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ABSTRACT

We succinctly summarize population ID information for common bottlenose dolphins Tursiops truncatus of the Pacific coast of South America, covering four coastal range states. Phylogenetic uncertainties relate primarily to offshore vs. coastal (inshore) ecotypes and biogeographic borders between the five proposed populations (2 offshore, 3 coastal): Colombia-Ecuador Offshore stock (probably = ETP Offshore), Peru-Chile Offshore, Ecuador Coastal, Peru Coastal and an unique community (Pod-R) on the north-central coast of Chile. Main questions concern the extent of gene flow between the offshore stocks at one hand, and with -and between- the three coastal populations at the other hand. Seven cranial characters, four non-metric (separation of occipital condyles, pterygoid bone development, exostosis of periotic) and three metric (tooth width, antorbital process length, maximum width palatines), dorsal fin shape, body stockiness, mt-DNA (control region), habitat, prey composition, parasite load, behaviour and prevalence of some infectious diseases differentiate coastal from offshore forms. 'Pod-R' is the southernmost (29°15'S) and only confirmed coastal form community in Chilean waters, albeit with an offshore (falcate) dorsal fin. Bottlenose dolphins which regularly transit nearshore in the Lagos and Aysén regions (Chilean Patagonia) and occasionally enter deep fjords, present an offshore morphotype. We suggest that two other coastal areas in Chile where bottlenose dolphins have been documented over decades, one a ca. 60 km stretch of coastline centered at Valparaiso/Laguna Verde (33°10'S) in central Chile, and a 190 km coastline around the Mejillones Peninsula (23°10'S) in northern Chile, may not host coastal but offshore form animals. The continental border of the Atacama Trench off northern and northcentral Chile leaves an extremely narrow, steep shelf with nearshore deep water, locally with strong coastal upwelling and increased productivity. This habitat seems to attract oceanic cetaceans, including offshore T. truncatus, sperm whales, large balaenopterids, and other species. The southern distribution range of true coastal morphotype bottlenose dolphins in Pacific South America remains unknown but off Chile distance-to-shore may not be the reliable indicator of ecotype as it is further north in the study region.

INTRODUCTION

Unlike for the Northeast Pacific, no nominal *Tursiops* species have been described for the Southeast Pacific, and scarce records are documented in pre-1980 historical literature (reviewed in Van Waerebeek *et al.*, 1990). Nonetheless, the common bottlenose dolphin *Tursiops truncatus* Montagu, 1821 is one of three most frequently captured cetacean species in Peruvian waters, consistently over a period of a quarter century (Read *et al.*, 1988; Van Waerebeek *et al.*, 1988, Van Waerebeek and Reyes, 1994a,b; 1997; García-Godos, 1993, 2007; Mangel *et al.*, 2010; Tzika *et al.*, 2010), is the second-most commonly bycaught cetacean in Ecuador (Félix and Samaniego, 1994; Van Waerebeek *et al.*, 1997) and is at least occasionally taken in Chile (Guerra *et al.*, 1987) and Colombia (Mora and Muñoz, 1994; Prieto, 1990; Avila *et al.*, 2008). Despite considerable fisheries-related mortality, merely a handful of studies have focused on population structure of *T. truncatus* in Chile, Peru and Ecuador, evaluating morphological variation (Van Waerebeek *et al.*, 1990; Santillán, 2003; Anchante *et al.*, 2008; Santillán *et al.*, 2008; Félix *et al.*, 2017a), molecular genetics (Sanino *et al.*, 2005; Bayas, 2015), distribution (Sanino and Van Waerebeek, 2008; Olavarría *et al.*, 2010) and feeding ecology (Van Waerebeek *et al.*, 1990; García-Godos *et al.*, 2007). All lines of evidence point to the existence of ecologically, morphologically and genetically distinct coastal (inshore) and offshore (oceanic) stocks in Ecuador, Peru, and Chile. No other region-wide review of *T. truncatus* has been presented since Van Waerebeek *et al.* (1990), hence an update is due.

Analysis of new specimen data is underway but no results are as yet available.

Considering a single *Tursiops* species in the SE Pacific Ocean, whose taxonomic identity (*T. truncatus*) is not disputed, we henceforth refer to 'the bottlenose dolphin'. Status at subspecific levels is less clear and the terms ecotype, form, population and stock are used here more or less interchangeably. Two ecotypes have been recognized, either coastal (inshore) or offshore (oceanic) (*sensu* Van Waerebeek *et al.*, 1990). 'Nearshore' is meant as a purely spatial indicator of habitat without phylogenetic connotations. 'Morphotype' emphasizes substantial morphological variation implying phylogenetic distance through reproductive isolation.

In terms of research effort (detailed below), most data from Ecuador were derived from dedicated boat-based surveys and some specimen collection; in Peru information was obtained primarily from necropsies of bycaught specimens at fishing ports, beach-combing, and some boat surveys; in Chile and Colombia primarily from dedicated boat-surveys and limited specimen collection. In all countries opportunistic shore-based sightings contributed to respective datasets. Genetics information is limited to insights from mtDNA (331bp control region) which evaluated relationships between four groups: Chilean inshore (n=8), Peruvian inshore (n=3), Chilean offshore (n=8) and Peruvian offshore (n=12) (Sanino *et al.*, 2005); as well as a population structure study of the coastal bottlenose dolphin from the inner estuary of the Gulf of Guayaquil and a phylogeographic study based on both mtDNA and microsatellite data of stranded and free-ranging animals that included both coastal and offshore specimens (Bayas, 2015).

COASTAL POPULATIONS

Colombia-Coastal

García *et al.* (2008) reported on the distribution of *T. truncatus* in Pacific Colombia (Chocó, Bahia Málaga, Isla Gorgona and Isla Malpelo) and Chiriqui Gulf, Panamá. Bottlenose dolphins were observed in small groups mostly in protected waters including bays. Near Isla Gorgona (Colombia) and Bahía Honda (Panama), the species was considered rare, while around Isla Malpelo it was common. In the Utría National Park and surrounding areas, Chocó (05°59'N, 77°21'W), coastal bottlenose dolphins were most commonly found in rocky areas and near mangrove forests, where they forage (Suárez, 1994). Two coastal surveys conducted in the north of Chocó (06°30'N, 77°40'W) in 2004-2008 report frequent presence, especially in March, with an encounter rate estimated at 15.3 individuals/h. Forming small groups (6-20 ind.) main behaviours observed were feeding and slow travel (Avila *et al.*, 2008; Avila, 2009). Palacios *et al.* (2012) compiled sighting data collected under various survey programmes and concluded that *T. truncatus* was well represented in Colombia's nearshore waters, but most encounters occurred north of 04°N.

More south, in Bahía Málaga (03°55'N,77°21'W), bottlenose dolphins also showed a preference for nearshore habitat (<1 km from shore) including inside the bay. Small groups (mean=7) were encountered during 38% of boat sorties. Activities included feeding, socializing, rest and slow transit (Rengifo *et al.*, 1995; Londoño, 2005).

Bottlenose dolphins and pantropical spotted dolphins (*Stenella attenuata*) are exploited for bait in the Colombian Pacific (Mora and Muñoz, 1994; Prieto, 1990; Avila *et al.*, 2008). Interviews in Bahía Solano showed that dolphins were used by artisanal long-liners (37% of registered fishermen) and that 16% of fishermen occasionally hunted them, taking up to 6 dolphins/month (Avila *et al.*, 2008). A description of regular landings of dolphins and human consumption, was provided by a member of the fishers community of Buenaventura port on 04-II-1990 (K.Van Waerebeek, unpubl. data). The present situation is unknown and needs to be re-evaluated.

No morphological variation data or genetics analysis have been presented for the Colombian Pacific, and no specimen reference collection is available. Photographs by one of us (ICA) of coastal *T. truncatus* in the Málaga area (Figure 1) demonstrate the same triangular-shaped dorsal fins with low falcateness as Ecuadorian and Peruvian coastal animals (Félix *et al.*, 2017a).



Figure 1. Common bottlenose dolphins slowly moving nearshore in the Málaga bay area, southern Colombia, on 15 July 2012. Small group size and triangular-shaped dorsal fins with minimal falcateness are consistent with the coastal forms of Ecuador and Peru. Photos © Isabel C. Avila.

Ecuador-Coastal

Since the early 1990s research on *T. truncatus* in Ecuador has focussed primarily on the ecology, population structure and abundance of a number of inshore communities in the interior estuary of the Gulf of Guayaquil and off Salinas port, on Ecuador's SW coast (e.g. Felix, 1994, 1997, 2001). A population of 637 animals (CI 95% 541-733) was estimated consisting of two types of communities, resident and non-resident (with seasonal occurrence), with an average of 115 animals (SD=37) per community (Félix, 1994, 1997). Resident communities exhibit many characteristics that are consistent with a coastal ecotype, while non-residents are of uncertain status (Félix, 1994, 1997, 2001) but most likely are also coastal. Cranial data (Santillán *et al.*, 2003) suggested a possible third, intermediate, morphotype, but evidence was not convincing. Variation in dorsal fin shape supports the occurrence of two morphotypes, coastal and offshore (Félix *et al.*, 2017a).

A fisheries interaction study found indications of an important incidental catch in the southern Gulf of Guayaquil (Puerto Bolívar), estimated at 227 bottlenose dolphins/year of unknown stock (Van Waerebeek *et al.*, 1997), however in retrospect considering the very wide 95% CI (0-665) the actual take may have been either overestimated or catches of additional dolphin species were included. From scars and injuries on the back and dorsal fins, some 2.2% of coastal bottlenose dolphins in the interior estuary of the Gulf of Guayaquil showed evidence of boat collisions or traumatic contact with fishing gear in the early 1990s. Incidence increased 5-fold over the past 25 years, presently reaching 11.1% (Félix *et al.*, in press).

The Gulf of Guayaquil population suffers a sustained decreasing trend as four population parameters (average community size, average group size, average encounter rate and average density) have declined between 39% and 54% in these 25 years (Félix *et al.*, 2017b). Another study in Posorja and El Morro yielded similar conclusions (Jiménez and Álava, 2014). In the northwestern part of the Gulf of Guayaquil (Salinas), a small community of coastal bottlenose dolphins (n=9) ranges nearshore over about 40km on both sides of the Puntilla de Santa Elena (Zavala *et al.*, 2016). This community also seems to be decreasing according to existing historical records (F. Félix, unpublished data). Occasionally groups of offshore ecotype can also be observed off the Puntilla de Santa Elena (F. Félix, unpublished data).

Between 1996 and 2010, 14 strandings of *T. truncatus* were recorded on Ecuador's central coast. In three cases the stranding was firmly associated with fisheries interaction and in one case with a collision (Félix *et al.*, 2011). Mortality in fishing nets has also been registered in Puerto López, Manabí (Castro and Rosero, 2010). In January 2017, three new cases of interaction with fishing gear were recorded in Morro, Gulf of Guayaquil, suggesting that the frequent fisheries-caused mortality as identified in the mid-1990s (Félix and Samaniego, 1994; Van Waerebeek *et al.*, 1997) persists, and probably affects the entire population of the Gulf of Guayaquil (Félix *et al.*, in press).

Stomach contents of coastal *T. truncatus* in the Gulf of Guayaquil included *Scynoscion* sp. and *Cetengraulis mysticetus* (Félix, 1994)

Peru-Coastal

Unlike in Chile, coastal morphotype bottlenose dolphins have a more or less continuous nearshore distribution along most of the central and northern Peruvian coast (Van Waerebeek *et al.*, 1990). Communities likely spatially overlap and interbreed. For instance, two individuals shared the same control region haplotype although they were landed in ports 556 km apart (Sanino *et al.*, 2005). The southern distribution boundary of the coastal ecotype in Peru is unclear but at least extends to Bahía Independencia (14°13'S, 76°09'W). Five strandings of *T. truncatus*, presumably dead from fisheries interactions, were reported for Tacna, southern Peru (Pizarro, 2010), but their ecotype is unknown.

Three metric and four non-metric cranial characters are diagnostic (Van Waerebeek *et al.*, 1990 and allow an almost complete separation between coastal and offshore specimens when the skull is available. During at-sea observations the typical triangular dorsal fin with low falcateness index (overhang/length base of DF) allows differentiation with a high degree of certainty (Félix *et al.*, 2017a). Only a single individual (MFB-185) with both cranial features and fisheries data confirming an offshore form, showed a DF with coastal phenotype. It was the only specimen to be misclassified after ocular inspection.

Mean group size, from small-boat surveys in the Paracas Bay area, was 8.7 (Reyes *et al.*, 2002). Most sightings occurred between the surf-zone and the 5m isobath. Paracas Bay appears to form the border between two local resident groups. A spatially wider sample, between Ancón (11°44'S) and Paracas (13°50'), yielded a mean group size of 6.5 (SE=1.0) (Van Waerebeek *et al.*, 1990). In the Paracas (Pisco) area, besides two resident groups, there is some evidence also for a rare transient community (Echegaray *et al.*, 1992). Comprehensive datasets remain to be analysed, but at one cliff-top observation platform on the central coast (Pucusana), over a 30-year period, mean sighting rates as well as mean group sizes have fallen dramatically, while boat traffic (and disturbance) increased and water pollution from

untreated sewage grew worse (K.Van Waerebeek, unpublished data).

The most common prey, in terms of both total prey items and frequency of occurrence (Van Waerebeek *et al.*, 1990) were Peruvian anchovy (*Engraulis ringens*), Patagonian squid (*Loligo gahi*), Peruvian weakfish (*Cynoscion analis*), and Pacific sardine (*Sardinops sagax*). Observations from the Cerro Azul pier, in 1991, showed that they preyed on mullet (*Mugil cephalus*) and horse mackerel (*Scomber japonicus*) (García-Godos, pers. observations).

Chile-Coastal

Pod-R of central-north Chile

The so-called 'pod-R' (for resident), a unique inshore occurring community in the central-north of Chile (González *et al.*, 1989; Capella *et al.*, 1999; Sanino and Yañez, 2001), originally consisting of some 28 photo-identified individuals moved ca. 27 km south from Isla Chañaral (29°02'S) to the area near Islas Choros, Damas and Gaviota (29°15'S) after one dolphin was illegally harpooned by swordfish fishermen (Sanino *et al.*, 2001). Genetically pod-R is highly divergent from both Peruvian offshore and coastal stocks but showed a relatively closer mt-DNA affinity with the Chilean offshore stock (Sanino *et al.*, 2005). We hypothesize that this coastal community may have diverged relatively recently from the large offshore population. It retains at least one 'ancestral' offshore morphologic trait, i.e a strong falcateness in dorsal fin shape, normally found in offshore bottlenose dolphins of the SE Pacific (Félix *et al.*, 2017a). Otherwise, the pod's long-term nearshore residency, their slender body, non-stubby rostrum and light colouration are consistent with the coastal morphotype in Peru and Ecuador.

Although one carcass stranded in Punta de Choros in April 2013 and several members have not been re-identified since several years, no cranial specimens have become available. The examination of even a single adult skull of Pod-R would be revealing. This community has been seen feeding on *Strangomera bentincki*, *Engraulis ringens* and *Mugil cephalus* (G.P. Sanino, pers. observations). Excessive pressure from incorrectly managed dolphin-watching led to evidence of stress and complete reproductive failure for at least three years (1995-1998) (Sanino and Yañez, 2000). Due to its small community size, unique genetic markers (Sanino *et al.*, 2001) and vulnerability to anthropogenic pressures, the Chilean government legally granted nearshore ecotype bottlenose dolphins Endangered/EN status while the rest is listed as Least Concern/LC (Ministerio del Medio Ambiente, 2016).

OFFSHORE POPULATIONS

Colombia-Ecuador Offshore (= ETP-Offshore?)

Walker (1981), based on NMFS/NOAA ship surveys, suggested that the eastern tropical Pacific (ETP) offshore population of bottlenose dolphins extends as far south as the waters off Colombia and Ecuador, including the Galápagos Islands. Except for general distribution, knowledge of the biology of *T. truncatus* in the Colombian Pacific is scarce (Avila *et al.*, 2013). The offshore population has been estimated between 3,548 - 14,493 (Gerrodete and Palacios, 1996) following sighting cruises in the 1980s and 1990s. Palacios *et al.* (2012) from later cruises (1986-2008) estimated an encounter rate (density) of 3.21 groups of *T. truncatus* per 1,000 km distance and between 3.97 - 11.43 groups per 100 hours observer effort. Among offshore sightings several occurred over the Malpelo Ridge.

Off Malpelo Island (03°56'N, 81°34'W) bottlenose dolphins have been sighted during all seasons of the year. Calves and juveniles of different sizes suggest they may breed near the island (Herrera *et al.*, 2007, 2011). Unfortunately, no photo-identification or telemetry studies have been carried out.

Near Gorgona Island (03°56'N, 78°12'W), separated by a 35 km wide, 270 m deep channel from mainland, bottlenose dolphins have only been reported from April to November (but not in June), in groups of 20-200 individuals (Flórez-González and Capella, 2001; Flórez-González *et al.*,2004). Their ecotype status is unconfirmed but large group size suggests offshore animals.

Offshore *T. truncatus* have also been recorded aboard Ecuadorian oceanographic cruises along the Ecuadorian coast in deeper water, and towards and around the Galapagos archipelago (Clarke *et al.*, 2001; Alava, 2002). By geographic argument, this population is identifiable with the nominal species *Tursiops nuuanu* Andrews, 1911 (type locality, 12°N, 120°W). Scott and Chivers (1990) recorded their offshore presence as far south as 15°S. Félix *et al.* (2017) demonstrated some dorsal fin shape difference between Ecuador offshore and Peru offshore. However, it is assumed that some degree of overlap (parapatry) and reproductive exchange occurs between the three large offshore, highly mobile stocks (ETP, Ecuador Offshore, and Peru-Chile Offshore) (see below). A phylogeographic analysis revealed that six specimens stranded on the central coast of Ecuador, presumably offshore ecotype, were closest related to Northeast Pacific animals (Bayas, 2015). The results of Bayas (2015) have not yet been compared with Sanino *et al.* (2007), for the control region sequence examined in the former was larger, but a comparison is due.

Peru-Chile Offshore stock

Although they shared only one control region haplotype, explainable because of very large population size, no significant differences were found in the mtDNA control region between Peruvian and Chilean offshore dolphins

(Sanino *et al.* 2005), prompting the authors to name this population the 'Peru-Chile offshore bottlenose dolphin stock'. Results from an IWC/SOWER cruise off Chile in 1997-98 (Findlay *et al.*, 1998) indicated large group sizes which ranged from 2 up to 2,000 individuals (mean= 108.5; SD=313.7; N=49; median=25). Off Peru, offshore bottlenose dolphins have been recorded during IMARPE cruises in groups up to at least 1,000 individuals (Table 1), in waters from 71 m to more than 1000 m deep, with mean SST 18.9°C, and with distances from shore ranging 12-65 nm (Márquez and Arias-Schreiber, 2001; Sánchez and Arias Schreiber, 1998). One of us (J.C. Reyes) during an experiment with longlines, confirmed that *T. truncatus* observed 60 nm off Pucusana, central Peru, showed indeed the offshore morphotype *sensu* Van Waerebeek *et al.* (1990).

Mean	SD	Min	Max	N	Source
50	119.7	1	440	18	Bello <i>et al.</i> (1997)
28.7	105.8	1	1000	92	Sánchez and Arias-Schreiber (1998)
142.1	194.2	10	500	9	Marquez and Arias-Schreiber (2000)
106.1	132.0	1	500	22	Ontón <i>et al.</i> (1997)

Table 1. Variation in group sizes for offshore *T. truncatus* reported off Peru during four IMARPE cruises in 1997-2000. With few exceptions groups are considerably larger than those seen in the coastal form.

At least three metric and four non-metric cranial characters (Table 2) have been identified that allow to discriminate between Peruvian inshore and offshore skulls (Van Waerebeek *et al.*, 1990; Anchante *et al.*, 2008). Three parameters, including antorbital process length, maximum width of palatines and tooth width showed no overlap between adults of the two forms which are thus diagnosably distinct (Table 2). Although the inshore sample was small, new specimens tend to confirm this. An evidently offshore skull from south of Bahía Inglesa (27°10'S,70°55'W) in northcentral Chile showed the same combination of cranial characters as Peruvian offshore specimens (Sanino and Van Waerebeek, 2008).

Three species of cestodes and one nematode affected most offshore animals and none, or a few, inshore dolphins (Table 2). Highly divergent helminth parasite loads serve as a powerful indicator of ecological separation. It is thought to be linked to different prey composition, as parasite larvae are thought to be transmitted through prey that function as intermediate hosts. For instance, readily diagnosable osseous lesions in cranial sinuses known as 'basket-like lesions' (Van Bressem *et al.*, 2007), caused by the nematode *Crassicauda* sp., are significantly more common in offshore animals.

Stomach contents analysis supports the vastly different diets between ecotypes (Table 2). In Peru, offshore bottlenose dolphins (n=22) consumed mainly slimtail lanternfish (39.2%), barracuda *Sphyraena* sp. (13.5%) and Pacific sardine *Sardinops sagax* (13.3%). The diversity index of the diet and temporal shifts in the main prey suggest an opportunistic feeding strategy, which take advantage of the locally most available epipelagic and mesopelagic schooling fish (García-Godos *et al.*, 2007).

Patagonian Offshore stock (Los Lagos, Aysén)

Bar one outlier (see below), the southernmost range of *T. truncatus* in Chile is at the southern part of Región de Los Lagos (Golfo Corcovado) and Región de Aysén (Aguayo *et al.*, 2006; Sanino and Van Waerebeek, 2008; Olavarría *et al.*, 2010; Viddi *et al.*, 2010). A mother-calf pair was sighted deep inside Comau fjord, at 42°22'S,72°24'W. A single skull showed the offshore morphotype, but morphological variation data are very limited. Three sightings between 43°-45°S (Corcovado Bay, Temuan Channel, Vera Sound) in January and December 2007 (Sanino and Van Waerebeek, 2008) were morphologically (stocky bodies with short, stubby snout; falcate dorsal fins; very dark overlay which obscured cape pattern in some) and behaviourally (large groups of 40-120 individuals; fast, high-energy swimmers) consistent with an offshore form, despite encountered inside fjords, one group almost 50 nmiles from open water. Individual variation in colouration pattern was significant, especially in the extent of the dorsal overlay. Dark eye patches were common. Variation in colouration remains to be quantified.

The temporary use of nearshore habitat is explainable because Patagonian fjords mimic slope waters due to their great depth, may reach several 100s of meters in the main channels and several tens of meters even in the smaller channels. The fjords may provide shelter from stormy waters of the South Pacific as well as abundant prey, associated with the numerous rivers. Three groups counted respectively 40, 100 and 120 individuals, which is consistent with the Chilean offshore form (Sanino and Van Waerebeek, 2008) and considerably larger than inshore form group sizes in central Peru (mean= 6.5; Van Waerebeek *et al.*, 1990), Paracas communities (mean =8.70), Ecuador (mean = 8.12, SD=4.48; Félix *et al.*, 2017b), i.e. where groups rarely exceed 15 individuals (K. Van Waerebeek, unpublished data). All groups were actively attracted to a rigid-hull inflatable and moved at high speed with frequent leaps.

Olavarría *et al.* (2010) reported several sightings for the Los Lagos (42°-44°S) and Aysén (44°-46°S) Regions and listed 4 encounters over one week in summer 2009 with (apparently) a single group of 5 individuals in the western Magellan Strait at 53°22′S,72°38′W. The authors suggest, and we concur, that these bottlenose dolphins probably originated from the Atlantic, considering their proximity to the western South Atlantic population in Argentina's Tierra del Fuego, and the complete lack of records in Chile's southern Aysén and Magallanes regions. The southernmost record then of Chilean bottlenose dolphins is at 45°49′S,74°59′W in Bahía Darwin (Aguayo-Lobo *et al.*, 2006).

INCERTAE SEDIS (IN NEARSHORE HABITAT)

Chile-Incertae sedis

Peninsula of Mejillones and surroundings, northern Chile

In the late 1980s, Guerra *et al.* (1987) first documented the nearshore presence of bottlenose dolphins in Chile. These authors reported five specimen records (3 bycatches, 2 strandings) over a *ca.* 190 km stretch of coastline centred around the Mejillones Peninsula (23°10'S, II Region, Antofagasta) in northern Chile. One very large (315 cm) harpooned female (AMM-017) stranded at Coloso was collected and is thought to be an offshore specimen. Recent observations confirm that bottlenose dolphins are regularly sighted in the Bay of Mejillones. Their movements, seasonality, population identity, and status are currently under study (Anna María García, University of Antofagasta, pers. comm. to KVW). Interestingly, fin whales have recently been documented to enter the Bay of Mejillones with some regularity (Pacheco *et al.*, 2015), possibly because of feeding opportunities due to strong local upwelling. We suggest that offshore bottlenose dolphins may access these nearshore, but fairly deep waters, for the same reasons (prey availability). The close examination of any new stranded or bycaught specimens will have high priority.

Laguna Verde and surroundings, central Chile

Bottlenose dolphins, locally known as 'delfines de Laguna Verde', are regularly sighted in nearshore waters near Valparaiso, central Chile (V Region) since at least the early 1990s until today. Confirmed observations, both land-based and boat-based, have been made off Caleta Barco, Quintay, Caleta los Docos, Bahía Laguna Verde, Bahía Valparaiso, Concón and Isla Mantagua (G.P. Sanino and Andrés Venegas, pers. observations; Table 3). Diaz-Aguirre et al. (2009) also reported sightings between Punta Angeles (33°01'S) and Punta Gallo (33°16'S), centered at Punta Curaumilla, in several periods between 2004-2007. Dolphins seemed to be feeding on neritic fishes near the surface. Diaz-Aguirre et al. (2009) did not provide group sizes nor photos, but an overall mean derived from reported total number of animals divided by total number of groups gives 25.8 ind./group, which is the median group size (25) for offshore T.truncatus off Chile (Findlay et al., 1998). 'Preliminary information on photo-identification suggests that some individuals are present year-round (Diaz-Aguirre et al., 2009), and 'the distribution and movement pattern [parallel to the coastline], according to Diaz-Aguirre et al. (2009), 'suggest that this population probably pertains to the coastal ecotype'. In view of the lack of published data, firm assignation to ecotype is premature, but we believe these animals are more likely incursing offshore form, similar to the Patagonia Offshore stock. Importantly also, the utilised coastal zone is considerably larger than reported and stretches at least from Caleta Barco in the south to Isla Mantagua off Concón (Figure 2). Data confirm long-term utilisation of the area by *T. truncatus*, from early 1990s till today, but a dedicated photo-ID study will be required to properly evaluate degree of residency.

Table 3. Associated data for 5 sightings of *T. truncatus* made from small-boats north of Bahía de Valparaiso, as plotted in Figure 2. Group sizes of 40 individuals and higher and deep water point to an offshore population.

Date	Time	Site	Position	Depth (m)	Group size
19. Mar. 2017	10:00:00	Roca oceánica	32.9382°S - 71.5827°W	171	40
7. Jan. 2017	08:17:00	Roca oceánica	32.9375°S - 71.5921°W	210	80
6. Aug. 2016	11:55:00	Isla Mantagua	32.8853°S - 71.5568°W	95	40
9. Apr. 2016	09:00:00	Cochoa	32.9251°S - 71.5914°W	157	60
26. Mar. 2016	09:00:00	Higuerillas	32.9047°S - 71.5728°W	151	120

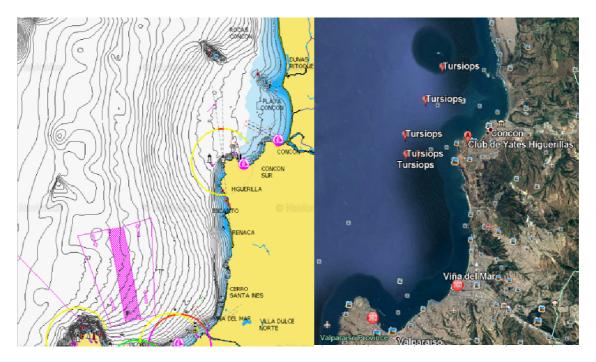


Figure 2. Recent sightings of bottlenose dolphins (made by AVA) north of Bahía de Valparaiso demonstrate the northern known limit of a ca. 60 km stretch of coastline utilized by *T. truncatus*, centered off Valparaiso and Laguna Verde. Although nearshore, habitat consists of fairly deep water (see Table 3).

DISEASES AS POTENTIAL STOCK INDICATOR

A variety of infectious and non-infectious diseases have been documented in *T. truncatus*. Below we summarize those with potential value as stock indicators in the study region, as some have shown widely differing prevalence levels between coastal and offshore populations.

Skin diseases

Tattoo skin disease, a dermatologic infection by cetacean poxviruses, was detected in offshore (prevalence 41.6%, n= 12) and coastal (n=1) bottlenose dolphins in central Peru (Van Bressem and Van Waerebeek, 1996).

Lobomycosis-like disease, with a clinical pattern highly reminiscent of lobomycosis (caused by an uncultivatable strain of *Paracoccidioides brasiliensis*), has been found in coastal dolphins in Peru (n=1), Ecuador and southern Colombia (Bahía Malaga, Tumaco) with varying prevalence levels, from 1.6% (n= 441, Gulf of Guayaquil) to 16.7% (n = 18, Salinas, EC) (Van Bressem *et al.*, 2007, 2015a). So far, it has not been detected in the offshore ecotype.

Pale dermatitis (PAD) of unknown aetiology affected 6.9% (n=87) of coastal bottlenose dolphins from Paracas Bay, central Peru (Van Bressem *et al.*, 2015b), but was not detected in the offshore form. A female from Palena, southern Chile (offshore), presented numerous skin vesicles (Viddi *et al.*, 2005, Van Bressem *et al.*, 2007).

Other infectious diseases

Penile warts likely due to papillomaviruses were observed in three of 8 offshore males (Van Bressem *et al.* 1996). Serum antibodies against dolphin morbillivirus were detected in 3 of 6 offshore specimens (Van Bressem *et al.* 1998). Cowpox virus neutralizing antibodies were reactive in 6 offshore dolphins tested (Van Bressem *et al.* 2006). Finally, serum antibodies against *Brucella* spp. were detected in 1 of 2 coastal and in 2 of 3 offshore dolphins caught off central Peru in 1993-1995 (Van Bressem *et al.*, 2001).

Osteological lesions

Lytic cranial lesions were the most frequently observed disease in coastal (26.9%, n= 26) and offshore (42.9%, n= 42) bottlenose dolphins, followed by hyperostosis and ankylosing spondylitis in offshore (31%) and inshore (15.4%) specimens. Prevalence of basket-like (lytic) osseous lesions in the skull caused by *Crassicauda* sp. was almost four times higher in offshore (26.2%) than in inshore (7.7%) specimens from Peru (Van Waerebeek *et al.*, 1990; Van Bressem *et al.*, 2007). Both ecotypes were affected by periodontal lytic disease to a similar degree (coastal 15.4%, offshore 16.7%). Traumas and fractures were also similarly prevalent in coastal (7.7%) and offshore (7.1%) specimens (Van Bressem *et al.*, 2007).

CONCLUSIONS

Uncertainties of taxonomy and phylogenetics concerning bottlenose dolphins occurring off the Pacific coast of South America are limited to populational/subspecific issues. Five populations (2 offshore, 3 coastal) are provisionally identified: Colombia-Ecuador Offshore stock (most likely identifiable with ETP-Offshore), Peru-Chile Offshore, Ecuador-Coastal (mainly Gulf of Guayaquil), Peru-Coastal and a unique isolated community (Pod-R) living nearshore on the north-central coast of Chile. In particular questions remain, at one hand, about the extent of gene flow between the Colombia-Ecuador Offshore stock and the large Peru-Chile Offshore stock at one hand, their relationship with the three coastal populations at the other hand, and finally the inter-coastal affinities.

At least seven cranial characters, four non-metric (separation of occipital condyles, pterygoid bone development, exostosis of periotic) and three metric (tooth width, antorbital process length, maximum width palatines), dorsal fin shape, body stockiness, mt-DNA (control region), habitat, prey composition, parasite load, behaviour and prevalence of some infectious diseases differentiate the coastal from the offshore forms. Several of the cranial characters are diagnosably distinct between morphotypes to such a degree that a brief ocular inspection of the skull, or the dorsal fin, is often sufficient to correctly allocate specimens to the correct form.

Pod-R from northcentral Chile, till date, is the only confirmed coastal form community in Chilean waters, and thus also the southernmost (29°S) off Pacific South America. Bottlenose dolphins regularly transiting nearshore in Chile's Patagonia and occasionally entering fjords in the Los Lagos and Aysen regions, exhibit both offshore morphotype (stocky body; stubby snout; falcate dorsal fin; dark overlay obscuring cape pattern) and offshore type behaviour (forming large groups; fast travel). Also we suggest that bottlenose dolphins utilizing some 60 km of coastline centered off Valparaiso/Laguna Verde (central Chile), and dolphins inhabiting nearshore though fairly deep waters over a 190 km stretch of coast centered around the Mejillones Peninsula in northern Chile may also belong to the offshore morphotype. Nonetheless confirmatory evidence will be required.

The continental border of the Atacama Trench off northern and northcentral Chile leaves an extremely narrow, steep continental shelf with deep water close to shore, locally with strong coastal upwelling favouring high productivity and prey concentration. This quasi-pelagic habitat seems to attract oceanic cetaceans, including offshore stock *T. truncatus*, sperm whales (*Physeter macrocephalus*), fin whales (*Balaenoptera physalus*) and other species. Unsurprisingly, sperm whales were successfully hunted in the 20th century from a shore-based whaling station at Quintay, located precisely at Laguna Verde where also bottlenose dolphins are reported, we believe from an offshore stock. The southern distribution range of true coastal form bottlenose dolphins in Pacific South America remains unknown but off Chile distance-to-shore may not be the reliable indicator of morphotype as it is further north in the study region (i.e. Peru and Ecuador).

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Table 2. Discriminatory biological characteristics for Peruvian coastal and offshore forms. Sources: (1) Van Waerebeek *et al.*, 1990; (2) Félix *et al.*, 2017; (3) García-Godos *et al.*, 2007; (4) Sanino and Van Waerebeek, 2008; (5) this paper; (6) Anchante *et al.* (2008). *Leuroglossus urotramus* is now considered a junior synonym of *L. stilbius*.

Data type	Parameter	Inshore Peru	Offshore Peru	Source
Cranial				
morphology	Tooth width	wide (8.55-9.60 mm)	narrow (6.55-8.55 mm)	(1)
	antorbital process length	short (49-57 mm)	long (58-67 mm)	(1)
	maximum width of palatine	narrow (50.3-54.4 mm)	broad (55.2-69.3 mm)	(1)
	pterygoids (development)	fragile, thinly walled	thickly walled	(1)
	pterygoid notch shape	wide, with rounded obtuse apex	narrow notch with subacute apex	(1)
	separation of occipital condyles	broad, U-shaped	narrow, V-shaped	(1)
	periotic bone	without exostosis	with frequent exostosis	(6)
External morphology	Dorsal fin shape	triangular; broad at mid- height; relatively low	strongly falcate, narrow at midheight; relatively high	(2,5)
	Body s hape	relatively slender	often heavy, stocky bodies	(1)
	Body length (largest Male)	308 cm	304.5cm (322cm, this paper)	(1)
	Body length (largest Female)	289 cm	289 cm (Chile: 315 cm)	(1)
	Pigmentation	light gray overlay, prominent dorsal cape	dark gray overlay, partially obscures dorsal cape	(1)
Parasitic load	Tetrabothrius forsteri (Cestoda)	16.7%	70.6%	(1)
	Phyllobothrium delphini (Cestoda)	0.0%	70.0%	(1)
	Monorygma grimaldi (Cestoda)	0.0%	80.0%	(1)
	<i>Crassicauda</i> sp. (Nematoda)	0.0%	68.8%	(1)
Prey species	Peruvian anchovy (<i>Engraulis ringens)</i>	frequent	frequent (22.7% FO)	(1,3)
	Patagonian squid (<i>Loligo gahi)</i>	frequent	indeterminate	(1)
	Peruvian weakfish (<i>Cynoscion analis)</i>	frequent	none	(1)
	Pacific sardine (Sardinops sagax)	frequent	very frequent (40.9% FO)	(1,3)
	Hake (<i>Merluccius gayi</i>)	occasional	frequent (13.6% FO)	(1,3)
	Mullet (<i>Mugil sp.)</i>	occasional	rarely (4.55% FO)	(1)
	Banded toadfish (<i>Aphos porosus)</i>	occasional	none	(1)
	<i>Anchoa</i> sp.	occasional	none	(1)
	Loma drum (<i>Sciaena deliciosa</i>)	occasional	none	(1)
	Minor stardrum (<i>Stellifer minor</i>)	occasional	none	(1)
	Kingcroaker (<i>Menticirrhus ophicephalus</i>)	occasional	none	(1)
	Inca scad -jack mackerel (<i>Trachurus murphyi</i>)	none	frequent	(1,3)
	California smoothtongue (<i>Leuroglossus urotramus</i>)	none	frequent	(1)
	Lumptail searobin (<i>Prionotus stephanophrys</i>)	none	occasional (4.6% FO)	(1,3)
	Slimtail lanternfish (<i>Lampanyctus parvicauda</i>)	none	very frequent (45.5% FO)	(3)
	Unidentified squids	none	frequent	(1)
	Barracuda (<i>Sphyraena</i> sp.)	none	very frequent (22.7% FO)	(3)
Behavioural ecology	Habitat	nearshore, shallow waters; often near surfzone	pelagic; mainly deep waters near continental slope	(1,2,4)
	Group size (range)	small groups (1-25)	large-very large groups (1-1000)	(1,2,4)
	Group size (mean)	6.5 (SE 1.0)	50 -106.1 (n=4 means)	(1,5)
		slow travel typically parallel	fast swimming (modal behaviour); travels long distances/day, any	
	Travel	to shoreline	direction	(4,5)