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Habitat use of south-eastern Pacific humpback whales (*Megaptera novaeangliae*; Borowski 1781) in Golfo Dulce, Costa Rica

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ABSTRACT

Context. Golfo Dulce is a wintering ground of the south-eastern Pacific population of humpback whales. Habitat use and spatial preferences of whales during their reproductive season must be addressed to effectively conserve this species. **Aims.** This study aims to determine spatial segregation depending on humpback whale group composition (groups that included mother–calf dyads versus adult-only groups). **Methods.** Spatial aggregation was assessed using sightings per unit of effort from June to October, 2010–2019. The group preferences were analysed as a function of water depth and distance from the coast, and habitat use was characterised using behavioural data. **Key results.** Our SPUE analysis showed important locations used by humpback whales. The mother–calf groups were present in waters <80 m deep, and their main behaviour was resting (nursing and social). Adult-only groups were in the deeper waters, and the main behaviours were social breaching and travelling. Spatial preferences and behaviour data allowed the identification of critical nursing areas near potential mating grounds. **Conclusions and implications.** Our study has highlighted the need for inshore habitat protection, and these habitat-use patterns should be considered when designing effective conservation and management strategies for marine spatial planning.

Keywords: behavioral ecology, breeding grounds, Central America wintering area, cetaceans, habitat use, humpback whale, resource management, spatial ecology.

Introduction

The humpback whale (*Megaptera novaeangliae*) is known for its long, seasonal migrations from its feeding grounds at high latitudes, to its wintering grounds in tropical waters, where breeding and calving occur (Flórez-González *et al.* 1998; Acevedo *et al.* 2017). South-eastern Pacific humpback whales have multiple wintering areas, including the Central American region (Oviedo and Solís 2008; Rasmussen *et al.* 2012; Acevedo *et al.* 2017; De Weerdt *et al.* 2018). Costa Rica receives whales from both the northern and southern hemispheres, and it has been hypothesised that gene flow is possible if there is spatio-temporal overlap (Baker *et al.* 1990, 1998; Rizzo and Schulte 2009). However, the north-eastern Pacific population migrates to lower latitudes between December and April, whereas the south-eastern Pacific population makes its journey to warmer waters between May and November, although some individuals have been observed into December (Bettridge *et al.* 2015).

The south-eastern Pacific population has its wintering grounds in Central American waters, such as the Pearl Islands and the Gulf of Chiriquí off the coast of Panama (Guzman and Félix 2017); the Pacific coast of Nicaragua (De Weerdt *et al.* 2020); and the southern Pacific coastline of Costa Rica, including Caño Island, Drake Bay and Golfo Dulce (May-Collado *et al.* 2005; Oviedo and Solís 2008). The first record of southern Pacific humpback whales in Costa Rica was documented by Acevedo and Smultea (1995).

Golfo Dulce is part of this large breeding habitat for humpback whales and has high numbers of records of mothers with calves, competitive groups of mature individuals and singing males (Herra-Miranda *et al.* 2016).

Habitat-use analyses are vital for the management and protection of cetaceans because they improve our understanding of the influence of the local environment and interactions with anthropogenic activities. There are two major risks to humpback whales in breeding areas that particularly affect juveniles and calves, namely, collision with vessels (Laist *et al.* 2001, 2014; Guzman *et al.* 2013) and entangling with fishing nets (Guzman *et al.* 2013). In the Golfo Dulce basin, both of these risks are present, given that there are two important national-level port facilities there Golfito and Puerto Jimenez (Herra-Miranda *et al.* 2016). As a measure to reduce the risk of collision between whales and vessels, the International Maritime Organization (IMO) adopted an area to be avoided (ATBA) in the coastal water off the Osa Peninsula, from Caño Island to the western entrance of Golfo Dulce. Since it was implemented in January 2018, merchant vessels >900 tonnes (Mg) have been excluded from the area. In addition, in February 2018, the Costa Rican government declared the 1366 km^2 ATBA located at the entrance of Golfo Dulce (decree numbers 41003-MOPT-SP-MINAE and 41086-MAG) as well as implementing a Traffic Separation Scheme at the entrance of the Golfo de Nicoya, increasing the protection of large whales from potential vessel collisions along the Pacific coast of Costa Rica (decree number 41003-MOPT-SP-MINAE and 41086-MAG; Guzman *et al.* 2020).

Therefore, the aim of this study was to determine whether there is spatial segregation of the south-eastern Pacific humpback whales in Golfo Dulce according to groups of whales that are composed completely of adults versus groups that contain mothers and calves. This information will allow identifying priority areas within Golfo Dulce, Costa Rica.

Materials and methods

Study area

Golfo Dulce is in the southern Pacific region of Costa Rica (8°33′N, 83°14′W). The gulf is of tectonic origin and has a length of 50 km and varies in width between 10 and 15 km wide, covering an area of ~750 km^2. The climate is tropical-humid with a rainy season from June to early November with an average monthly precipitation of ~100–700 mm and stable and uniform sea-surface temperature of ~30°C (Svendsen *et al.* 2006; Herra-Miranda *et al.* 2016). Golfo Dulce receives runoff from several rivers, particularly the Coto-Colorado, Tigre, Esquinas and Rincón rivers. This large embayment has generally been divided into two areas defined by the bathymetry and oceanographic conditions, namely, the inner basin, and the sill (Fig. 1*a*). The inner basin encompasses 65% of the embayment (~450 km^2) with a maximum depth of 250 m and with currents below 5 cm s^{-1} (Morales-Ramírez *et al.* 2015). The sill area (~200 km^2) is located ~20 km from the mouth of Golfo Dulce and is characterised by shallower depths of ~60 m, as well as strong currents associated with tidal cycles (Quirós-Alvarez 2003; Svendsen *et al.* 2006). The sill is a particularly important topographic feature for the local oceanography because it reduces water exchange between Golfo Dulce and the adjacent oceanic waters, producing a calm interior that occasionally creates anoxic conditions at the bottom of the inner basin (Brenes-Rodríguez and León-Coto 1988; Quirós-Alvarez 2003; Svendsen *et al.* 2006).

Data collection

The surveys were conducted from June to October each year from 2010 to 2019. The maximum number of surveys conducted in a season was 57 in 2013 and the minimum was four in 2014. The average number of surveys conducted per season was 23 ± 16. Surveys were conducted in a 7-m fibreglass boat with a 115-hp outboard engine within the inner-basin waters and sill area of Golfo Dulce. The ports of departure and landfall were at Rincon Bay, Golfito and Puerto Jimenez, and surveys were conducted between 08:00 and 13:00 hours. The area was navigated specifically in search of whales; however, to monitor our location and assess detectability conditions (for behaviour and acoustic sampling), geographic position and sea-state readings according to the Beaufort scale were taken every 30 min (stations), and the presence or absence of cetaceans was monitored for 5 min. Whenever a group of whales was sighted, the boat came within ~100 m of the sighted group. Date, time, geographic position, size and group composition were recorded. The first recorded behaviour was at the time of the encounter. After 10 min, behaviour was noted again, and, if it was the same as the previous behaviour, then a behavioural observation was performed (Fig. 1*b*). We did not conduct behavioural sampling if abrupt changes in behaviour were displayed due to our presence. Three behavioural categories were defined (rest, social and travel), which are described in detail in an ethogram (Table 1). Behavioural sampling duration lasted 30 min, on average, particularly with groups containing mother–calf pairs. In most cases, at least two 10-min behavioural bouts were conducted spaced by 5-min intervals. Following Herra-Miranda *et al.* (2016), we defined the following four group types: mother and calf pair (MC); mother, calf and an escort (MCE); mother, calf and two or more escorts (MCE+); and non-calf groups composed of adults only. The project was conducted under the permit number INV-ACOSA 032-16 from the Ministerio de Ambiente. The Smithsonian Animal Care and Use Committee approved tagging procedures.

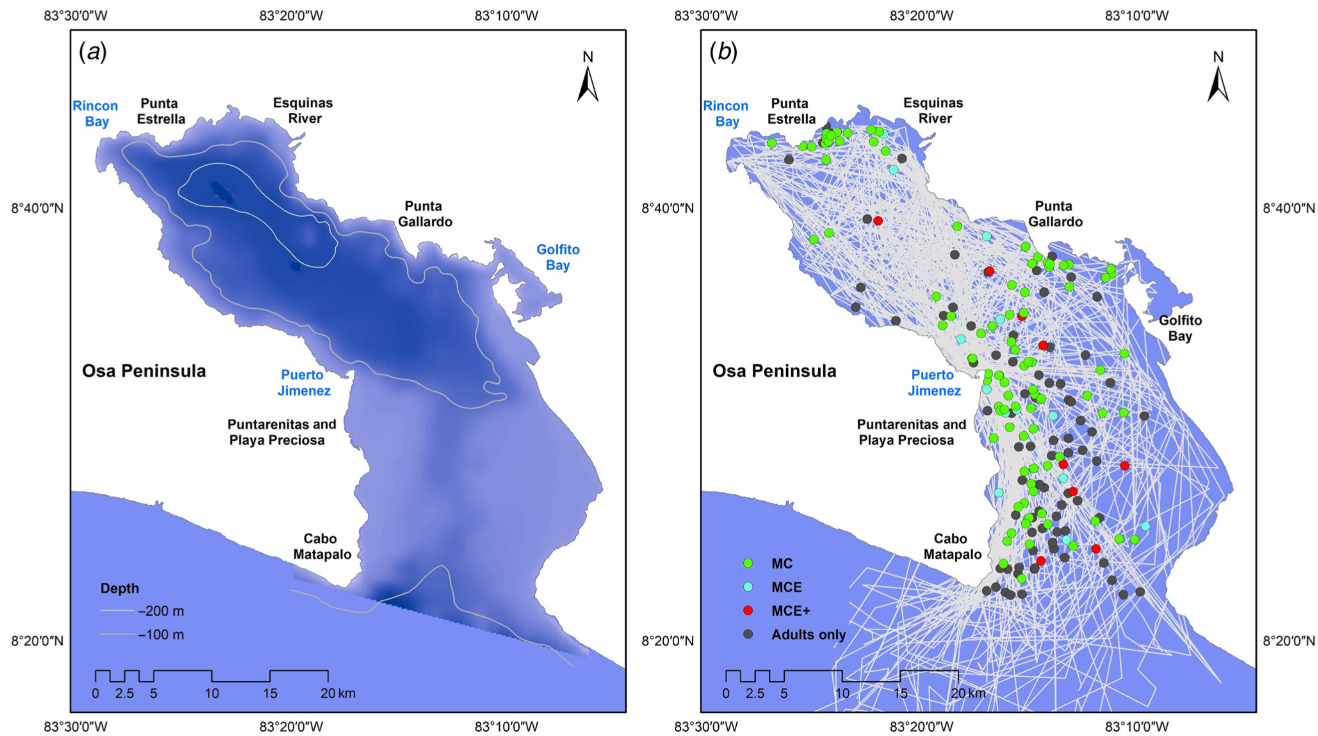

Fig. 1. (*a*) Golfo Dulce bathymetry and main localities. (*b*) Sampling effort between 2010 and 2019 (grey lines) and the distribution of whale sightings (points) during the study period, on the basis of group composition: mother + calf (MC, green), mother + calf + escort (MCE, blue), mother + calf + escort + adult males (MCE+, red) and adult-only (grey).

Table 1. Humpback whale ethogram in Golfo Dulce.

Behavioural category	Variations of surface behaviour
Rest: whale motionless in the same location for >1 min	*Rest-nurse*: mother stays still in the same location, whereas calf surfaces periodically and dives to nurse for <1 min. Sometimes a milky plume can be observed in the surface
	Rest-social: mother stays still in the same location, whereas calf shows abundant surface behaviours adjacent to the resting mother
Social: passive or active interaction between two or more whales, adults including mother and calves, with surface events	*Social-breach*: an individual or several individuals repeatedly propelling two-thirds of their body out of the water
	Social-sing: an individual or several individuals surfacing over a specific location where extended vocalisations (songs) were confirmed and recorded
	Social-competition: Three or more individuals engaging in agonistic interactions with abundant surface events such as fluke slaps and thrashing. Usually, there is a mother–calf pair within the vicinity of competitive males
Travel: whale(s) showing directional movement	An individual or several individuals swimming with a directional movement. There may be an arching of the body into a dive, usually showing the fluke

Data analysis

The distribution of humpback whales in Golfo Dulce (2010–2019) was assessed with sightings per unit of effort (SPUE). First, the survey routes were outlined using the 30-min stations described above. Then, the effort was computed as a function of the total distance travelled into each cell of a regular grid of ~2 × 2 km. The number of sightings by group type (MC, MCE, MCE+ and only adults) within a cell was counted and divided by the previously computed effort to obtain the final SPUE. This procedure was performed with the package 'raster' (ver. 3.5-15, R. J. Hijmans, see https://CRAN.R-project.org/package=raster) in R (ver. 4.2.0, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/).

The distance from the coast was calculated considering the closest point to the coast by using the ArcGIS Desktop (ver. 9.3, see https://webhelp.esri.com/arcgisdesktop/9.3/index.cfm?TopicName=welcome), and the depth of each whale sighting location was determined using the global multi-resolution topography data synthesis (http://www.marine-eo.org/portals/gmrt/; Ryan *et al.* 2009). To determine whether there was spatial segregation among groups of humpback whales that differed in composition (MC, MCE, MCE+ and only adults), we used the information on depth, distance from the coast and behavioural categories (Rest, Social and Travel) recorded in each sighting. To assess whether there were differences among groups of whales and among the main behaviours in function of distance from coast and depth, Kruskal–Wallis tests were performed, followed by Dunn's test of multiple comparisons with Bonferroni adjustment. The analyses were performed in R (R Foundation for Statistical Computing) using 'FSA' package (ver. 0.9.3, D. H. Ogle, J. C. Doll, P. Wheeler and A. Dinno, see https://github.com/fishR-Core-Team/FSA).

The spatial trends resulting from the computed SPUE were qualitatively reinforced by two different approaches to confirm that they are not due to biases from our sampling methods. First, we overlapped the tracks of three adult female humpback whales that were satellite-tagged in Golfo Dulce in September 2015 by using Wildlife Computers SPOT5 tag models AM-S193 (tag numbers 456, 459 and 462). The three females corresponded to mother–calf groups. The geographic positions of the female humpback whales were obtained from an ARGOS satellite system with an error range <5 km. Satellite data were analysed using the Satellite Tracking Analysis Tool software and Kalman algorithm (Coyne and Godley 2005; Lopez *et al.* 2014; Guzman and Félix 2017). Tracks were plotted over the SPUE maps, and only positions within Golfo Dulce and surrounding areas were considered. The second qualitative validation was performed by plotting sighting records from an independent marine megafauna survey (n = 25 days, 191 h) conducted in July–August 2011 (Bessesen 2015). That study yielded several humpback whale encounters (n = 11), including eight mother–calf groups and nursing records.

Results

Spatial preferences according to humpback whale group composition

From 2010 to 2019, 120 mother–calf and 77 adult-only groups, in total, were recorded. The average of all groups was two (s.d. = 2) individuals per sighting. According to our SPUE, mother–calf groups were located near the coast, with an average depth of 63 m, whereas adult-only groups were concentrated in the central part of the mouth of the gulf, with an average depth of 73 m (Fig. 2*a*–*d*).

The general spatial trend in Golfo Dulce between 2010 and 2019 showed a major occurrence of humpback whales in the sill area within ≤100-m isobaths. Mother–calf groups aggregated primarily in the western portion of the sill area between Puerto Jimenez and Cabo Matapalo. Two additional areas of aggregation were identified by the spatial usage trend, including (1) the coastline from the entrance of Golfito towards Punta Gallardo, and (2) along the northern coast of Golfo Dulce from the western side of Punta Estrella towards the Esquinas River. The geographic positions of humpback whale sightings from an independent marine megafauna survey (see Supplementary Fig. S1) and the tracks of three satellite-tagged whales coincide with the sill area where we obtained the highest SPUE values (Fig. 3).

Behaviour characterisation

The four group types differed in their behaviours. For all three groups with calves, particularly MC and MCE, rest behaviour was more frequent than social behaviour. For MCE+ and adult-only groups, resting behaviour was infrequent and social behaviours (including competitive groups and singing males aggregations) were more frequent. For all groups, travelling accounted for over 40% of the behavioural observations (Table 2).

The four group types differed in the depth of the locations where they were sighted (Kruskal–Wallis test, χ^2 = 9.4, d.f. = 3, P = 0.025), their distance from shore (Kruskal–Wallis test, χ^2 = 26.66, d.f. = 3, P = 0.001), and the behavioural categories they performed (Kruskal–Wallis test, χ^2 = 26.35, d.f. = 3, P = 0.001; Fig. 4).

MC groups were found in significantly shallower waters than were MCE+ groups (Dunn test, Z = 2.67, P = 0.044). MC groups were found at significantly shorter distances from the coastal waters than were adult-only groups (Dunn test, Z = 3.71, P = 0.001) and MCE+ groups (Dunn test, Z = −4.24, P = 0.001). The MCE groups were also found at shorter distances from the coastal waters than were MCE+ groups (Dunn test, Z = −2.99, P = 0.016). Finally, the main differences in the behavioural categories represented were between the MC and adult-only groups (Dunn test, Z = −4.99, P = 0.001).

We also found that there were differences in habitat characteristics among the behavioural categories. Depth (Kruskal–Wallis test, χ^2 = 9.86, d.f. = 2, P = 0.007) differed between the Rest and Travel (Dunn test, Z = −2.64, P = 0.025) and between the Social and Travel (Dunn test, Z = −2.79, P = 0.016) categories. Distance from the coast (Kruskal–Wallis test, χ^2 = 20.41, d.f. = 2, P = 0.001) differed between the Rest and Travel (Dunn test, Z = 4.21, P = 0.001) and Social and Travel (Dunn test, Z = 3.51, P = 0.001) categories. The Travel category was recorded in deeper waters and farther from the coast than were the rest of the categories.

Discussion

Habitat use of south-eastern Pacific humpback whales in Golfo Dulce

This work shows that spatial analysis of SPUE considering social structure and habitat use can be useful in defining

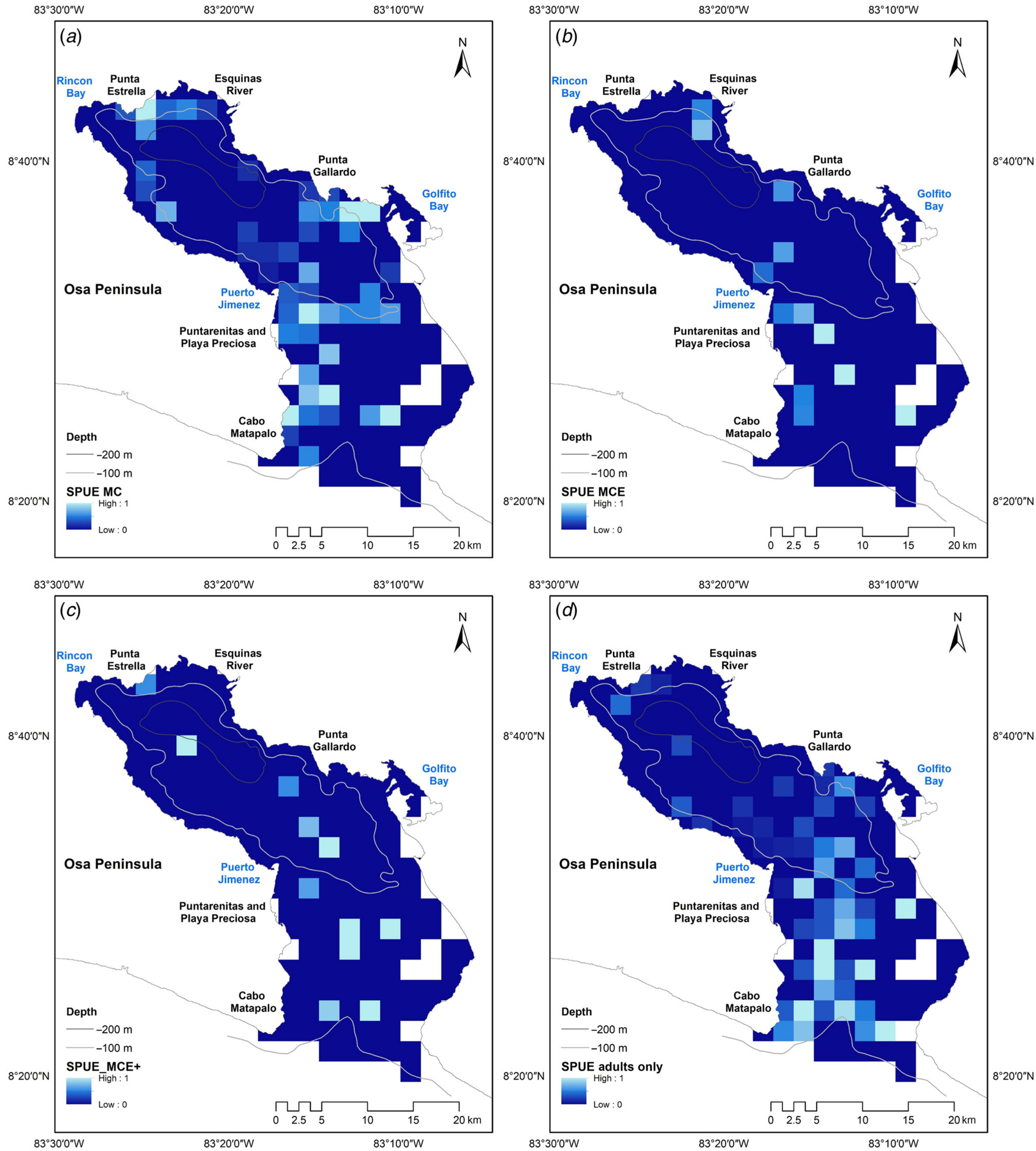

Fig. 2. Sightings per unit effort of humpback whale groups: (*a*) mother + calf (MC), (*b*) mother + calf + escort (MCE), (*c*) mother + calf + escort + adult males (MCE+) and (*d*) adult-only group.

main breeding areas for humpback whales in Golfo Dulce, Costa Rica. Our analysis highlighted the sill as the main area used by humpback whales within the gulf. The spatial patterns described are further supported by the independent data set of Bessesen (2015) and by the tracks of three satellite-tagged humpbacks whales. The highest frequency of both mother–calf and adult-only groups were recorded in waters with depths less than 80 m within the sill area, with a distance from coast of ~2–5 km. Similar preferences for shallow and near-the-coast habitats have been

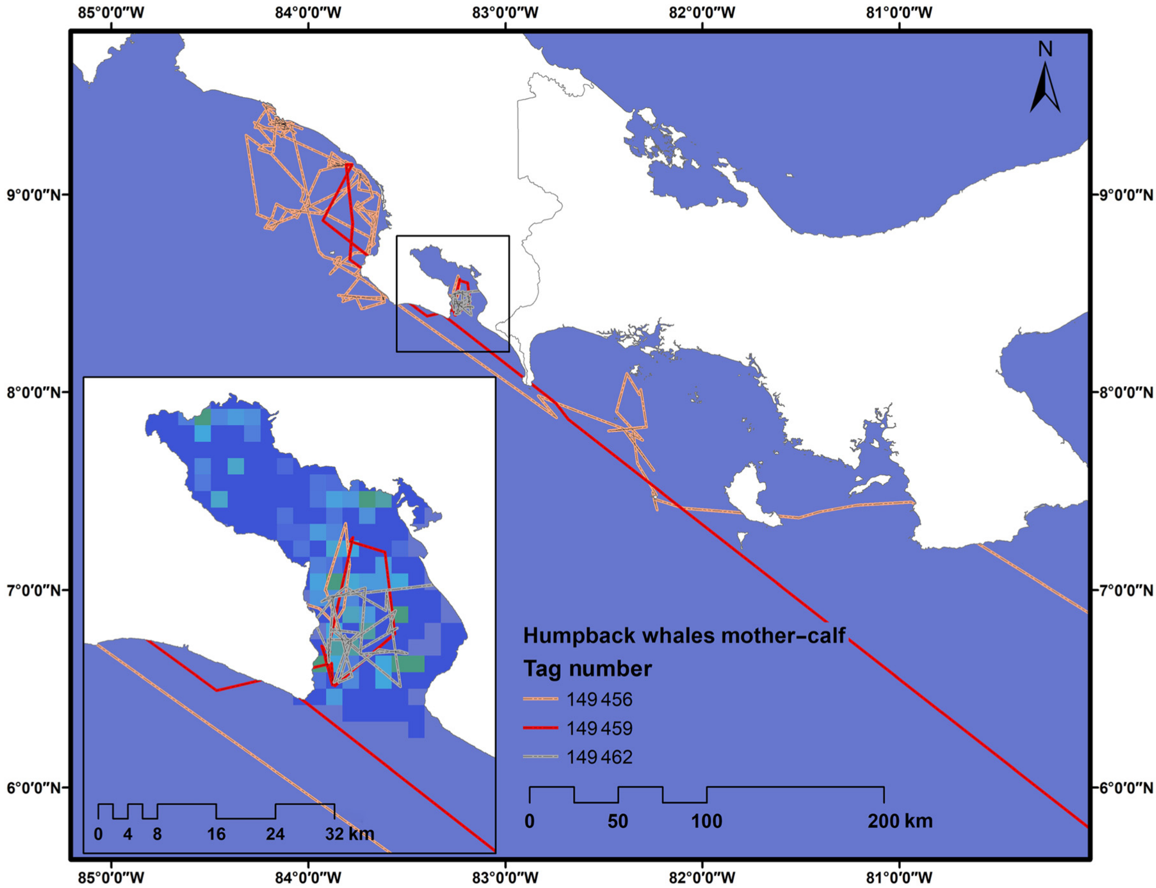

Fig. 3. Tracks of the three satellite-tagged whales (mother–calf pairs) during the 2015 breeding season.

Table 2. Behaviour categories according to humpback whale group composition and habitat characteristics recorded during the reproductive seasons between 2010 and 2019 in Golfo Dulce.

Group composition	Behaviour category	Number of events	Percentage	Depth (m) $\bar{x} \pm$ s.d.	Distance to coast (m) $\bar{x} \pm$ s.d.
MC (*n* = 93)	Rest-nurse	6	6	27 ± 18	1644 ± 443
	Rest-social	48	52	51 ± 45	1984 ± 1626
	Social-breach	10	11	77 ± 50	2957 ± 1458
	Travel	29	31	68 ± 60	2954 ± 1486
MCE (*n* = 15)	Rest-social	5	33	37 ± 37	1787 ± 791
	Social-breach	4	27	75 ± 60	2693 ± 1604
	Travel	6	40	71 ± 49	3955 ± 1942
MCE+ (*n* = 12)	Rest-social	1	8	192	4317
	Social-breach	2	17	68, 192	5423, 5227
	Social-competition	2	17	191, 205	5306, 4982
	Travel	7	58	84 ± 67	5903 ± 1101
Adults only (*n* = 77)	Rest	13	17	41 ± 47	2645 ± 1774
	Social-breach	14	18	77 ± 63	3145 ± 1503
	Social-sing	3	4	60 ± 32	5265 ± 2152
	Social-competition	4	5	93 ± 57	5331 ± 2657
	Travel	43	56	81 ± 61	3840 ± 2028

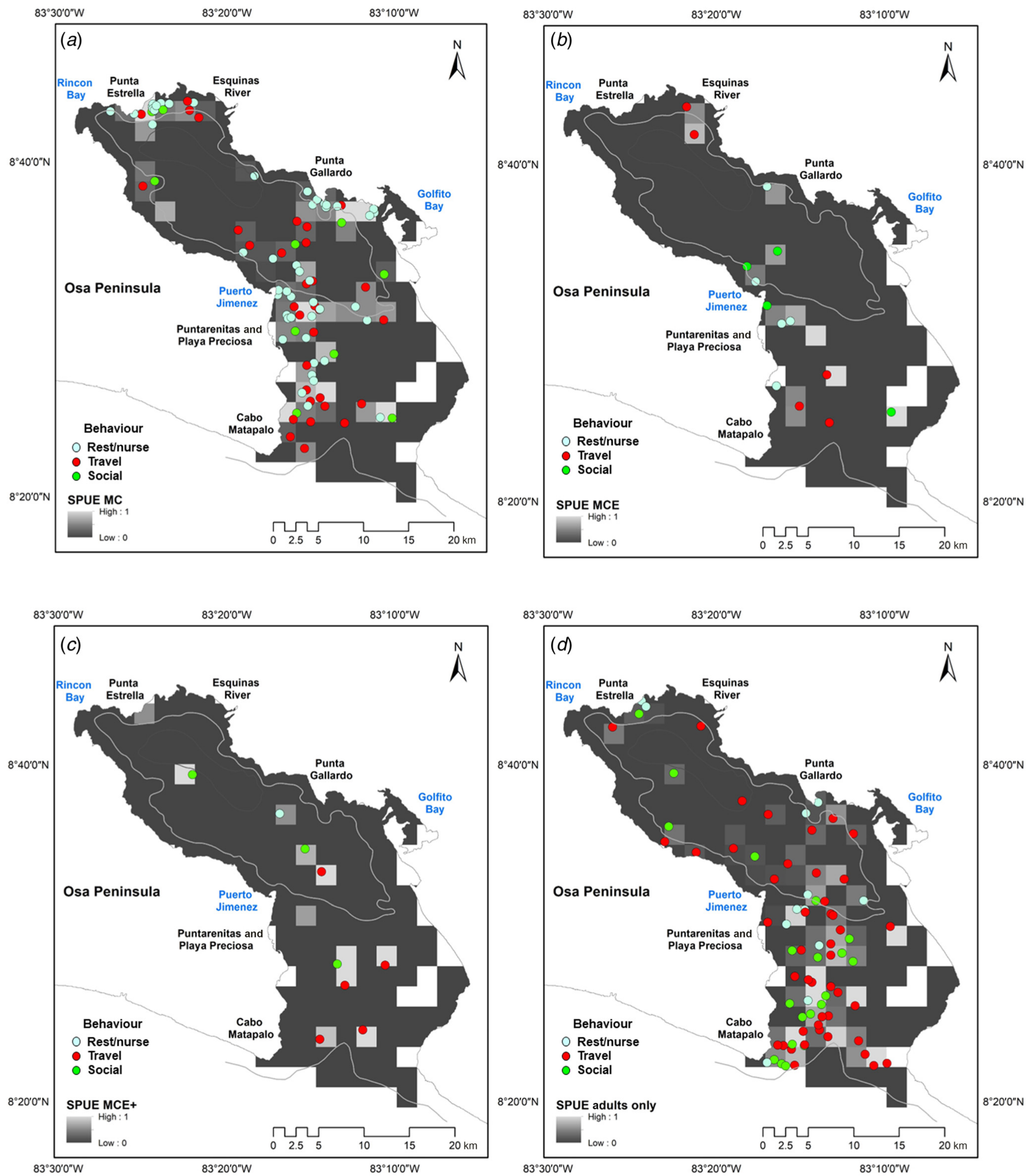

Fig. 4. Main behaviours of humpback whale groups: (*a*) mother + calf (MC), (*b*) mother + calf + escort (MCE), (*c*) mother + calf + escort + adult males (MCE+) and (*d*) adult-only group.

observed in other populations of humpback whales (Cartwright *et al.* 2012; Trudelle *et al.* 2018; Pacheco *et al.* 2021).

Despite this general pattern of habitat use by all group types, there was important spatial partitioning, which may be explained by the differences in behaviour among group types (Martins *et al.* 2001; Ersts and Rosenbaum 2003; McCulloch *et al.* 2021). For example, MC groups were found closer to shore and at shallower depths than the adult-only groups. This pattern may be due to mother–calf pairs avoiding courting males (Sullivan and Cartwright 2009). Likewise, the areas of aggregation at Punta Gallardo and along the northern coast could be the result of calving females moving away from the sill area, where they are most likely to encounter males. Movements towards the inner basin could also lead to more favourable water conditions for nursing. Avoidance of males and nursing in calm waters could increase the probability of calf survival, whereas being exposed to courting males could increase calves' energy expenditure, potentially decreasing their survival (Sullivan and Cartwright 2009; Félix and Botero-Acosta 2011).

Adult-only groups may have been composed mainly of males looking for females to mate. As a result, travelling could be as frequent as social behaviours that arise from male–male interactions and competitive groups. If males exhibit mating preference for non-lactating females, they may avoid the waters nearest the coast to remain in the area where the probability of encountering non-lactating females is higher (Craig *et al.* 2002). Indeed, the latter could be a factor driving the depth distribution of all groups. Despite the absence of any direct records of mating, it is very likely that mating occurs in Golfo Dulce, where competitive groups and singing males have been observed mainly in the sill area (Herra-Miranda *et al.* 2016). Our data add to the existing evidence that Golfo Dulce is a critical nursing and breeding area for humpback whales, which includes previous assessments and direct observations of calving (Márquez-Artavia *et al.* 2012; Bessesen 2015; Herra-Miranda *et al.* 2016). The high proportion of calves found at Golfo Dulce (54%) is similar to that in the adjacent calving areas of Chiriquí Gulf (52%, Rasmussen and Palacios 2013), Drake Bay and Isla del Caño (58%; Vida Marina Foundation, unpubl. data, 2001–2006), and is considerably higher than in the calving areas of Gorgona Island, Colombia (26.5%, Flórez-González *et al.* 1998), central Ecuador (20.3%, Scheidat *et al.* 2000; Félix and Haase 2005), northern Peru (23.3%, Pacheco *et al.* 2021). Moreover, the high proportion of travelling whales and the number of sightings recorded during our 10-year study period suggest that Golfo Dulce could be part of a larger calving area encompassing the wintering grounds reported off Caño Island and in Panama (the Gulf of Chiriquí and Pearl Islands).

A regional interpretation: Golfo Dulce as part of the Central American wintering area

Golfo Dulce provides suitable conditions for nursing and mating for humpback whales, such as stable sea temperature ~30°C and favourable waters between 20 and 80 m deep. However, individual-level data suggest short residence times in Golfo Dulce, namely, 1–3 days on the basis of individual photo identification (CEIC, unpubl. data), and 2–14 days on the basis of satellite tags. Additionally, proximity to other calving areas such as Isla del Caño, Las Perlas Archipelago and the Gulf of Chiriquí suggests that the humpback whales observed in Golfo Dulce could be transiting the whole Central America wintering area of the south-eastern Pacific population. This is consistent with short habitat-use patterns, namely, movements of 200–350 km along coastal zones performed by humpback whales during the breeding season. For example, humpback whales that breed in Panama have been shown to move short distances over the shelf and along the coasts of Costa Rica, Panama and Ecuador, and tagged individuals were shown to move in and out of a given wintering area while transiting between different regions (Guzman *et al.* 2015; Guzman and Félix 2017). The distance from the mouth of Golfo Dulce to Caño Island or to Coiba Island in Panama is ~90 and ~200 km respectively; so, there may be high connectivity within the Central America wintering area.

The analysis of habitat use can be approached through short- and long-distance patterns, and both must be considered to improve the management and conservation plans of a species. Long-distance patterns refer to the annual migrations performed by humpback whales between the polar regions and the equatorial band, and short-distance habitat-use patterns, such as the one addressed in this work, allow the identification of specific areas for calving, courtship and competition among adult males. We expect that our study, which spanned a decade and assessed both spatial segregation and behaviour, will contribute to the conservation of the habitat as a whole because habitat use by cetaceans is frequently the scientific basis for the establishment of marine protected areas. The response of mother–calf groups to the structure of the available calving habitat in Golfo Dulce adds to previous evidence of active reproduction and is further supported by behavioural displays associated with reproduction, such as competitive groups or singing, as documented in Herra-Miranda *et al.* (2016). Our study has highlighted the need for inshore habitat protection, and this information is the basis for several potential management strategies such as Marine Spatial Planning, the extension of current protected areas such as Piedras Blancas National Park or Preciosa-Platanares Wildlife Refuge, and, ultimately, the establishment of a new marine protected area in Golfo Dulce.

Supplementary material

Supplementary material is available online.

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