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Feeding of humpback whales at low latitudes of the Southeast Pacific Ocean

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ABSTRACT

Humpback whales perform long migrations from their breeding and nursing areas at low latitudes to feeding grounds at high latitudes. Nonetheless this strictly dichotomous paradigm of migration is challenged by accumulating examples of occasional or regular feeding in tropical or subtropical areas for several stocks worldwide. Here we report multiple lines of evidence of IWC 'Stock G' humpback whales feeding in coastal waters at low latitudes of the Southeast Pacific Ocean. Lunge-feeding behavior was observed in Ecuador, while both lunge- and trap-feeding in pursuit of Peruvian anchovy was documented in northern Chile. Five records of substantial defecation in a key breeding ground in Ecuador also demonstrates local foraging. In addition mark-recapture analysis of one individual feeding at high and mid latitudes of Chile suggested potential site fidelity to two foraging areas. Whether these behaviors are novel due to changes in prey distribution, intensifying competition for food from a growing humpback whale population, or rather reflect vastly increased research effort in a poorly studied region, remains unknown. Further research into the feeding ecology of 'Stock G' should help reveal historic and potentially novel feeding grounds, prey composition and precise migration paths.

KEYWORDS: *Megaptera novaeangliae*, feeding grounds, trap-feeding, lunge-feeding, Humboldt Current, Peruvian anchovy, phylopatry.

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Humpback whales perform long migrations from high latitude feeding grounds to their breeding and nursing areas in low latitudes [1,2,3], with the notable exception of the non-migrating Arabian Sea population that remains year-round in the Arabian Sea and Persian Gulf [3,4]. However the paradigm of this long migration for feeding or breeding strategies is under discussion as an increasing number of studies show humpback whales feeding in formerly unrecognized mid or low latitudes [5,6,7,8,9,10]. Some authors highlight the need for whales to find new localities to feed due to increasing population abundance, the potential consequences of climate change on humpback whale prey distribution or the learning of new feeding areas among individuals [10]. However, there is no evidence that occasional low-latitude feeding is novel behavior in the SE Pacific and may just have remained unnoticed, partly because whaling had severely depleted most populations and partly because before 2000 research effort on humpback whales was scarce in western South America [6].

Humpback whales are generalist predators which exibit different foraging strategies related to high primary and secondary productivity areas [11,12]. Feeding strategies depend on the target prey, for example Alaska humpback whales engage in coordinated lunge-feeding where they feed on euphausiid crustaceans (*Euphausia pacifica*) and herring (*Clupea harengus*). In the NE Atlantic Ocean humpback whales perform swimming lunging and bubbling in group associations or individuals alone [13]. Both feeding strategies are used to maintain naturally occurring concentrations of preys. Off British Columbia (Vancouver) humpback whales trap-feed on small and less concentrated herring schools [14]. The whales set a trap for juvenile fish when they are in small diffuse schools. The fishes are collected near or in the mouth of the whales while hiding from predation by diving birds, then the whales use their pectoral fins to herd the fish towards their mouths. High fidelity to feeding sites has been demonstrated in the NE and NW Pacific humpback whales by genetic and photo-

identification studies [15,16,17]. Genetic analysis demonstrated finer site fidelity between two different feeding sites spaced 500 km apart in Russia [17]. In addition, humpback whales showed different feeding strategies in the 2 feeding sites, as near Karaginsky Island they foraged on schooling fishes and around the Commander Islands they foraged on euphausiids [18].

In the SE Pacific Ocean the IWC-named breeding "Stock G" of humpback whales perform long migrations from high latitudes in the Corcovado Gulf (42ºS), Magellan Strait (54ºS) and Antarctica (70ºS) in summer to their breeding and nursing grounds in low latitudes in northern Peru (04ºS), Ecuador, Colombia, Panama and Costa Rica (12ºN) during austral winter [19,20,21,22,23,24,25]. Recently, photo identification studies have shown that humpback whales feeding in Antarctic waters breed in northern Peru, Ecuador and Colombia whereas humpback whales feeding in Magellan Strait breed in Costa Rica and Panama [2,26]. Genetic studies also showed genetic structuring between breeding and feeding areas of the Stock G [27]. However, occasional humpback whale sightings in low latitude upwelling areas during summer may indicate that not all whales migrate to high latitudes for feeding [6,28]. The Humboldt Current marine ecosystem is recognized for its exceptionally high secondary productivity of small pelagic fishes such as the Peruvian anchovy (*Engraulis ringens*) due to its year-round high primary productivity upwelling system [29]. It extends from 04-07ºS in northern Peru to 37ºS off central Chile. Distinct upwelling cells occur within Chile and one of the most intense and permanent is the Mejillones Peninsula Upwelling System (MPUS at 23ºS) [30]. Coastal upwelling is the key oceanographic process promoting a rich habitat for pelagic organisms, which serve as prey for baleen whales. Recently, the presence of fin whales (*Balaenoptera physalus*) has been documented engaging in feeding behavior at the Mejillones Peninsula, northern Chile, during austral summer [31,32], while humpback whales

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have been reported travelling on their northward or southward migration [32]. This study reports the first authenticated record of humpback whales performing lunge and trap-feeding behavior in northern Chile, and presents evidence of lunge-feeding and also defecating in a key breeding ground in coastal Ecuador.

Northern Chile. Over five days, from 10 March to 4 April 2019, two adult humpback whales were observed side-by-side performing feeding behavior on Peruvian anchovy in Mejillones Bay (23°1'45"S, 70°29'44"W, Figure 1). Observations were made opportunistically from a 7 m vessel equipped with a 50 HP outboard engine during fishing or ecotourism activities. Photo-ID images of the flukes were taken with a CANON T5i Reflex camera and geographic coordinates were recorded with a Garmin Etrex 10 GPS.

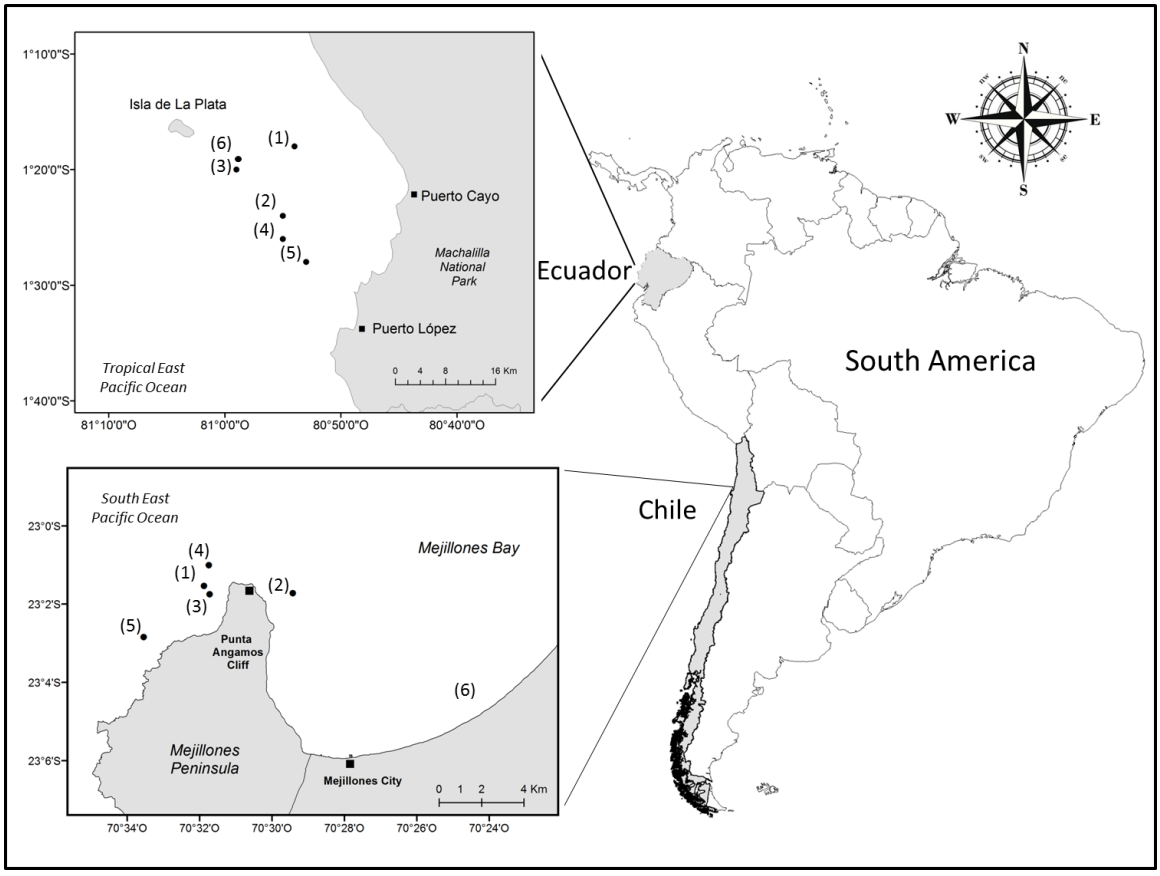

Figure 1. Map of Machalilla National Park in Ecuador and Mejillones Península in northern Chile showing the geographic positions (black dots) of humpback whales performing feeding

 doi:10.20944/preprints202012.0446.v1

behavior. Numbers indicate the dates observed in Ecuador: (1) 21 June 2005 (2) 11 July 2008 (3) 13 August 2008 (4) 15 July 2011 (5) 10 August 2016 (6) 13 August 2017. Numbers indicate the dates observed in Chile: (1) 10 March 2019 (2) 12 March 2019 (3) 16 March 2019 (4) 17 March 2019 (5) 23 March 2019 (6) 18 April 2020.

During the observation period anchovies were grouped in big schools of small-sized, juvenile, individuals and both whales performed coordinated lunge-feeding and trap-feeding strategies (Figure 2). Lunge-feeding consisted of dives of 2 min, followed by the anchovies leaping off the water surface and the whales suddenly breaking the surface simultaneously in close proximity to the center of the school, the mouth wide agape and with distended throat (Figure 2E). Whales rised up to one-third of their body length before falling back to the water. No bubbles were observed, however the emergence of schools of anchovies at the surface one to two seconds before the whales broke the surface suggests that the whales herded the school of fishes with a bubble net. Observations and photographs of prey at the surface and inside the buccal cavity of the whales and the presence of South American sea lions (*Otaria flavescens*) and seabirds including Inca terns (*Larosterna inca*) and gray gulls (*Leucophaeus modestus*) were registered (Figure 2G). Trap-feeding consists in humpback whales remaining close to the surface with open mouth for an extended period of time (minimum 4 s) compared to lunge-feeding [14]. Humpback whales were observed performing both lunge and trap-feeding in the same observation time. Both whales were preying on schooling immature Peruvian anchovy. When humpback whales started trap-feeding, Inca terns and gray gulls approached the whales' mouths to prey on anchovies. In the Southern Hemisphere, lunge-feeding strategy has been described previously in humpback whales from Magellan Strait but none performed trap-feeding [33]. One of the humpback whales observed in March 2019 was recaptured in April 2020 in the portuary area of Mejillones Bay with another humpback whale performing

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lunge and trap-feeding (Figure 2H, I) on peruvian anchovies. We were able to collect several Peruvian anchovies of size range 8-12 cm with fishing line and small hook (Figure 5), at the exact location and time when humpback whales were seen preying on anchovies.

Figure 2. Lunge-feeding and trap-feeding behaviors by two humpback whales as documented

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off the Mejillones Peninsula, northern Chile. (A) One of the whales observed trap-feeding for the first time (10 March 2019) with mouth kept open for longer than 4 seconds. Peruvian anchovy at the surface were herded towards its mouth with pectoral fins. (B) The same two humpback whales observed on a second day (12 March 2019) performing trap-feeding behavior on schools of Peruvian anchovy. The whales remained in parallel position at the surface with mouths wide agape. (C) Trap-feeding by the same two humpback whales recorded on a third day (16 March 2019). (D) Lunge-feeding performed by the same two whales on 17 March 2019. Note anchovies (white arrows) escaping from one whale's mouth. (E) Lunge-feeding observed off Mejillones Peninsula on 17 March 2019. Whales emerged in synchrony, one exposing one third of body while the other engaged in lateral lunge-feeding. Seabirds fed on anchovies herded to the surface. (F) Lunge-feeding documented for the last time (23 March 2019). White arrows indicate how the whale forcefully expels water through the baleen by closing its mouth. (G) Propeller scars of the bigger humpback whale encountered off Mejillones Peninsula. Note abundant grey gulls hovering above the whale. The individual performing lunge and trap-feeding behavior in March 2019 (H) was recaptured and seen lunge-feeding in April 2020 (I).

Coastal Ecuador. On 21 June 2005, two humpback whales were observed lunge-feeding in protected coastal waters (at 01°18'S, 80°54'W) of the Machalilla National Park, Ecuador (Figure 1). The sighting from 10:47 till 11:40 was made opportunistically by one of us (CC) from an 11m fiberglass whale-watching boat equipped with two 115 HP outboard engine, on the Puerto Lopez - Isla de la Plata route. Initially the whales moved slowly together, changing behavior at 11:21 when both started side lunge-feeding. Six times in a row the whales, slowly moving on one side, broke the surface with wide open mouth and extended ventral pleats (Figure 3) before closing mouths while still at the surface. Only one whale lifted

 doi:10.20944/preprints202012.0446.v1

its tailstock and flukes above water before diving and considering that the whales did not surface in synchrony, possibly they were diving to different depths. At 11:42 the whales surfaced with mouths shut and resumed their prior behavior of slow travel. No prey species could be seen but, as usual at that time of the year, turbidity was very high. The whales photo-identified (by flukes) as EC666 and EC667 in the PWF Ecuadorian catalogue were compared with some 600 individuals from Ecuador, 342 individuals in the catalogue of Fundación Yubarta (Colombia), 36 whales in the Fundación Sentir catalogue (Colombia) and with 65 photos by CEQUA (Chile), but no matches were found. Although feeding had not been observed before, nor since, on other whale-watching excursions in the Machalilla National Park, one local fisherman offered a detailed description of a behavior he observed which can only be interpreted as a bubble net feeding humpback whale. That occasional feeding off Puerto López may not be so exceptional is suggested by documented observations of locally defecating humpback whales.

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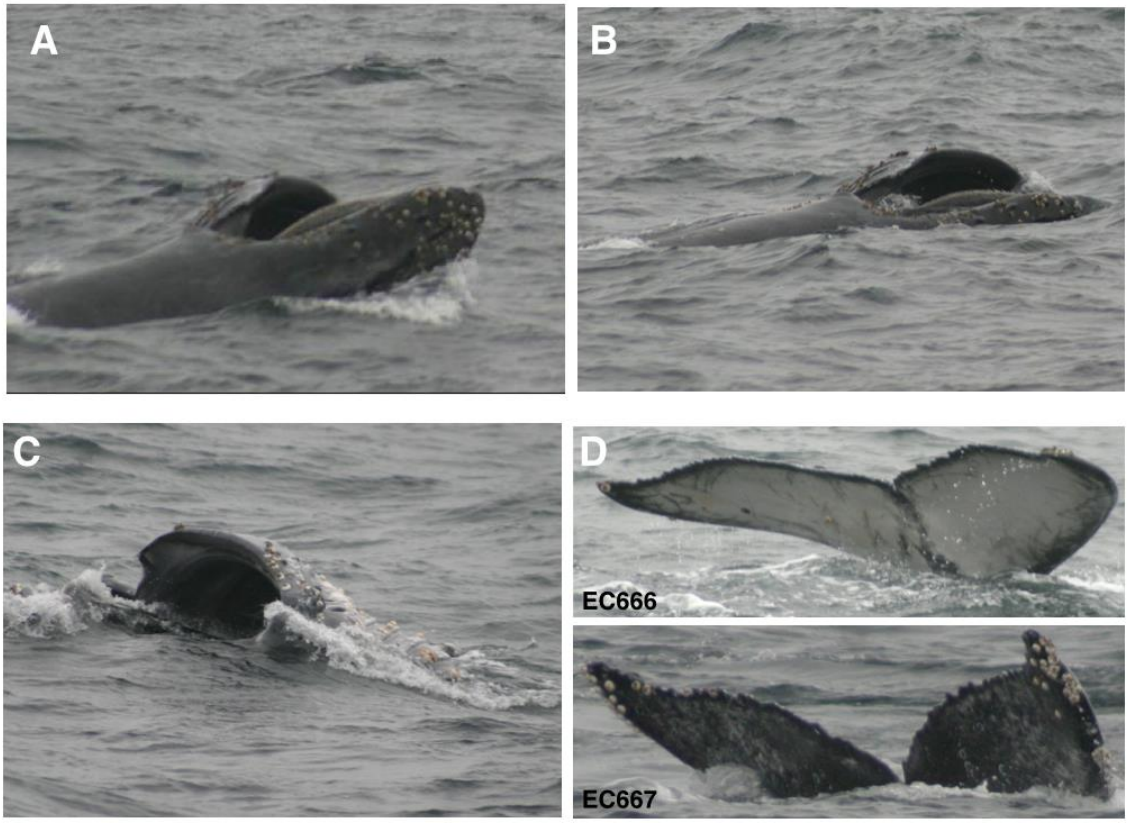

Figure 3. (A) Humpback whale lunge-feeding in protected coastal waters (01°18S,80°54'W) of Machalilla National Park, Ecuador. (B) Slow-moving whale, tilted 90º on its right side, opens mouth and starts lunge-feeding. (C) Whale surfacing with wide open jaws and expanded throat pleats; closing jaws after a few seconds. (D) Flukes photo-ID of feeding humpback whales EC666 and EC667 on 21 June 2005 (Photos: C. Castro – PWF).

Faecal matter was observed on five occasions, as follows. An adult whale EC1373 sighted at 01°24'S,80°55'W on 11/07/2008 (Figure 4A) and adult EC1504 (one of two whales) recorded at 01°21'S,80°59'W on 13/08/2008 were both photographed with faeces sticking to their dorsal fins or dorsum. Another adult whale was sequentially photographed, surfacing first without, and then with, green-brown faeces sticking to its dorsal fin at 01°26'S,80°55'W on 15/07/2011.

A group of three adult humpback whales was encountered slapping pectoral fins on

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the sea surface at 01°28'S,80°53'W on 10/08/2016. After 10 min, the sea around one individual suddenly became discolored by the evident release of a large quantity of green-brown faeces (Figure 4B). Shrimp boats were fishing in the immediate vicinity (< 500m) and may provide a clue as to a potential prey target.

The 5th case was on 13/08/2017, an adult whale in a small group of two whales was clearly observed defecating very close to the boat at 01°20'S,80°59'W. An attempt to sample the green-brown faeces failed, however video # 5847 recorded by one of us (C.C.) documented the event.

Figure 4. Evidence of humpback whale defecation at Machalilla National Park, Ecuador: (A) Whale EC1373 at 01°24'S,80°55'W on 11/07/2008 with green-brown faeces sticking to dorsal fin. (B) Humpback whale sighted at 01°28'S,80°53'W on 10/08/2016 when suddenly releasing a cloud of green-brown faeces (Photos: C. Castro - PWF).

Considering that freshly expulsed whale faeces may have positive buoyancy, the

 doi:10.20944/preprints202012.0446.v1

surfacing through a large floating faecal cloud, may explain the momentary tainting (befouling) of parts of the whale's dorsum and dorsal fin. The speed of digestion and transition of ingested food through a whale's gastrointestinal tract is rapid [34]. Digestion of a full stomach in baleen whales has been estimated at about 15 hours [35]. The whales observed defecating evidently must have fed locally on the breeding ground.

Trap-feeding is considered a novel foraging strategy of humpback whales off Vancouver Island, Canada [14] and this is the first record of Stock G whales performing this strategy. It has been suggested that foraging strategies may vary among humpback whale populations depending on their prey type, abundance and geographical area [33,36,37] For example, in the Magellan Strait whales were bubble net feeding on Fuegian sprat (*Sprattus fueguensis*). In the Antarctic Peninsula, bubble net and lateral lunge-feeding were performed to capture Antarctic krill (*Euphausia superba*), and skimming/lunge-feeding to capture lobster-krill (*Munida rugosa*) [21]. In western Canada humpback whales used both trap-feeding and lunge-feeding while targeting juvenile Pacific herring (*Clupea pallasi*) [14, 38]. However, the preference of one feeding strategy versus another depending on the type of prey may also be influenced by a variety of factors such as bottom slope, abundance of prey, individual preferences, prey distribution in the water column and shape of the prey school [38,39,40,41,42]. McMillan et al. (2018) also showed that when herring schools were less abundant, humpback whales utilized trap-feeding instead of lunge-feeding. Trap-feeding is a less energetic cost feeding strategy to capture less abundant schooling fishes [43]. In British Columbia, Canada, the number of humpback whales engaging in trap-feeding increased in consecutive years, suggesting that it might be learned from others (horizontal or cultural transmission) [44,45]. Maternal transmission and/or cultural transmission have been observed as calves practice the same feeding behavior used by their mother [11,46]. Whether this

foraging strategy has been adopted by Stock G humpback whales from another population is unknown.

A photo identification analysis of the two humpback whales recorded in Mejillones Bay in March-April 2019 matched one of them with a humpback whale observed feeding on krill (*Euphausia* sp.) in the Gulf of Corcovado, Chile's northern Patagonia, during the 2017 austral summer (Paulina Bahamonde, personal communication to AMGC). The same individual was recaptured in Mejillones Bay in April 2020 with another whale, both lunge-feeding on schools of Peruvian anchovy (Figure 2H,I). The recapture of the same whale feeding in the same period (early autumn) in consecutive years suggests feeding site fidelity to Mejillones Bay, possibly on its northward migration to Eastern Tropical Pacific coasts. Humpback whales tend to have higher site fidelity to their feeding grounds than to the breeding grounds in both Northern and Southern Hemispheres [26, 47,48,49]. Site fidelity to the Magallanes Strait feeding ground has been described for Stock G [21,26]. The discovery of new feeding habitats for humpback whales have been attributed to climate change effects presumably modifying prey distribution [50, 51,52] or the expansion of humpback whale populations increasing competition for food compelling whales to find new feeding grounds [10]. However, local fishermen from Mejillones described humpback whales performing lunge-feeding behavior before industrial fishing started in the 1980s. The decrease of fish abundance due to industrial fisheries and the severe depletion of humpback whales in the SE Pacific following a century of whaling until 1968 [53,54] might have masked a natural behavior of at least occasional feeding in low latitudes. Moreover, before 2000 dedicated research on SE Pacific humpback whales was minimal [6]. Nonetheless, humpback whales were previously reported feeding at low latitudes in the year-round upwelling system of Peruvian coastal waters [6,28]. For three days in mid-summer (17-20 February 1996),

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biologists A. Garcia-Godos and C. Zavala observed two humpback whales from cliffs at San Juan de Marcona (15°20'S) in south-central Peru. The whales, pursued by numerous seabirds, were repeatedly seen feeding at the surface, as well as breaching [6]. One humpback whale sighted in Bahia San Jorge, 200-300m inshore of southern Antofagasta (23°28.5'S) on 14 March 1987 [55] apparently neither had undertaken a southbound summer migration. We speculate it might have been feeding at the adjacent Mejillones Bay. In addition the individual showed a propeller scar on its dorsal fin in 2019 but not in 2017 (Gustavo Chiang, personal communication to AMGC). Humpback whales that oversummer, while feeding along the coasts of Chile and Peru are subjected for extended periods to anthropogenic threats such as vessel collision [32] and fishing gear entanglement [59]. For instance, their small-scale distribution has been demonstrated to overlap with the navigation paths of large cargo vessels entering and exiting the major portuary area of Mejillones Bay [32].

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Figure 5. Peruvian anchovies (*Engraulis ringens*) sampled simultaneously when humpback whales were lunge- and trap-feeding in Mejillones Bay, northern Chile, in April 2020.

In conclusion, we here present novel evidence of humpback whales occasionally feeding at three low-latitude coastal locations in the SE Pacific, i.e., at Mejillones Peninsula in northern Chile (ca. 23°S), at San Juan de Marcona in south-central Peru (ca. 15°S) and in waters of the Machalilla National Park, Ecuador (ca. 01°S).

Further research will need to clarify humpback whale migration patterns and feeding ecology in the SE Pacific Ocean, and allow us to understand whether these parameters have been modified significantly by climate-change influence on prey distribution and availability. It is

necessary to unravel also how the intense industrial purse-seine fishery of small pelagic fishes in Mejillones Bay (personal observations) is affecting the local abundance of Peruvian anchovy and generally whether fishing effort is disturbing whale distribution and habitat use in nearby areas of the Humboldt Current System. Moreover the recent propeller scar observed in one of the humpback whales underlines the high risk of collision with maritime traffic, particularly in Chile's Mejillones Bay. The relatively high navigation speed of industrial fishing boats in the bay may put at risk the survival of humpback whales and disturb their feeding behavior [32]. A Marine Spatial Planning effort is needed in Mejillones Bay for transiting vessels to avoid the feeding area of humpback and fin whales. Moreover, a ban on industrial purse-seine fishing for small pelagics in the bay would greatly favour the conservation of locally feeding humpback and fin whales [31,32] as well as small cetaceans such as the dusky dolphin *Lagenorhynchus obscurus*, the common bottlenose dolphin *Tursiops truncatus* and the Burmeister's porpoise *Phocoena spinipinnis*, all of which inhabit Mejillones Bay [55], Garcia-Cegarra thesis) and are thought to commonly prey on anchovies as they do in Peruvian waters [56,57,58].

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Disclosure statement

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