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RESEARCH ARTICLES

KICKER ROCK: BOOT, WHALE OR SEAMARK?

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SUMMARY

With a few exceptions, the origins of the English names of the Galapagos Islands have been clearly elucidated. Kicker Rock (León Dormido) is one of the exceptions. It is sometimes assumed that the name Kicker derives from the boot-like shape of the islet, but no historical evidence for this has been found. Here I argue that Kicker Rock got its name instead from a famous pair of 17th century British seamarks, the Kickers of Portsmouth Harbour.

RESUMEN

Kicker Rock: ¿bota, ballena o marca de navegación? Con algunas excepciones, los orígenes de los nombres ingleses de las Islas Galápagos han sido bien dilucidados. Kicker Rock (León Dormido) es una de las excepciones. A menudo se asume que el nombre se derive de la forma de bota que tiene el islote. Sin embargo no se ha encontrado evidencia histórica para apoyar esto. Aquí propongo en cambio que el nombre Kicker Rock fue inspirado por un par de famosas marcas de navegación británicas que datan del siglo 17, las Kickers del puerto de Portsmouth.

INTRODUCTION

Modern lore has it that Kicker Rock (known in Spanish as the sleeping lion, León Dormido) got its English name from its resemblance to a boot or foot (*e.g.* Dodd 1930, Pinchot 1930, Boyce 1998, Woram 2016). This is a plausible explanation, because from some angles it does appear shoe-like (Fig. 1), but it is not supported by historical evidence. Captain James Colnett, who labelled the islet for the first time on his 1798 map of Galapagos, never likened the formation to a piece of footwear. When he first sighted it, on the afternoon of 25 June 1793 (recorded as 26 June in Colnett's logbook, because he used the nautical day which ran from noon to noon), he remarked that it resembled a "Sperm Whales head mouth open & up" (Colnett 1794). Kicker might therefore mean whale, perhaps one kicking up from the deep (as in breaching or spy-hopping). However, there is no supporting evidence in the historical literature that Kicker was ever slang for whale, while kicking is not a historical whaling term and kick feeding (also known as lobtail feeding, a foraging behaviour specific to a North Atlantic population of humpback whales) did not become part of cetological terminology until the end of the 20th century (Weinrich *et al*. 1992, Greenberg 2003). What therefore is the origin of the name?

As revealed in his book about the voyage (Colnett 1798), Colnett named several other islands in the Galapagos, all after British peers, or admirals of the Royal Navy:

Hood and Chatham islands after "Lord [Samuel] Hood" and "Lord Chatham" (John Pitt, 2nd Earl of Chatham); Gardner, Caldwell, Barrington, Duncan and Jervis (spelt Jarvis in the text of Colnett's book, and Jervis in the accompanying map) islands after Admirals Alan Gardner, Benjamin Caldwell, Samuel Barrington, Adam Duncan and John Jervis. This suggests there should be an eminent Lord, Captain or Admiral Kicker in the annals of British history. I could find none, but did find two prominent Kickers of a different kind.

THE KICKERS OF ENGLAND

Gill-Kicker and Kicker-Gill (also spelt Gilkicker and Kickergill, and collectively known as "the Kickers") were a pair of famous purpose-built seamarks, erected in Hampshire on the south coast of England in the 17th century, to help ships safely navigate the Solent between Portsmouth Harbour and the Isle of Wight (Avery 1721, Mackenzie 1821, Le Fevre *et al*. 1995) (Fig. 2). This well-fortified but shallow and narrow stretch of the English Channel was the "favourite rendezvous of the British navy, and the point from which the fleets of Nelson, Howe, St. Vincent, and Rodney…often set forth" (King 1858). The Kickers were prism-shaped towers, made of whitewashed stone, plaster and brick, standing between 15 and 38 m tall (at various times in their history) and set roughly 1 km apart (Grose & Astle 1784, Le Fevre *et al*. 1995). Gill-Kicker was the older, seaward mark,

Figure 1. Kicker Rock (León Dormido), from the east (photo by KTG, 2014).

Figure 2. Google Earth image of the entrance to Portsmouth Harbour, England, showing the locations of the Kicker seamarks and South Sea (now Southsea) Castle.

erected by Admiral Robert Rich, Earl of Warwick, in or soon after 1643, as deduced from the inscription it bore which, although only partially legible when recorded in print over a century later (Grose & Astle 1784), referred to Robert and to "Captaine chard blie senior [probably Captain Richard Blith senior] his captaine in the Prince Royal"; Blith and the *Prince Royal* were under Warwick's command only in 1643 (Powell 1962). Kicker-Gill was the landward back mark, erected in or just before 1698 (Le Fevre *et al*. 1995). Gill-Kicker presented a rectangular front, with its other two sides sloping downwards so that the rear point of the triangle was lower (Grose & Astle 1784), whereas Kicker-Gill was of even height on all three sides, until a triangular pediment was added on top of the front in later years (Pevsner & Lloyd 1967) (Fig. 3). Gill-Kicker was dismantled late in 1779 and replaced by a fort (Fort Monckton), while Kicker-Gill remained standing until 1965 (Anon. 1779, Grose & Astle 1784, Le Fevre *et al*. 1995). Eighteenth and 19th century directions for entering Portsmouth Harbour specified lining up the two Kickers (later, Kicker-Gill and Fort Monckton on "Kicker Point") "in one", or in combination with a nearby church or castle (Avery 1721, Norie 1839, Hobbs 1859). Several ships' logbooks from this period include bearings taken off one or both of the Kickers (Le Fevre *et al*. 1995). For example, the log of HMS *Bounty* for 3 December 1787 reads: "at 2 pm came to anchor and moored in 5 fathoms the Kicker NNW1/2N and South Sea Castle EbS" (Galloway 2012).

Colnett would have been familiar with the Kickers. He joined the Royal Navy in 1770, sailed on several of its ships (*e.g.* HM Ships *Hazard*, *Scorpion* and *Resolution*), and from 1783 to 1786 was based at Portsmouth on harbour duty aboard HMS *Pégase* (Galois 2004). Portsmouth was also the harbour where, in late December 1792, Colnett boarded the merchant ship *Rattler* and began his voyage to Galapagos (Colnett 1798). That he didn't record a bearing off Kicker-Gill in the *Rattler*'s log is explained by the fact he didn't start writing in it until already at sea (on 5 January 1793).

THE KICKER OF GALAPAGOS

The importance of the Kickers to the British Navy, and by extension, to Colnett, is indisputable, but did Colnett really name Kicker Rock in Galapagos after them? Points suggesting that he may have done so include the fact that Kicker Rock, like the Portsmouth Kickers, is a prominent seamark, *i.e.* an object visible from the sea, which serves to aid sailors in navigation. Logbooks show that many of the 19th century ships following in Colnett's wake, *e.g.*
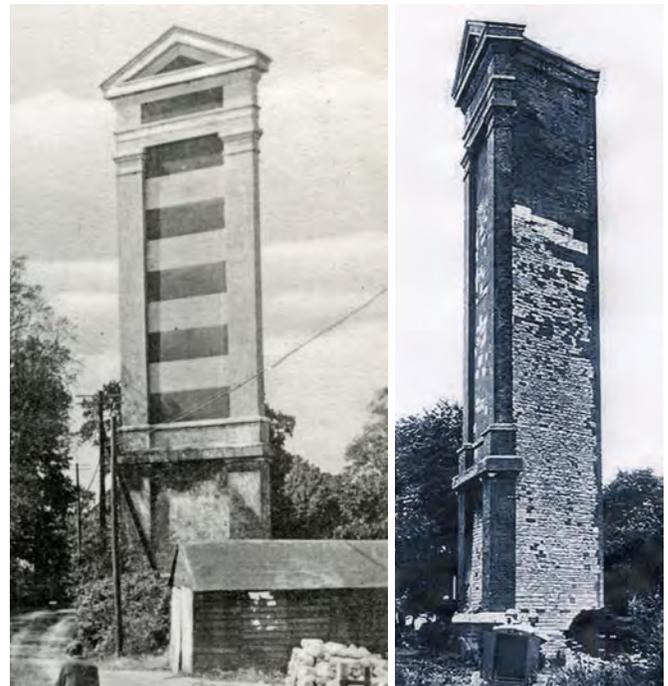
Figure 3. Kicker-Gill tower, Clayhall Road, Alverstoke, England. Left: front view (cropped from a postcard mailed in 1910, unknown photographer: KTG's collection). Right: side view (unknown photographer, 1965: Gosport Society).

HMS *Tagus* (Pipon 1814) and HMS *Beagle* (FitzRoy 1835–6), oriented themselves with compass bearings recorded off Kicker Rock, and even today, the U.S.A.'s National Geospatial-Intelligence Agency's 2014 sailing directions for Galapagos specify Kicker Rock, "a sheer, high rock shaped like a church with a high, square tower", as a principle navigation target for the area. Another indication that Kicker Rock was named after the Kicker towers of England is that when Colnett first mentioned the name in his Galapagos account he wrote that the feature resembled "one of the Kickers" (Colnett 1794), in the plural.

Colnett saw Kicker Rock on two different occasions. The first time, on 25 June 1793, was from a distance of more than 17 km, when the *Rattler*, after closely rounding the northeastern head of San Cristóbal and stopping briefly near Hobbs Bay, came to anchor off the northwest coast, in front of the tuff cone today known as Pan de Azúcar (Fig. 4). He did not give the rock a name, but merely wrote, "... Ex[tent] of Land from S 13 W to E 34 N. a Rock of[f] the SW point like a Sperm Whales head mouth open & up W 33 S." (Colnett 1794). The *Rattler* did not get any closer to Kicker Rock that year, but Colnett did send some men in a small boat to Stephens Bay, off which the rock lies, in search of freshwater. Spelt Stephen's Bay in Colnett's book, this was probably named for Sir Philip Stephens, First Secretary of the Admiralty, to whom Colnett dedicated his book. Two days later the *Rattler* weighed anchor, headed off to the northeast, tacked back southwards around the eastern tip of San Cristóbal, passed within 5 miles of

Española (on 30 June), and then headed eastward, out of the archipelago.

The second time was on 12 March 1794 when the *Rattler* re-entered the Galapagos archipelago after 8.5 months along the western coasts of Central and North America. This time Colnett sailed the ship directly into Stephens Bay (Fig. 4). In the following insufficiently punctuated and somewhat ambiguous entry for that day, Colnett (1794) recorded the name Kicker for the first time (bold type added by KTG):

*"Moderate Breezes at NE stood along to the SW with an Intention to pass to the W^t of **a Remarkable Rock resembling in Hight & Size & shape in several points of view one of the Kickers which lay N of a Deep Bay in which one of the Boats had good sound^{gs} when here before** off the Rock to the N of it 2 Cables lengths 19 f^m Rocky as we rounded in to the W^d & S^d no Sound^{gs} with 50 f^m Line & the wind hauling more to E prevented now our getting into the E^t Corner. we at last got sound^{gs} within a Mile of the Shore in the W^t Corner a low point at 29 f^m Rocky hauld out to beat up - I set out with a Boat to sound the Bay found good bottom at the E part 5 or 6 Miles from the Shore 21 f^m sand two points of the Bay NE & SW **the Kicker Rock** WNW 2 ½ miles. got on Board & fetched into the bay with the ship & came too on the same Bearings - At daylight sent two Boats away one to the NE other SW to search the Lee side of the Isle for Salt. the Jolly Boat also went a fishing under the big Rock - & in a short time caught great numbers of large Cod which form 10 to 30 weight & also sea Breams."*
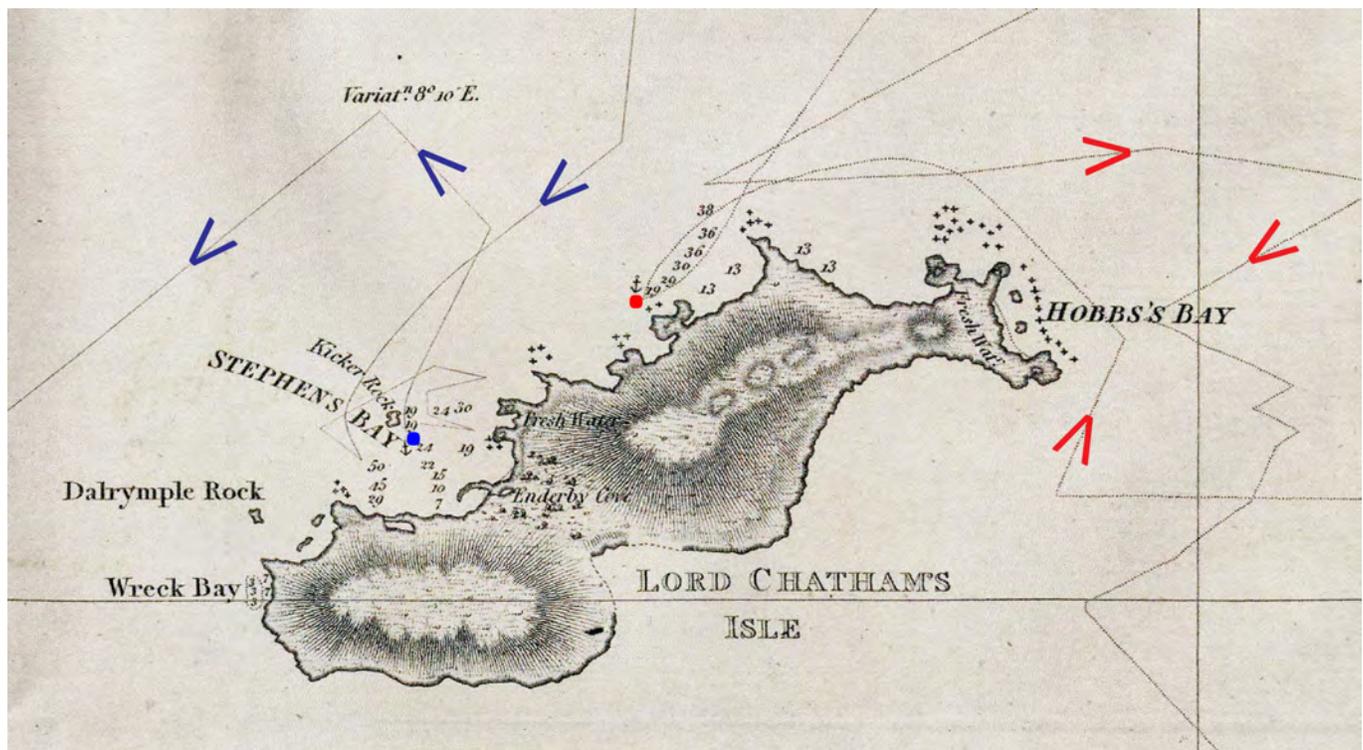
Figure 4. San Cristóbal Island, taken from Colnett's 1798 map of Galapagos, showing the tracks and anchorages of the *Rattler* (with coloured arrows and dots added by the author) in June 1793 (red) and March 1794 (blue), as they correspond to the ship's logbook.
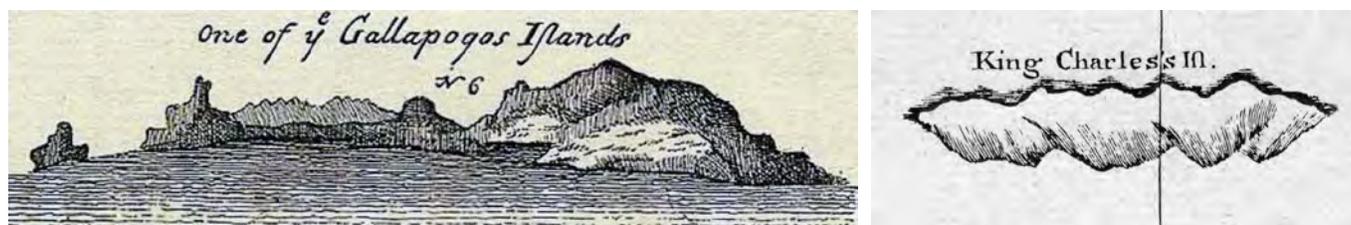
Figure 5. Left: Edward Cooke's 1709 sketch of San Cristóbal, with Kicker Rock and Cerro Brujo on the left, viewed from a position southwest of Stephens Bay. Right: Cowley's depiction of San Cristóbal, from map in Hacke (1699).

The "Remarkable Rock" is "the Kicker Rock", so what did Colnett mean by likening it to "one of the Kickers"? There can be three interpretations of this. In the phrase in bold, Colnett could have been referring to two or more formations in Galapagos, which had either (1) already been named Kicker by a previous visitor, or which (2) he had named himself in 1793; alternatively (3) he could have meant that the "Remarkable Rock [*i.e.* Kicker Rock] ... lay N of a Deep Bay" (which it does: Stephens Bay) and the intervening mention of the resemblance to "one of the Kickers" referred to some other Kickers, elsewhere in the world.

The first possibility, that Colnett was referring to some Galapagos formations named Kicker by someone else, is unlikely. Colnett (1795) had on board the *Rattler* a map of the islands, copied from a Spanish chart of the South Seas (item MPI 1/400/4, National Archives, London). He also had several "purchased … voyages of former navigators", which, from clues in his book, almost certainly included Woodes Rogers' and Edward Cooke's separate accounts of their cruise with William Dampier through the islands in 1709 (Cooke 1712, Rogers 1712). He may also have had accounts of Dampier's earlier voyage to Galapagos with Ambrose Cowley in 1684 (Dampier 1729), and a version of Cowley's chart of the Galapagos Islands first published by William Hacke (Hacke 1699). However, none of these references contains the word or name Kicker. Furthermore, although Rogers noted a "little Rock appearing like a Sail" and a "great Rock" off a large island, which from their descriptions and geographical positions relative to each other were undoubtedly Dalrymple, Kicker Rock and San Cristóbal respectively, Colnett failed to recognise them. Nor did Colnett recognize Cooke's illustration of San Cristóbal, which Cooke (1712) "call'd Marqueses Island", nor Cowley's depiction of it, which he named "King Charles's Island" (Hacke 1699) (Fig. 5). Colnett believed that the principal Galapagos islands he saw in 1793 (San Cristóbal and Española) were uncharted and therefore free to be named, stating, with reference to San Cristóbal (which he dubbed Chatham) and Española (which he named Hood), that "I could not trace these isles by any accounts or maps in my possession" (Colnett 1798).

The second possibility, that Colnett was referring to some Galapagos formations that he or his crew had already nicknamed "the Kickers", but not recorded in writing, also lacks support. There are several prominent formations (rocks and headlands) around San Cristóbal and Española that could be regarded as seamarks, and thus potential candidates for a second Galapagos "Kicker", but with no evidence in favour of Colnett naming any of them as such, so we can only guess which one(s) he might have. Dalrymple Rock (Roca Cinco Dedos in Spanish, meaning Five Fingers Rock), the most likely choice due to its proximity and physical similarities to Kicker Rock, can almost certainly be discounted. Dalrymple and Kicker Rock are both off-shore tuff islets lying at an equal distance (*c.* 5 km) from the coast of San Cristóbal (Fig. 4), and they are often paired in print, as for example, by Captain Tanner (1890) of USSFS *Albatross*, who likened the taller (145 m) Kicker Rock to a "square-rigged vessel" and the smaller and lower (19 m) Dalrymple Rock to "a boat with lug sail" (Fig. 6). However, Dalrymple lies 15 km southwest of Kicker Rock. Colnett could not have seen it in 1793 (the *Rattler* was anchored too far north), and although the men he sent to Stephens Bay that year might have (because Dalrymple is faintly visible from the northern end of the bay), Colnett made no mention of it in his logbook, nor in the text of his book. Dalrymple is only included (and labelled as such) on his map as a result of the survey of the southwestern coast of San Cristóbal conducted by his whaling master and chief mate on 13–15 March 1794, with the name probably provided after the voyage by someone in the Admiralty, presumably in honour of Alexander Dalrymple, first hydrographer of the Admiralty (Woram 2016). On the other hand, Wreck Bay, off which the rock lies, was more likely named by Colnett during the voyage, for "a part of the wreck of a ship" that his men found there (Colnett 1798); coincidentally, Rogers (1712) recorded "some of the Wreck and Rudder of a Vessel" on this same stretch of coastline 85 years earlier.

Figure 6. Two views of Dalrymple Rock, topped with a 20th century beacon (photos by KTG, 1996).
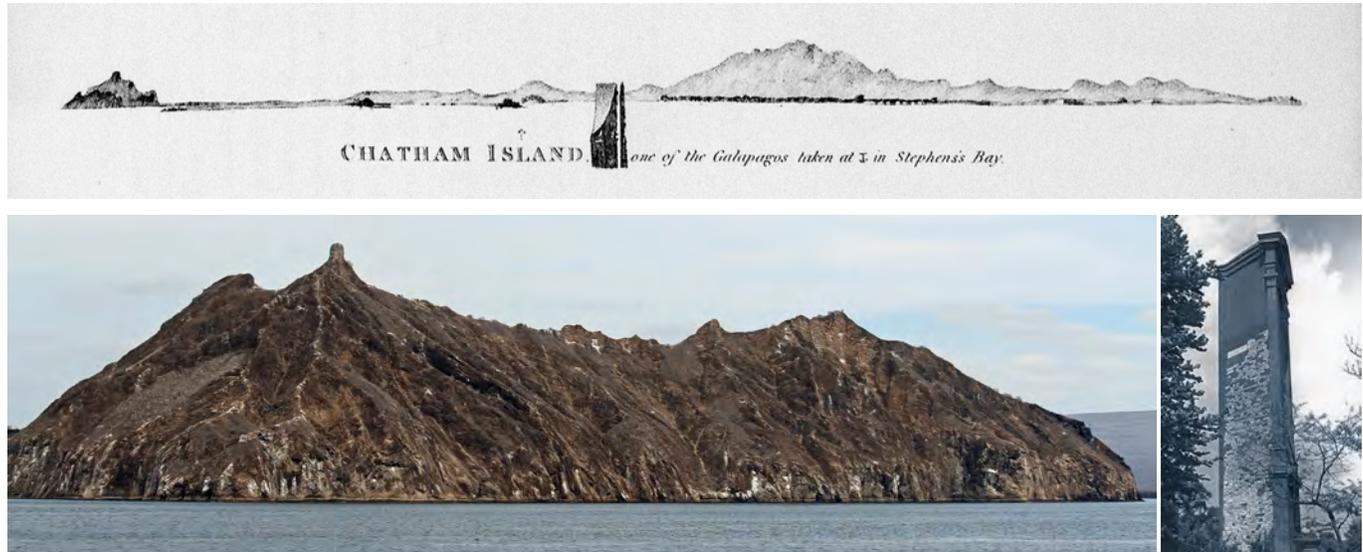
Figure 7. Top: Colnett's illustration of San Cristóbal as viewed from a position somewhat seaward of the *Rattler*'s anchorage in Stephens Bay, 12–16 March 1794, with Kicker Rock in centre front, and Cerro Brujo (with its knob exaggerated) on the far left (Colnett 1798). Bottom left: Cerro Brujo with its tower-like projection on the summit (photo by KTG, 2016). Bottom right: Kicker-Gill tower, photographed by Eric Lane, 1965 (Hampshire Record Office).

The third interpretation implies that Colnett was likening Kicker Rock to some "Kickers" elsewhere in the world. If so, these were almost certainly Gill-Kicker and Kicker-Gill, as I have been unable to find any land formation or manmade structure called Kicker in the 18th century, save for these seamarks. Evidence in support of this interpretation exists in two island profiles of San Cristóbal (Figs 7 & 8), drawn by Colnett and included in his book (Colnett 1798). One (Fig. 7 top) is a panorama of Stephens Bay with a stylised representation of Kicker Rock in the foreground. As depicted, the rock bears a resemblance to Kicker-Gill, as it was just before the seamark's demolition in 1965 (Fig. 7 bottom right). Note the rectangular face, the horizontal "belt" and chisel top

of both the rock and the seamark. Gill-Kicker, which lacked Kicker-Gill's triangular pediment in front, was probably an even closer match to Colnett's sketch. With the exaggerated peak of Stephens Bay's northern headland (Cerro Brujo: Fig. 7 bottom left) appearing like a second, back mark in the distance (6 km from Kicker Rock), the allusion to the British Kickers is strong.

Colnett's other island profile shows the northwestern coast of San Cristóbal with Kicker Rock on the far right, as it was first viewed by Colnett from the distance, at his anchorage off Pan de Azúcar in June 1793 (Fig. 8). Here, Kicker Rock and Cerro Brujo's peak are depicted as twinned features, the peak a miniature version of the rock, and a compass bearing is written over each. It is
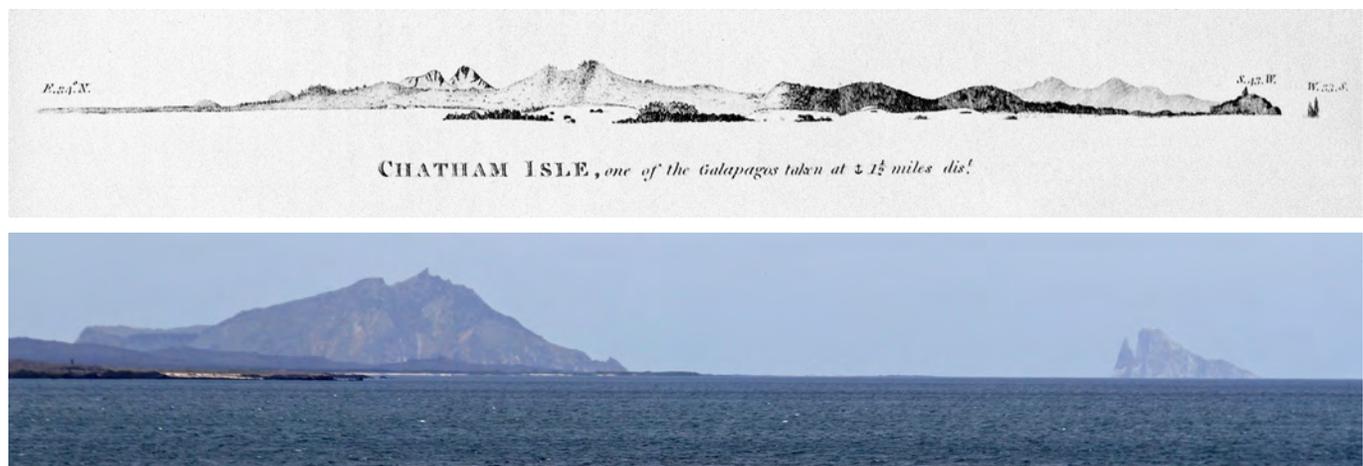
Figure 8. Colnett's sketch of San Cristóbal as viewed from the *Rattler*'s anchorage far to the northeast of Stephens Bay on 25 June 1793, showing Cerro Brujo and Kicker Rock on the far right (Colnett 1798). Bottom: magnified shot of Cerro Brujo and Kicker Rock, taken from a similar angle and distance (photo by KTG, 2016).

easy to imagine Colnett regarding the two formations as a pair of seamarks equivalent to the Kickers of England; the rock and peak signal the entrance to Stephens Bay, just as Gill-Kicker and Kicker-Gill once did for Portsmouth Harbour. The analogy would have been reinforced when Colnett's men were sent to Stephens Bay in 1793, for they would have seen that Cerro Brujo's summit projection resembles a man-made watch tower or navigation beacon (Fig. 7 bottom left). Colnett did not name this projection but only referred to Cerro Brujo as "the bluff", a "Mountain …[that] appears like an island" and at one point "Mineral Mount" for the sand full of yellow "topazes", actually olivine, that his men found at its base, a bucketful of which was brought back to England, to assess their value (Colnett 1794, 1795, 1798). However, Captain FitzRoy of HMS *Beagle* later dubbed it Finger Peak (FitzRoy 1835–6), while Darwin (1835) called the headland itself Finger Hill and Finger Point, a name still sometimes used today, as in the list of navigational landmarks of the USA's National Geospatial-Intelligence Agency (2014): "Punta Finger … a conspicuous dark colored cliff topped by a pinnacle rock".

In final support of a link between Kicker Rock and the Kickers of England is this telling description of the islet written by Commander David Porter of the United States Frigate *Essex*, after seeing it in 1813:

> "*This rock is very remarkable in its appearance, and is the* **surest mark for finding the bay***. It is very high,* **flat on the top***, and from some points bears strongly the* **appearance of a castle***. On the western side the rock is split from the summit to the base, and the part detached stands* **like an obelisk** *on a very narrow base.*"(Porter 1815; bold type added by KTG).

If Porter hadn't been American (and an enemy of the British in the war of 1812–15) one could almost believe he was thinking of the entrance of Portsmouth Harbour when choosing the words for this passage.

CONCLUSION

So, boot, whale or seamark? There is no evidence that Colnett was thinking of a foot when he chose the name Kicker; that appears to be a 20th century interpretation. He imagined a whale when he first looked at Kicker Rock from a distance, but there is no evidence linking the word Kicker (which Colnett did not record until the following year) to a cetacean. Colnett did not refer in his book to the likeness to a whale, and his close up illustration of the rock bears no resemblance to one. Colnett may thus have been alluding to the Kicker seamarks of England, famous among British mariners of the time, when he used the word Kicker for the Galapagos rock. This is supported by the connection of the name to the Royal Navy and thus to the other Galapagos island names that Colnett chose; Colnett's logbook reference to more than one Kicker but his application of the name in Galapagos to only one; the islet's importance as a navigation mark, both then and now; and the resemblance of Colnett's illustration

of Kicker Rock to Kicker-Gill and probably to Gill-Kicker too, with the obvious utility of Cerro Brujo's peak as a second mark. The historical record is sketchy, and we may never know the origin of the name for certain, but this possibility seems strong.

ETYMOLOGY

There is no certain explanation why the seamarks in England were called Gill-Kicker and Kicker-Gill. However, a possible answer lies in the etymology of the words gill and kicker. The place-name "gill" means a stream or small wooded glen, and Gill-Kicker, the first seamark to be constructed, was backed by a marshy creek (now dammed and known as Gilkicker Lake), while Kicker-Gill stood above a wooded slope by Alverstoke creek (now Stoke Lake). The surname "Kicker" derives from the Middle English word "kiken", meaning "to watch or spy" (Reaney & Wilson 2006). From the same root come English and Scots dialect "keeker" and Dutch "kijker", all meaning "watcher" and from which the 17th-century application of the word Kicker to the seamarks could have derived. In a sense they were "watching" (facing) the sea, were "watching over" sailors (assisting in safe navigation) and were themselves objects that sailors "watched for". The interpretation is thus at least logical, and we might think of the Kicker Rock in Galapagos as the watching rock or the rock to watch for, when locating and navigating Stephens Bay.

The origin of its more recent Spanish name "León Dormido" is another story...

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BANCO TUZO: AN ANCIENT GALAPAGOS ISLAND AND POTENTIAL STEPPING STONE FOR SPECIES DISPERSAL

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SUMMARY

Banco Tuzo is a flat-topped seamount that lies 360–400 m below sea level, between the shallow volcanic platform of the main Galapagos archipelago and the northern islands of Marchena and Pinta. Recovered basalt fragments include rounded rocks with morphology that suggests exposure to a tidal environment. Ages of the lavas determined by ^{40}Ar–^{39}Ar dating vary from 2.0 ± 0.5 Ma to 1.1 ± 0.5 Ma ($\bar{x}$ ± SD). The subsidence rate calculated from the radiometric ages is similar to that estimated for young oceanic lithosphere. Our observations indicate that Banco Tuzo is an ancient, now submerged, island that formed close to the current position of Wolf Volcano, the northern end of Isabela Island. This ancient island may have provided a pathway for species dispersal between the main Galapagos Archipelago and the present-day northern islands.

RESUMEN

Banco Tuzo: antigua isla de Galápagos y posible escala intermedia para la dispersión de especies. El Banco Tuzo es un monte submarino de cima plana que se encuentra a 360–400 m bajo el nivel del mar, entre la plataforma volcánica poco profunda de la parte principal del archipiélago de Galápagos y las islas norteñas de Marchena y Pinta. Los fragmentos basálticos recuperados incluyen rocas redondeadas con morfología que sugiere exposición a un medio ambiente con mareas. Las edades de las lavas determinadas por el método de ^{40}Ar–^{39}Ar varían de 2.0 ± 0.5 Ma a 1.1 ± 0.5 Ma ($\bar{x}$ ± SD). La tasa de hundimiento calculada mediante las edades radiométricas es similar a la estimada para litosfera oceánica joven. Nuestras observaciones indican que el Banco Tuzo es una antigua isla, ahora sumergida, que se formó cerca de la actual posición de Volcán Wolf, el extremo norte de la Isla Isabela. Esta antigua isla podría haber proporcionado una vía para la dispersión de especies entre la parte principal del archipiélago de Galápagos y las actuales islas del norte.

INTRODUCTION

Ocean islands play a critical role in our understanding of the evolutionary biology of terrestrial species. Such islands are subject to processes including magmatism, tectonic plate movement, thermal subsidence, and changes in sea level, which create a geography that is dynamic over millions of years (*e.g.* Whittaker *et al*. 2008). As a result, constraining the emergence location and age of current and past (drowned) islands is critical to understanding species dispersal between islands and how this affects evolution over millennia.

The Galapagos Archipelago is one of the world's most studied oceanic island groups and served as inspiration for the theory of evolution by natural selection (Darwin 1859). The islands include a concentrated region of active volcanoes in the west, with a chain of older volcanoes extending eastward in the direction of Nazca plate motion (White *et al*. 1993, Sinton et al. 1996). The erupted lavas have distinctive compositions (White et al. 1993) and the islands are underlain by mantle with anomalously slow velocities according to seismic tomographic imaging (Hooft *et al*. 2003, Villagómez *et al*. 2007, 2014). These observations indicate that the islands are formed by magma generated by the partial melting of an upwelling mantle plume. Unlike an idealized plume with volcanism focused on one or two islands, magmatism occurs well east and north of the youngest volcano, Fernandina. For example, relatively recent (last several hundred years) lava eruptions have occurred in the central islands of Santiago and Santa Cruz. To the north, there is a collection of islands (Wolf, Darwin, Pinta, Marchena, Genovesa) and seamount lineaments between the Galapagos Spreading Center (GSC) and the main Galapagos Platform to the south (Fig. 1). This results in a broad spatial distribution of the currently emergent islands. Prior to *c*. 4 Ma before

present (BP), the GSC was situated over the plume that produced the Carnegie and Cocos aseismic ridges, which trend to the east and northeast, respectively, from the Galapagos Islands (Wilson & Hey 1995).

As late as 1985, studies on the evolution of the terrestrial species that inhabit the Galapagos Islands were based on the geography of the currently emergent islands (Geist *et al*. 2014). With the understanding that some oceanic archipelagos, like the Galapagos, are created by hotspots and that there is a continuum of new islands

that eventually become drowned seamounts, historical biogeographers realized that evolutionary timescales can be extended beyond the age of the extant islands (Heaney 2000). Detailed bathymetric mapping, rock sampling, and radiometric age determination of drowned seamounts on the Carnegie and Cocos Ridges (Fig. 1) demonstrated that we cannot assume a static distribution of islands. Christie *et al*. (1992) first recognized drowned islands that are 5–9 Ma old, east and northeast of the current platform. This in turn gave evolutionary biologists a basis to extend the

Figure 1. Map of the Galapagos region showing the major islands, lineaments, the Galapagos Platform carrying most of the main islands, and the Galapagos Spreading Center. The red rectangle encloses the area shown in Fig. 2.

age of evolution of terrestrial Galapagos species (Grant *et al.* 1996, Rassmann 1997). Werner *et al.* (1999) observed a 14 Ma-old drowned island on the Cocos Ridge (Fig. 1), which further extended the potential time for evolution on the islands (Parent *et al.* 2008).

In 2010, the MV1007 cruise of the research vessel *Melville* mapped for the first time a large seamount (Fig. 2) nestled within the islands. This seamount has been named Banco Tuzo by the Instituto Oceanográfico de la Armada of Ecuador to honor the Canadian geophysicist J. Tuzo Wilson. It is flat-topped and lies between the main Galapagos Platform and the northern island of Marchena (Fig. 1). We report new bathymetric imaging and ^{40}Ar–^{39}Ar radiometric dating of basalts dredged from the seamount, which show it to be a drowned island. We suggest that this former island was a stepping-stone from the islands of the main Galapagos platform to the northern islands of Pinta and Marchena, permitting the radiation of species, such as marine iguanas and giant tortoises.

METHODS

The morphology and surface characteristics of Banco Tuzo were determined using multibeam and side-scan sonars and a towed camera. Bathymetric data were collected using a hull-mounted EM122 12 kHz multibeam sonar along ship tracks oriented at 140° with typical swath widths of 3–5 km. We generated side-scan sonar imagery from the EM122 data, on which we interpret low reflectivity areas to be areas covered with > 1 m of sediment, and areas of high backscatter reflectivity to be lava flows with thin to no sediment cover. In order to obtain a closer view of the surface of the seamount, photographic imaging was obtained using the Woods Hole Oceanographic Institution's TowCam system (Fornari 2003), along a short transect (TC1) between 665 and 623 m depth at the hummocky eastern side of the southern margin terrace (Fig. 2). The camera sled was deployed using the ship's cable, and a combination of forward ship motion and winch operation was used to place the camera within *c.* 5 m of the seafloor. Still photos were taken from the camera every *c.* 10 seconds as the ship was underway at 0.5 knot. Rocks were dredged using a standard frame and chain system.

For the ^{40}Ar–^{39}Ar radiometric dating, rock samples were crushed and any large mineral crystals (phenocrysts) were manually removed under an optical microscope. The remaining groundmass (the fine material that solidified
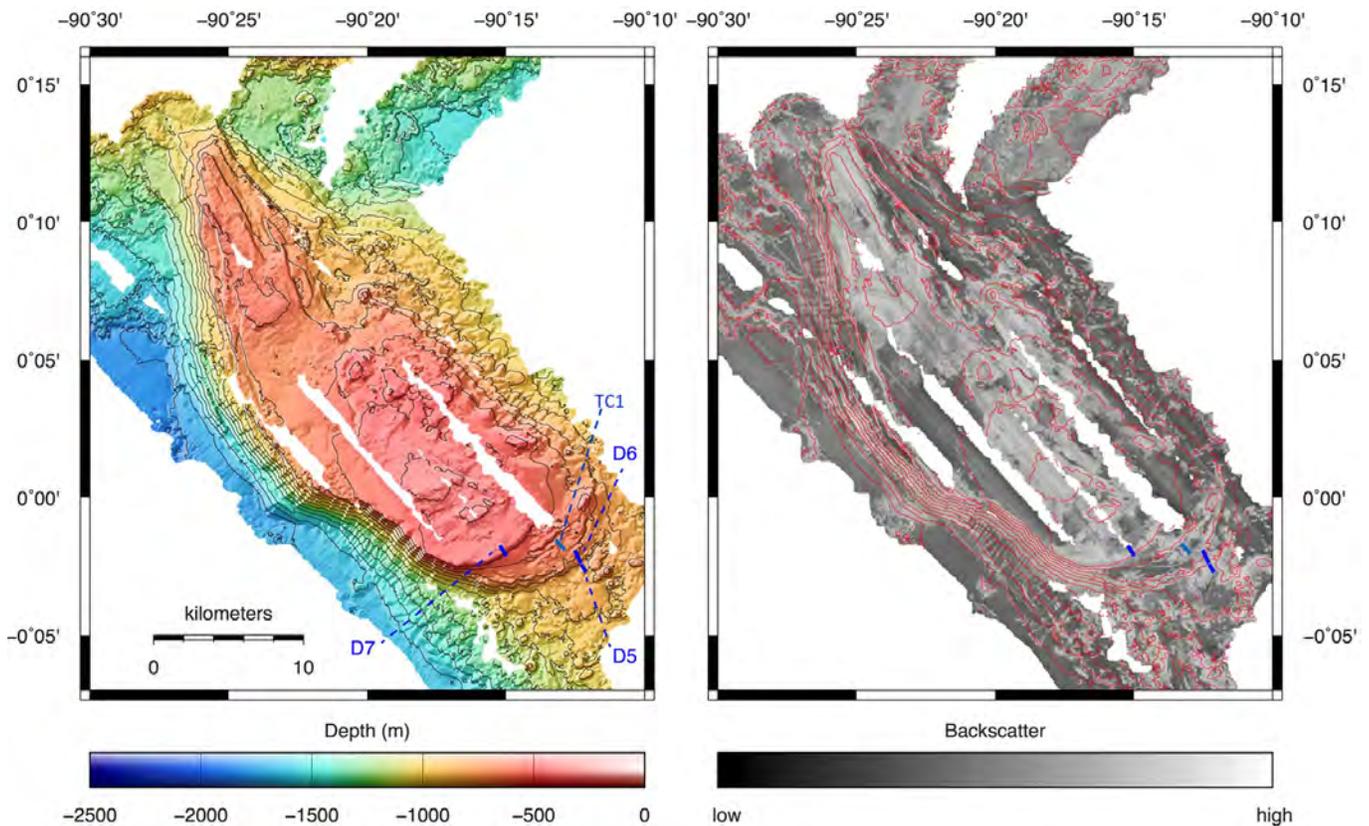
Figure 2. Left: bathymetric map generated using data from the hull-mounted EM122 multi-beam system; the map is illuminated (hill-shaded) so any individual color may be expressed from pale to dark as shown on the scale bar. Right: side-scan sonar imagery from the EM122 data, where the darker shades represent low backscatter reflectivity and the lighter shades are higher reflectivity. On both charts the white areas are where no data were collected, the contours are 100 m isobaths, and the four transects (D5–7, TC1) are marked by the thick undashed blue lines.

upon eruption) was cleaned by a series of HCl and HNO_3 leaching steps in an ultrasonic bath followed by handpicking to remove any altered grains and remaining phenocrysts (Koppers *et al.* 2011). The samples were packed in a glass tube which was evacuated then irradiated for 7 h in the TRIGA CLICIT nuclear reactor at Oregon State University and the irradiation flux was monitored using the FCT-3 biotite standard (28.03 ± 0.18 Ma) (Renne *et al.* 1998). Incremental heating of the samples was done by scanning a defocused 10 W CO_2 laser over the samples and the resulting gas was analyzed in a single-collector MAP 215-50 mass spectrometer. Before analyzing a sample, and after every three heating steps, system blanks were measured. J-values for each sample were calculated by parabolic extrapolation of the flux monitor samples and their height in the glass tube. Incremental heating plateau ages and isochron ages were calculated using ArArCALC software (Koppers 2002). All errors on the ages are reported at the 95% confidence level (± SD) including 0.3–0.4% SD in the J-value. K/Ca values were calculated as weighted means for the age spectra or as total fusion K/Ca values by combining the gas analyses. All ages were calculated using the corrected Steiger & Jäger (1977) decay constant of $5.530 ± 0.097 × 10^{-10}$ per year as reported by Min *et al.* (2000).

RESULTS

Morphology of Banco Tuzo
The EM122 data (available through the Marine Geoscience Data System <http://www.marine-geo.org/tools/search/entry.php?id=MV1007>) show that Banco Tuzo is an elongate (NW–SE trending), flat-topped feature *c.* 40 km long and *c.* 20 km wide. The shallowest part of the seamount is at the southeastern end, consisting of a flat-topped hill, 4–5 km in diameter, which is 360 m below sea level (bsl) at its shallowest point (Fig. 2). The boundary between the flat top and steep flanks of the seamount lies at 500–600 m bsl. A steep slope that drops from 500 m bsl to a relatively shallow-sloped terrace between 600 m bsl and 900 m bsl characterizes the southeastern margin of Banco Tuzo. The western flank drops much more steeply (15–30° slopes) from the flat top to the *c.* 1800 m bsl depth of the surrounding seafloor. There are sub-parallel channels running down this slope and the high backscatter reflectivity of the channels indicates that they are bare rock, perhaps scoured by debris flows. In contrast with the western escarpment, the eastern edge of the seamount has a relatively gentle slope (< 10°), but it

also has channels. There are several small volcanic cones rising from this flank with the largest *c.* 2 km in diameter. The northern end of the seamount pinches to a narrow saddle that is *c.* 1000 m bsl before the seafloor rises up the southern flank of Marchena Island.

Unlike the summits of most active, emergent Galapagos islands (*e.g.* Isabela), Banco Tuzo does not exhibit primary volcanic features such as scoria cones and spatter ramparts. High backscatter reflectivity (Fig. 2) over much of the top of the seamount indicates a surface dominated by bare rock. The southwestern edge of the seamount top, however, displays low backscatter reflectivity and is probably a large sediment-covered plain. The TowCam images revealed that a large proportion of transect TC1 was covered with light-colored sediment, often with ripple marks (Fig. 3). Lava was observed as isolated mounds in the sediments, as pillow flows, short layered flows and blocky piles (Fig. 3). The pillow structures, which were a common substrate in the flat regions of the TowCam trajectory, and the layered flows (Fig. 3 top) appear to be primary features that have not been rotated. While some of the blocky piles of basalt could be debris from mass wasting, overall the terrace appears to be a constructional feature. Abundant marine life was observed with the TowCam system. The hard surfaces hosted many sessile organisms, such as yellow sea-lilies (Crinoidea) and a variety of Anthozoa including anenomes, black coral (Antipatharia) and soft and hard corals (Fig. 3). The soft sediment hosted spider crabs (Decapoda), pencil urchins (Cidaroida) and sea cucumbers (Holothuroidea).

Recovered rock samples
Three dredge transects on the southeastern margin of Banco Tuzo (Fig. 2, Table 1) recovered rock fragments with basaltic compositions (K. Harpp unpubl. data). Dredge D5 (836–834 m bsl) recovered fresh, moderately vesicular pillow basalt fragments that are aphyric with rare plagioclase glomerocrysts. Dredge D6 (828–682 m bsl) recovered three aphyric, non-vesicular pillow basalts and one aphyric but vesicular pillow basalt fragment (sample D6D) that has a higher MgO content than the other D6 basalts. The shallowest dredge, D7 (529–430 m bsl), sampled the slope break and margin of the flat seamount top and recovered at least two distinct groups of basalts. One group consists of highly vesicular, plagioclase-phyric, sub-rounded basalt clasts (samples D7A, B and C) that are moderately weathered (Fig. 4). The morphology is similar to rocks from wave-eroded beaches with rounded gouges and fluted features produced by bio-eroding organisms

Table 1. Dredge (D) and towcam (TC) transect locations.

Transect	Start position	Start depth (m)	End position	End depth (m)
D5	0°2'43.1"S, 90°12'6.7"W	836	0°2'25.4"S, 90°12'17.3"W	834
D6	0°2'23.5"S, 90°12'18.0"W	828	0°1'54.7"S, 90°12'30.9"W	682
D7	0°2'7.5"S, 90°14'59.0"W	529	0°1'44.8"S, 90°15'13.1"W	430
TC1	0°2'15.2"S, 90°12'28.0"W	665	0°1'48.7"S, 90°13'4.2"W	623
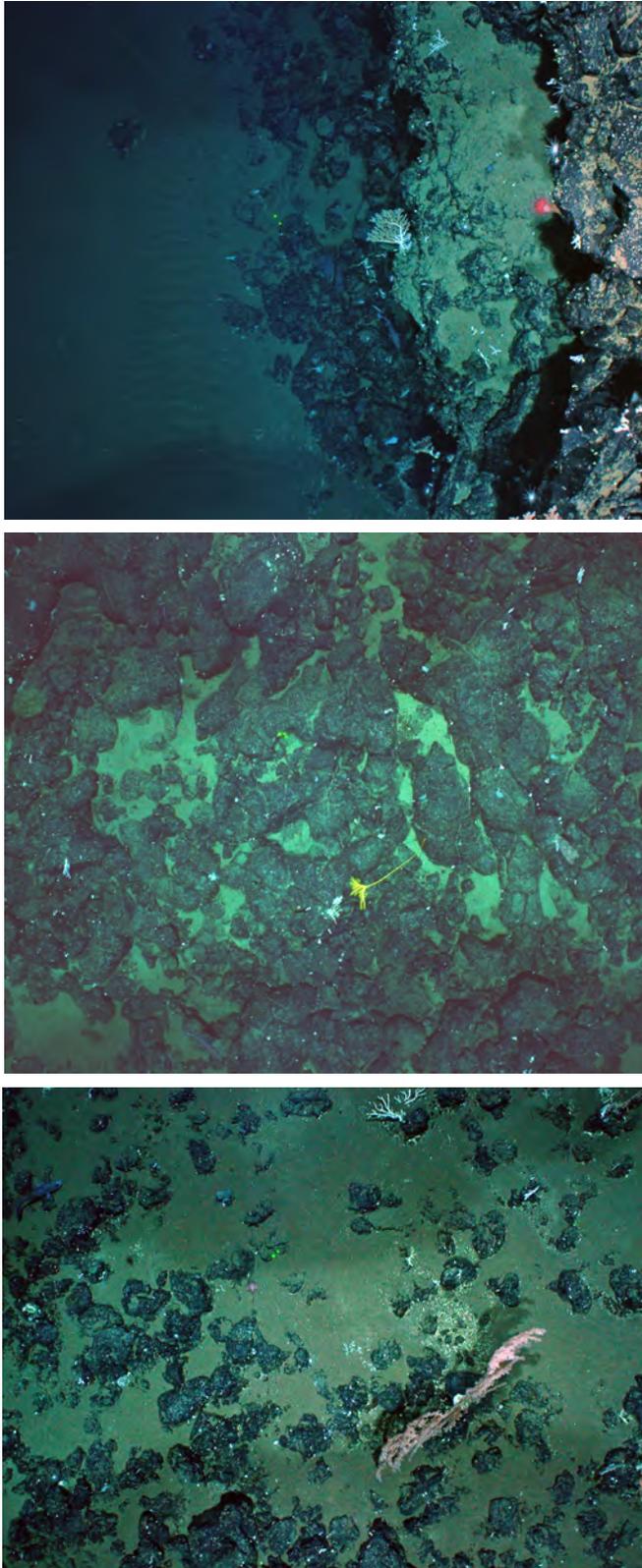
Figure 3. Representative photographs taken during the towed camera transect TC1. Top: an undersea cliff showing several basalt flows hanging over rippled sediment cover, with an orange anemone and a white coral attached to the lava. Middle: pillow basalts partially covered with sediment, with a yellow crinoid on the exposed lava. Bottom: basalt cobbles and blocks partially covered with sediment.

Figure 4. Rocks from dredge D7. The white scale bar in each image represents 1 cm. The top image shows a cut face illustrating the vesicularity that is common to most of the D7 rocks. The other images show the rounded edges and large bores, gouges and fluted features consistent with a tidal or beach environment.

such as sea urchins (Echinoidea) (Asgaard & Bromley 2008, Ramalho *et al*. 2013). The vesicularity of the lavas is consistent with subaerial origins as hydrostatic pressure can inhibit the exsolution of volatiles during submarine eruption, although this depends on the volatile content of the magma. Taken together, the morphology of these clasts suggests past exposure to a tidal environment. The other D7 rocks are nonvesicular, slightly plagioclase-phyric pillow basalt fragments. One of these lavas contains a xenocryst of the weathered basalt, indicating that it is younger than the first basalt group.

⁴⁰Ar–³⁹Ar ages

Four samples of the compositionally distinct basalts from two dredges (D5 and D7) yielded reliable crystallization ages using ⁴⁰Ar–³⁹Ar techniques (Table 2, Fig. 5; detailed data for the ⁴⁰Ar–³⁹Ar ages are available on the Geochron database <http://www.geochron.org/>). A sample (D7C) from the shallowest dredge, which shows the rounded and pitted morphology, has the oldest age of 2.0 ± 0.5 Ma. The other three ages (1.1 ± 0.5, 1.3 ± 0.8, 1.6 ± 0.8 Ma) are from pillow basalt fragments. On the basis of these ages and uncertainties, we can conclude that Banco Tuzo magmatism occurred at least 1–2 Ma BP.

DISCUSSION

Evidence for a drowned island

The elongate shape and relatively smooth, flat top of Banco Tuzo make it unique in comparison to other seamounts

Table 2. Incremental heating ⁴⁰Ar–³⁹Ar analyses of basalts dredged from Banco Tuzo.

| Sample | N | n | Plateau Age | | | | Total Fusion | | Inverse Isochron | | |
			Age (Ma)	³⁹Ar %	K/Ca	MSWD	Age (Ma)	K/Ca	Age (Ma)	⁴⁰Ar/³⁶Ar intercept	MSWD
D6B	8	7	1.6 ± 0.8	98.8	0.009	0.03	2.0 ± 0.9	0.025	1.6 ± 0.9	295.5	0.04
D6D	6	6	1.3 ± 0.8	100	0.007	0.17	1.3 ± 0.8	0.007	1.3 ± 0.9	295.9	0.20
D7C	7	4	2.0 ± 0.5	89.9	0.008	0.01	6.0 ± 1.4	0.018	2.0 ± 0.6	296.2	0.02
D7F	7	5	1.1 ± 0.5	82.5	0.008	0.02	2.0 ± 0.7	0.038	1.1 ± 0.6	296.1	0.02

N = total number of incremental heating steps for each sample.
n = number of steps included in the age plateau and isochron calculations.
MSWD = mean square weighted deviation values for the plateau ages (df = n–1) and inverse isochrons (df = n–2).
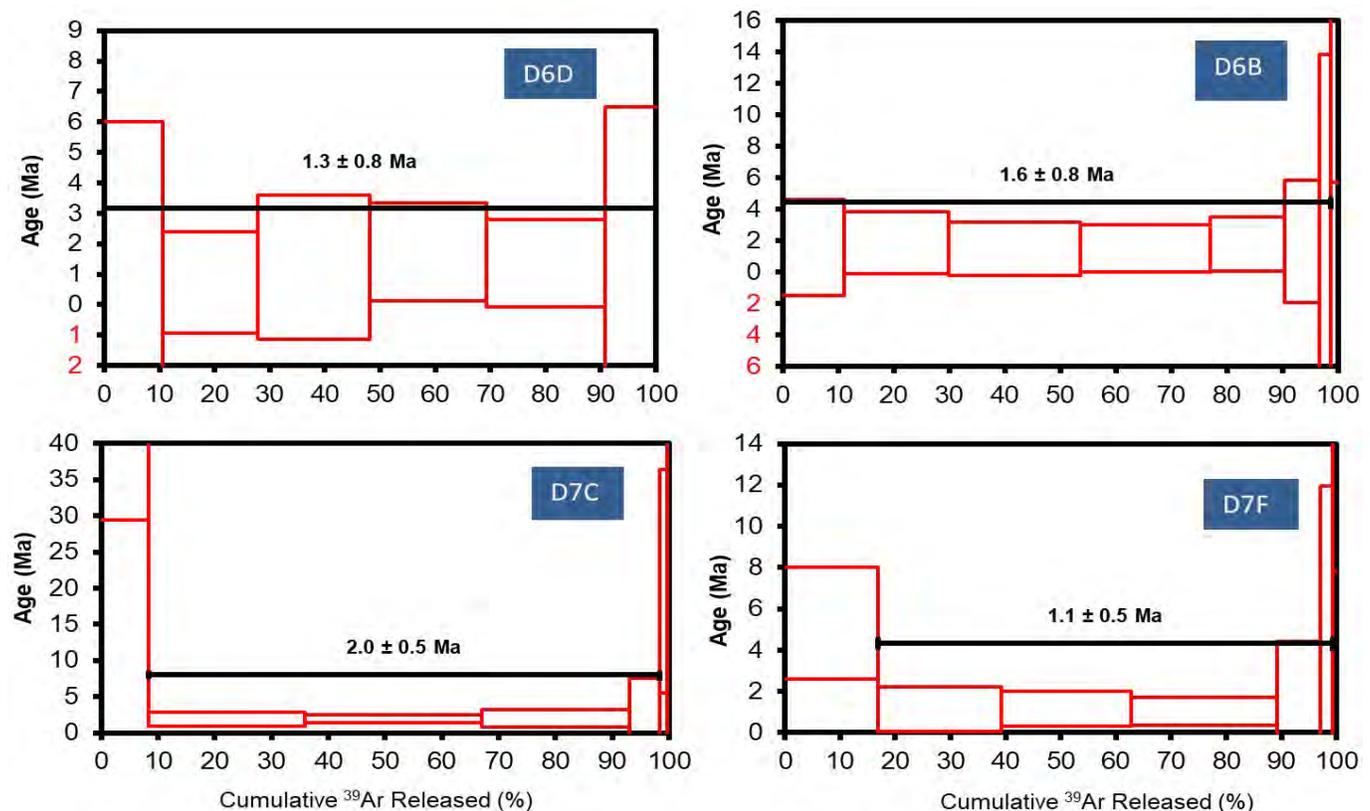
Figure 5. Step age spectra for the ⁴⁰Ar–³⁹Ar analyses of basalts dredged from Banco Tuzo. Black lines show the steps used in calculating the age given above the line, and are positioned arbitrarily relative to the *y*-axis.

in the region. The seamounts that lie between the main Galapagos platform and the GSC appear to be either cones (sometimes with defined calderas) or composite edifices with discrete flows and rift zones (Mittelstaedt *et al.* 2012). The flat top of Banco Tuzo is suggestive of the guyots (drowned islands) in the western Pacific but, by itself, a flat seamount top does not necessarily indicate past subaerial erosion, as this feature is evident in other Pacific seamounts where it has been caused by sedimentation and filling of surface topography (Karig *et al.* 1970) or by lava ponding within a caldera (Fornari *et al.* 1984, Clague *et al.* 2000, Mitchell 2001). However, the exposure of hard rock inferred from the Banco Tuzo backscatter data (Fig. 2) does not support sediment filling. Furthermore, the lava ponding mechanism is often invoked in smaller (4–5 km basal diameter), near-ridge volcanoes that have roughly circular shapes, whereas Banco Tuzo is much larger, far from circular, and morphologically unlike a single volcano with a central caldera. The combination of the flat top, the lack of primary volcanic features, and the morphology of the dredge D7 rocks, is best explained by previous subaerial exposure and erosion of the volcano.

The thin longitudinal channels on the eastern and western flanks of Banco Tuzo (Fig. 2) support a subaerial past as well. Similar features are present on the flanks of Wolf and Darwin Islands (Harpp *et al.* 2014). Thin channels several km long that have been observed on the submarine slopes of the volcanic island of La Réunion appear to be from sediment flows caused by the unstable buildup of clastic sediment along the edge of slopes

(Saint-Ange *et al.* 2013). A plausible explanation for the thin channels on Banco Tuzo is that they carried flows of volcaniclastic sediment created by coastal erosion during subaerial exposure.

Size and location of the ancient island

The age of the oldest sample constrains the paleoposition of the ancient Banco Tuzo island as well as its subsidence rate. Using an eastward plate velocity of 59 ± 1 km/Ma (O'Connor *et al.* 2007, Geist *et al.* 2014) for the Nazca Plate within the hotspot reference frame, we determine the position of Banco Tuzo at 2 Ma BP to be *c.* 120 km west of its current position. This would place it close to where Wolf Volcano, the northern end of Isabela Island, now lies (Fig. 6).

In order to determine the subsidence rate and the age at which Banco Tuzo became submerged, we first assume that the ancient shoreline is at or below the depth where the rounded rocks were recovered (dredge D7, 530–430 m bsl) but above the other transects where no weathered rocks were found, and therefore probably at the sharp bathymetric break between the flat top and the steep slopes on the western and eastern margins, at about 600 m bsl. We also assume that thermal subsidence due to cooling began after the youngest lava aged 1.1 Ma erupted, which we assume was the cessation of magmatism. Therefore Banco Tuzo has subsided *c.* 600 m in the past 1.1 Ma. This is slightly faster than the 380 m of subsidence for oceanic lithosphere derived from mid-ocean ridges during 1.1 Ma (Stein & Stein 1992), but slower than the 1195 m
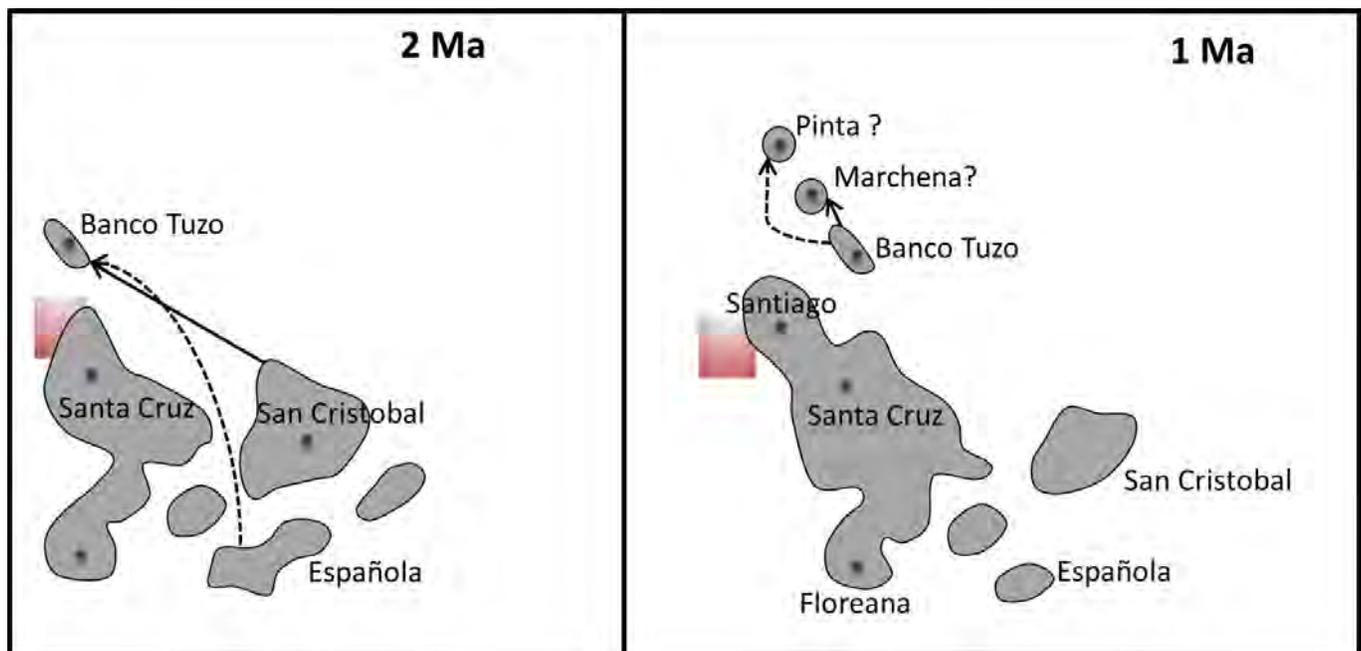
Figure 6. Possible paleogeography of the Galapagos region for 2 and 1 Ma BP based on Geist *et al.* (2014), updated with data presented here. Shadowed black circles indicate volcanoes that were active during that time increment. The pink shaded box is the estimated location of the Galapagos hotspot. The solid arrow represents a possible pathway of migration of the lava lizard clade currently comprising *Microlophus habeli* (Marchena) and *M. bivittatus* (San Cristóbal). The dashed arrow represents a possible pathway of migration of the tortoise lineage *Chelonoidis hoodensis* (Española) and *C. abingdoni* (Pinta).

of subsidence using the rate of the Galapagos Platform (Geist *et al*. 2014). This disparity between the subsidence of Banco Tuzo and the main archipelago suggests that the northern volcanoes, such as Pinta and Marchena, which are not located on the Galapagos Platform, may subside more slowly than the main islands.

To estimate the size of the ancient Banco Tuzo island, we assume that the slope break at 600 m bsl represents the ancient shoreline. At *c.* 1.1 Ma BP the summit of the island would have reached *c.* 350 m above sea level (not accounting for any erosion) and would have had the approximate land area and height above sea level of Marchena. At this time, the westernmost island on the main Galapagos Platform was a landmass composed of what is now Santa Cruz and Floreana (Geist *et al*. 2014). Banco Tuzo island would have been located just north of this landmass (Fig. 6), until it subsided. Using a subsidence rate of 550 m/Ma based on the above calculations, the island would have subsided 350 m over 0.6 Ma and therefore reached present-day sea level at *c.* 0.5 Ma BP. The emergence dates of Pinta and Marchena are not clear but recent radiometric ages of lavas dredged from the flanks of the two islands are *c.* 1 Ma (C. Sinton unpubl. data) and the oldest radiometric (K–Ar) dates from the subaerial lavas are 0.9 ± 0.2 Ma BP for Pinta and 0.56 ± 0.04 Ma BP for Marchena (White *et al*. 1993). Therefore Pinta and likely also Marchena were probably contemporaneous islands with Banco Tuzo.

Impact on species dispersal

Dispersal of species between islands in oceanic archipelagos is imperative for the evolution of a diversity of subspecies (Cowie & Holland 2006). Due to its location between the main archipelago and the northern islands, Banco Tuzo may have served as a stepping-stone for terrestrial flora and fauna between them. The inter-island radiation of terrestrial species is a prominent aspect of evolution in Galapagos and the timing of island emergence is a key determinant of this (Parent *et al*. 2008). At least two specific radiations could have been facilitated by Banco Tuzo. Mitochondrial DNA sequencing shows a relationship between the giant tortoises of the southeasterly island of Española (*Chelonoidis hoodensis*) and of Pinta in the north (*C. abingdoni*) (Caccone *et al*. 2002). An emergent Banco Tuzo at 2 Ma BP could have hosted the ancestors of these tortoises before Pinta emerged as an island (Fig. 6). Banco Tuzo may also have played a role in the radiation of lava lizards *Microlophus*. The divergence of the genetically related species on San Cristóbal (*M. bivittatus*) and Marchena (*M. habeli*) has been given an age of 0.4 Ma (Benavides *et al.* 2009) based on what they considered was the age of Marchena. This age can be extended if lava lizards migrated from San Cristóbal to Banco Tuzo 1–2 Ma BP and then later to Marchena after it emerged above sea level (Fig. 6).

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VERTEBRATE DIVERSITY ON FLOREANA ISLAND, GALAPAGOS

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SUMMARY

We report on the status of vertebrates on Floreana Island and Gardner-by-Floreana islet, Galapagos, comparing the species that we recorded in 2010 at 29 count points and while walking between them, with records from the previous two centuries compiled from the literature. On Floreana, we recorded 33 of the 50 indigenous species that had been recorded historically, of which 17 species were recorded on the 29 point counts. On Gardner-by-Floreana we recorded 20 indigenous species in total, of which nine on the single point count. The most abundant species were the Galapagos Flycatcher *Myiarchus magnirostris* on Floreana and the Great Frigatebird *Fregata minor* on Gardner. On Floreana we recorded ten of the 13 introduced vertebrate species that had been recorded previously, two of them on point counts. No introduced vertebrates were found on Gardner.

RESUMEN

La diversidad de vertebrados en la isla Floreana, Galápagos. Presentamos una actualización de los registros de especies de vertebrados en Floreana y Gardner-por-Floreana, Galápagos. Se comparó los datos de nuestro estudio en 2010, colectados en puntos de conteo y al caminar entre ellos, con la información obtenida de la literatura desde hace dos siglos. En Floreana observamos 33 de las 50 especies indígenas registradas históricamente, de las cuales 17 fueron registradas en los 29 puntos de conteo. En Gardner-por-Floreana registramos 20 especies indígenas, incluidas nueve en el punto de conteo. Las especies más abundantes fueron el Papamoscas *Myiarchus magnirostris* en Floreana, y la Fragata menor *Fregata minor* en Gardner. En Floreana registramos diez especies introducidas de las 13 que habían sido registradas anteriormente, dos de ellas en los puntos de conteo. No hubo registros de vertebrados introducidos en Gardner.

INTRODUCTION

Biodiversity inventories are an important means of tracking changes over time (Magurran & McGill 2011). Comparisons of historical records with contemporary studies allow tracking of extinctions and new invasions in fragile ecosystems. Inventories can also help to document threats to native species and prioritise conservation efforts in the long term.

Inventories of vertebrates in the Galapagos Archipelago have been conducted since the early 19th century, when the islands' unique fauna was first thoroughly described (see references below). Galapagos was visited by whalers and buccaneers in the decades leading up to the first permanent human settlements in Galapagos, initially on Floreana Island in 1832, when the archipelago became an Ecuadorean possession (Idrovo 2005).

Floreana is an island of *c*. 173 km² in the south of the archipelago (1°17'S, 90°26'W) with, in 2017, a human population of about 145 people, whose agriculture-based livelihood continues to influence the island's ecosystem (O'Connor *et al*. 2010). In Galapagos the vegetation is zoned according to altitude and aspect (Snell *et al*. 1996, Trueman & d'Ozouville 2010). The majority of Floreana

falls into the Dry Zone (up to between 80 and 120 m in elevation), the Transition and Humid zones comprise the interior portions of the island at higher elevations, where there is enough water for agriculture (Fig. 1), while the Coastal zone occupies a relatively small proportion of the island. Gardner-by-Floreana (1°19'48"S, 90°17'18"W) is a 76.5 ha islet located 8 km to the east of Floreana (Snell *et al*. 1996, Jiménez-Uzcátegui *et al*. 2011).

In Galapagos, 121 indigenous (endemic or native) vertebrate species have been recorded since the mid-1800s, of which 15 are now considered extinct (Jiménez-Uzcátegui *et al*. 2008a, 2017). The only extinct vertebrate unique to Floreana Island was the Floreana Giant Tortoise *Chelonoidis niger*. Other species considered extirpated from Floreana are extant in other parts of the archipelago or on islets close to Floreana, including the Galapagos Hawk *Buteo galapagoensis*, Floreana Mockingbird *Mimus trifasciatus*, Large Ground-Finch *Geospiza magnirostris* (last record 1957) and Sharp-beaked Ground-Finch *G. difficilis* (Jiménez-Uzcátegui *et al*. 2008a, 2011, Dvorak *et al*. 2017). Harris (1973) recorded the Galapagos Rail *Laterallus spilonotus* on Floreana but it has not been seen there since 1983 (Castro & Phillips 1996), and the Little Vermilion Flycatcher *Pyrocephalus nanus* has not been
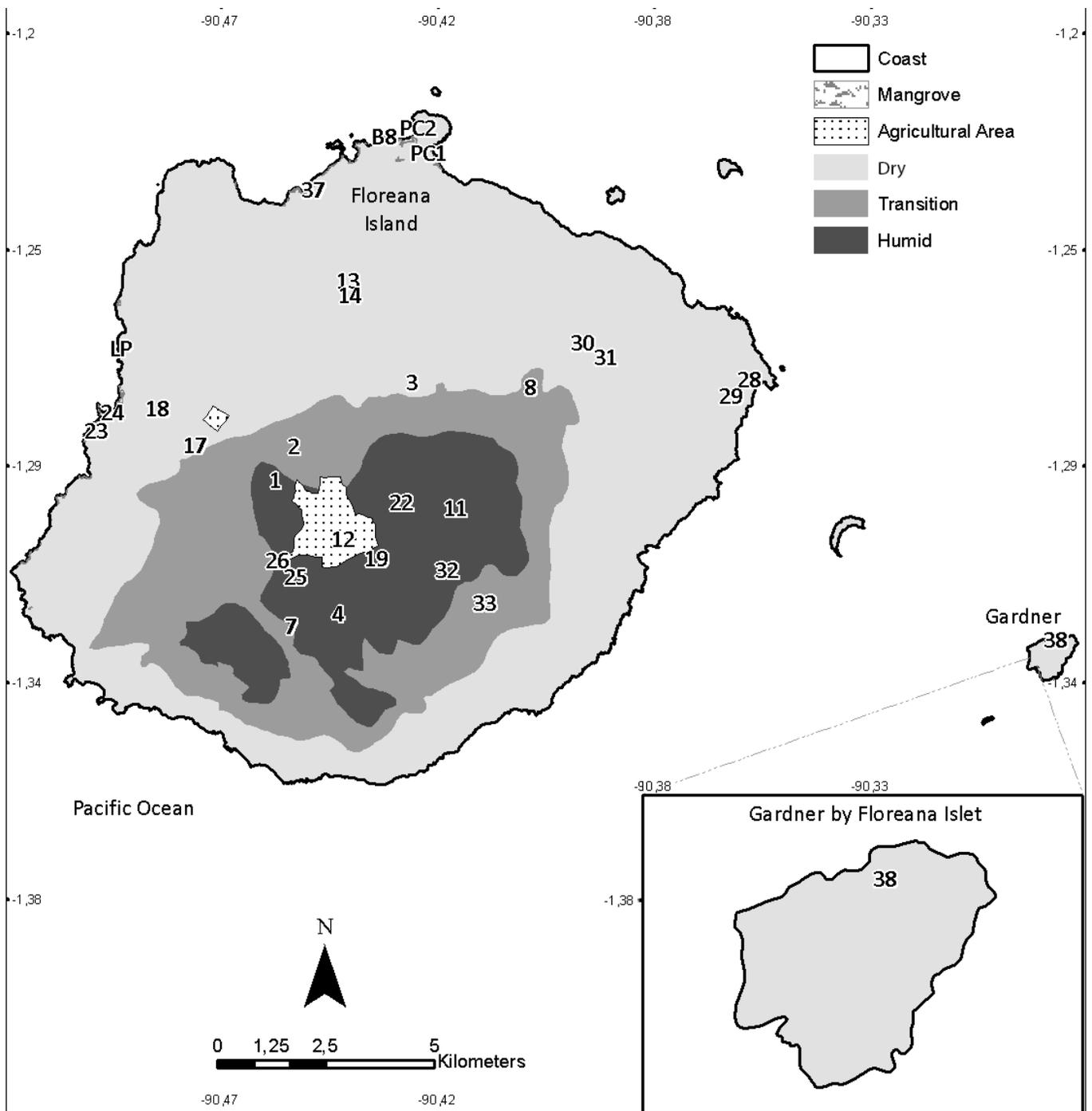
Figure 1. Map of Floreana and Gardner-by-Floreana showing point-count locations and vegetation zones.

seen there in the last decade (Wiedenfeld 2006); they are considered Vulnerable and Near-Threatened respectively (IUCN 2017). Southern Red Bat *Lasiurus blossevillii* (syn. *L. borealis brachyotis*) was recorded in 2004 after decades of no records (Brosset 1963, McCracken *et al*. 1997, Key & Sangoquiza 2008). Six other threatened vertebrate species are present on Floreana: the Critically Endangered Galapagos Petrel *Pterodroma phaeopygia* and Medium Tree-Finch *Geospiza pauper*, and the Endangered East Pacific Green Turtle *Chelonia mydas*, Galapagos Penguin

Spheniscus mendiculus, Galapagos Martin *Progne modesta* and Galapagos Sealion *Zalophus wollebaeki* (IUCN 2017).

An essential step towards identifying potential conservation or management actions for Galapagos is to track biodiversity across time and space, to gauge the effects of anthropogenic changes in the system, such as landuse change and the success of conservation efforts. Accordingly, the objectives of our study were to describe changes in the vertebrate fauna on Floreana and Gardner-by-Floreana since the 19th century, and to compare

species diversity across vegetation zones, predicting that diversity of indigenous species would be lower in zones where human influences such as introduced species and habitat change have been more conspicuous.

METHODS

Our field study

We used 29 count points on Floreana and one on Gardner-by-Floreana (Fig. 1), which had been established as part of a study of land snails carried out in 2009 (C.E. Parent & S. Cárdenas unpubl.). The points on Floreana were in the following vegetation zones: Coastal (n = 3, including one in mangrove), Dry (n = 11), Transition (n = 6) and Humid (n = 9). The point on Gardner-by-Floreana was in the Dry Zone.

We surveyed all points once, from 11 to 27 January 2010. Three 5-min. observation periods were carried out at each point, the first from the point itself, then the other two at positions 10 m from the point, in directions selected depending on the terrain. In each 5-min. period, we recorded every vertebrate species seen (on substrate or flying) or heard (only for species with distinct songs) at up to *c.* 50 m from the point. When possible, we recorded sex, age (juvenile, adult), and abundance if individuals occurred in groups. After the third count, we played from the central point 5-min. recordings of songs of the Medium Tree-Finch and Galapagos Rail, in order to improve the likelihood of detecting these species of particular conservation interest. Most point count data were collected between 6h00 and 10h00 and the rest between 15h00 and 18h00. For each point, we derived the cumulative number of vertebrate species and individuals by summing the tallies for the three counts plus playback responses at that point. In addition, we recorded vertebrates that we saw or heard as we walked between points, at distances of up to 20 m from us, at any time of day.

Other historical and recent data

From the literature we compiled records of vertebrate species that have been observed on Floreana since 1835,

and summarised these into lists by century (19th, 20th, 21st), applying modern taxonomy and nomenclature to all three periods. The list for the 19th century was compiled primarily from records in Darwin (1839), Sundevall (1871), Salvin (1876), Ridgway (1889), Van Denburgh & Slevin (1913), Gifford (1919), Wiedenfeld (2006) and Jiménez-Uzcátegui *et al.* (2011); for the 20th century from Van Denburgh (1912, 1914), Van Denburgh & Slevin (1913), Swart (1931), Slevin (1935), Brosset (1963), Lévêque (1964), Harris (1973), Franklyn *et al.* (1979), Hoeck (1984), Barnet (1986), Curry (1986), Steadman (1986), Steadman *et al.* (1991), McCracken *et al.* (1997), Petren *et al.* (1999), Wiedenfeld (2006) and Jiménez-Uzcátegui *et al.* (2008a, 2008b, 2011); and for the 21st century from Carrillo *et al.* (2005), Wiedenfeld (2006), Jiménez-Uzcátegui *et al.* (2008a, 2008b, 2011), Key & Sangoquiza (2008), Farrington & Petren (2011), Frías *et al.* (2014), Torres-Carvajal *et al.* (2014), Carmi *et al.* (2016), Dvorak *et al.* (2017), McCracken & Jiménez-Uzcátegui (2018) and Zaher *et al.* (2018). In addition, records from the secondary sources Castro & Phillips (1996) and Jiménez-Uzcátegui *et al.* (2017) were included, but records from these two sources that were not also reported in any of the foregoing primary sources are regarded as unconfirmed.

RESULTS

In total, 50 indigenous and 13 introduced vertebrate species have been reported on Floreana including its offshore islets (Table 1: records for Gardner-by-Floreana are reported separately only for our 2010 study).

At the 29 points on Floreana, we found 17 indigenous and two introduced vertebrate species. Adding the species that we found between plots, we recorded in total 33 indigenous and ten introduced species. On Gardner-by-Floreana we found nine indigenous species on the point count, 20 indigenous species overall, and no introduced species.

Of the 19 vertebrates on the point counts on Floreana, we counted 421 individuals. The most abundant species

Table 1. Vertebrate species reported on Floreana Island and Gardner-by-Floreana. * = extinct on Floreana; R = recorded in the primary sources listed in Methods; R? = unconfirmed record (see Methods); NR = not recorded; P = recorded on our point counts; W = recorded by us off-point.

	19th c.	20th c.	21st c.	Floreana This study	n obs. (%)	Gardner This study	n obs. (%)
NATIVE REPTILES							
Phyllodactylus baurii Baur's Leaf-toed Gecko	R	R	R	W		W	
Microlophus grayii Floreana Lava Lizard	R	R	R	**P**	9 (2.1)	W	
Amblyrhynchus cristatus Marine Iguana	R	R	R	W		W	
Pseudalsophis biserialis Galapagos Racer	R	R	R	NR		NR	
Chelonoidis niger Floreana Giant Tortoise*	R	NR	NR	NR		NR	
Chelonia mydas East Pacific Green Turtle	R?	R	R	W		W	
NATIVE BIRDS							
Anas bahamensis White-cheeked Pintail	R	R	R	W		NR	
Phoenicopterus ruber Greater Flamingo	R	R	R	W		NR	
Phaethon aethereus Red-billed Tropicbird	R	R	R	**P**	2 (0.5)	W	

	19th c.	20th c.	21st c.	Floreana This study	n obs. (%)	Gardner This study	n obs. (%)
Zenaida galapagoensis Galapagos Dove	R	R	R	P	1 (0.2)	P	6 (10.7)
Coccyzus melacoryphus Dark-billed Cuckoo	R	R	R	P	3 (0.7)	NR	
Laterallus spilonota Galapagos Rail	NR	R	NR	NR		NR	
Neocrex erythrops Paint-billed Crake	NR	R[1]	R	NR		NR	
Gallinula galeata Common Gallinule	NR	R	R	NR		NR	
Spheniscus mendiculus Galapagos Penguin	R	R	R	W		NR	
Hydrobates castro Band-rumped Storm Petrel	R?	R	R	NR		NR	
Pterodroma phaeopygia Galapagos Petrel	R?	R	R	W		NR	
Puffinus subalaris Galapagos Shearwater	R	R	R	W		W	
Nyctanassa violacea Yellow-crowned Night Heron	R	R	R	W		W	
Butorides striatus Striated Heron	R	R	R	P	2 (0.5)	NR	
Ardea herodias Great Blue Heron	R?	R	R	W		NR	
Pelecanus occidentalis Brown Pelican	R	R	R?	P	5 (1.2)	W	
Fregata minor Great Frigatebird	R?[2]	R	R?	P	25 (5.9)	P	17 (30.4)
Fregata magnificens Magnificent Frigatebird	R?[2]	R	R?	P	2 (0.5)	W	
Sula sula Red-footed Booby	R	R	NR	W		P	1 (1.8)
Sula nebouxii Blue-footed Booby	R?	R	R?	P	7 (1.7)	W	1 (1.8)
Sula granti Nazca Booby	R	R	R	W		P	7 (12.5)
Himantopus mexicanus Black-necked Stilt	R	R	R	NR		NR	
Anous stolidus Brown Noddy	R	R?	R?	W		W	
Creagrus furcatus Swallow-tailed Gull	R	R	R	NR		NR	
Asio flammeus Short-eared Owl	R	R	R	W		P	2 (3.6)
Buteo galapagoensis Galapagos Hawk*	R	NR	NR	NR		NR	
Myiarchus magnirostris Galapagos Flycatcher	R	R	R	P	94 (22.3)	NR	
Pyrocephalus nanus Little Vermilion Flycatcher	R	R	R	NR		NR	
Progne modesta Galapagos Martin	R	R	R	W		NR	
Mimus trifasciatus Floreana Mockingbird*	R	NR	NR	NR		P	14 (25.0)
Setophaga petechia Yellow Warbler	R	R	R	P	84 (20.0)	P	1 (1.8)
Certhidea fusca Grey Warbler-Finch	R	R	NR	NR		NR	
Platyspiza crassirostris Vegetarian Finch	R	R	R	P	2 (0.5)	NR	
Camarhynchus psittacula Large Tree-Finch	R	R	NR	NR		NR	
Camarhynchus pauper Medium Tree-Finch	R	R	R	P	32 (7.6)	NR	
Camarhynchus parvulus Small Tree-Finch	R	R	R	P	2 (0.5)	NR	
Geospiza fuliginosa Small Ground-Finch	R	R	R	P	55 (13.1)	NR	
Geospiza fortis Medium Ground-Finch	R	R	R	P	69 (16.4)	P	7 (12.5)
Geospiza magnirostris Large Ground-Finch*	R	NR	NR	NR		NR	
Geospiza scandens Common Cactus-Finch	R	R	R	P	9 (2.1)	NR	
Geospiza difficilis Sharp-beaked Ground-Finch*	R	NR	NR	NR		NR	
NATIVE MAMMALS							
Zalophus wollebaeki Galapagos Sea Lion	R	R	R	W		W	
Lasiurus blossevillii Southern Red Bat*	R	R?[3]	R	NR		NR	
Lasiurus cinereus Hoary Bat	NR	R[4]	R	NR		NR	
INTRODUCED BIRDS							
Crotophaga ani Smooth-billed Ani	NR	R?	R	P	16 (3.8)	NR	
Bubulcus ibis Cattle Egret	NR	R?	R	P	2 (0.5)	NR	
Gallus gallus Domestic Chicken	R	R	R	W		NR	
Meleagris gallopavo Turkey	NR	R?	R	NR		NR	
INTRODUCED MAMMALS							
Capra hircus Goat	R	R	R	W		NR	
Sus scrofa Pig	R	R	R	W		NR	
Bos taurus Cattle	R	R	R	W		NR	
Equus caballus Horse	R	R	R	NR		NR	
Equus asinus Donkey	R	R	R	W		NR	
Felis catus Cat	R	R	R	W		NR	
Canis domesticus Dog	R	R	R	W		NR	
Rattus rattus Black Rat	R?	R	R	W		NR	
Mus musculus House Mouse	R?	R	R	NR		NR	

[1]First record 1953.
[2]One or both of these species were recorded as "*Fregata aquila*" in the 19th c.
[3]Reported by Brosset (1963) but without details.
[4] First confirmed in the 1990s.

were the Galapagos Flycatcher *Myiarchus magnirostris* (94 individuals = 22.3 %), followed by the Yellow Warbler *Setophaga petechia* (84 individuals, 20.0 %) and the Medium Ground-Finch *Geospiza fortis* (69, 16.4 %) (Table 1). Of the nine vertebrates on the point count on Gardner-by-Floreana, we counted 56 individuals. The most abundant species were the Great Frigatebird *Fregata minor* (17 individuals, 30 %), followed by the Floreana Mockingbird (14, 25 %) and the Medium Ground-Finch and Nazca Booby *Sula granti* (7 individuals each, 12 %) (Table 1).

DISCUSSION

Floreana has experienced recent ecosystem changes, including a great fire in the 19th century and a cool period in 1860–1954 (Nickerson 1984, Dunbar *et al*. 1990), frequent visits by whalers and buccaneers before the first permanent human settlements, then settlement and the development of agriculture since the early 19th century (Idrovo 2005). People brought introduced species that have affected the indigenous species (Jiménez-Uzcátegui *et al*. 2011). These changes contributed to the extinction of five species on Floreana in historical times (Galapagos Hawk, Large Ground-Finch, Sharp-beaked Ground Finch, Floreana Mockingbird and Floreana Giant Tortoise), none of which was registered in our contemporary surveys (Table 1).

Our results revealed that our point sampling regime was not satisfactory for assessing species diversity. In our 29 points counts we recorded only 17 of the 50 indigenous species that have been recorded on Floreana (including the five extinct species mentioned in the previous paragraph), but we recorded an additional 16 indigenous species between plots. Our point sampling effort was limited over space and season, taking place over ten days during the warm season (Trueman & d'Ozouville 2010) in a single year, and probably covering < 0.001 % of the total surface area of Floreana. It is important to increase this effort, complement this method with others such as transects, and extend the survey throughout the seasons.

The 17 indigenous species not recorded in our study include the five extinct species mentioned above, plus the Galapagos Rail and Little Vermilion Flycatcher (neither of which has been recorded recently), the Paint-billed Crake *Neocrex erythrops*, Common Gallinule *Gallinula galeata*, Band-rumped Storm Petrel *Hydrobates castro*, Black-necked Stilt *Himantopus mexicanus* and Swallow-tailed Gull *Creagrus furcatus* (all species from coastal and lagoon habitats where we made few observations), Grey Warbler-Finch *Certhidea fusca* and Large Tree-Finch *Camarhynchus psittacula* (species with small and decreasing populations: Fessl *et al*. 2017), the nocturnal Hoary Bat and Southern Red Bat, and the Galapagos Racer snake *Pseudalsophis biserialis* (species difficult to find) (Table 1).

On the other hand, the Medium Tree-Finch, recently categorized as Critically Endangered because its population is decreasing, was fifth in abundance with 32 individuals (8.7 %) and it has been shown not to be restricted to the *Scalesia* forest (Fessl *et al*. 2017). However, this Floreana endemic may still be susceptible to climate change, introduced species and diseases.

The reasons behind the declines and disappearance of indigenous vertebrate species on Floreana remain controversial (Curry 1986, Jiménez-Uzcátegui *et al*. 2011), but the relict distributions of some taxa, such as the Floreana Mockingbird and Galapagos Racer snake, which are now limited to Champion and Gardner-by-Floreana islets, suggest that the introduction of predators such as rats *Rattus* spp. and cats *Felis catus* has led to local extirpations (Jiménez-Uzcátegui *et al*. 2008a, 2011; Table 1). On these islets, no species are known to have disappeared, and no introduced vertebrates (except Smooth-billed Ani) or pathogens (except canary pox-virus) have been recorded, but when La Niña or El Niño events have taken place, their vertebrate populations fluctuated (Curry 1986, Jiménez-Uzcátegui *et al*. 2011). Climate change and pathogens may compound these effects (Thiel *et al*. 2005, Jiménez-Uzcátegui *et al*. 2011).

The management of introduced species, including cats, rats, goats *Capra hircus*, and plants such as Hill Blackberry *Rubus niveus* and Lantana *Lantana camara*, among others (Guézou *et al*. 2014), remains a high priority to avoid more extinctions on Floreana, while the protection of pristine sites such as the islets of Gardner-by-Floreana and Champion, which effectively conserve some species extinct on the main island, remains essential. Long-term monitoring of these sites and species is important, to register changes over time and allow managers to direct resources to conserve them (Jiménez-Uzcátegui *et al*. 2019).

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EFFECTS OF THE 2016 EL NIÑO ON THE GALAPAGOS ARTISANAL COASTAL FIN-FISH FISHERY

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SUMMARY

El Niño events heavily influence the Tropical Eastern Pacific and lead to a decrease in nutrient and phytoplankton concentrations and variation in the composition of the marine trophic web. The target species of the Galapagos coastal fishery include demersal fish, several of which are listed as threatened on the IUCN Red List. At present it is unclear how El Niño events influence artisanal fisheries in the Galapagos. To study this influence, catch composition at the largest dock on Santa Cruz Island was recorded during March and April in 2013, 2014 and the El Niño year 2016. Compositions were significantly different between 2016 and both 2013 and 2014, but not between 2013 and 2014. These differences were due to the appearance of uncommon demersal species such as Grape-eye Seabass *Hemilutjanus macrophthalmos* and Pacific Dog Snapper *Lutjanus novemfasciatus* in 2016. Size frequency distributions also varied, with significantly larger sizes of several species observed in 2016 when compared to 2013 or 2014. At present, the immediate mechanism behind the observed changes in fish communities is unclear; however, because many demersal fish have conservative life histories and there are no species-specific regulations governing the take of fin-fish within the Galapagos Marine Reserve, fishing during El Niño events may have profound effects on such populations by eliminating the largest individuals.

RESUMEN

Efectos de El Niño de 2016 en la pesquería artesanal de peces costeros de Galápagos. Los eventos de El Niño tienen una gran influencia en el Pacífico Este Tropical y conducen a la disminución en la concentración de nutrientes y fitoplancton y a la variación en la composición de la red trófica marina. Las especies objetivo de la pesquería costera de Galápagos incluyen peces demersales, varios de los cuales están considerados amenazados en la Lista Roja de la UICN. Todavía no está claro cómo influyen los eventos de El Niño en la pesca artesanal en las Galápagos. Para estudiar esta influencia, se registró la composición de la captura en el muelle más grande de la isla de Santa Cruz durante marzo y abril de 2013, 2014 y del año de El Niño 2016. Las composiciones fueron significativamente diferentes entre 2016 *vs*. 2013 y 2014, pero no entre 2013 y 2014. Estas diferencias se debieron a la aparición en 2016 de especies demersales poco comunes, como el Serrano ojo de uva *Hemilutjanus macrophthalmos* y el Pargo prieto *Lutjanus novemfasciatus*. Las distribuciones de frecuencia de tamaño también variaron, con tamaños significativamente más grandes de varias especies observados en 2016 en comparación con 2013 o 2014. En la actualidad, el mecanismo inmediato detrás de los cambios observados en las comunidades de peces no está claro; sin embargo, debido a que muchos peces demersales tienen historias de vida conservadoras, y a que no hay regulaciones específicas para estas especies que rijan su captura dentro de la Reserva Marina de Galápagos la pesca durante los eventos de El Niño podría tener efectos profundos en dichas poblaciones al eliminar a los individuos más grandes.

INTRODUCTION

The oceanography of the Tropical Eastern Pacific (TEP) is dominated by the El Niño-Southern Oscillation (ENSO) cycle and its effect on inter-annual sea surface temperature variability (Wang & Fiedler 2006). During El Niño years, Kelvin waves originate in the warm western equatorial Pacific and travel eastwards, bringing unusually warm waters to the west coast of South America. The physical effects of El Niño events include increases in sea surface temperature, precipitation and sea surface height, and a deepening of the thermocline (Wang & Fiedler 2006, Liu *et al*. 2014). These changes produce a decrease in nutrient and phytoplankton concentrations and variation in the composition of the marine trophic chain (Wang & Fiedler 2006).

While El Niño events have historically occurred at a decadal time scale, in the last thousand years they appear to have increased in strength in the TEP, with record temperatures observed over the last half century (Conroy *et al*. 2009, Edgar *et al*. 2010, Wang *et al*. 2017). This trend is expected to continue as extreme El Niño events are predicted to occur more frequently owing to climate change (Conroy *et al*. 2009, Wang *et al*. 2017, Cai *et al.* 2018). The changes in environmental conditions observed during El Niño years have been linked to changes in the abundance and distribution of multiple species, many of them of high economic importance for fisheries, from pelagic species such as the Jack Mackerel *Trachurus symmetricus* (Arcos *et al.* 2001) or the Jumbo Flying Squid *Dosidicus gigas* (Alabia *et al.* 2016), to entire coastal fish assemblages (Ñiquen & Bouchon 2004, Rojo-Vázquez *et al.* 2008, Adams & Flores 2016).

The Galapagos islands, located in the TEP *c.* 1000 km west of the coast of mainland Ecuador, are in the path of cold and warm oceanic currents, mainly the cold eastward-flowing Cromwell (Equatorial) Undercurrent that upwells in the western side of the archipelago, and the westward South Equatorial Current (SEC) (Schaeffer *et al.* 2008, Sachs & Ladd 2010, Liu *et al.* 2014). The SEC transports warm waters from the Panama Current entering from the north, particularly during the hot season (December–May), and cool upwelled waters from the Humboldt Current entering from the south, particularly during the cool season of June–October. These currents provide the waters of the archipelago with a high input of nutrients and plankton, levels of which can be above those observed in tropical Pacific open ocean waters even during El Niño events (Schaeffer *et al.* 2008, Wolff *et al.* 2012). High production allows abundant sea life of tropical, temperate and southern ocean origin to occur (*e.g.* >550 inshore fish species) including a large proportion (*c.* 20 %) of endemic species (Wellington 1984, Bustamante *et al.* 2000, McCosker & Rosenblatt 2010, Schiller *et al.* 2013, Salinas-de-León *et al.* 2016).

Productivity in the Galapagos can be strongly reduced by El Niño events; in particular, the 1982–3 and 1997–8 El Niño events exhibited extreme thermal anomalies that altered intertidal shores and shallow rocky reefs and reduced phytoplankton productivity (Robinson 1985, Glynn *et al.* 2001, Vinueza *et al.* 2006). This precipitated a drastic reduction of biomass at the base of the marine trophic pyramid (Robinson & Del Pino 1985, Wolff *et al.* 2012). The resulting lack of food led to sharp population declines of endemic vertebrates such as the Galapagos Penguin *Spheniscus mendiculus* and Galapagos Fur Seal *Arctocephalus galapagoensis* (Trillmich & Limberger 1985, Vargas *et al.* 2006).

Climate change will also likely affect ecosystems through intense and periodic extreme events, rather than a gradual change in ocean climate (Reaser *et al.* 2000, Boer *et al.* 2004, Edgar *et al.* 2010). Since the effects of El Niño events are clearly identified in the Galapagos islands (Wang & Fiedler 2006), the archipelago provides a good opportunity to evaluate both short-term (El Niño events) and long-term (climate change) impacts on ecosystems.

Since the establishment of the *c.* 138,000 km^2 Galapagos Marine Reserve (GMR) in 1998 (Heylings *et al.* 2002), commercial fishing has been banned and artisanal fishing permitted only in areas delimited by the zonation scheme approved in 2001 (Castrejón *et al.* 2014). In 2016, the Galapagos National Park Directorate (GNPD) recorded 1121 licensed fishers and 337 registered fishing boats, of which only *c.* 400 of the licensed fishers are active (Zimmerhackel *et al.* 2015, DPNG 2017). The fisheries for lobsters (*Panulirus gracillis*, *P. penicillatus* and *Scyllarides astori*) and fin-fish are the most important source of income since the collapse of the *Isostichopus fuscus* sea cucumber fishery in the 2000s, and together are worth *c.* US$ 4 million a year (Hearn *et al.* 2007, Castrejón *et al.* 2014; Zimmerhackel *et al.* 2015). The coastal-demersal fishery targets species that include demersal predatory fish such as the endemic Galapagos White-spotted Sandbass *Paralabrax albomaculatus* and regional endemic Sailfin Grouper *Mycteroperca olfax* (on the IUCN Red List as Endangered and Vulnerable, respectively: Castrejon *et al.* 2005, Robertson *et al.* 2010, Erisman & Craig 2018), together with the regional endemic Mottled Scorpionfish *Pontinus clemensi* and the widely distributed Misty Grouper *Hyporthodon mystacinus* (Reck 1983, Bustamante 1998, Schiller *et al.* 2015, Zimmerhackel *et al.* 2015).

The fin-fishery is mostly conducted using the traditional hook and line method ("empate" in Spanish), as used by most Galapagos fishers during the daytime (Zimmerhackel *et al.* 2015, Usseglio *et al.* 2015). This unregulated, multi-species (>60 species caught), small-scale artisanal fishery shows clear signs of over-exploitation, low selectivity and high by-catch that have had a severe impact on slow-growing bottom-dwelling fish populations such as groupers (Schiller *et al.* 2015, Zimmerhackel *et al.* 2015, Usseglio *et al.* 2015, 2016). Currently, landing statistics for this fishery are scarce (Reck 1983, Bustamante 1998, Velasco Plaza *et al.* 2014), and no information on the effect of environmental variability on the population dynamics of the main exploited species is available (Castrejón *et al.* 2014, Zimmerhackel *et al.* 2015, Usseglio *et al.* 2016).

Despite general negative effects on the ecosystem, certain fisheries in the Galapagos benefited during and immediately after the 1998–9 El Niño. The fin-fishery then had similar total landings as previous years but catch composition included more species than in 1997 (77 *vs* 65 species: Bustamante *et al.* 1999). Not only were more *M. olfax* caught during the El Niño but on average they were larger when compared to 1997, 1999 and 2001, perhaps because fish were moving to shallower waters attracted by higher water temperatures that may have acted as a spawning cue (Nicolaides & Murillo 2001, Nicolaides *et al.* 2002). Among other effects, Defeo *et al.* (2013) found that the biomass of lobsters (*P. penicillatus* and *P. gracilis*)

and sea cucumbers (*I. fuscus*) increased considerably after the 1998–9 event, probably due to higher than average recruitment during the El Niño.

The above led us to expect that the Galapagos fin-fishery catch would exhibit a different composition during further El Niño events, with a higher proportion of larger demersal fish. In the present study, we tested this by comparing catch composition and length distribution of the most common species landed at the main port of Santa Cruz, Galapagos, during three years: 2013, an average oceanographic year, 2014, a year of weak warming, and 2016, an El Niño year (Wang *et al.* 2017). We also identified species indicative of each year, and correlated variability in the catch composition with water temperature and the Multivariate ENSO Index (MEI). We did not compare individual species or total catches among years because annual fishing effort variability was unknown.

MATERIALS AND METHODS

Data Collection

Fish catches were recorded by an observer at Pelican Bay in Puerto Ayora, the major landing dock of Santa Cruz Island (Fig. 1). The observer recorded all catches landed from 7h30 to 17h00, Monday to Friday, during March and April of 2013 and 2016, and in April 2014. Data were collected during these months because they are part of the Galapagos hot season, when the influence of El Niño events is more strongly experienced in the TEP (Wang & Fiedler 2006, Liu *et al.* 2014). Fish were identified using Molina *et al*. (2004) and Grove & Lavenberg (1997). We excluded pelagic species from further analysis because, during 2013, the GNPD and local fishers conducted a pilot study to determine the feasibility and impacts of long-line fishing inside the GMR (DPNG 2014). Pelagic species were taken directly to continental Ecuador to be sold, and therefore were poorly represented during this year in our dataset. Participation by some fishers in this long-line study also influenced fishing effort during 2013, not allowing us to compare fish catch abundance among years. Besides quantifying the species collected, the observer recorded fork length (FL, 1 mm precision) of all fish caught and name of the fishing boat. During 2013 and 2014, fishers also shared their approximate fishing locations (Fig. 1).

We obtained water temperature data for the study period measured at the Charles Darwin Research Station located in Academy Bay, Puerto Ayora (Fig. 1, data available at <www.darwinfoundation.org/datazone/climate/>). These data are recorded daily and have been found to be representative of temperature changes in the archipelago and well correlated with temperatures throughout the TEP (Wolff 2010). The MEI is an index used to monitor ENSO across all El Niño regions, where negative values represent the cold ENSO or La Niña phase, and positive values represent the warm or El Niño phase (Wolter & Timlin 1998). This index is developed

Figure 1. Map of the Galapagos Archipelago showing the main oceanographic currents and 2013–14 fish catch locations included in this study. The inset shows the northern outlying islands of Darwin and Wolf at larger scale.

using data on sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky, considered the main observed variables over the tropical Pacific (<www.esrl.noaa.gov/psd/enso/mei/>, consulted 29 Jan 2019).

Statistical Analysis

A Multi-Response Permutation Procedure (MRPP) was used to test variation in catch composition among years. Because annual fishing effort was unknown, catch composition data were first transformed into percentages (McCune & Mefford 2011), with species present in only one sample excluded. Our percentage-transformed catch composition data met the homogeneity of dispersion assumption, which was tested using multivariate homo-geneity of groups dispersion analysis (Oksanen *et al.* 2013). The daily averaged percent catch composition, calculated by adding the catches of all boats for the day and dividing by the number of boats, was used as the unit of comparison because daily oceanographic conditions likely influenced the catch of all boats similarly, and therefore the catch of individual boats would not have been independent. To conduct the MRPP, we used the Bray–Curtis coefficient to create a dissimilarity matrix among samples in multidimensional space, and with a *P*-value determined using 4999 permutations. The Bray–Curtis index was used because its sensitivity does not decrease when using a heterogeneous dataset and its sensitivity towards outliers is low (McCune & Mefford 2011). We

corrected the *P*-value using Tukey's honestly significant difference test due to multiple pairwise comparisons.

A multi-dimensional scaling (MDS) ordination was used in order to visualize MRPP results and explore the relationship between catch composition and environmental variables. This was constructed with the Bray-Curtis distance measure in two-dimensions and catch percentage composition. The stress of the ordination was 0.17, which is below maximum recommended levels (0.2: McCune & Mefford 2011). To explore the relationship between landing compositions and oceanographic conditions, Pearson correlations between water temperature and MEI with ordination axes were computed. Because the environmental conditions that influenced fish movement might have occurred prior to the day of capture, we also included one day and one month lagged values for these variables, and averaged over the one (2014) or two (2013 and 2016) months surveyed each year.

An Indicator Species Analysis (ISA) was used to determine whether certain species were indicators of each year. The ISA combines species information on abundance and frequency of occurrence in a particular group (McCune & Mefford 2011). This analysis provides indicator values (IV) that express the proportional and relative frequency of a species in a particular group as a percentage (*i.e.* range 0–100). We determined the *P*-value using a Monte-Carlo test with 4999 randomizations. Only species with a *P*-value ≤ 0.05 were considered in further analysis. The MRPP, MDS and ISA analyses were conducted using the statistical software package PC-ORD 6.0 (McCune & Mefford 2011).

We ran Kolmogorov-Smirnov two-way tests (K-S) to compare the size frequency distribution of *P. clemensi, P. albomaculatus, M. olfax*, Grape-eye Seabass *Hemilutjanus macrophthalmos*, *Hyporthodon mystacinus*, Ocean Whitefish *Caulolatilus princeps* and *L. novemfasciatus* in 2013, 2014 and 2016 (Sokal & Rohlf 2012). These species were selected as they were the most abundant or were found to be year indicators (see Results section). K-S tests were run using R Core software (v. 2.15.3: <www.r-project.org>). Means are given ± SD where appropriate.

RESULTS

We recorded 4923 individual fish (1886, 676 and 1418 in 2013, 2014 and 2016 respectively) on 62 fishing days (37, 15 and 10, respectively) from 43 different fishing boats (13 % of boats registered in Galapagos) at Pelican Bay (28 in 2013, 22 in 2014 and 7 in 2016). During this period, we documented 36 species which belonged to 12 families, the most common being Serranidae (eight species) and Scombridae (seven species, Table 1).

Considering all species caught (*i.e.* including those present in only one sample), on average, 2.88 ± 1.72 species of fish were recorded per day in 2013, 3.25 ± 2.38 in 2014 and 3.86 ± 2.41 in 2016. The most commonly caught species were *P. clemensi* (31 % of individuals, Fig. 2) in

Table 1. All fish species recorded at Pelican Bay dock, Puerto Ayora, Santa Cruz Island, during March and April 2013, April 2014, and March and April 2016. *Species found in more than one sample, considered in full statistical analysis.

Carangidae	**Scombridae**
*Alectis ciliaris**	*Acanthocybium solandri*
Seriola peruana	*Euthynnus lineatus*
Seriola rivoliana	*Sarda orientalis*
Coryphaenidae	*Scomberomorus sierra*
Coryphaena hippurus	*Thunnus albacares*
Haemulidae	*Thunnus obesus*
*Haemulon scudderii**	*Thunnus alalunga*
Xenichthys agassizi	**Scorpaenidae**
Xenocys jessiae	*Pontinus clemensi**
Istiophoridae	*Scorpaena mystes*
Makaira mazara	**Serranidae**
Labridae	*Cratinus agassizii**
*Bodianus diplotaenia**	*Dermatolepis dermatolepis**
Semicossyphus darwini	*Epinephelus cifuentesi**
Lutjanidae	*Epinephelus labriformis**
*Lutjamus guttatus**	*Hemilutjanus macrophthalmos**
*Lutjanus argentiventris**	*Hyporthodon mystacinus**
*Lutjanus novumfasiatus**	*Mycteroperca olfax**
*Lutjanus viridis**	*Paralabrax albomaculatus**
Malacanthidae	*Paranthias colonus*
*Caulolatilus affinis**	**Sphyraenidae**
*Caulolatilus princeps**	*Sphyraena idiastes*
Mugilidae	
Mugil galapagensis	

2013, *M. olfax* (31 %) in 2014 and *P. clemensi* (41%) in 2016. These fish had been caught at 54 fishing sites in 2013 and at 32 in 2014; collection site data were not available for 2016. Sites were located near ten major islands, mostly around Floreana (50 % of the 954 catches where location was provided, Fig. 1), Isabela (17 %) and Santiago (9 %). During the sampling period, water temperature at the CDRS and MEI were lowest in 2013 (25.4 ± 1.0°C and 0.28 ± 0.42, respectively, mean ± SD) and highest in 2016 (26.7 ± 0.1°C and 2.01 ± 0.06).
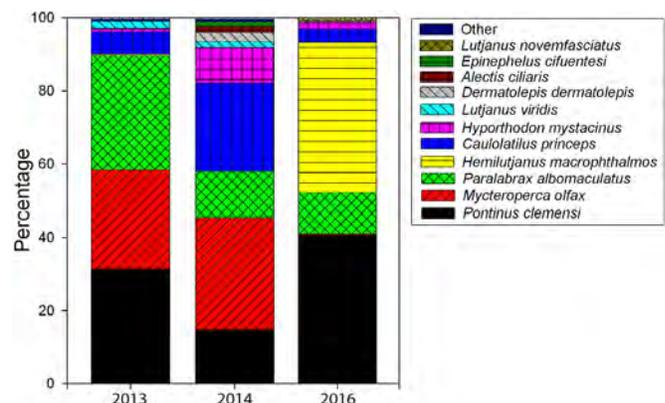
Figure 2. Percentage composition of the Galapagos fin-fishery catches recorded during March and April 2013, April 2014, and March and April 2016.

Of the 36 species recorded, 18 were observed on more than one day and are demersal, and were therefore used in the further analyses below. The catch composition varied significantly among years (MRPP, A = 0.10, P = 0.0002). Pairwise comparisons found differences between 2016 and 2013 and between 2016 and 2014 (P = 0.001 and 0.0003, respectively) but not between 2013 and 2014 (P > 0.05). In the MDS ordination, data were divided by year on axis 1 with 2016 on the right side, and 2013 and 2014 towards the left side of the axis (Fig. 3). Axis 1 was most strongly correlated with MEI values per month (r = 0.53, P < 0.01) followed by MEI values lagged by 1 month (r = 0.50, P < 0.01). *H. macrophthalmos*, which was present on all 2016 days, and *L. novemfasciatus*, present only in 2016, were indicator species for 2016 (IV = 99.3 and 28.6, P = 0.0002 and 0.02).

We found significant differences in the size frequency distribution of all species analyzed (Fig. 4). Size frequency distribution of *P. clemensi*, *H. macrophthalmos* and *H. mystacinus* differed between 2016 and 2013, with larger sizes in 2016, while size distribution of *P. albomaculatus*, *M. olfax* and *C. princeps* varied between 2016 and both 2013 and 2014, with larger sizes always observed in 2016 (Table 2). We were not able to compare *P. clemensi*, *H. macrophthalmos* and *H. mystacinus* sizes from 2016 with 2014 as not enough individuals were recorded. We were also not able to compare size frequency distribution of *L. novemfasciatus* among years because they were only recorded during 2016; during that year fish measured between 58 and 102 cm FL (77.5 ± 15 cm FL).

DISCUSSION

The present study is one of the first to analyze the impact of El Niño events on demersal fin-fishery catch composition for the Galapagos (Bustamante 1999, Nicolaides & Murillo
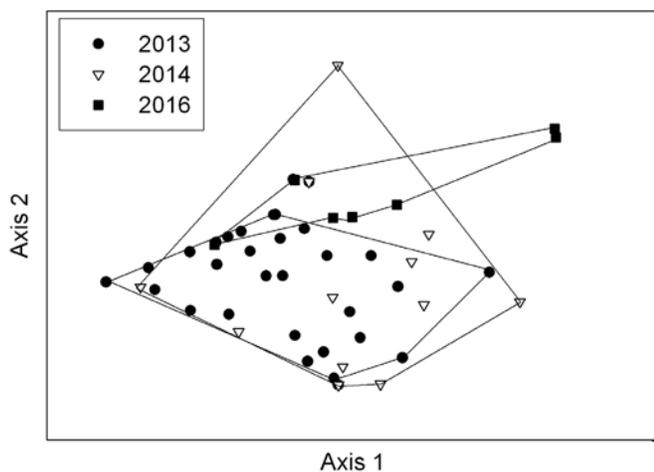
2001, Nicolaides *et al.* 2002) and globally (for pelagics see Godínez-Domínguez *et al.* 2000, Rojo-Vázquez *et al.* 2008, Adams & Flores 2016). Our results provide evidence that the catch composition of the Galapagos artisanal coastal fin-fishery changed during 2016, an El Niño year. This change was mainly driven by an increase in size and the presence of uncommon demersal fish species in the catch during 2016.

Changes in the catch composition of fin-fish fisheries during El Niño events have been observed in other parts of the Pacific (*e.g.* Ñiquen & Bouchon 2004, Rojo-Vázquez *et al.* 2008, Adams & Flores 2016). These authors have suggested that their results could have been caused by mortality or migration of the target species or their prey. In Galapagos, studies have observed that during El Niño events there is a reduction in primary production and the populations of small pelagic fish, and larger sizes of *M. olfax* are caught (Nicolaides & Murillo 2001, Nicolaides *et al.* 2002, Wolff *et al.* 2012, Vargas *et al.* 2006), suggesting that similar mechanisms may be taking place in the archipelago.

Demersal species such as groupers and snappers have been shown to exhibit size-depth distribution with larger fish inhabiting deeper waters (Aburto-Oropeza *et al.* 2009, Misa *et al.* 2013, Lindfield *et al.* 2014). Nicolaides & Murillo (2001) hypothesized that during the 1998–9 El Niño, larger and mature *M. olfax* were moving to shallower warmer waters to spawn, making them more vulnerable to the fishery, but provided no evidence to support this. Another hypothesis could be that during El Niño events larger fish moved to feed in shallower waters where production is higher (Wolff *et al.* 2012). The fact that *H. macrophthalmos* and *L. novemfasciatus*, two relatively shallow-water species (10–50 m and < 30 m in depth: Grove & Lavenberg 1997, Smith-Vaniz *et al.* 2010), were indicators of 2016 supports the hypothesis that hunger may have played a role in our results, as these species were attracted to bait in 2016 but not in prior years. Changes in feeding behavior due to hunger, leading to an increase in attacks on fishing bait, have been found to occur in other marine fish species (Stoner 2003, 2004). In Pacific Halibut *Hippoglossus stenolepis*, a benthic species, hungrier individuals were found to detect and

Figure 3. Multidimensional scaling ordination of Galapagos artisanal fisheries catch composition recorded during 2013, 2014 and 2016 (stress = 0.17). To highlight the three groups, convex polygons were added to the figure.

Table 2. Results of Kolmogorov-Smirnov two-sample test comparing size frequency distribution of fish species caught by Galapagos artisanal fishers in 2013, 2014 and 2016.

	2013 *vs* 2014		2013 *vs* 2016		2014 *vs* 2016	
	D	n	D	n	D	n
Caulolatilus princeps	0.12	127	0.37***	193	0.41***	206
Hemilutjanus macrophthalmos	n/a	n/a	0.65***	279	n/a	n/a
Hyporthodon mystacinus	n/a	n/a	0.77***	48	n/a	n/a
Mycteroperca olfax	0.15	313	0.77***	262	0.67**	65
Paralabrax albomaculatus	0.09	331	0.3***	405	0.37**	138
Pontinus clemensi	0.21	462	0.17***	1244	0.11	860

*P < 0.05; **P < 0.01; ***P < 0.001; n/a = comparison not possible.
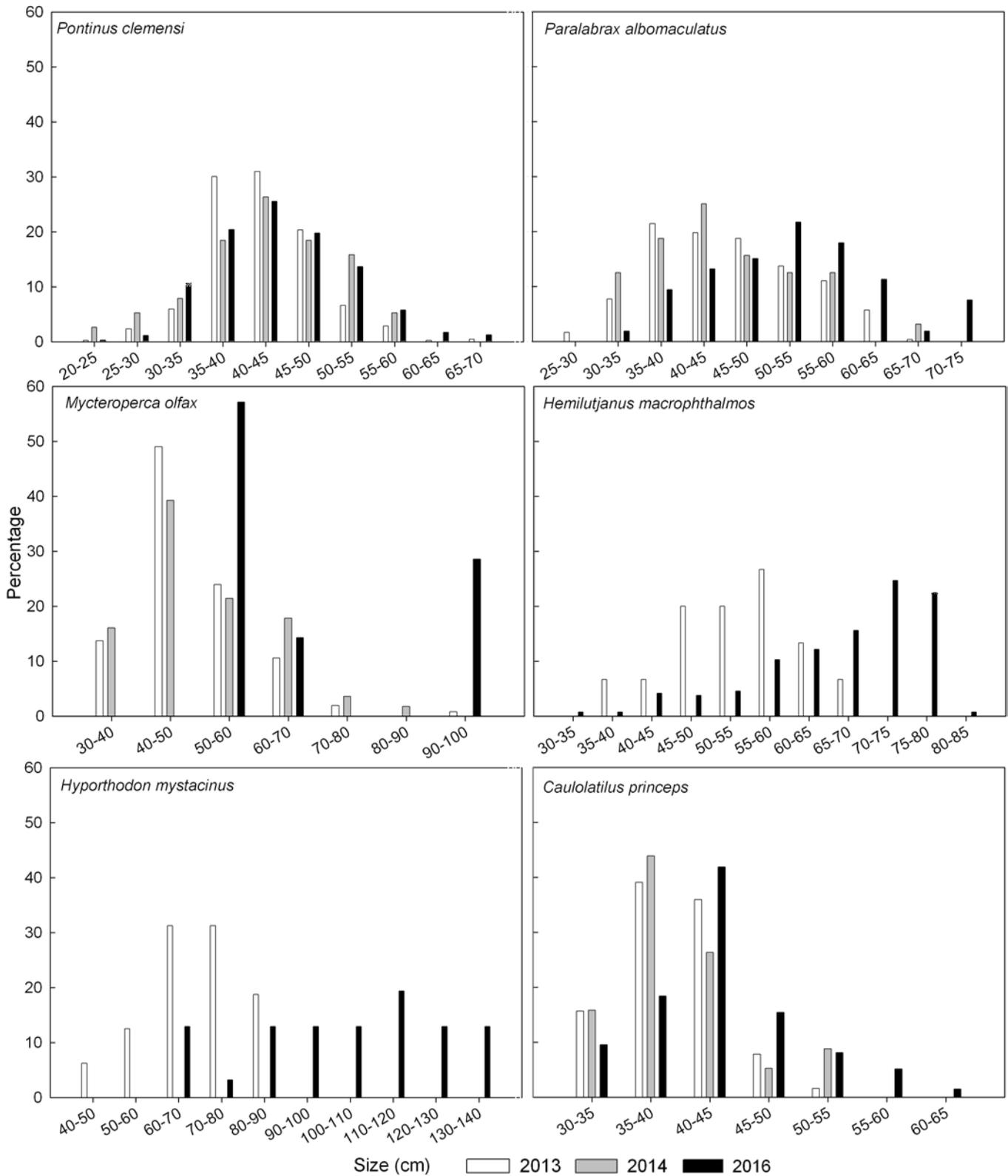
Figure 4. Size frequency distribution (%) of six demersal fish species caught by Galapagos artisanal fishers during 2013, 2014 and 2016. Statistical comparison was conducted with K-S test as detailed in the text and Table 2.

attack bait more quickly (Stoner 2003). Furthermore, the lower primary production observed during El Niño events may have enhanced visibility, allowing fish to locate and

attack baits more easily, increasing the probability of them being caught. In laboratory studies, Stoner (2003) and De Robertis et al. (2003) found that prey detection-attack

time decreased and capture success by *H. stenolepis* and the demersal Sablefish *Anoplopoma fimbria*, increased in clearer water resulting from lower levels of phytoplankton. Higher water clarity was reported in the GMR during the 1998 El Niño event (Wellington *et al.* 2001) and during the peak of the 2016 El Niño (Salinas-de-León, pers. obs.). We were not able to compare visibility rigorously but we were able to compare MEI, which is calculated using several variables that influence water clarity such as surface wind and total cloudiness fraction of the sky, and lower values were observed during 2016 than 2013 or 2014. Therefore, because El Niño events have effects throughout the trophic web, including reducing primary production and prey availability and increasing water clarity, which may lead larger, hungrier fish to move closer to shore, where they are more likely to attack bait and consequently are more vulnerable to the fishery.

The elimination of larger individuals from small populations can have ramifications for fisheries management as it may influence stock productivity and stability; it may also have evolutionary consequences (Berkeley *et al.* 2004, Enberg *et al.* 2012, Hixon *et al.* 2014). These effects may occur in all species caught in the Galapagos artisanal fishery with phenotypic traits potentially being expressed earlier in life, and the elimination of "big old fat fecund females" (Berkeley *et al.* 2004, Enberg *et al.* 2012). In particular, such effects may be especially detrimental for the Vulnerable *M. olfax*. This species is a protogynous hermaphrodite (*i.e.* largest individuals are males) whose population in the Galapagos has a highly skewed sex ratio (< 0.025 males : 1 female) and which has suffered sharp declines due to over-fishing, including the direct targeting of spawning aggregations, over the last century (Reck 1983, Coello & Grimm 1993, Salinas-de-León *et al.* 2015, Usseglio *et al.* 2015, 2016). These characteristics make the Galapagos population of *M. olfax* especially vulnerable to fishing, particularly during El Niño events.

Our results suggest that Galapagos artisanal fishers catch a different assemblage of larger individuals during El Niño events. The 2016 El Niño had on average lower MEI values than the 1983 and 1998 events (<www.esrl.noaa.gov/psd/enso/mei/>, consulted 13 Apr 2019); therefore the results we observed may occur regularly during these events. Because El Niño events provide a unique opportunity to evaluate the possible impacts of climate change on ecosystems, future work should focus on evaluating regulations that could alleviate fishery pressure on threatened demersal predatory fish species in the short (El Niño events) and long term (climate change) in the Galapagos Archipelago.

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OBSERVATIONS ON THE NESTING OF THE GALAPAGOS DOVE *ZENAIDA GALAPAGOENSIS* IN GALAPAGOS, ECUADOR

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SUMMARY

Roosts and nesting sites of the endemic Galapagos Dove *Zenaida galapagoensis* were found on Santa Cruz, Daphne Major and Baltra Islands. At Las Grietas (0°45'26"S, 90°18'56"W), a tourist visitor site on Santa Cruz, roosts and a nesting site were found in 2017, in cracks and cavities of difficult access. The nest was observed for 24 days. Two adults incubated but the nest was abandoned in the late incubation phase. The nest, comprising twigs and dry leaves, contained two fertilised eggs and one broken shell, and the reason for abandonment is unknown. It contained no larvae or pupae of the parasite *Philornis downsi*. We observed up to ten doves at this site, including eight juveniles. In 2019, a second nest with two eggs was found in a hollow cactus trunk adjacent to the Charles Darwin Research Station on Santa Cruz. This nest was observed from incubation to fledging of both nestlings. We found 13 pupae of *P. downsi* in this nest, the first report of this invasive species parasitizing the Galapagos Dove. One nest was found on Daphne Major and another on Baltra Island, each with two eggs. These nests did not contain plant material and had no traces of *P. downsi*.

RESUMEN

Observaciones de la anidación de la Paloma de Galápagos *Zenaida galapagoensis* en Galápagos, Ecuador. Se encontró dormideros y sitios de anidación de la especie endémica Paloma de Galápagos *Zenaida galapagoensis* en las islas Santa Cruz, Daphne Mayor y Baltra. En Las Grietas (0°45'26"S, 90°18'56"W), un sitio de visita turística en Santa Cruz, se encontró en 2017 dormideros y un sitio de anidación, en grietas y cavidades de difícil acceso. El nido fue observado por 24 días. Dos adultos incubaron, pero el nido fue abandonado en la última fase de incubación. El nido, compuesto por ramitas y hojas secas, contenía dos huevos fertilizados y un cascarón roto, y se desconoce el motivo de abandono. El nido no contenía larvas ni pupas del parásito *Philornis downsi*. Se observó hasta diez palomas en el sitio, incluyendo ocho juveniles. En 2019, encontramos un segundo nido con dos huevos en el tronco hueco de un cactus ubicado cerca a la Estación Científica Charles Darwin, Santa Cruz. Este nido fue observado desde la incubación hasta que los dos polluelos abandonaron el nido. Se encontró 13 pupas de *P. downsi* en el nido, el primer registro de esta especie invasiva parasitando la Paloma de Galápagos. Un nido fue encontrado en Daphne Mayor y otro en Baltra, cada uno con dos huevos. Estos nidos no contenían material vegetal y no tenían rastros de *P. downsi*.

INTRODUCTION

The Galapagos Dove *Zenaida galapagoensis* is the only member of the Columbidae resident in the archipelago. It is listed as Least Concern on the IUCN Red List (BirdLife International 2016) and occurs on all of the main Galapagos islands and in all types of habitat, but is reported as rare on the inhabited islands (Fessl *et al*. 2017). Possible explanations of its decline on inhabited islands include predation by introduced species such as the cat *Felis catus* (Konecny 1987), diseases (Deem *et al*. 2008, Padilla *et al*. 2004, 2006), competition and risk of disease transmission from domestic pigeons *Columba livia* (Harmon *et al*. 1987, see also Padilla *et al*. 2004), although the latter were successfully eradicated from Galapagos in

2006 (Phillips *et al*. 2012). There have been no reports of Galapagos Dove as a host of the avian parasite *Philornis downsi*, whose blood-sucking larvae attack the chicks of 20 bird species in Galapagos (Fessl *et al*. 2018, D. Anchundia unpubl., S. Knutie pers. comm.).

There is little information about the ecology of the Galapagos Dove. Its diet varies and includes seeds, caterpillars and cactus flowers (Grant & Grant 1979). On Santiago, Marchena and certain other islands, they roost under rocks near the shore and fly in the mornings to the highlands to forage (DA & BF pers. obs,). The only published information on its reproductive behaviour comes from a study in 1978 on Genovesa Island, a small, arid island without introduced mammals (Phillips *et al*. 2012). There, they nested in the hot season, with

egg laying starting approximately one month after the first notable rain, laying 1–3 eggs (median 2). Half of the nests were found in old nests of Galapagos Mockingbird *Mimus parvulus* and the rest on the ground under plate-like pieces of lava (Grant & Grant 1979). Our field observations around a nest and roosts are the first for Santa Cruz and Baltra, both islands with predators including rodents and cats (the latter eradicated from Baltra in 2003: Phillips *et al*. 2005).

METHODS

Between May and June 2017, we searched for Galapagos Doves and their nests in the agricultural zone of Santa Cruz Island and in the dry vegetation zone around Puerto Ayora. One nest was found, at the tourist visitor site Las Grietas, and 24 days of nest observation comprising 2–4 h per day were made at different times of the day totalling 62 h of observation. The observations, all by AC, were made from a distance of 10 m from the nest.

In January 2019, we noticed a Galapagos Dove entering a semi-hollow dead cactus (0°44'26.3"S, 90°18'07.8"W, 22 m elevation) at El Barranco, adjacent to the Charles Darwin Research Station, Santa Cruz Island. After the dove left, we filmed inside the cavity and confirmed that there were two eggs being incubated. We visited this nest every 1–3 days throughout the incubation, nestling and post-fledging phases, and recorded Galapagos Dove activity in the area. After the young fledged, we collected the cactus fibre material at the base of the nest cavity and searched it for evidence of *P. downsi*.

Baltra and Daphne Major Islands were visited in July and October 2017 to look for bird nests in crevices in rocks and to set traps for *Philornis downsi*. One nest was found at 0°25'32"S, 90°22'16"W on Baltra in July and another at 0°25'14"S, 90°16'47"W on Daphne Major in October. Both were checked for evidence of *Philornis* parasitism.

RESULTS

Las Grietas nest
The nest was inside a rocky cavity, inaccessible to tourists. Every 20–30 min. (n = 24 observations) two adult doves took turns at incubation. After ten days with no activity at the nest, it was assumed that it had been abandoned and the nest and its eggs were collected. The cause of the abandonment could not be determined. We also observed rats *Rattus* sp. and cats at Las Grietas.

The nest cavity was 50 cm deep and the entrance gap measured *c*. 10 cm vertically. The nest was 30 cm from the entrance and consisted of a flat platform of dry twigs, each no more than 15 cm long and not interwoven, with a few dry leaves mixed with soil, feathers and small rocks.

The nest contained two eggs and the broken shell of a third (Fig. 1), although no trace of a nstling was observed. The two intact eggs were similar in colour and size and showed a visible network of blood vessels through the

Figure 1. Nest at Las Grietas, collected June 2017. Photo: AC.

shell when observed against a light. The eggs measured 27.4 x 21.4 mm (3.49 g) and 27.0 x 21.3 mm (3.45 g).

During observations at this nest during late afternoon (17h00) ten individual doves were observed to fly between the rocks and the water, alighting and walking into the cracks in the rocks. In these cracks, small branches similar to the incubated nest were found, but with no traces of eggs or shells (Fig. 2). Of the ten individuals, only two were adults (the pair that incubated the nest) and the rest juveniles. The juveniles were identified by their dull brown head and mantle, speckled breast, dark eye-ring, and pale pink tarsus and claws. The adults showed a more intense brown on head, mantle and breast, iridescence on the cheeks, bright blue eye-ring and bright red tarsus and claws (Fig. 3).

When feeding, the juveniles were more active and exploratory, picking up many items, and they were less fearful towards people compared with the adult birds.

El Barranco nest
The El Barranco nest was found on 31 Jan 2019, when we observed two doves at the nest cavity standing on

Figure 2. Roosting site of *Zenaida galapagoensis* at Las Grietas, May 2017. Photo: AC.

Figure 3. Juvenile (top) and adult *Z. galapagoensis*, June 2017. Photos: AC.

Figure 4. Semi-hollow cactus trunk in which a *Z. galapagoensis* nest was found. January 2019. Photo: CP..

the rim of a 2.6-m tall, semi-hollow cactus trunk (Fig. 4). The nest cavity was approximately 33 cm deep and contained two eggs that were laid directly on the cactus material, without added nesting material. Two nestlings were observed in the cavity from 18 to 23 Feb 2019. Their hatch date is unknown, but on 23 Feb they appeared to have well-developed plumage on the head and body and to be more than half the size of adult doves. On 25 Feb the nest was empty (Fig. 5) and 13 *Philornis downsi* closed pupae were found in the nest material collected. The next day, two fledglings were seen within 10 m of the nest cavity, being fed by an adult dove.

During the incubation phase, we observed a dove enter the cavity and stay inside for at least 1 h 23 min., when our observation ended. An adult dove was seen many times foraging alone within 15 m of the nest during incubation phase. During subsequent observations in the incubation and nestling phases, we did not see a second dove. After fledging, five Galapagos Doves, including three adults and two fledglings, were seen foraging together many times within 25 m of the nest site.

Baltra and Daphne Major nests

Both nests were on the ground, each under a large rock. The nest on Baltra contained eggs but no incubation

Figure 5. Inside the semi-hollow *Opuntia* cactus. February 2019. Photo: CP.

activity was observed. A few doves were seen in the area, but none approached the nest or showed any defensive behaviour. We left the area, returned an hour later and observed the nest from a distance, but still no activity was seen. Roost sites, similar to that at Las Grietas shown in Fig. 2, were also found on Baltra (Fig. 6).

Figure 6. Roosting site of *Zenaida galapagoensis* on Baltra, May 2017. Photo: AC.

The nest on Daphne Major (Fig. 7) was found with an individual incubating. Neither nest was observed further since the visits to these islands were of only one day. These nests did not contain any plant material and the eggs were placed directly on the ground. Three months later the two islands were visited again: both nests were empty, but the one on Daphne contained down feathers so it might have had chicks. No traces of *P. downsi* were found in either of these nests.

DISCUSSION

Galapagos Doves were regularly seen in the area of Las Grietas from 17h00 onwards, after most tourists had left. Despite the presence of rats and cats, the species nests and apparently roosts there. Even though the observed nest failed, observations of juvenile doves suggested it had recently bred successfully in the area.

Parasitism by subcutaneous *Philornis* species has been reported in other columbids, including *P. angustifrons* on

Columbina talpacoti, *Leptotila verreauxi* and *L. rufaxilla*, *P. sanguinis* on *L. verreauxi* (Dodge & Aitken 1968), and an undetermined *Philornis* sp. on *Zenaida macroura* (Glasgow & Henson 1957). Our study is the first evidence of a columbid species parasitized by the semi-haematophagous species *P. downsi*, whose second and third instar larvae do not attach permanently to the host but stay in the nesting material during the day and blood-feed during the night.

Galapagos Doves may use old Galapagos Mockingbird nests, build their own stick nest in a cactus, or nest on the ground (Grant & Grant 1979) using plant material as on Santa Cruz, or placing eggs directly on the soil as found on Daphne Major and Baltra. These differences in nesting behaviour may make it difficult for *P. downsi* to parasitize all types of Galapagos Dove nests, although the fly seems to be opportunistic, as its larvae and pupae have been discovered in various nest types. We found that *P. downsi* larvae are capable of surviving in natural cactus fibres combined with dove faeces. The impact of *P. downsi* on the Galapagos Dove is still unknown, and although the information presented here adds to knowledge of nesting sites, more studies on breeding, feeding ecology and movement between nesting and feeding sites are needed.

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DRIFTING MARINE SNAKES AROUND THE GALAPAGOS ARCHIPELAGO

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SUMMARY

A female Yellow-bellied Sea Snake *Hydrophis platurus* of 720 mm total length and 172 g was found dead at James Bay, Santiago Island in March 2018. Based on an analysis of this and other specimens of the species collected in the archipelago since 1970, we consider their probable origins as drifters on currents from coastal waters between Costa Rica and the Ecuadorian mainland. Identifiable gut contents of Galapagos specimens consisted of fish larvae. The new specimen is stored in the Vertebrate Collection of the Charles Darwin Research Station.

RESUMEN

Serpientes marinas a la deriva en el Archipiélago de Galápagos. Una serpiente marina *Hydrophis platurus*, hembra, de 720 mm de largo y 172 g, fue encontrada muerta en Bahía James, Isla Santiago, en marzo de 2018. En base a un análisis de este y otros especímenes colectados en el archipiélago desde 1970, consideramos sus orígenes probables y la posibilidad de que fueran arrastrados por las corrientes desde aguas costeras entre Costa Rica y el Ecuador continental. El contenido estomacal que se ha podido identificar en los especímenes de Galápagos consiste de larvas de peces. El nuevo espécimen está almacenado en la Colección de Vertebrados de la Estación Científica Charles Darwin.

INTRODUCTION

The Galapagos Islands are well known for their highly productive marine habitats (Guzmán *et al* 2008), resulting from the meeting of three main surface currents and one undercurrent (Liu *et al.* 2014). The cold Humboldt Current flowing from the southeast, combined with the westward-flowing South Equatorial Current, brings nutrient-rich surface water through the Archipelago. The warmer Panama Current brings less productive water from the Central American coasts. The Pacific Equatorial Undercurrent or Cromwell Current, flowing

from west to east, brings nutrient-rich, cool deep water to the surface, especially on the western side of the islands. The influence of the currents varies during the year and defines two clearly distinguished seasons, a warm season from January to May, dominated by the Panama Current, and a cool season from July to November dominated by the Humboldt Current; the months of June and December are considered transitions between seasons (Banks 2002).

Many species intentionally pass through the archipelago on their migrations, while others passively drift with the currents and are occasionally encountered (Shillinger *et al*. 2008, Plotkin 2010, Bessudo *et al*. 2011, Ketchum *et al*. 2014). The Yellow-bellied Sea Snake *Hydrophis platurus* is an example of the latter, with the first sighting in Galapagos made in February 1906 between San Cristóbal and Española islands (reported by J.R. Slevin *in* Van Denburgh 1912) and the first specimen collected in 1970 (Duffy 1982, Reynolds & Pickwell 1984). The Vertebrate Collection of the Charles Darwin Research Station (VCCDRS) houses 11 specimens (10 entire bodies and one skeleton) of Yellow-bellied Sea Snake collected opportunistically from 1970 to 1998, all representing sporadic sightings (Charles Darwin Foundation 2018) rather than resulting from specific searches; only one such search appears to have been carried out, for two months in 1968–9, when no sea snakes were found (Dunson & Ehlert 1971). The specimens were collected over the central area of the archipelago between the islands of Genovesa, Santiago and San Cristóbal (Reynolds & Pickwell 1984) (Fig. 1). One other specimen, collected at Caamaño Islet in June 1977 and housed at the San Diego Society of Natural History (SDSNH), California (Reynolds & Pickwell 1984) was not examined for the present study.

We report a new finding of a Yellow-bellied Sea Snake in Galapagos waters and review past records of sea snakes found within the Galapagos Marine Reserve (GMR). We discuss their possible origins and investigate the diet in the archipelago by analysing the gut contents of all specimens in the VCCDRS.

METHODS

Snake identification was based on standard morphological characters (Cundall *et al*. 2016, Guinea *et al*. 2017, Uetz *et al*. 2007, Uetz 2010) and specimens in the VCCDRS (Jiménez-Uzcátegui *et al*. 2017). We examined the 11 earlier sea snake specimens in the VCCDRS (Table 1) and for the ten specimens in spirit we determined their
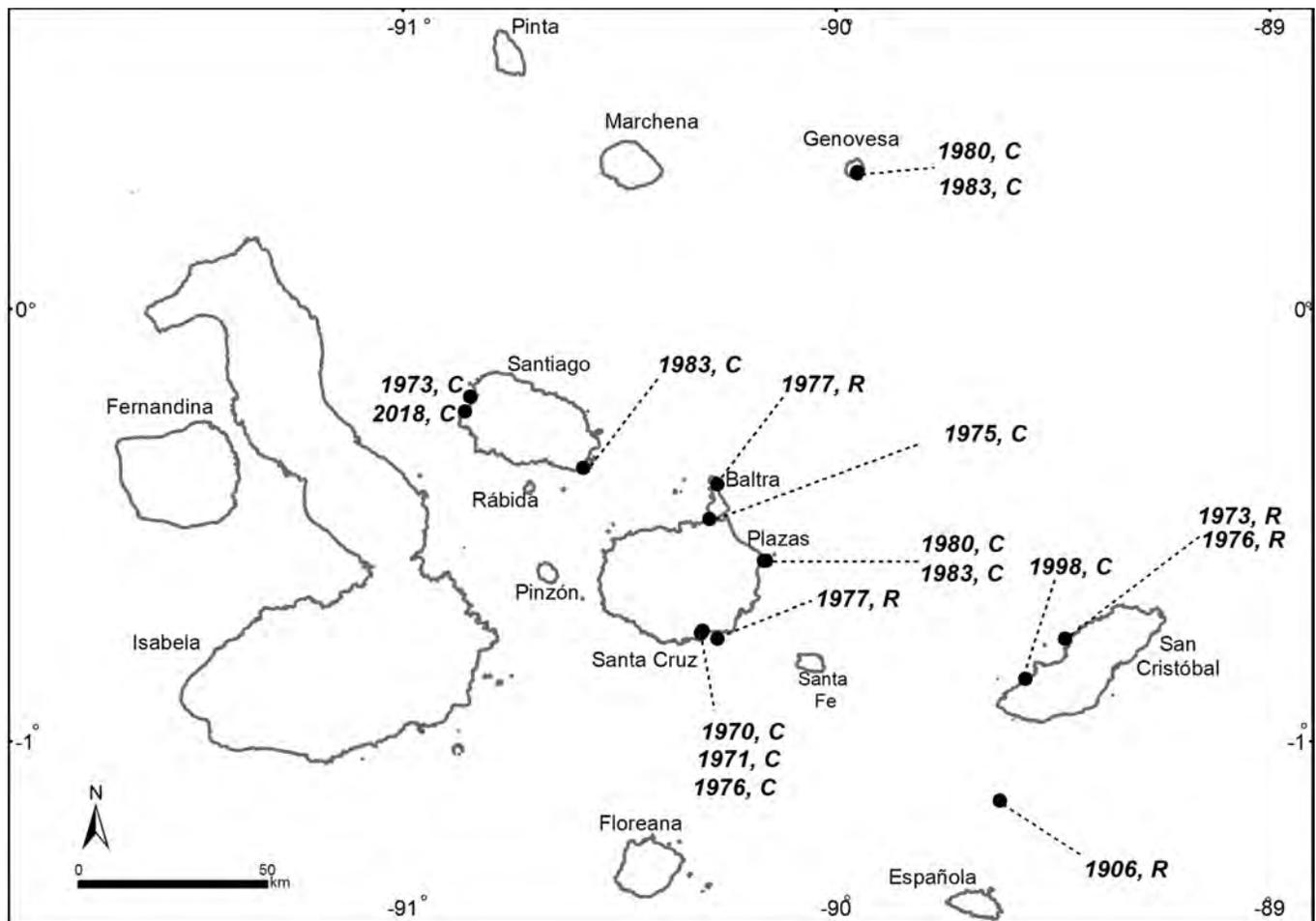
Figure 1. Locations of Yellow-bellied Sea Snakes collected (C) and reported (R) around the Galapagos Islands since 1906.

Table 1. Collection data, measurements (mm), weights (g) and gut contents of Yellow-bellied Sea Snakes in the VCCDRS. Bold dates were during El Niño events. A = adult, F = female, J = juvenile, M = male.

Specimen	Collection date	Location	Age	Sex	Total length	Snout-vent	Tail	Paddle height	Head	Weight	Gut content	Comments on voucher label
VCCDRS 363	10 Aug 1970	Academy Bay (Santa Cruz)	A	?	588	522	66	15	23	69.	2 fish, granular contents.	Found alive on beach.
VCCDRS 359	14 Nov 1971	Academy Bay (Santa Cruz)	A	M	458	403	55	12	24	50	Empty digestive tract.	Collected on sandy beach.
VCCDRS 362	**17 Mar 1973**	James Bay (Santiago)	J	?	355	313	38	8	15	19	14 fish.	Brought on board the *Beagle III* by a lava gull; still alive.
VCCDRS 360	10 Feb 1975	South Channel (Santa Cruz)	A	F	662	616	-	11	25	106	2 fish heads, 3 fish tails.	Collected dead.
VCCDRS 361	**27 Mar 1976**	Academy Bay (Santa Cruz)	A	M	540	476	64	15	22	87	Undetermined fully digested.	In the water near the shore.
VCCDRS 557	20 Apr 1980	Genovesa	A	?	-	-	-	-	-	-	-	Collected 400 m inland; dry specimen-preserved as skeleton.
VCCDRS 558	8 May 1980	South Plaza Islet	A	?	765	683	82	18	35	197	Digestive tract not preserved.	Found alive on water.
VCCDRS 1093	**10 Feb 1983**	Plaza Islets	A	F	623	558	65	12	22	66	2 partially digested fish.	Swimming on the surface.
VCCDRS 2241	**20 Mar 1983**	Darwin Bay (Genovesa)	A	F	512	454	58	11	20	34	1 fish head.	-
VCCDRS 1094	**15 Jun 1983**	Sombrero Chino Islet	J	?	267	233	34	9	13	13	Undetermined fully digested.	Found dead on beach.
VCCDRS 1247	**3 Feb 1998**	San Cristóbal	A	?	-	-	-	-	-	-	Digestive tract not preserved.	Decomposed specimen.
2018 specimen	21 Mar 2018	Santiago	A	F	720	650	73	10	30	172	12 fish.	Dead before collection.

sex (based on presence or absence of hemipenes), life stage and gut content, weighed them to the nearest 0.1 g, and took measurements to the nearest mm with a tape measure on a wooden platform as follows: total length = tip of snout to end of tail; snout to vent = tip of snout to the slit of the cloaca; head = tip of snout to posterior end of parietal scale; tail = slit of cloaca to end of tail; paddle height = maximum height of tail.

RESULTS

The new specimen

The specimen was found dead, entangled in a propeller of a small motorboat of the *Endeavour II* tourist vessel on 21 March 2018. The collision was determined to have taken place close to James Bay, Santiago Island (0.206°S, 90.836°W), where the motorboat had been transporting tourists from the *Endeavour II* to the island (Fig. 1). The sea depth in the area lies between 0 and 50 m over a sandy bottom with rocky reefs (G. Bohorquez pers. comm.).

The specimen, of total length 720 mm and weight 171.7 g (Table 1), bore wounds on the lower mandible, middle of the body and tail. It had a dark dorsum and yellow-brown venter, a fine white line along the body starting behind the head and ending anterior to the cloaca. The paddle-like tail was white (same colour as

the centre-body line) with scattered black spots. The specimen was identified as a Yellow-bellied Sea Snake and deposited in the VCCDRS. Its size indicated that it was an adult (Kropach 1975, Vallarino & Weldon 1996), dissection showed that it was a female and the ovaries were in an almost quiescent state.

Previous records

The 11 previous Yellow-bellied Sea Snake specimens at the VCCDRS date from 1970 to 1998. Nine of them were adults (considered such by their total length, as described in Kropach 1975, Vallarino & Weldon 1996), of which three were females, two males and four (including the skeletal specimen) of unknown sex; the other two were juveniles (Table 1).

In addition to specimens, Reynolds & Pickwell (1984) reported a number of other observations of the species (summarised in Table 2).

Diet in Galapagos

Gut contents revealed a fish diet for six of the specimens (Table 1). All the fish were < 50 mm long (snout tip to tip of caudal fin rays) and apparently in larval phase. Three snakes had an empty digestive tract or fully digested content while in the other two the digestive tract had not been preserved. Specimen 1247 had granules covering the full length of its digestive tract.

Table 2. Reports of Yellow-bellied Sea Snakes seen in Galapagos but not collected.

Date	Locality	Observations	Observer
Feb 1906	Between San Cristóbal and Española	Swimming	J.R. Slevin
Between 1973 and 1976	Bahía Sardinas (San Cristóbal)	Two observations, each of one swimming	B. Schreyer
14 Jun 1977	Seymour Islet	Mummified	T.W. Brown
c. 1977	Caamaño Islet	1–2 dead in sea-lion resting places	K. Trillmich

DISCUSSION

The presence of this species in the archipelago is suggested to result from passive drift from their breeding grounds near the continent (Dunson & Ehlert 1971, Duffy 1982, Reynolds & Pickwell 1984, Vallarino & Weldon 1996). They could have been brought to the archipelago from breeding populations along the Eastern Tropical Pacific coast (from Costa Rica south to the Ecuadorian mainland) by the Panamá Current, assisted by the Equatorial Current. These currents are at temperatures that would allow the snakes to survive (Reynolds & Pickwell 1984).

The 1906 sighting and eight of the 11 VCCDRS specimens (including the latest) occurred during the warm months of February to May. Two of the remaining specimens were collected during the August–November cool season, while one VCCDRS specimen and the SDSNH specimen were collected in the transition month of June. Sea surface temperature (SST) during March 2018 at Santiago Island was between 28.5°C and 28.7°C. Readings at the same site in 2003 oscillated between 24.5°C and 28.7°C (NOAA/NESDIS 2003). Six specimens were collected during four El Niño events out of the nine that occurred from 1965 to 1998 (Table 1). SST readings during these events were between 25.0°C and 28.6°C for February and March 1973, 1976, 1983 and 1998 (Charles Darwin Foundation 2018). A global decadal increase of 0.19°C in the period 1979–1998 (Vargas *et al*. 2007), in which two of the strongest El Niño events occurred in the archipelago, had great impacts on marine biodiversity (Trillmich & Limberger 1985, Nelson *et al*. 2004, Vargas *et al*. 2006) and may have affected the dispersal ability of species that actively or passively move through the archipelago.

The infrequency of sightings of the Yellow-bellied Sea Snake around the archipelago contrasts with its potentially extensive habitat range and occasional long-distance dispersal. This ability to disperse over large distances and to feed on small fish that seek shelter under drifting structures (Rasmussen *et al*. 2011, Brischoux & Lillywhite 2013) together with its bearing of live young (Vallarino & Weldon 1996), might suggest that the species is a good coloniser. Its establishment in Galapagos may be prevented only by water temperature, since surface waters below 20°C can limit its reproduction (Dunson & Ehlert 1971, Graham *et al*. 1971, Lillywhite *et al*. 2015). Outside the February to May warm period, SST in Galapagos may be too low for its reproduction or even survival (Dunson & Ehlert 1971, Reynolds & Pickwell 1984). Reynolds &

Pickwell (1984) note that cool season SST at Academy Bay (Santa Cruz) is usually *c*. 20–21°C, while the species may cease feeding below 23°C. Passive drifting to the islands on warm currents may thus represent a dead-end trap for the snakes.

The measurements of the specimens indicated that the majority were adults or at least sexually mature. It remains difficult to conclude that the species does not sometimes breed in the archipelago. The gut contents confirmed that the species eats small fish, of a size limited by its relatively small jaw opening (Klawe 1964).

The present work generated some questions. Does the species show habitat preferences in Galapagos? What is the fate of such species with long-distance dispersal in the face of predicted temperature rises of oceanic waters (García-Molinos *et al*. 2015)? Shall we see more Yellow-bellied Sea Snakes in the Galapagos as oceans warm and El Niño events take place more frequently?

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GALAPAGOS COMMENTARY

FLAMINGOS IN GALAPAGOS: SR JACINTO GORDILLO'S MISPLACED REPORT

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SUMMARY

In a report which has only recently come to light, Jacinto Gordillo described his observations on the flamingo of the Galapagos archipelago, starting *c*. 45 years ago. His findings and inferences are in accord with the results of detailed studies subsequently carried out by others.

RESUMEN

Flamencos en Galápagos: el informe perdido del Sr. Jacinto Gordillo. En un informe que sólo recientemente ha salido a la luz, Jacinto Gordillo describe sus observaciones sobre el flamenco del archipiélago de Galápagos empezando *c*. 45 años atrás. Sus conclusiones e inferencias concuerdan con los resultados de estudios detallados efectuados subsecuentemente por otros.

A report compiled from observations made between 1967 and *c*. 2007, but which had remained overlooked since then, came to light in 2016. The report is by Jacinto Gordillo, a warden in the Galapagos National Park Service for much of his working life, who also spent some time as an employee of the Charles Darwin Research Station. The report is in two parts. The first part addresses the biology of the American Flamingo *Phoenicopterus ruber* in the Galapagos archipelago from studies carried out during 1967–72. The second part addresses management and conservation issues of the flamingo population during 1978–2007. Little was known of the flamingo in Galapagos prior to Jacinto's studies apart from the occasional censuses carried out by the National Park Service and the Charles Darwin Research Station. The first census in 1968 recorded a population of *c*. 500 adult and juvenile birds.

We, and others with whom we had discussed the Galapagos flamingos, were unaware of this report prior to our 1976–9 study of these birds and thereafter, and in fact we do not know when the first part was actually written up in report form., Thus, the report is not acknowledged in Tindle *et al.* (2016), though we did cite what appears to be an early abridged version (Gordillo 1973).

Although Jacinto does not give details of the methods he used, it can be gleaned that he made frequent visits to lagoons where flamingos were recorded, and apparently some longer visits, particularly to sites where breeding occurred. He recorded his observations on the distribution, feeding ecology and breeding biology, and

hypothesized that the flamingos moved among islands in the archipelago in search of suitable feeding and breeding lagoons. He deduced that conditions for breeding persisted for about nine months of the year, and showed that low water level in lagoons was the principal determinant of the onset of breeding and that flooding of nests (by rainwater) contributed significantly to breeding failure. He noted the similarities in the feeding ecology and reproduction of *P. ruber* in Galapagos to what had been reported on the *P. ruber* populations in the Caribbean (Allen 1956, Rooth 1965). Anatomical and genetic studies have since shown that the Caribbean *P. ruber* is the likely parent population of *P. ruber* in Galapagos (Frias-Soler *et al.* 2014).

Unlike Jacinto, we had the benefit of spending much more time, *c*. 14,500 nest-h of observation, at all major colonies, with up to 20 h of observation per day. But analysis of these more substantial data upheld all of the inferences and predictions that Jacinto had made from his limited data. Our methods of course also allowed us to touch upon areas which Jacinto was unable to address, including the direct association between the spatial and temporal availability of food items and the distribution of flamingos, the differing breeding behaviour between lagoons where parents fed and those from which parents "commuted" to distant lagoons to feed, the duration of attentive periods at the nest by individual male and female parents, and the timing of parental feeding of offspring.

Jacinto's attention to detail was exemplary. Nowhere was this more apparent than in his description of the

flamingo group display which heralds the onset of breeding. Group display is a complicated affair, with which avian ethologists did not get to grips until Studer-Thiersch's (1975) detailed analysis on captive *P. ruber*. Jacinto, in his report, had identified many of the display movements under the much more difficult circumstance of observations in the wild.

Perhaps influenced by the observation that the breeding success of small isolated populations of flamingos is lower than that of larger populations (summarised in Duplaix-Hall & Kear 1975), Jacinto was pessimistic about the future of *P. ruber* in Galapagos. After all, he witnessed "colonies" with as few as three nests! Our later population dynamics data, and the quasi-annual censuses over the succeeding *c*. 45 years, have indicated that his fears were largely groundless. Those fears were also driven by the threats that Jacinto witnessed, from man and introduced animals, to the largest concentration of flamingos on southern Isabela island, where he did much of his work. At Quinta Playa lagoon, introduced cats, dogs and pigs took flamingo chicks and trampled nests. However, flamingos nesting on a small mud islet in the centre of the lagoon, rather than at the edge of the lagoon, were safe from the predators (A. Tupiza pers. comm.).

Las Salinas lagoon is among the network of lagoons close to the village of Villamil. As its name suggests it was used by the local people as a source of the salt deposited by sea-water evaporation, which they used for domestic purposes and salting fish. Later, in 1978, an amplification and redistribution of the power network of Villamil village saw electric cables erected at a height of 8 m in the direct flight path of flamingos coming into the lagoon. The number of flamingo fatalities caused by flying into the cables was considerable. Jacinto records the multiple skeletal injuries sustained by one such unfortunate bird. In accord with the wishes the National Park, the overhead wires were later replaced by subterranean wires. More human incursion was yet to come, including the construction of a road to the lagoon to encourage tourists, the allocation of land for human habitation alongside the lagoon, and a proposal for sewage management. Fortunately, today, < 5% of the flamingo population is directly impacted by human activities, and the flamingo population, though likely constrained by availability of

suitable feeding habitat within the archipelago, is more stable than Jacinto had imagined.

Jacinto's report is a testament to this intelligent man. Though he did not have the opportunity of a formal education in wildlife and conservation, many of us more fortunate in this regard have much to learn from his acute powers of observation and dedication. It is fitting that accolades from wildlife scientists around the world poured in when he passed away in 2016. His report (Gordillo 1967–2007) has now found its rightful home in the library of the Charles Darwin Research Station.

ACKNOWLEDGMENTS

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CHARLES DARWIN
AND THE CASE OF THE MISSING CORMORANTS

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SUMMARY

Why did Darwin not comment on the Flightless Cormorant *Phalacrocorax harrisi* during his visit to Galapagos in 1835? This paper explores some possible reasons, including lack of attention to birds, and population reduction caused by one or more of El Niño events, harvesting, predation and volcanic eruptions.

RESUMEN

Charles Darwin y el caso de los cormoranes indetectados. ¿Por qué Darwin no hizo ninguna referencia al Cormorán no volador *Phalacrocorax harrisi* durante su visita a las Galápagos en 1835? Este informe examina las posibles causas, incluyendo inatención a las aves, y reducción de la población debido a uno o más de eventos de El Niño, explotación, predación y erupciones volcánicas.

INTRODUCTION

Charles Darwin's one-month visit to the Galapagos Islands in 1835 is regarded as seminal to the development of the theory of evolution by natural selection. During his stay, he learned that the giant tortoises and mockingbirds varied between islands. Later, after his return to England, Gould's descriptions of the various species of what came to be known as Darwin's finches further reinforced his thinking (Sulloway 1982). However, among the most striking examples of evolution in the islands is one he didn't comment on: the Flightless Cormorant *Phalacrocorax harrisi*. This species is presently found only on Fernandina and Isabela islands on the west side of the archipelago, its distribution matching the cold-water upwelling resulting from the Equatorial Countercurrent (Harris 1979, Tindle *et al*. 2013).

The *Beagle* made landfall in the Galapagos on 15 September 1835 and departed 20 October 1835. Darwin spent only one day, 1 October, ashore in the present range of the cormorant, south of Tagus Cove (Banks Cove), Isabela Island (Estes *et al*. 2000), but did not report cormorants. There has been speculation about this oversight (Murphy 1936, Grant & Estes 2009). The cormorant can be obvious, sitting on the shoreline, extending its stumpy wings to dry in the sun. There are several possibilities: Darwin overlooked the cormorants, did not think them worthy of mention, or they were scarce or absent because of physical events or human actions. This note examines these possibilities.

OVERLOOKED OR NOT WORTH NOTING?

Could Darwin simply not have been interested in seabirds? Vogt (1942) wondered why Darwin did not comment on the vast numbers of seabirds in the Humboldt Upwelling off the coast of Peru, but that may have been because of his seasickness while on the open sea. Colnett (1798), visiting the Galapagos in 1793, noted "The various kinds of seabirds which I have seen on the coast of Peru, we found here, but not in equal abundance." Darwin did pay enough attention to Galapagos seabirds to find them similar to the seabirds of Peru and therefore less interesting than the rest of the islands: "The great Pelican & common gannet as at Callao & other species of latter, beautifully white & black." (Keynes 2000).

Grant and Estes (2009) suggested that Darwin was pre-occupied with the geology of the islands on his one day ashore in the range of the cormorant at Beagle Crater. They noted that he wrote as much about his geological observations that day as he did for the ten days he spent on Santiago Island. Returning to the *Beagle* after a very full day, he may have been tired and dehydrated, so an ordinary-looking cormorant in the water might not have been worth noting. He might have had no opportunity to note the stubby wings of the Galapagos Cormorant if none happened to be sunning as he made his way to the ship.

NOT PRESENT?

El Niño

El Niño events, by altering marine conditions, can have major effects on Galapagos seabirds (Duffy & Merlen 1986). The Equatorial Counter Current that provides cool, nutrient rich water to generate the upwelling ecosystem of the western Galapagos islands slows or disappears during El Niño (Firing *et al*. 1983) leading to decreases in marine productivity and changes in fish and seabird populations (Wolff *et al*. 2012). During the major event of 1982–3, Flightless Cormorant numbers decreased by 50 % (Valle & Coulter 1987) but were not affected by the very strong 1997–8 event (F.H. Vargas pers. comm.). We

now know that El Niño events vary both in strength and in local effects, so cormorant response may be similarly variable following different events.

King (2013) suggested Darwin did not see the cormorants because he was there during or after an El Niño year, but the evidence is weak. Quinn (1992) and Ortlieb (2000) both reported a very strong El Niño event in 1828, a moderately strong event in 1832 and a moderate event in 1835–6. However, FitzRoy noted that orographic intercept of winds led to "dry and barren" habitats in Galapagos, as in coastal Peru and northern Chile during non El Niño years, and Darwin mentioned trade winds (Keynes 1988) which would have been greatly reduced or absent during an El Niño. Both observations suggest the absence of El Niño conditions during the *Beagle*'s visit, but the possibility remains of a delayed cormorant population recovery following the 1828 or 1832 events.

Harvesting

Sailing vessels, including the *Beagle*, had two priorities when in the Galapagos: fresh water and fresh food, particularly giant tortoises (Townsend 1925, Hickman 1985), but ships' companies did not limit themselves to tortoises (Salvin 1876). Darwin reported "Sailors wandering through the woods in search of Tortoises, always take delight in knocking down the small birds" (Barlow 1963). Byron (1826) noted that his crew killed "some seals, pelicans, and penguins." David Porter, Captain of the *U.S.S. Essex*, wrote that "We soon however discovered them [iguanas] to be the most timid of animals, and in a few moments knocked down hundreds of them with our clubs, some of which we brought on board, and found to be excellent eating, and many preferred them greatly to the turtle." (Porter 1822). Porter (1822) also reported his crew killing flightless cormorants in 1813 at Essex Point on southern Isabela and at Punta Vicente Roca at the north end of the island: "We also found plenty of birds called shags, which did not appear alarmed in the slightest degree at our approach, and numbers of them were knocked down by our people with clubs, and taken on board." Cormorants are no longer present at Essex Point.

The over-harvesting of tortoises and land iguanas led to extinctions of entire island populations and may well have resulted in scarcity of other species such as Flightless Cormorants during and after Darwin's visit. Failure to recover following over-exploitation may explain why the Flightless Cormorant was not formally described to science until the late 19th century. Livezey (1992) mentions a series of reports of post-Darwin expeditions that did not note or collect cormorants (Sclater & Salvin 1870, Salvin 1876, 1883, Sharpe 1877, Ridgway 1890, 1894, 1897, *in* Livezey 1992). The first scientific description of the bird was based on specimens collected rather casually in 1897 in the surf off Fernandina: "We saw several specimens of a bird, probably a cormorant, and secured three. The birds were wild and kept in close to the breakers, so

no more could be obtained" (Rothschild 1898). Despite intensive collecting of birds in Galapagos, no cormorants were reported or collected in the Tagus Cove area by the same expedition.

Predation

In addition to direct exploitation by humans, the introduction of cats and dogs may have reduced the cormorant population. The first human colony was established in 1832 on Charles Island and it is likely that cats and dogs were introduced then (Salvin 1876). Dogs were reported as abandoned on Isabela in 1835 (Barnett 1986) but may have been present earlier. Habel, visiting in 1868, observed a cat at Tagus Cove and was told that there were "many" feral cats and dogs on Isabela (Salvin 1876). Dogs were not reported north of the Perry Isthmus on Isabela, which may explain why the bulk of the present-day cormorant population remains in this area and on predator-free Fernandina (Barnett 1986 and pers. comm.).

Fernandina eruption

Finally, volcanic eruptions may have played a part. In February 1825, Morrell (1832), while anchored in Tagus Cove, experienced a major eruption of Fernandina. He stated that "the whole atmosphere on the lee side of the bay appeared to be one mass of flame". A month later (27 March) Byron in HMS *Blonde* observed on Fernandina that "near the beach a crater was pouring forth streams of lava, which on reaching the sea caused it to bubble in an extraordinary manner."

The southeast and east sides of Fernandina have experienced frequent eruptions, often of very short duration (Kurz *et al*. 2014, <http://volcano.si.edu/volcano.cfm?vn=353010> consulted 14 Nov 2019). Five of the six volcanoes on Isabela Island have been active in recent times, although historical documentation is scarce (<http://volcano.si.edu/list_volcano_holocene.cfm> consulted 14 Nov 2019). One or more eruptions may account for Byron's comment "all this amidst volcanoes which are burning around us on either hand".

Morell (1832) claimed sea temperatures approaching 150°F (66°C) threatened his vessel. Unlike Darwin's factual writings, Morrell was writing a sailor's yarn for the public and may have exaggerated or borrowed interesting stories from others. During a Fernandina eruption in 1995 (Rowland *et al*. 2003) reported water temperatures of 45°C just offshore, well above lethal temperatures, especially for fish from cool upwelling waters. During the voyage of the *Oaxaca* in 1938, a fish kill was observed following a lava flow that reached the sea on the southeastern coast of Fernandina (Slevin 1959). Over time, local populations of flightless cormorants on Fernandina and parts of western Isabela might have been incinerated or starved after their prey parboiled as lava reached the sea. The low gene flow in the species (Duffie *et al*. 2009) suggests that recolonization might have been slow, such that cormorants might have been scarce or localized when Darwin visited in 1835.

IN CONCLUSION

Almost two centuries after his visit, a definitive answer as to why Darwin did not see the cormorant is not possible. Darwin may have been too focused on the geology of Tagus Cove and Beagle Crater to bother with cormorants. It is equally likely that Darwin could not notice what wasn't there. An earlier El Niño may have temporarily reduced the population of Flightless Cormorants or they might not have recolonized the area after one or more recent eruptions. Or they may have been so overhunted that they persisted only in refugia remote from sites where sailors went ashore to collect water or food. Being flightless, reoccupying their range would have been slow; their mean post-natal dispersal (to first breeding site) was estimated at 6.3 km (Valle 1995). Even today, there are genetic differences between birds on Isabela and Fernandina and between locations on both islands (Duffie *et al*. 2009).

It appears that we should not fault Darwin for lack of observation. We can only speculate on the impact on the development of his ideas had the cormorants been there and been noticed, drying their spread wings in Tagus Cove in 1835.

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Galapagos Research

INSTRUCTIONS FOR AUTHORS

Galapagos Research (formerly *Noticias de Galápagos*) is the research journal of the Charles Darwin Foundation for the Galapagos Islands. It publishes Research Articles, archival value news items ("News from Academy Bay") and more general or popular articles ("Galapagos Commentary") covering any topic relevant to science or nature conservation in Galapagos, including natural history, biology, ecology, evolution, systematics, conservation biology, geology, geography, history, human activity, and the management of biological diversity. Material from other geographical areas may also be considered, if it is of immediate relevance to science or conservation in Galapagos.

Contributions are accepted in English. Editorial assistance will be made available to authors whose first language is not English, but this does not include full translation from other languages; it is the author's responsibility to have the paper translated into English prior to submission. Manuscripts should be submitted by email to the Editor at <**alantye@gmail.com**>. Consult the Editor for further advice.

Research Articles must be original contributions that deal with subjects of relevance to Galapagos science or conservation (including all the subject areas listed above). Material published or accepted for publication elsewhere, in whole or in part, will not normally be accepted. Wherever possible, manuscripts should have been critically scrutinised by at least one specialist in the relevant field, before submission to the journal. Papers from Charles Darwin Research Station staff and volunteers should be reviewed by their Progamme Leader prior to submission. Submitted manuscripts will be sent by the Editor to at least one expert referee (normally two) for critical review.

News from Academy Bay items should not normally exceed 1000 words. News items may include notices of happenings in the islands that affect science or conservation, recent or forthcoming major events or publications about Galapagos (including book reviews), achievements in Galapagos science or conservation etc.

Galapagos Commentary items include opinion or discussion of Galapagos science or conservation issues, and more general or popular articles that have relevance to Galapagos science or conservation.

Format of tabular material, numbers, metric units, references, *etc*. should match recent issues. Note particularly: dates should be in the form 2 Feb 1990 but months standing alone in text may be written in full; times of day are written 6h45, 17h32 and coordinates in the form 0°46′N, 1°4′W (no leading zeros); numbers up to ten are written in full, except when followed by abbreviated units (*e.g.* 6 m), numbers from 11 upwards are written in figures except at the beginning of a sentence. All references mentioned in the article, and only such, must be entered in the bibliography.

Locality names should be widely recognised and in current use where possible. Articles citing older names, or localities that are not widely known, should contain a map or gazetteer, including all such localities mentioned. **Scientific names** should follow a recognised authority, which should be cited in papers dealing with taxonomic issues or lengthy species lists. Scientific names of **plants** should follow P.M. Jørgensen & S. León-Yánez (1999) Catalogue of the Vascular Plants of Ecuador. *Monographs in Systematic Botany from the Missouri Botanical Garden* 75 (see http://www.tropicos.org/ for database), unless sound reasons for following a different scheme are presented.

Figures should be prepared as for final reproduction, allowing for reduction to fit column or page size. Figures prepared in or scanned into an appropriate graphics format, saved at high resolution and submitted electronically are preferred. Figures should not be included in a Word file. Low-resolution files or poor-quality scans will not be accepted. When designing Figures, pay attention to *Galapagos Research* column size and page-shape. Authors are encouraged to submit **photographs** that illustrate salient points of their articles. Photographs should be high-contrast (for publication in monochrome) and high resolution. Photographs should be supplied in graphics file format (*e.g.* jpg or tif) and should not be pasted into a Word file. Photographers other than the paper's authors should be credited. Consult the Editor for further advice.

All Research Articles (but not News items or short Commentary notes) should include a **Summary**, not exceeding 5% of the paper's length. The Summary should briefly refer to the major findings of the paper and not simply outline what was done in the study. Summaries will be published in both English and Spanish and will be translated if necessary by the editorial team.

Accepted articles will be published **Online First**, on the CDF website, and cannot be altered further thereafter. They will normally be included in the next printed issue, which then becomes the definitive version. **Offprints** will not be supplied, but authors will be sent one copy of the issue in which their article appears, and a pdf file of their article, free of charge.

Central Galápagos Archipelago

Contour Invervals 100m.

Kilometers
0 10 20 30 40 50

Roca Redonda

Cerro Ecuador

Isla Fernandina

Bahia
Banks

Canal
Bolívar

Volcán Wolf

Volcán Darwin

Volcán Alcedo

Isla Santiago

Isla Marchena

Isla Pinta

Isla Genovesa

Cerro Azul

Isla Isabela

Bahía Elizabeth

Sierra Negra

Puerto
Villamil

Isla Tortuga

Islotes Cuatro
Hermanos

Bahía Cartago

Islotes Guy Fawkes

Isla Rabida

Rocas
Beagle

Isla Pinzon

Isla
Daphne
Major

Rocas Bainbridge

Isla Bartolomé

Isla Seymour Norte

Isla Baltra

Isla Santa Cruz

Puerto Ayora

Isla Santa Fe

Puerto Velasco
Ibarra

Islote
Campéon

Islote Enderby

Isla Caldwell

Isla Gardner
por Floreana

Isla Floreana

Puerto Baquerizo
Moreno

Isla San Cristóbal

Isla Gardner por Española

Isla Española

1°00'
0°30'
0°00'
0°30'

91°30'
91°00'
90°30'
90°00'
89°30'

Map by Tom Giermakowski
& Howard Snell
(University of New Mexico)