

Master Thesis

Drivers influencing bottlenose dolphin (*Tursiops truncatus*) group size and composition in the waters off La Gomera

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Einflussfaktoren auf die Gruppengröße und zusammensetzung Großer Tümmler

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Abstract

This paper provides findings of 26 years (1995-2020) of research on bottlenose dolphins' distribution and the factors influencing group size and composition in the southwest coast of La Gomera, Canary Islands. Data was collected repeatedly in all months of the years using boats of a whale watching operator as platforms of opportunity, in an area encompassing and extending beyond the current Special Area of Conservation (SAC), where an estimated stable resident population of 50 animals inhabits. The relationship between grouping pattern and environmental and topographic variables (sea surface temperature, chlorophyll-a, salinity, benthic slope, bathymetry and distance to coast), social structure (presence of calves and juveniles), temporal variation (months and years) and group behavior were analyzed using different models. Group size ranged between 1 and 500 individuals (mean = 18.96, median = 13), including residents and non-residents, and varied significantly within months and across years. Significant monthly and inter-annual variations in bottlenose dolphin abundance and group composition were also observed. Abundance and larger group sizes with the presence of calves and juveniles were higher during the summer months (July-September). Sea surface temperature, bathymetry and the presence of calves and juveniles were identified as the best predictors, positively influencing bottlenose dolphins' group size. Overall, larger group sizes tended to occur in warmer waters (> 22°C) and where bathymetry is up to 1500 m. Sea surface temperature was the only variable affecting groups with calves and juveniles, which tended to prefer warmer waters. The observed patterns are likely to be related to breeding seasonality, calving protection and prey availability. Larger groups foraging/feeding, resting, or socializing were also observed, suggesting that individuals can benefit from an increase in foraging efficiency, protection against predators and mating opportunities. This study reveals how different variables can influence bottlenose dolphin grouping patterns in the waters off La Gomera and highlights the importance of oceanic islands and coastal areas for calving and habitat use. However, the results support the need for further investigations to better understand population trends, movement patterns and prey distribution to guide potential management conservation. Finally, the present study illustrates the importance of mitigating the increasing anthropogenic threats to this species and recommends an improvement of regulations inside its borders.

<u>Keywords</u>: Tursiops truncatus, group size, abundance, group composition, seasonality, sea surface temperature, bathymetry, group behavior, La Gomera.

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1. Introduction

Cetaceans are essential in shaping and maintaining the balance of marine ecosystems, therefore comprehending how biotic and abiotic factors influence their distribution and habitat choices can provide valuable information to guide conservation management. MacLeod (2009) suggested that most species' distribution is explained by the relation between environmental conditions and their ecological niches, which for cetaceans is mainly defined by water depth, water temperature and elements influencing the availability and abundance of their prey. He argued that out of these factors, water temperature has the strongest influence on defining geographic ranges of cetaceans, while the other factors would mainly influence their distribution within their ranges. Nevertheless, is still poorly known why cetacean species' distributions are so often related with water temperature and whether changes in geographic ranges are, in fact, due to changes in water temperature (MacLeod, 2009). Changes in environmental and trophic variables, can influence cetacean densities in a particular area, resulting in seasonal and/or inter-annual variation (Griffin & Griffin, 2004). While species can exhibit inter-annual site fidelity to coastal areas (Oudejans et al., 2015), peaking abundance in some months of the year suggests that the studied area does not represent their whole population's range. In fact, as top predators that are able to swim great distances, their homerange is expected to be large (Ingram & Rogan, 2002). Seasonal patterns may additionally differ according to sex and age (McHugh et al., 2011).

Common bottlenose dolphins (*Tursiops truncatus*) are a cosmopolitan species, occurring both inshore and offshore (Defran & Weller, 1999; Shirihai & Jarrett, 2006; Wells & Scott, 1999). MacLeod (2009) defined them as "warmer water-limited (WWL) species", as their range is limited by their inability to exist in colder waters within the same ocean. In other words, WWL species have a temperature limit to their range, which can vary amongst species. Around oceanic islands, their distribution can range from small to large displacements and is mainly explained by prey availability, reproduction, nursing, season and species niche (Tobeña et al., 2014). Adult male home ranges are usually influenced by the distribution of reproductive females and mating purposes (Sprogis et al., 2016). Females on the other hand, tend to influence habitat selection and range patterns of their offspring, as juveniles bottlenose dolphins have been observed to have a high degree of fidelity to birth area (McHugh et al., 2011). Seasonal movements may reflect prey abundance and distribution (Griffin & Griffin, 2004). Other factors such as salinity (Mintzer & Fazioli, 2021; Tynan et al., 2005; Waring et al., 2023), chlorophyll-

a concentration (Smith et al., 1986; Torreblanca et al., 2022), bathymetry (Ingram & Rogan, 2002; MacLeod, 2009; Ritter & Bünte, 2015; Vermeulen, 2018), distance to coast (Haughey et al., 2021) and benthic slope (Ingram & Rogan, 2002) have been proved to influence the distribution of cetaceans. Despite being commonly found in shallow and coastal waters, a diverse environment might influence the habitat use of bottlenose dolphins (Ingram & Rogan, 2002; Louis et al., 2018). For instance, dolphins in Shannon statuary, Ireland, exhibit a preference for steep benthic slopes and deep statuary waters (Ingram & Rogan, 2002), whereas resident dolphins in Bahía San Antonio, Argentina, stay in shallow waters but move to intertidal zone during high tide to feed (Vermeulen, 2018). Factors such as predation risk and social interactions may also influence movement patterns and habitat use of such societies (McHugh et al., 2011; Ritter & Bünte, 2015; Smit et al., 2010). Coastal bottlenose dolphins can form resident (Simões-Lopes & Fabian, 1999) and semi-resident populations (Cheney et al., 2013; Ingram & Rogan, 2002). The range of resident groups tends to be narrow, probably because of their reliability on food resources (Pérez-Alvarez et al., 2018). On the other hand, offshore species rarely appear in the same site (Oudejans et al., 2015).

Many cetacean species, including bottlenose dolphins, are constituted by fission-fusion societies, in which dynamic, short term associations change daily or even hourly. Nevertheless, these social clusters can also be very distinct and long-lasting (Louis et al., 2018). Associations among cetaceans can be particularly influenced by ecological factors (Galezo et al., 2018; Louis et al., 2018; Oudejans et al., 2015) and seasonal aspects (La Manna et al., 2023; Sprogis et al., 2016). Resident dolphins in shore habitats tend to live in small groups (Pérez-Alvarez et al. 2018), while pelagic species tend to be found in larger groups (Bouveroux et al., 2018; Defran & Weller, 1999). Previous studies have reported the main variables influencing bottlenose dolphin group size to be foraging strategy, presence of calves, presence of predators, underwater noise and water temperature (Gowans et al., 2007; La Manna et al., 2023; Mann et al., 2000; Methion et al., 2023). Females with calves, for example, are more often present in larger groups, probably because it may increase the survival rates of their calves (Heiler et al., 2016). Group size and composition can also vary significantly and may be formed by individuals that share similar characteristics such as age (Louis et al., 2018; Wells et al., 1987), kinship (Azzellino et al., 2016; Diaz-Aguirre et al., 2018), reproductive state (Wells et al., 1987) or sex (Diaz-Aguirre et al., 2018; King et al., 2018). Nevertheless, residents of the Normano-Breton Gulf (English Channel) are associated preferentially with individuals showing a similar foraging strategy rather than individuals that are related or of the same sex (Louis et al., 2018). These associations are usually a trade-off between the costs and the benefits of group-living (Methion et al., 2023). Social structures can provide benefits to animals, such as increasing foraging efficiency (Azzellino et al., 2016; Galezo et al., 2018; Louis et al., 2018), protection against predators (especially in the presence of calves) (Louis et al., 2018; McHugh et al., 2011), reproductive opportunities (Louis et al., 2018), epimeletic behavior (De Moura et al., 2009), social learning (Rossman et al., 2015), and task solving (Kuczaj et al., 2015), encouraging cetaceans to engage in cooperative behavior. On the other hand, social structures can also be costly to animals as intra-group competition for resources, food, and mates increases, as well as the spread of diseases (Louis et al., 2018), which in turn affects group size. Knowledge about grouping pattern is fundamental to better understand their social systems (Methion et al., 2023).

The waters of the Canary Islands archipelago are home to an extraordinary diversity of cetaceans. About one third (28) out of the 87 species of cetaceans around the world have been recorded in this region (Ritter et al., 2011), of which 23 species were documented in the waters off La Gomera (See Appendix A). This fact makes the coastal waters off La Gomera unique and highly important for cetaceans residing in and visiting the area. The area studied here is located in the southwest of La Gomera, lying on the lee side of the island, characterized by calm waters, where cetaceans can find places to rest and care for their calves. In addition, the nearby deep waters, reaching up to 2,000 meters, only a few kilometers away from the coast (Ritter, 2001), are an important habitat for preys as well as species that live on the high seas. The interaction between the Canary Current and African coastal upwelling, added to presence of cyclonic and anti-cyclonic eddies that are shed from the lee sides of the islands, contribute to the vertical and horizontal transport of nutrients to the oligotrophic waters of the region (Arístegui et al., 1997). This in turn may increase zooplankton productivity, possibly contributing to this remarkable environmental density (Barton et al., 1998; Mason et al., 2006; Ministerio para la Transición Ecológica y el Reto Demográfico [MITECO], 2013). The higher surface concentration of chlorophyll-a between January to March, which is attributed to the erosion of the thermocline (Arístegui et al., 1997), might attract species during this time of the year.

The bottlenose dolphins are found throughout the year in these waters southwest off La Gomera, usually in small groups (Ministerio para la Transición Ecológica y el Reto Demográfico [MITECO], 2013). Their various resident groups are estimated to have a stable population totaling about 50 individuals (Boletín Oficial del Estado, 2011). The bottlenose dolphins in this

archipelago do not seem associated to an island, but rather moving between the various islands (Papale et al., 2015). The species prefers a bathymetric range between 100-500 meters; it is the only species found regularly close to the coast and seen from the shore (M.E.E.R. e.V., 2008). In the high seas they are often associated to other species, e.g.: with pilot whales (Globicephala *macrorhynchus*). The bottlenose dolphin is classified as vulnerable at the national level (Spain) and regional level (Canary Islands). In the International Union for the Conservation of Nature (IUCN) Red List the species is currently classified as Least Concern (IUCN Red List, 2022a). Also listed in Annex II of the EU Habitats Directive (Spanish Law 42/2007), it requires special measures for their habitat protection through the establishment of Special Area of Conservation (onwards SAC), a subset of Natura 2000 sites (Council Directive 92/43/EEC). In compliance, the SAC Franja Marina Santiago-Valle Gran Rey (onwards FMSGR), located in the southwest coast of La Gomera, was established in 2011 (Boletín Oficial del Estado, 2011). The corresponding management plan and conservation measures include the regulation of uses and activities, and promotion of best practices inside the SAC (Boletín Oficial del Estado, 2011). SACs are established on the European level as a type of Marine Protected Area (MPA). MPAs on the other hand, are a tool on the international level, which have been created to manage anthropogenic threats while supporting the sustainable use of marine resources, as well as safeguarding the biodiversity of marine ecosystems (Haughey et al., 2021). Protected areas have been considered as fundamental tools for the successful implementation of strategies for nature and biodiversity conservation (Spiliopoulou et al., 2021). A model MPA complementing and enhancing the existing management was proposed by Ritter (2012). The focus of this proposal is a long-term development of whale watching tourism in a sustainable way. Meanwhile, a new management plan for the SAC was approved by the Spanish government in December 2022, aiming to promote biodiversity and activities that are compatible with their conservation goals (Boletín Oficial del Estado, 2022).

Although the area is considered a hotspot for biodiversity and as being part of a Natura 2000 Network, marine mammals are under pressure and subjected to many threats such as bycatch, marine pollution, underwater noise, and vessel collisions (Herrera et al., 2021). More recently, bottlenose dolphins and other cetaceans have been increasingly exposed to whale-watching activities (Dinis et al., 2016). Despite being regulated in many places and being promoted as ethically acceptable, whale-watching activities have been shown to exert short-term negative impacts on the behavior of cetaceans (Eskelinen et al., 2016). Dolphins tend to avoid areas of high levels of traffic and underwater disturbance, adversely affecting bottlenose dolphins'

distribution (Pirotta et al., 2013) and group composition (Heiler et al., 2016). Nevertheless, the potential effects of whale-watching activities on dolphins remain poorly understood (Dinis et al., 2016). Bottlenose dolphins in the Canary Islands were also reported to be highly exposed to organic pollution caused by anthropogenic sources (García-Alvarez et al., 2014). In addition, many species are believed to change their distribution as a reaction to changes in their environment, such as global climate change (GCC) (MacLeod, 2009). Therefore, understanding trends in population ecology, habitat use (key areas within a population range), geographical patterns and a species' niche are extremely important to improve the identification of areas of connectivity and when making recommendations towards the conservation management of marine mammals. They can also offer information on the effectiveness of conservation efforts (Vargas-Fonseca et al., 2020). Since marine mammals are highly mobile species occupying a wide-range niche, the inclusion of spatial distribution and biological environmental factors that affect their distribution are essential in guiding management decisions on their conservation (Haughey et al., 2021).

Despite bottlenose dolphins being one of the most-studied marine mammal species, few studies have focused on the causes of variation in their group size. The objectives of this study were: (1) to examine the monthly and interannual variation in distribution (occurrence and frequency), abundance and group size of bottlenose dolphins occurring in La Gomera during the period of 1995-2020; (2) to analyze the seasonal and interannual variation in groups with the presence of newborns, calves and juveniles between 1995-2020, and to determine whether their presence affect group size; (3) to test significant differences in group size according to group behavior between 1995-2020; and (4) to determine whether and how oceanographic and topographic variables affect their grouping behavior (size and composition) during the period of 2000-2020. Based on the data collected throughout the years, I hypothesize that bottlenose dolphins in La Gomera will display a seasonal pattern with higher occurrence during spring months. Furthermore, non-adults are predicted to be present in larger groups. Groups are expected to vary significantly depending on group behavior. Larger groups are also expected to be found further away from the coast and in deeper waters, while all environmental variables are presumed to have a significant impact on group size and composition. Finally, I will discuss anthropogenic threats that are likely to affect bottlenose dolphins' group size.

2. Materials & methods

2.1 Study area

The study area is located in the coastal waters southwest of La Gomera (17°15'W-17°21'W and 28°1'N-28°14'N), in the western part of the Canary Islands Archipelago (Figure 1). The archipelago is an autonomous region of Spain in the Northeast Subtropical Atlantic Ocean extending out 90 - 400 km from the West African coast. It comprises seven main islands, each of them steep independent volcanoes with deep channels in between and high peaks above the sea (Barton et al., 1998; Ritter, 2001). The presence of a narrow continental shelf also means that very deep waters (up to almost 4000 meters) are relatively near the coast (Ritter, 2001). The islands are influenced by the Canary Current, which is part of the eastern limb of the North Atlantic Subtropical Gyre; and by the north-eastern trade winds. These characteristics affect both oceanic and atmospheric currents while shaping the complex oceanographic conditions of the region (Barton et al., 1998; Mason et al., 2006).



Figure 1: Location of La Gomera in the Canary Islands archipelago.

The study site greatly overlaps, extending beyond the borders of the SAC FMSGR ([ES7020057], Figure 2), which spans a total of 13,139.09 hectares of surface delimited by its inner boarder, extending from Playa del Inglès and Playa de Santiago, and its outer boarder following the coast 7.13 km (3.85 nautical miles [nm]) into the sea (Macaronesian Maritime Spatial Planning, 2019; Ritter, 2012). The area, despite being in a region where the African

coastal upwelling regime is absent, lies in the lee of the island with warm and calm water most of the year, water temperature averaging 18°C in winter and 23°C in summer (Ritter, 2002), making the area suitable for marine species to rest and transit (Boletín Oficial del Estado, 2011). Despite the seasonal or annual occurrence of many species, some of them can be seen during the whole year, including a few resident populations (Ritter, 2012). Most sightings are of small and medium sized toothed whales; however, several baleen whales have also been recorded (Ritter, 2012). The five most abundant species by La Gomera between 1995-2007 were the bottlenose dolphin (*subject of this study*), the short-finned pilot whale (*G. macrorhynchus*), the Atlantic spotted dolphin (*Stenella frontalis*), the rough-toothed dolphin (*Steno bredanensis*) and the short-beaked common dolphin (*Delphinus delphis*, M.E.E.R. e.V., 2008).



Figure 2: SAC Franja Marina Santiago-Valle Gran Rey (ES7020057), La Gomera Island (Ministerio de Agricultura, Pesca y Alimentación (2010).

FMSGR has been part of the Network Natura 2000 (European Union Habitats Directive 92/43/EEC) since January 2002 (Boletín Oficial del Estado, 2011). It was first accepted as a Site of Community Importance (Decision 2002/11/EC of the European Commission), then in

2011 declared as a SAC, reflecting its importance for cetaceans, especially for bottlenose dolphins which, alongside loggerhead turtles (*Caretta caretta*), were declared as a species of community interest (Anexo II de la Ley 42/2007, Boletín Oficial del Estado, 2011). It is an important place for feeding, breeding and resting for this species (Boletín Oficial del Estado, 2011). SACs aim to guarantee the long-term survival of the most threatened species and habitats of Europe while contributing to the mitigation of biodiversity loss caused by anthropogenic activities (Ministerio para la Transición Ecológica y el Reto Demográfico [MITECO], 2013). Therefore, this SAC is operated to ensure the protection of natural habitats and species of community interest found in the area through the sustainable use and practices in the area (Ministerio para la Transición Ecológica y el Reto Demográfico [MITECO], 2013).

2.2 Study species

Bottlenose dolphins are marine mammals that belong to the family of oceanic dolphins or *Delphinidae* of the sub-order *Odontoceti* (toothed whales), which comprise the major group of the order *Cetacea*. The genus "*Tursiops*" means "dolphin-like", suggesting they were amongst the original types of dolphins (Shirihai & Jarrett, 2006). They were known among ancient Greeks and Romans, and today they are popular for their social behavior towards men, including performances for the benefit of the observers (Wells & Scott, 1999). Bottlenose dolphins are found worldwide from tropical to temperate waters and are only absent in polar waters (Shirihai & Jarrett, 2006; Wells & Scott, 1999). They can be found both inshore and offshore, with individuals usually differing morphologically (Defran & Weller, 1999; Shirihai & Jarrett, 2006) and genetically (Pérez-Alvarez et al., 2018).

Bottlenose dolphins are fast swimmers and can dive up to around 500 m deep for as long as 12 min (Shirihai & Jarrett, 2006). They tend to form flexible group patterns (fission-fusion dynamics) where individuals aggregate or split temporarily depending on social and environmental factors (Methion et al., 2023). Their groups range usually between 10-20 animals, but they can reach groups of up to 1,000 individuals or be seen frequently solitarily, while their social units can be mixed, including nursery groups and juveniles (Shirihai & Jarrett, 2006). They herd fish cooperatively by disorientating and pushing them towards the shore, occasionally taking advantages of small-scale human-fisheries (Shirihai & Jarrett, 2006). Their diet is varied, mainly consisting of krill, fish, octopus, squid and shrimp (Ministerio para la Transición Ecológica y el Reto Demográfico [MITECO], 2013).

Color, shape, and size can vary greatly between regions, but they are amongst the largest dolphins, as full-grown they can reach up to 4.1 m and weigh up to 650 kg (Shirihai & Jarrett, 2006). Females sexually mature at 5-13 years old, while males mature at 8-15 years old and their lifespan can be up to 52 years (Shirihai & Jarrett, 2006). Gestation takes 12 months and they give birth every 2-6 years, usually in the warmer months (Wells & Scott, 1999). The strong bond between mother and calf can last up to 7 years, even though they are usually dependent up to a year old; in addition, females sometimes care for other calves (Shirihai & Jarrett, 2006).

2.3 Data collection

The dataset of the cetacean sighting used in this study was obtained from M.E.E.R e.V., which has been conducting data collection in that region since 1995. Data collection was done in cooperation with a local whale watching operator, in the beginning Club del Mar, and since 2006 OCEANO Whale Watching La Gomera, which holds the appropriate license to operate commercial whale watching trips (yellow flag "Barco Azul"). The studied period was between 1995 to 2020, until the day whale watching trips were not allowed anymore due to COVID restrictions. Most of the time the whale watching boats operated on a daily basis, once or twice per day, depending on weather conditions and sea states (mostly Beaufort sea state \leq 3), and departed from the harbor in Vueltas in the municipality of Valle Gran Rey. Boat trips averaged between 3-4 hours to a maximum of 8 hours (occasionally), usually reaching out up to 9.3 km (5 nm) from the shore.

During the period different boats were used as platforms for data collection, most of them being motor vessels up to 10 m long, including former wooden fishing boats and a former fiber diving school boat, carrying a maximum of 12 passengers at a time, including a guide and the skipper. They all had a maximum speed of 8 kn, which varied depending on sea conditions. When a sighting occurred, observation and approaching followed the Canary Islands' Code of Conduct in the whale watching zone. The Canary Islands government enacted a law (Law 7/1995) in 1996 to regulate the cetacean sightings, which was revised in 2002. The Canary Islands whale watching regulations states that a boat must, upon encounter with a cetacean or group of cetaceans, not interrupt the trajectory of the animals, not separate nor disperse the group, keep a distance of at least 60 m and avoid the presence of more than three vessels within 200 m away from the cetaceans, not chase nor harass the animals (Gobierno de Canarias, 2000), among

others. Regarding the approaching methods, a vessel must reduce speed when less than 300 m of distance, not be faster than the slowest animal of the group, approach gradually converging towards the direction of the animals and conduct observation parallel to the group trajectory, avoid abrupt change of speed or direction (Gobierno de Canarias, 2000). Once sighted, the group was approached slowly and carefully to avoid disturbances and lasted for a maximum of 30 min.

Data was collected systematically based on the species identification through observation from the boats in the study area. The observations occurred during daylight hours by one or two experienced observers on board which visually scanned the area. In case of a sighting, animals were identified at the lowest taxonomic level possible. Sightings were systematically recorded on prepared data entry sheets (See Appendix B). Posteriorly data was added into an access data base or later in an Excel spreadsheet database. Data collected for each sighting included date, time, duration of sighting, sea state, geographical position (using a board global positioning system – GPS, as part of boat equipment), estimation of group size and composition. A group or school was defined as all animals of one species visible at one time independent of their behavior, while a subgroup was defined as smaller aggregations of animals within the same group (Mann, 2000). In addition, group structure, group behavior, encounter category and behavior of individuals were recorded (definitions on section 2.4 Analysis variables).

2.4 Analysis variables

2.4.1 Bottlenose dolphin behavior

Group behavior, individual behavior and encounter category were recorded describing the group characteristics/behavior at the beginning of an encounter. When change(s) of behavior was (were) observed during the sighting, those were also occasionally recorded. Group behavior was defined as the behavioral state of the group (majority) and were classified in seven broader categories (Table 1).

Behavioral state	Definition
(group)	
Resting	Slow movements, low activity, animals mostly close to surface
Travelling	Continuous movement into +/- direction
Milling	Movement into subsequently changing directions
Forage/Feeding	High activity, animals chasing prey (e.g.: fish), fast and erratic movements, often
	with seabirds present
Diving	Most or all animals repeatedly leaving the surface for longer periods of time
	(minutes)
Social	High activity, animals "deal with each other", frequent direct physical contact
	(e.g.: chasing, rubbing, copulating, etc.)
Mixed	Different animals of the same group do different things

Table 1: Definitions of behavioral states used to report surface group behavior during bottlenose dolphins sightings in this study (definitions according to Shane, 1990; Weaver, 1987).

Most observations included a common behavior of a bottlenose dolphin group (group behavior); however, frequent behavioral events of individuals were also recorded. Some of the behaviors were related to the presence of a boat; in those cases, the requirements were that the animals initiated the behavior, that behavior involved action or reaction and that it was directed to the boat (Ritter, 2002). Despite 39 different types of behavior having been recorded during this study, the description is given only for the most commonly observed events (Table 2).

Table 2: Ethogram defining behavioral events used to report surface behavior of individuals during the bottlenose dolphins sightings in this study (definitions according to Connor, 1990; Herzing, 1995; Östman, 1987; Weaver, 1987).

Abbreviation	Behavior	Definition
	(Individual)	
BOR	Bow ride	Gliding/swimming on pressure wave in front of the boat
LEP	Leap	Re-entering water headfirst after having gained horizontal
		distance in air
TSL	Tail slap	Hitting the surface with ventral surface of the fluke
SPY	Spy hop	Head and eyes above water, body in vertical position
BRE	Breach	Lifting most of the body above surface. Noisy re-entry by hitting
		the surface with the lateral body surface
FIS	Fish hunt	Obvious fishing activity close to surface
APP	Approach	Moving towards the boat

BOW	Bow	Re-entering water headfirst within a body width of where leaving
		water
SOC	Socialize	Two or more animals having body contact e.g.: by rubbing each
		other
SUF	Surfing	Gliding/swimming in a wave or swell
DIV	Dive	Leaving the surface
BUS	Belly up swim	Swimming close to the surface in an inverted position
SCO	Scouting	Brief approach towards the boat up to a few meters and then
		moving away

The encounter category described the reaction of the majority of group members towards the boat. It was categorized according to the degree of boat-related behavior and was defined as: avoidance, no response, proximity, or interaction (Table 3).

Table 3: Definitions of boat-related group behavior used to report encounter category during bottlenose dolphins sightings in this study (definitions according to Würsig et al., 1998).

Category	Definition
Avoidance	Movement away from the boat or disappearing by diving
No response	No apparent response to the approach of the boat. Animal(s) keep(s) a certain
	distance without disappearing. Boat-related behaviors rare or missing
Proximity	Movement of animal(s) towards the boat. Short distance (< 10 m) between animals
	and boat. Boat-related behaviors possible, but not frequent
Interaction	Frequent movement of animal(s) towards the boat. Boat-related behaviors frequent
	(e.g.: during > 50 % of time)

2.4.2 Dependent variables, sighting, sighting effort, and correction factor

The dependent variables used for statistical analysis were group size (definition in Table 4) or groups with the presence of newborns, calves, or juveniles (definitions in Table 5). For the statistical analysis, missing values for group size in a sighting were substituted for the mean group size value of the respective month, and then rounded to closest integer number. Sighting and correction factor variables were used in the descriptive analysis, while sighting effort was used in both descriptive and in the statistical analysis as a random factor (definitions in Table 4).

The correction factor for each month or year was calculated by dividing the equal percentage of tours per month or year (total sighting effort = 100 % equally divided per months or years), by the percentage of tours recorded in that specific month or year. It was applied in the descriptive analysis to adjust the differences of sighting effort between different periods, making them comparable based on the assumption that a higher number of tours in a certain period result in higher numbers of cetacean sightings and abundance.

Variable	Definition	
Sighting	Each individual bottlenose dolphin group encountered, regardless of its group	
	size or whether it occurred in the same tour	
Sighting effort	Number of tours, considering that all tours were an average of 3.5 hours	
Correction factor	Adjustment applied to the recorded number of sightings and abundance of	
	bottlenose dolphins to account for the variation in sighting effort, allowing the	
	data to be standardized by obtaining comparable estimates in relation to	
	number of tours	
Group size	Total number of individuals in a sighting, which may include groups with	
	newborns, calves and/or juveniles present	

Table 4: Variables used for descriptive and statistical analysis in this study and their definitions.

Group composition refers to groups with the presence of newborns, calves and/ or juveniles and had their age classes defined according to their relative body size (Table 5). Despite the estimated group size having been recorded, the number of non-adults were not counted separately but simply recorded as present in the group when that event occurred (presence-absence data).

Age class	Definition
Adults	Large and robust animals approximately 2.5–3 m long
Juveniles	Animals with body length about 2/3 of adults, swimming independently.
Calves	Animals with body length less than 2/3 of adults, mostly swimming in close relationship to
	an adult (presumably its mother)
Newborns	Animals of very small size, always swimming close to an adult, fetal folds may be visible,
	floppy fin and fluke, animals surface in a clumsy way.

Table 5: Definitions of age classes used to report group composition during bottlenose dolphin sightings in this study (definitions according to Bearzi, 1994; Caldwell et al., 1990).

2.4.3 Oceanographic and topographic data

In order to identify the effects of potential drivers of bottlenose dolphins' change, time series of sea surface temperature (in degrees Celsius, °C; onwards "SST"), chlorophyll-a concentration at sea level (in µg/l; onwards "chl-a") and seawater salinity concentration (in permille, ‰; onwards "SAL") were analyzed. In addition, the effects of the following topographic variables, bathymetry (in meters, onwards "depth"), benthic slope (in degrees, °; onwards "slope") and distance to coast (in meters but retrieved in degrees, onwards "distance") on bottlenose dolphins change were also analyzed. These variables were chosen in this study because they have been reported or suggested to affect dolphins' abundance, group size and distribution (Haughey et al., 2021; Herzing, 1995; Ingram & Rogan, 2002; La Manna et al., 2023; MacLeod, 2009; Mintzer & Fazioli, 2021; Smith et al., 1986; Torreblanca et al., 2022; Tynan et al., 2005; Vermeulen, 2018). The variables were retrieved accordingly to the coordinates reported at the beginning of each sighting from the period between 2000-2020.

SST (°C) data was obtained from a reanalysis service provided via the University of Reading, which is based on the sea surface daily temperature product provided through the Copernicus Mission with resolution \pm 14 km² (C. Merchant & Embury, 2020; C. J. Merchant et al., 2019). Information on chl-a (µg/l) concentration was from the Global Ocean 3D Chlorophyll-a dataset from the European Union-Copernicus Marine Service (2020) with a resolution \pm 4 km². SAL (‰) was obtained from European Union-Copernicus Marine Service (2018).

Bathymetry data was obtained by GEBCO Grid at a resolution of 15 arc seconds (GEBCO Bathymetric Compilation Group 2022, 2022). Slopes were calculated from the GEBCO dataset in the open-source GIS software QGIS (QGIS Development Team, 2020). Distance was calculated in GIS.

2.5 Statistical analysis

Group size was not normally distributed; thus, I used a Kruskal-Wallis test to determine if there are significant differences in group sizes between months and years. Comparisons between month-to-month and year-to-year effects were performed using Dunn's test on rank sums with a Bonferroni correction. Kruskal-Wallis test was also used to analyze significant differences in group size according to group behavior, followed by post-hoc pairwise comparisons using

Dunn's test with Bonferroni correction. For the analysis of environmental and topographic predictors, a series of steps were involved to select the most significant predictors influencing bottlenose dolphins' size: (1) randomly subsampling the data to remove temporal autocorrelation from the data, (2) collinearity testing between environmental variables to exclude correlated predictors from the same model, (3) model building and (4) model selection for fixed effects.

Data (n = 3866) was checked for autocorrelation using ACF plots and Durbin-Watson statistics. Since the data was found to be autocorrelated (Durbin-Watson = 0.19584, p < 2.2e-16), I subsampled the data to 500 observations (Swihart & Slade, 1985), which removed autocorrelation from the data (Durbin-Watson = 1.863, p = 0.06245). To subsample the data, only observations between 2000-2020 (21 years) were considered, since environmental and topographic variables were not available outside that period. Values for continuous variables were scaled (z-transformation) for the analysis and back transformed to produce intuitive plots of predictions. In addition, values of distance to coast were converted from degrees to meters (1 degree = 111,139 m). Distances above 20,000 m from the coast were excluded. Since environmental and topographic variables were retrieved based on the coordinates from the sightings, the observations with missing or false coordinates were excluded, as well as the observations from the months with missing tours. As a result, the subsample was taken from n= 2450 observations and all plots for Linear Mixed Models (LMM) and Generalized Linear Mixed Models (GLMM) were done from this dataset (n = 2450).

In order to build the models, I tested for collinearity between the environmental variables (Zuur et al., 2010) using non-parametric tests (Spearman), to remove variables that were strongly correlated from the same model using "corrplot" package (Wei & Simko, 2021). Chl-a and SST were excluded from being in the same model since these variables have high intercorrelation ($\rho = -0.64$, See Appendix C).

Linear Mixed Models (LMM) from package lme4 (Bates et al., 2015) were used to model predictor variables that influenced bottlenose dolphin group size (response variable). Modelling started with a full LMM including all predictor variables that could have influenced bottlenose dolphin group size as fixed effects (except for SAL, slope and groups with newborns, which were removed from the full model to simplify the model selection, since those variables had no significant effect on the response variable). To investigate the effect of groups with calves and

juveniles on the total group size of bottlenose dolphins, another LMM was used. Total tours and "months of years" (months nested in years) were included in the models as random effects to have the data corrected by sighting effort per month and to account for temporal variation on the fixed effects.

To investigate the effects of different predictors on groups with calves and juveniles, different approaches were taken. To explore the monthly variation on bottlenose dolphin groups with calves and groups with juveniles I used a univariate logistic regression model (GLM output). To analyze the best environmental and topographic predictors on these groups, Generalized Linear Mixed Models (GLMM) were performed, with sighting effort and "months of years" as random factors to have the data corrected by sighting effort per month and to account for temporal variation on the fixed effects.

The selection of the optimal LMM and GLMM was done by sorting out fixed effects using likelihood test Akaike Information Criteria (AIC) from "MuMIn" package (Bartón, 2023) in a model selection framework. I determined the best model with the lowest AICc as a criterion. Visualization of plots were used to check model assumptions by inspection of residuals against fitted values and regression fits. Validation was also carried out by checking overdispersion in the LMM models.

All statistical analyses were performed using the free software RStudio Version 2023.03.1+446 (Posit Software, 2023).

3. Results

3.1 Total tours (sighting effort) and sightings

Overall, 11,362 boat tours (sighting effort) were conducted over 252 months between September 1995 to March 2020, with an average duration of 3.5 hours per tour. During this period, 3,998 groups of bottlenose dolphin (sightings) were recorded (Figure 3). All numbers of sightings refer only to bottlenose dolphin groups and not to other species. Most of the sightings were recorded at a distance of up to 8,000 m from the coast (92.38 %; mean \pm SD 4385.45 \pm 2711.28 m, range: 3 – 19,985 m, n = 3111), at a bathymetry between 22 to 400 m (44.89 %; mean \pm SD 696.32 \pm 646.44 m, range: 22 – 4105 m, n = 2862) and where slope is



between 0 and 10° (50.3 %; mean \pm SD 13.46 \pm 10.69°, range: 0.12 – 54.5°, n= 3199, see Appendix D).

Figure 3: Map of bottlenose dolphin sightings during the study period in the coastal waters southwest off La Gomera, Canary Islands (M.E.E.R e.V. 2023).

Monthly comparison showed that most tours took place in spring (March 9.88 % and April 11.45 %) and summer (August 10.60 %; mean \pm SD: 946,83 \pm 198,3 tours, range: 703 - 1301 tours, N_{TOTAL} = 12), which mainly reflect the high peak of touristic activities. Likewise, most sightings of bottlenose dolphin groups occurred in similar months, April (11.11 %), July (11.16 %) and August (13.48 %; mean \pm SD: 333.2 \pm 108.3 sightings, range: 183 - 539 sightings, N = 12). Applying the correction factor to correct for different sighting effort, also favored the summer months of July and August for most sightings (Figure 4).



Figure 4: Total number of tours per month (sighting effort, blue line); total number of sightings per month (bottlenose dolphin group sightings, orange line); calculated corrected number of sightings per month (corrected for sighting effort, grey line) between 1995-2020 in the coastal waters southwest off La Gomera, Canary Islands.

The interannual pattern of tours and sightings of bottlenose dolphin groups shows that most tours occurred in 2003 (8.7 %), 2005 (8.6 %) and 2006 (8.7 %; range: 87 - 992 tours, mean \pm SD: 473.41 \pm 254.77 tours, n= 24). Nevertheless, the years with most sightings did not follow the same pattern, with peaks occurring in 2015 (8 %) and 2016 (8.13 %; range: 11 - 325 sightings, mean \pm SD: 153.8 \pm 72.3 sightings, N_{TOTAL} = 26). Applying the correction factor to correct for different sighting effort not only favored the years 2015 and 2016, but also 1998 for most sightings (Figure 5).



Figure 5: Total number of tours per year (sighting effort, blue line); total number of sightings per year (bottlenose dolphin group sightings, orange line); calculated corrected number of sightings per year (corrected for sighting effort, grey line) between 1995-2020 in the coastal waters southwest off La Gomera, Canary Islands. 1995*, 2004* and 2020* tour data are incomplete, for 2007 and 2008 tour data is not available.

During the study period SST ranged from 18.09 °C to 25.96 °C, chl-a from 0.009 μ g/l to 0.40 μ g/l and SAL from 36.36 ‰ to 37.20 ‰ (Figure 6). Correlation analysis showed that SST and chl-a were strongly negatively correlated (ρ = - 0.64), SST and SAL were weakly correlated (ρ = 0.23), while there was a lack of correlation between chl-a and SAL (ρ = 0.04, see Appendix C).



Figure 6: Time series for sea surface temperature, chlorophyll-a and salinity in the southwest coastal waters off La Gomera from 2000-2020.

3.2 Bottlenose dolphin behavior

The most observed group behaviors of bottlenose dolphins at the beginning of a sighting were travelling (33 %) and foraging/feeding (24 %, n = 1714; Figure 7). Most of the time, the groups did not change their behavior after boat approach. However, some groups started engaging in other activities (n = 395), for instance, groups that were initially travelling subsequently started foraging and/or feeding (7 %), engaging in social behavior (6 %) or diving (5 %). The groups that were initially foraging and/or feeding, 5 % changed to social behavior while 2 % dove. Out of the group with initial social behavior, 18 % started foraging and/or feeding and 15 % started travelling.



Figure 7: Behavioral state of bottlenose dolphin groups observed at the beginning of a sighting during this study in the coastal waters southwest off La Gomera, Canary Islands (n = 1714).

Within a bottlenose group sighting, the frequent behavior of certain individuals was also recorded (n = 1166). In total, 39 distinct behaviors of bottlenose dolphins were recorded following the ethogram used in this study (see ethogram on table 3 for abbreviations and
definitions). Individuals in the same group could present different behaviors, therefore some sightings had more than one behavior recorded. For this report, I am only presenting the thirteen most commonly observed behaviors, representing 96 % of total behaviors. The most observed aerial behaviors were leaping [LEP] (28 %) and breaching [BRE] (4 %), while the most common boat-related behaviors were bow riding [BOR] (41 %) and spy hopping [SPY] (6 %). Tail slapping was the most common type of slap observed during our study [TSL] (10 %) (Figure 8).



Figure 8: Most frequent behavior of bottlenose dolphin individuals in a group sighting during this study in the coastal waters southwest off La Gomera, Canary Islands (n = 1166). See table 5 for ethogram.

The most observed boat-related reactions of the group upon encounter were "proximity" (44 %) or "no response" (39 %, n = 2748; Figure 9). In most of the occasions, there was no observed change in group reaction; nevertheless, some positive change of reaction was observed (n = 196), such as 10 % of groups that initially showed proximity towards the boat, subsequently changed to interaction with the boat. In addition, 4 % of groups with initially no response to the boat, changed reaction to proximity towards the boat.



Figure 9: Boat-related group behavior of bottlenose dolphin groups observed upon encounter with the boat during this study in the coastal waters southwest off La Gomera, Canary Islands (n = 2748).

3.3 Bottlenose dolphin abundance and group size

In total, 69,233 bottlenose dolphins, including resighting, were recorded in 3,651 sightings of bottlenose dolphin groups (group size was missing in 347 sightings) during the study period, throughout the study area. The monthly abundance of bottlenose dolphins peaked in July (14.7%), August (17.9%) and September (11.4%) for both observed and corrected numbers (Figure 10a), which coincided with the higher number of boat tours and sightings during the summer months, but not during the spring season. The lowest abundances were observed during the winter months (December to March). Throughout the studied years, there was a moderate increase in abundance until peaks (both observed and corrected) in 2015 and 2016 (Figure 10b), which also had the greatest number of sightings recorded. After that, abundance started to decrease. However, the abundance was also relatively lower in 2010.

The monthly average group size was also bigger from July to September, similarly to abundance, and with two other peaks in February and November (Figures 10a). The smallest

average group size was in March. Yearly comparisons show a moderate decreasing trend in average group size from 2003, except for peaks in 2006, 2009 and 2016 (Figures 10b), from which only 2016 also had a peak in abundance. On the other hand, average group sizes were particularly smaller in 1998, 2010 and 2019.



Figure 10: A): Group size (mean, orange line), observed abundance (blue bars) and corrected abundance (grey bars) of bottlenose dolphins per month between 1995-2020 in the coastal waters southwest off La Gomera, Canary Islands. B): Group size (mean, orange line), recorded abundance (blue bars) and corrected abundance (grey bars) of bottlenose dolphins per year between 1995-2020 in coastal waters southwest off La Gomera, Canary Islands. 1995*, 2004* and 2020* tour data are incomplete, for 2007 and 2008 tour data is not available.

Group size ranged from 1 to 510 dolphins (mean \pm SD: 18.96 \pm 21.40 individuals per group, median = 13, n = 3651), with 96 % comprising of groups up to 50 individuals. The most common group size was 1-10 dolphins (n = 1651). One large sighting of 510 animals was reported, while some sightings of large groups > 50 individuals (n= 160) were recorded (Figure 11).



Figure 11: Frequency of bottlenose dolphin group sizes between 1995-2020 in the coastal waters southwest off La Gomera, Canary Islands (n = 3651).

3.3.1 Inter-annual and monthly variation in group size

There were significant differences in the monthly pattern of bottlenose dolphin group sizes (Kruskal-Wallis, chi-squared = 216.68, p < 2.2e-16, df = 11 with Dunn's multiple comparison; Figure 12a) with larger groups during the summer months (July to September). There was also a significant difference in group sizes across the years (Kruskal-Wallis, chi-squared = 290.92, p < 2.2e-16, df = 25 with Dunn's multiple comparison; Figure 12b, see Appendix E for posthoc test).



Figure 12:A) Boxplot of bottlenose dolphin groups size across months during the study period in the coastal waters southwest off La Gomera, Canary Islands. B) Boxplot of bottlenose dolphin groups size across years during the study period in the coastal waters southwest off La Gomera, Canary Islands (N = 3998). Box = inter-quartile range; lower and upper bound of the box = first (25 %) and third (75 %) quartiles; middle quartile = median; dots = outliers.

3.3.2 Environmental and topographic predictors influencing group size

Larger bottlenose dolphin groups were positively associated with SST, depth, presence of calves and presence of juveniles (Table 6). On the other hand, distance, slope and SAL were not significant predictors of bottlenose dolphins' group size. Larger groups preferred temperatures above 22 °C (Appendix F) and waters where depth was below 1,500 m (Figure 13). The model's total explanatory power is moderate 16 % (conditional $R^2 = 0.16$), while the part related to the fixed effects alone is 3 % (marginal $R^2 = 0.03$). Groups with the presence of calves and/ or juveniles were observed in larger groups (Table 6; Figure 14). The model's explanatory power related to the fixed effects alone is 21 % (marginal $R^2 = 0.21$).

Table 6: Analysis of bottlenose dolphins group size from 2000-2020 in the coastal waters southwest off La Gomera, Canary Islands, based on Linear Mixed Models (LMM) performed on a subsample of 500 observations. Random effects were tours (sighting effort) and months of each year. Fixed effects were sea surface temperature, water depth, presence of calves and presence of juveniles. $\tau_{00} =$ variance of random effects. $\sigma^2 =$ residual of random effects. ICC = Intraclass Correlation Coefficient.

		GROUP SIZE						
Predictors	Estimates	CI	р	Estimates	CI	p		
(Intercept)	0.00	- 0.13 - 0.14	0.942	-0.48	-0.660.30	<0.001		
Sea surface temperature	0.14	0.04 - 0.23	0.006					
Bathymetry	0.15	0.04 - 0.26	0.009					
Calves				0.46	0.27 - 0.65	<0.001		
Juveniles				0.60	0.41 - 0.78	<0.001		
Random Effects								
σ^2	0.84			0.71				
$ au_{00}$	0.05 month:year 0.05 tours			0.00 month:year				
				0.09 TOURS				
	0.02_{YEAF}	0.02 _{YEAR}			0.05 year			
ICC	0.13							
Ν	157 _{mont}	157 _{month} : year			157 _{MONTH: YEAR}			
	65 _{TOURS}			65 _{tours}				
	18 year			18 year				
Observations	500			500				
Marginal R ² / Conditional R ²	0.032 / 0	.155		0.207 / NA	1			



Figure 13: A) Effect of sea surface temperature on bottlenose dolphins group size during the study period in the coastal waters southwest off La Gomera, Canary Islands. B) Effect of bathymetry on bottlenose dolphins group size during the study period in the coastal waters southwest off La Gomera, Canary Islands. Black dots represent each bottlenose dolphin group. Blue linear regression line of best fit with confidence interval. Showing groups < 250 individuals per group (n=2450).



Figure 14:A) Boxplot of bottlenose dolphin mean group size (blue dot) with the presence/absence of calves during the study period in the coastal waters southwest off La Gomera, Canary Islands. B) Boxplot of bottlenose dolphin mean group size (blue dot) with the presence/absence of juveniles during the study period in the coastal waters southwest off La Gomera, Canary Islands (n = 2450). 0 = absence of calves/ juveniles and 1 = presence of calves/ juveniles. Box = inter-quartile range; lower and upper bound of the box = first (25 %) and third (75 %) quartiles; middle quartile = median; dots = outliers.

3.3.3 Group size variance according to group behavior

Bottlenose dolphin group sizes differed significantly with group behavior (Kruskal-Wallis, chisquared = 99.626, p-value < 2.2e-16, df = 6, with Dunn's multiple comparison; Figure 15, see Appendix G for post-hoc test). Groups with mixed behavior had the largest group size mean, with an average of over 25 individuals per group. However, their behaviors were not specified. Groups foraging/feeding, resting and in social behavior were also large, averaging over 20 individuals per group. On the other hand, groups diving, milling and travelling tended to be smaller.



Figure 15: Boxplot of bottlenose dolphin mean groups size (blue dot) according to the group behavior during the study period in the coastal waters southwest off La Gomera, Canary Islands (n = 1714). Box = inter-quartile range; lower and upper bound of the box = first (25 %) and third (75 %) quartiles; middle quartile = median; dots = outliers.

3.4 Bottlenose dolphin group composition

From the total number of sightings of bottlenose dolphin groups ($N_{TOTAL} = 3998$), newborns were present in 2.8 %, calves in 27.2 % and juveniles in 53.8 % of the groups. Monthly comparison showed that groups with newborns, calves and juveniles were seen year-round, but mostly observed from July to September, with a peak in August. Inter-annual comparison showed that newborns observations had a moderate increase until peaking in 2016 (30.4 %), decreasing since then. Observations of groups with calves and juveniles peaked in 2015 (14.2 % and 11.3 % respectively), and also similarly in 2016 (13.5 % and 10.2 % respectively; Figure 16).



Figure 16: A): Monthly distribution of bottlenose dolphin groups with the presence of newborns, calves, and juveniles between 1995-2020 in the coastal waters southwest off La Gomera, Canary Islands. B) Yearly distribution of bottlenose dolphin groups with the presence of newborns, calves, and juveniles between 1995-2020 in the coastal waters southwest off La Gomera, Canary Islands.

Groups with presence of calves and juveniles were best predicted as a positive function of SST (Table 7, Figure 17). Depth, distance, slope and SAL were not significant to either of the groups. None of the variables were significant to predict groups with newborns present.

Table 7: Analysis of bottlenose dolphin groups with presence of calves and juveniles between 2000-2020 in the coastal waters southwest off La Gomera, Canary Islands, based on Generalized Linear Mixed Models (GLMM) performed on a subsample of 500 observations. Random effects were tours (sighting effort) and months of each year. Fixed effects were sea surface temperature. $\tau_{00} =$ variance of random effects. $\sigma^2 =$ residual of random effects. ICC = Intraclass Correlation Coefficient.

	Calves			Juveniles			
Predictors	Odds Ratios	CI	р	Odds Ratios	CI	р	
(Intercept)	0.32	0.18 - 0.54	<0.001	1.46	0.91 - 2.34	0.114	
Sea surface temperature	1.53	1.20 – 1.94	0.001	1.30	1.05 - 1.62	0.018	
Random Effects							
σ^2	3.29			3.29			
$ au_{00}$	0.29 MONTH:YEAR			0.24 month:year			
	0.00 tours			0.00 _{TOURS}			
	$0.92 _{\rm YEAR}$			0.77 _{YEAR}			
Ν	157 month: year			157 month: year			
	65 _{tours}			65 _{TOURS}			
	18 year			18 _{YEAR}			
Observations	500			500			
Marginal R ² / Conditional R ²	0.054 / NA			0.022 / NA			



Figure 17: A) Effect of sea surface temperature on bottlenose dolphin groups with presence of calves during the study period in the coastal waters southwest off La Gomera, Canary Islands. B) Effect of sea surface temperature on bottlenose dolphin groups with presence of juveniles during the study period in the coastal waters southwest off La Gomera, Canary Islands (n = 2450). 0 = absence of calves/juveniles and <math>1 = presence of calves/juveniles.

The results from the univariate logistic regression model indicated that spring months were significant negative predictors (OR < 1) for groups with newborns and juveniles, May for newborns and March and April for juveniles. On the other hand, summer and autumn months (July to September and November) were positive predictors (OR > 1) of groups with calves (Table 8, Figure 18).

Table 8: Analysis of presence of calves and juveniles in bottlenose dolphins groups between 2000-2020 in the coastal waters southwest off La Gomera, Canary Islands based on univariate logistic regression (n = 3998). The coefficients are converted (exponentiated). Pseudo R-squared statistics are shown in the bottom. Numbers in bold indicate significant values.

	Newborns			Calves			Juveniles		
Predictors	Odds Ratios	CI	р	Odds Ratios	CI	р	Odds Ratios	CI	р
(Intercept)	0.03	0.01 - 0.06	<0.001	0.28	0.20 - 0.39	<0.001	1.27	0.97 – 1.66	0.079
February	0.17	0.01 - 1.01	0.102	0.81	0.50 - 1.30	0.390	0.75	0.51 - 1.10	0.139
March	0.21	0.03 - 0.93	0.059	0.66	0.43 - 1.03	0.064	0.45	0.32 - 0.64	<0.001
April	0.57	0.19 – 1.78	0.312	0.75	0.51 - 1.13	0.171	0.45	0.32 - 0.63	<0.001
May	0.11	0.01 - 0.63	0.038	0.95	0.63 - 1.45	0.818	0.97	0.69 – 1.37	0.864
June	0.70	0.20 - 2.37	0.567	1.31	0.86 - 2.00	0.215	1.17	0.81 – 1.69	0.403
July	1.31	0.53 - 3.71	0.573	1.87	1.29 – 2.74	0.001	1.28	0.92 – 1.77	0.144
August	2.38	1.06 - 6.37	0.054	2.11	1.47 - 3.06	<0.001	1.36	0.98 - 1.86	0.062
September	1.98	0.82 - 5.51	0.152	2.02	1.38 – 2.99	<0.001	1.36	0.97 – 1.92	0.077
October	0.57	0.18 - 1.83	0.331	1.35	0.92 - 2.01	0.131	0.83	0.59 – 1.16	0.273
November	0.99	0.34 - 3.04	0.983	1.61	1.08 - 2.43	0.020	1.05	0.74 - 1.49	0.790
December	1.41	0.46 - 4.44	0.547	1.30	0.82 - 2.05	0.268	0.85	0.57 – 1.26	0.418
Observations	3998			3998			3998		
R ² Tjur	0.014	0.029			0.037				





Figure 18: Probability of presence of A) newborns, B) calves and C) juveniles bottlenose dolphins during each month between 1995-2020 in the coastal waters southwest off La Gomera, Canary Islands. 0 = absence and 1 = presence. Purple bars: confidence intervals. Arrows show comparison among the means.

4. Discussion

The results show monthly and inter-annual variations in abundance, group size and composition indicating shifts in distribution and grouping patterns, with higher occurrence, larger groups and presence of newborns, calves and juveniles during summer months (July- September). Throughout the years, a moderate decreasing trend in group size was observed, while a gradual increase in abundance as well as groups with presence of newborns, calves, juveniles could be noted until 2016, from which the trend started to decrease. In addition, significant differences in group size were found according to the group behavior. The results of the best models revealed that bottlenose group size was positively influenced by multiple factors: sea surface temperature (SST), bathymetry (larger groups preferred warmer and shallower waters) and presence of calves and juveniles. Group composition was also primarily influenced by SST

(groups with calves and juveniles tend to prefer SST > 22° C). Nevertheless, salinity, distance to coast and slope were not significant factors to predict bottlenose dolphin group size or composition. This study reveals the importance of addressing different variables that might influence their grouping pattern. These results will be further discussed in the next sections.

4.1 Inter-annual variation

Most of the bottlenose dolphin groups in La Gomera consisted of 1-10 dolphins (mean = 18.91, median = 13). Similar group sizes were reported off the coast of San Diego (mean = 19.8, Defran & Weller, 1999), Azores (mean = 21.3, Silva et al., 2008) and Madeira Archipelago (median = 12, Dinis et al., 2016), while smaller groups were observed in Sarasota Bay (mean = 7, Wells et al., 1987) and Carragas Archipelago (mean = 13.7, Lodi, 2012). In the waters off La Gomera, large groups equal to or exceeding 50 or even up to 500 individuals were observed sporadically (8 % of the sightings). Such large groups consisting of up to 600 *T. aduncus* were frequently sighted in Eastern Cape (mean = 52, Bouveroux et al., 2018). Variation in group size is common to this type of fission-fusion society and the reasons can be various, including response to unstable and patchy food resources (Defran & Weller, 1999; Gowans et al., 2007; Tobeña et al., 2014), predation pressure (Bouveroux et al., 2018) or reproductive cycles. The influence of predictors can also vary significantly depending on season and year, indicating that habitat preferences can be spatially and temporally complex (Haughey et al., 2021).

In this study there were random fluctuations in group size throughout the years, showing no visible pattern. On the other hand, total abundance and groups with non-adults present had a moderate increase until reaching a peak in 2016, then a decrease ever since. The abundance of bottlenose dolphins in La Gomera was also considerably lower in 2010 than in other years in this study. Similarly, the average group size was relatively small in 2010. While there were no observed anomalies in SST nor salinity in that particular year, chlorophyll-a (chl-a) concentration in 2010 was the lowest recorded during winter, compared to the same season in other years in the time series in this study. Variations in the chl-a levels could be related to the presence/ absence of cyclonic or anti-cyclonic eddies affecting the transport of nutrients from bottom to the surface. Increase in abundance but decrease in group size in La Gomera suggests a possible strategy to avoid intra-group competition. Conversely, a decrease in abundance but increase in the mean group size suggests that most dolphins leave the area to follow their prey, whereas larger groups gather to forage cooperatively. The decline in population and group size

during some years could be attributed to a depletion of resources, interspecies competition, low reproduction rates, attacks from predators, environmental change, as well as anthropogenic impacts such as increase in tourism and degradation of habitat quality (Azzellino et al., 2016; Bearzi et al., 2003; Lodi, 2012; Vargas-Fonseca et al., 2020). Therefore in 2010, when both abundance and mean group size were reduced, it is possible that bottlenose dolphins left the area to find more productive and less competitive foraging sites, as interspecific competition can be problematic when resources are low (Azzellino et al., 2016). Inter-annual changes may also be caused by fluctuations in mortality and recruitment (Griffin & Griffin, 2004).

The fluctuation in group size in La Gomera is also likely to be affected by the resident dolphins, which have been estimated to be in a stable population of around 50 animals (Boletín Oficial del Estado, 2011), similar to that reported in the Azores (44, Silva et al., 2008). Travelers may also show site fidelity to an island, as in the case of western Canary islands, including La Gomera, where at least 10 % of individuals are reported to travel between islands, possibly due to the oligotrophic waters influencing prey distribution (Tobeña et al., 2014), and consequently affecting bottlenose dolphin group size and distribution. Bottlenose dolphins' high mobility within the archipelago also suggests that their home ranges may include more than one island (Tobeña et al., 2014). In addition, the visit of transient pelagic dolphins might contribute to an increase in group size in the waters off La Gomera in some years and especially during the summer. Low site fidelity but new dolphins visiting an area spanning years might be due to different habitat structures and prey distribution than areas where the animals have site fidelity (Defran & Weller, 1999). In the waters off San Diego for instance, bottlenose dolphins are observed throughout the year but they are not year-round nor seasonal residents, i.e., they are mainly transient (Defran & Weller, 1999). On the other hand, in southern Brazil, most bottlenose dolphins were reported to be residents (Simões-Lopes & Fabian, 1999). Segregations of bottlenose dolphins into communities that share habitat and resources might explain the different patterns of occurrence (Dinis et al., 2016), the recurrent appearance of top predators in an area may also indicate high biological productivity, i.e., high prey availability (Alves et al., 2019). The waters in the Canary Islands have been considered a hot spot for cephalopod species diversity (Escánez et al., 2021), possibly contributing to the presence of resident large marine mammals.

In sum, bottlenose dolphin group sizes observed in La Gomera are consistent with typical patterns seen in this species. Inter-annual variations in abundance and group size in the study

area indicates that bottlenose dolphins are primarily driven by prey diversity and distribution, impacting their foraging strategies, and influencing the distribution of resident, semi-resident, and transient dolphins. Environmental changes and habitat degradation may further contribute to yearly variance. As these factors vary across years and seasons, they contribute to the behavior and spatial complexity of bottlenose dolphin distribution.

4.2 Monthly variation and environmental factors

Larger groups of bottlenose dolphins with the presence of newborns, calves and juveniles were mostly observed off La Gomera during the summer months, similarly, their total abundance peaked between July and September. These results are consistent with previous reports showing that larger groups and groups with newborns are mostly found during summer (and early autumn) months (Dinis et al., 2016; Methion et al., 2023). Seasonal variations in abundance, group pattern, distribution and habitat use are most likely due to varying environmental conditions, to the forementioned prey availability and interspecies competition, and also due to reproduction and nursing season (Azzellino et al., 2016; Griffin & Griffin, 2004; Haughey et al., 2021; Liu et al., 2021a). While there was no noticeable long-term trend in the environmental variables during the study period, there was an evident seasonal pattern. In waters off La Gomera, SST is likely the main reason affecting seasonal grouping pattern directly or indirectly, as it had a significantly positive effect on group size and on groups with presence of calves and juveniles. In the study area, larger groups preferred temperatures above 22 °C, consistent to other studies (Haughey et al., 2021; Mintzer & Fazioli, 2021). Groups with presence of calves and juveniles also tended to prefer warmer waters, suggesting a preferable season for birthing and calving (Dinis et al., 2016; Sprogis et al., 2016). In Sarasota Bay and Shark Bay groups with calves were also seasonal, and despite being born throughout the year, a peak in birth occurred from late spring to early autumn and were related to water temperature (Mann et al., 2000; Wells et al., 1987). Wells et al. (1987) suggested that thermoregulation or related energetic limitations may be fundamental drivers in determining seasonality of births, as mothers may spend much less energy in summer to maintain body temperature of her own and her newborn. Birthing and calving season is likely one of the main reasons for the increase in abundance and group size during the summer months in La Gomera. In addition, male home ranges during the breeding season are also influenced by reproductive females (Sprogis et al. 2016), possibly contributing to larger clusters during summer in the waters off La Gomera, as larger mixed-sex clusters offer higher reproduction opportunities. Reproductive females in turn may depend on food availability and safety from predators (Diaz-Aguirre et al., 2018), while their reproduction success was suggested to be influenced by environmental variables (Rossman et al. 2015).

The strong negative correlation between SST and chl-a implies that chl-a is negatively associated with an increase in bottlenose dolphin group sizes. The Canary waters are usually regarded as nutrient poor, but the eddies created by perturbances in current flow and wind on the lee sides of the islands transport nutrient water from the deep to the surface, even though dispersion is usually more common than retention (Mason et al., 2006). In the waters off La Gomera primary production and chl-a concentration are relatively low throughout the year but relatively high chl-a values on the surface were observed from January to March (nutrient bloom), coinciding with the erosion of the thermocline (Arístegui et al., 1997). In addition, the Canary Current is stronger in winter in the west of the Canaries (Arístegui et al., 1997), facilitating the transport of nutrients from the east. These nutrient-rich waters with higher amounts of plankton may attract planktivorous consumer, which themselves are consumed by larger fish, thus supporting top predators, such as cetaceans (M.E.E.R. e.V., 2008). This process of changes in the primary production to reach dolphin prey through the various trophic levels may take some time (Methion et al., 2023). A study by Methion et al. (2023) reported larger groups of bottlenose dolphins 60 days after the peak in medium concentration of chl-a in the surface water. In waters off La Gomera, despite the low abundance of bottlenose dolphins on this time of the year (winter and early spring) and their average group size being only slightly larger in February compared to other months in winter and spring, several other cetacean species have been observed to forage more often near the surface during spring time. (Ritter, 2001). This season coincides with the main season for tuna fisheries in the area, indicating high prey availability (Ritter, 2001); and with the period of maximum extension of the mixed surface layer, increasing primary production in this region (Arístegui et al., 1997). The lower density of bottlenose dolphins in La Gomera during spring might be explained by their dispersion to find other foraging sites and avoid competition. Summer on the other hand, is the period of strongest water stratification in the study area and lowest values of chl-a (Arístegui et al., 1997). The increase in abundance and in larger bottlenose dolphin groups during this period could be influenced by an increase in abundance of their prey species (i.e., krill, fish, cephalopods and crustaceans) and/ or attempt of maximizing foraging efficiency. Despite chl-a being related to abundance and distribution of fish, the larger densities of bottlenose dolphins observed during

summer, when chl-a levels are typically low, indicate that chl-a is not the main factor in predicting group size and composition in La Gomera.

Oscillation in salinity is usually influenced by drought, precipitation or the alteration of water masses (Griffin & Griffin, 2004). Nevertheless, in this study, salinity was a not a significant factor in determining group size or group composition. In estuarine areas, which are important feeding grounds for many coastal populations of bottlenose dolphins, salinity was reported to affect dolphin density, i.e., higher occurrences at higher salinity concentration, probably due to higher prey availability (Mintzer & Fazioli, 2021).

Briefly, the hypothesis of higher bottlenose dolphin occurrence in the waters off La Gomera during spring was rejected, as their abundance and presence in larger groups with calves and juveniles were higher during the summer months. This can be attributed to the dolphins' preference for warmer waters during the birthing and calving season, providing more breeding opportunities, potentially attracting their prey and attempt to enhance foraging efficiency. In contrast, smaller group sizes and lower abundance of bottlenose dolphins were observed in winter months when the chl-a levels are high, indicating a potential migration to warmer waters and other foraging areas to avoid inter-specific competition. Salinity did not affect group size and composition, rejecting the hypothesis that all studied environmental variables would significantly influence on group size and composition.

4.3 Topographic variables

In La Gomera larger groups preferred waters where bathymetry was up to 1,500 m; however, most sightings occurred where waters are less than 400 m deep. The hypothesis that larger groups would be found in deeper waters could only be partially met, since 1,500 m is relatively deep, but group size was positively associated with bathymetry. In other words, larger groups tend to be found in shallower waters. Reports of a higher occurrence of this species where the sea floor is between 300-1500 m deep was possibly because cephalopod prey are usually found in outer-slope habitats (Azzellino et al., 2016). The high cephalopod diversity reported in the Canary Islands waters could explain the presence of larger groups occurring also offshore (Escánez et al., 2021). Larger groups of short-beaked common dolphin (*Delphinus delphis*) were also reported around the shelf edge, even when not feeding (Cañadas & Hammond, 2008). On the other hand, bottlenose dolphins were recorded in much shallower waters: 10-30 m in

San Diego (Defran & Weller, 1999), 7-13 m in Western Australia (Haughey et al., 2021), 9-20m in Eastern Cape (Bouveroux et al., 2018). Shallow waters can also be advantageous for foraging both demersal fish and schooling pelagic fish (Dinis et al., 2016; Silva, 2007), while providing favorable habitats for nursing and calving (Cañadas & Hammond, 2008; Lodi, 2012; Mann, 2000). In this study bathymetry was not a significant predictor of groups with presence of calves and juveniles. Therefore, the significant effect of bathymetry on group sizes in La Gomera suggests a relation to foraging strategies on the vertical distribution of prey (Dinis et al., 2016).

Bottlenose dolphins as well as other species in the region, tend to concentrate near the coast and prefer the lee side of the island(s) where SST and chl-a concentrations tend to be higher (Herrera et al., 2021). However, distance to coast was not a significant factor influencing group size or composition in this study; therefore, rejecting the hypothesis that larger groups would be found further away from the coast. The occurrence of large groups are usually reported farther from the coast or part of transient pelagic populations of dolphins (Dinis et al., 2016). In La Gomera most of the sightings were on a distance up to 8,000 m from the shore, which means that they occur both near and far away from the coast, in waters outside the current SAC Franja Marina Santiago-Valle Gran Rey (FMSGR). In Haughey et al.' (2021) study, a distance within 7,000 m to boat ramp was also identified an area of high occurrence of Indo-Pacific bottlenose dolphins and one of the most influential variables on their distribution. The occurrence of bottlenose dolphins farther from the shore might be related to prey availability and lack of predators (Bouveroux et al., 2018), and the occurrence of larger groups in offshore waters is possibly related to foraging strategies changing from solitary prey in shallow waters to schooling fish in open waters. On the other hand, higher occurrence of bottlenose dolphins closer to the coast (within 2,000 m of distance) were also observed in other studies (Defran & Weller, 1999; Haughey et al., 2021). In the Canary Islands, studies indicate that they mainly feed in coastal waters, though offshore feeding may also occur (Fernández et al., 2009).

One of peculiarities of the study area is the steep slopes due to the presence a narrow continental shelf. Steep slopes can be provide larger concentrations of prey and be advantageous for dolphins' foraging techniques (Ingram & Rogan, 2002). Most bottlenose dolphin groups in this study were found where the gradient is not steep, however benthic slope was not a significant predictor of group size. Oceanic islands are also known to have high species richness, as the narrow shelves and steep slopes allow coastal, benthic and oceanic species to overlap (Escánez

et al., 2021), suggesting that besides the rich diversity of cephalopods in the Canary Islands, a high prey diversity exists for the cetaceans in this area. A study from Azzellino et al. (2016) suggest that the intermittent use of an area could be due to temporary sources of food induced by zooplankton accumulation in the slope region, making the animals move in and out, which in turn, could be beneficial by reducing the overlap of habitats and consequently, also reducing interspecific competition.

In short, this study shows that the distribution range of bottlenose dolphin includes waters also beyond the current SAC Franja Marina Santiago-Valle Gran Rey. The hypothesis that larger groups would be found where bathymetry is higher was partially met, as larger groups were found in deep waters, but they tended to be even larger in shallower waters. The significant effect of bathymetry on group size is possibly related to the vertical distribution of bottlenose dolphin prey and foraging strategies. The hypothesis of larger groups being farther from the coast was rejected, suggesting that they feed in both inshore and offshore due to the variety of prey, e.g., a high diversity of cephalopods, and absence of predators. While steep slopes can provide benefits such as the variety of prey, it was not a significant predictor of group size, indicating that bottlenose dolphins use various foraging techniques and grouping patterns in these habitats. None of the variables were significant to groups with calves or juveniles present.

4.4 Group composition and behavior

Social interactions can also influence group size and like other species (e.g.: Risso's dolphins, Azzellino et al., 2016), bottlenose dolphins are very social and spend considerable amount of time with related individuals. As hypothesized, larger bottlenose dolphin groups were positively associated with the presence of calves and juveniles, supporting previous studies (Augusto et al., 2012; Heiler et al., 2016; Methion et al., 2023). Larger groups in La Gomera are possibly formed as a strategy for protection i.e.., ensuring calves' survival, as well as reproduction success (Augusto et al., 2012; Liu et al., 2021a). The connection between mother and calves tends to decrease when the calf is 3-4 years old; however, they still seemed to be with their mother occasionally until to 9-10 years of age (Wells et al., 1987). While the reason for separation is unknown, birth of new calves did not appear the be the main reason (Wells et al., 1987). In Sarasota Bay, bottlenose dolphin group size was observed to decrease with increasing dolphin age until sexual maturity (Wells et al., 1987). In La Gomera, juveniles were present in larger groups, indicating that they remain associated to their mothers and conspecifics or that

they stay in larger groups for protection and social motives. Larger group sizes can also be beneficial for social learning, which can be passed from mother to calf as observed when female bottlenose dolphins exhibited highly individual specialization in foraging habits that tended to be the same as when they were calves (Rossman et al., 2015). Nevertheless, vertical social learning was observed to be more important for daughters, while also reflecting sex-specific foraging and social tactics (Miketa et al., 2018).

Associations may also be related to social preferences, even if it results in overlapping ranges, which in this case creates opportunities for interaction (Louis et al., 2018). The most common observed behaviors of bottlenose dolphin groups in this study were travelling or foraging/feeding, which is consistent with other studies (Bouveroux et al., 2018; Liu et al., 2021a). Group size can vary significantly depending on the group behavior. In the waters off La Gomera, larger groups were observed foraging/feeding, resting or engaged in social behavior. Larger groups when foraging and socializing might provide more benefits for the individuals such as foraging efficiency, i.e., large foraging aggregations possibly form to feed on large schools of fish (Galezo et al., 2018); and reproductive opportunities. In a study by Galezo et al. (2018) larger groups tended to be comprised of mixed-sexes. Larger groups resting could provide them protection against predators. In other studies dolphins tended to gather to rest and socialize in large groups, but forage in smaller groups, probably to reduce competition (Azzellino et al., 2016; Galezo et al., 2018). While larger density of groups travelling and socializing are usually observed in deep waters, groups feeding tend to prefer coastal waters (Cañadas & Hammond, 2008). In addition, associations may extend to interactions with other species e.g., bottlenose dolphins are often sighted with pilot whales in La Gomera, possibly looking for protection, feeding opportunities and social interactions, which tend to influence bottlenose dolphin grouping pattern. (Ritter & Bünte, 2015; Smit et al., 2010)

In brief, the study confirmed the hypothesis that non-adults are present in larger groups. The presence of calves and juveniles in larger groups indicates that they form as a protective measure for the calves, which tend to last for years until they reach maturity. Moreover, the larger groups observed during foraging/feeding, resting, and socializing in the study area suggest that this type of association offers significant benefits to individuals, including enhanced foraging efficiency, protection against predators, and increased opportunities for reproduction.

4.5 Anthropogenic threats

This study indicates that the clustering behavior of bottlenose dolphin in this area is shaped by environmental and seasonal fluctuations, their habitat preferences, and social interactions. Nevertheless, dolphins with distribution in inshore areas and shallower waters are also particularly vulnerable to increasing cumulative pressures from anthropogenic activities, such as habitat loss and degradation, pollution (chemical/ organic, debris and underwater noise), maritime traffic and interaction with fisheries, often leading to population fragmentation (Alves et al., 2019). Although this study did not analyze the impact of anthropogenic threats on bottlenose dolphins distribution and grouping pattern, it has been argued that about a third of the cetaceans deaths in the Canary Islands were related to human activities (Díaz-Delgado et al., 2018). These threats added to ongoing climate change might further contribute to the destabilization of marine species and ecosystems (Azzellino et al., 2016; García-Alvarez et al., 2014).

The increasing exposure to organic pollutants originated from anthropogenic sources was reported to be the main stressor in the bottlenose dolphin population dynamics in the Canary Islands (García-Alvarez et al., 2015). García-Alvarez et al. (2014) suggested that the origin might be from intense maritime traffic or discharge from agriculture activities. As top predators they can accumulate contaminants, thus reflecting the health status of lower levels in the trophic cascade (Wells et al., 2004); hence, the importance to monitor and protect this species and other marine mammals. Analysis of contaminants should continue to be performed in order to assess their vulnerability and exposure to different pollutants. In addition to organic pollutants, underwater noise pollution has been reported to significantly affect bottlenose dolphins' occurrence and distribution (Heiler et al., 2016; Pirotta et al., 2013). In La Gomera most sources of noise come from shipping traffic (Ritter, 2012). Animals tend to avoid areas of high levels of traffic and underwater disturbance, resulting in changes in their behavior, especially in the presence of calves (Heiler et al., 2016; Pirotta et al., 2013). As marine mammals rely on acoustic communication, the continuous and increasing exposure to underwater noise may have long-term negative effects on their populations.

Underwater noise and organic pollution are not the only negative outcome from maritime traffic. Strikes with ships and high-speed ferries, as well as disturbances from whale watching tourism are serious threats to cetaceans in the Canary Islands waters, where collision is a major

problem affecting nearly 10 % of the animals with wounds (Carrillo, 2007). Even though responsible whale watching tourism has been promoted as ethically acceptable and as a platform for education and conservation efforts, compared to captive facilities, the negative impacts on cetacean behavior associated with boat-interactions are numerous, including group directional change, alterations in group size, group dispersion, changes in vocalization and increased dive times (Haughey et al., 2021; Papale et al., 2015; Vargas-Fonseca et al., 2020). Such shifts in behavior result in seasonal and long-term displacement of cetaceans (Haughey et al., 2021). The chances of collision with vessels increase dramatically as the number of boat and traffic increases, overlapping with cetaceans' habitat use (Haughey et al., 2021). In La Gomera, the situation is similar, despite the regulation of whale-watching tourism limiting the number of boats and special requirements for operation such as the yellow flag "Barco Azul", activity remains high especially during the summer, coinciding with peaks in bottlenose dolphins' density including the presence of calves. Due to a lack in speed regulation, dolphins are increasingly at risk of collisions with vessels inside the SAC, but also outside especially in the area between Tenerife and La Gomera (Herrera et al., 2021; Tobeña et al., 2014). However, the true effects and dimension of these activities remain unknown.

Global Climate Change (GCC) has been proposed to have a favorable outcome to bottlenose dolphins due to a possible geographic range expansion towards the poles (MacLeod, 2009). Nevertheless, the effects of GCC possibly include changes in migration seasons and reproductive success of cetaceans in this region (Herrera et al., 2021). Some species migrate very far for calving and breeding, from feeding areas, but the reasons are not well understood. In addition, seasonal and inter-annual environmental changes, including global warming, resulting either from anthropogenic impacts or from oceanographic variation, are likely to cause shifts in prey distribution and abundance, consequently affecting bottlenose dolphin range patterns. Bearzi et al. (2003) argue that shifts on dolphins' range and distribution are primarily a response to prey availability, thus indirectly related to warming water temperatures. Since during the study period there was no noticeable long-term trend in SST pattern, warming was possibly not a factor.

All in all, in addition to the environmental variables, habitat preferences and social behavior influencing bottlenose dolphins' grouping behavior (size and composition) as well as their distribution (occurrence and frequency) in La Gomera, it is has been demonstrated that this species are also affected by anthropogenic threats such as organic pollution and underwater noise. The absence of a speed limit for maritime traffic within the SAC boundaries poses a further threat to this species, increasing the risk of collisions with vessels. In addition, climate change will likely affect their distribution, migration season and reproduction success in this region. It highlights the need for conservation efforts to mitigate anthropogenic impacts and protect the well-being of these marine mammals.

4.6 Limitations of the study

Determining an accurate group size can vary among observers and be challenging depending on the sea state, distance to the group and behavior of the group, as it can be more challenging when they are feeding or dispersed (Bouveroux et al., 2018). Estimation of group size by traditional methods (observer-based and photo-identification) can also be affected by methodology (Liu et al., 2021b), which can in turn influence the examination of the effect variables have on group size and composition. Bottlenose dolphins in this study also lacked individual parameters such as age, sex and reproductive condition data which could have influenced group size, group composition and distribution. Since they were not known as distinguished individuals, population size could not be investigated nor discussed, but only the probability of meeting certain group sizes under certain circumstances. Consequently, the term migration must be used carefully as nothing is known about home ranges and movements of individual dolphins. Despite this study missing values, temporal autocorrelation and data reduction, the significance of the results indicates that the real effects are probably stronger than obtained from the analyses.

Results regarding newborns, calves and juveniles must be treated carefully since in the raw data it cannot be distinguished whether they were absent or merely unobserved, only if they were present; therefore, there is a probability of a high number of non-available (NA) entries instead of 0 (absence). In the case of presence, it was also not reported how many were present, but simply that there was at least one present. The sample size of groups with newborns was considerably smaller compared to groups with calves and groups with juveniles, which could have resulted in non-significance in the models, especially when using the subsample. Newborns surfacing on the far side of their mothers may be difficult to be observed, thus could have been missed (Wells et al., 1987). Furthermore, newborns only have visible characteristics of newborns for a short period of time, making it more difficult and rarer to be observed.

4.7 Implications for conservation and management and conclusions

As marine mammals are usually considered keystone species and sentinels of healthy, productive and diverse ecosystems, protecting them likely benefits other species and the ecosystem in general (Wells et al., 2004). Marine mammals are highly mobile species occupying a wide-range niche, therefore the inclusion of spatial and temporal movements, as well as biological environmental factors and anthropogenic threats that affect their distribution, are essential to guide management decisions on the conservation of species. Ultimately, conservation actions will potentially contribute to maintaining their cultural and economic values (Haughey et al., 2021).

Significant variation in abundance, group size and composition of bottlenose dolphins among seasons and across years in La Gomera are likely a response of resident, semi-residents, and transient dolphins mainly to resources availability, but also to environmental change and degradation of habitat. Their higher density and distribution including groups with calves and juveniles in warmer waters during summer months indicates that breeding season is an important period for bottlenose dolphins in this area, therefore particular conservation measures are recommended during the summer. The observed variation in group size could also be the result or interaction of other variables not monitored in this study. Hence, the importance of long-term monitoring to identify possible environmental changes, as climate change will likely contribute to future changes in their distribution, migration season and reproduction success in this region; and possible ecological factors, such as the presence or absence of other species, affecting their behavior.

This study suggests that oceanic islands and coastal ecosystems are particularly important to bottlenose dolphins, consequently identifying areas of high use are fundamental to determine which sites and to which extent MPAs/SACs boundaries should be delineated (Haughey et al., 2021). The higher occurrence of larger groups in shallower waters is possibly related to foraging techniques and vertical distribution of prey, as large groups were also occurred in deeper waters. However, due to insufficient data on prey and predators, as well as bottlenose dolphins' diet in La Gomera it is difficult to speculate further on the main factors influencing distribution and the behavior of grouping patterns.

While the SAC FMSGR does seem to encompass a large proportion of the area used by bottlenose dolphin habitat, large displacement and distribution beyond the limit of a SAC, indicates that the current SAC is not large enough to protect these species (Herrera et al., 2021). Therefore a large MPA that includes their offshore habitat is recommended, like the one proposed by Ritter (2012). Incorporating Natura 2000 objectives into spatial planning is crucial, in particular, to maintain or improve connectivity between sites (European Environmental Agency, 2022). Herrera et al. (2021) highlighted the importance for conservation management and evaluation of current SACs, as well as the need of MPAs to connect the offshore habitats between the islands.

Protected areas (PA) have been considered as fundamental tools for the successful implementation of strategies for nature and biodiversity conservation (Spiliopoulou et al., 2021). The most recent achievement in marine conservation, the UN High Seas Treaty, agreed upon by United Nations member states in March 2023 and adopted in June 2023 commits to protect and ensure the sustainable development in waters that lie beyond national jurisdictions (United Nations [UN], 2023). The agreement is an important step towards protecting the ocean and its biodiversity, and fundamental for achieving the ocean related targets of the 2030 Agenda for Sustainable Development, which pledged to protect at least 30 % of the planet's land, coastal areas and oceans by 2030 (United Nations Environment Programme [UNEP], 2022). In order to optimize protection efforts and designate more efficient networks of PAs, initiatives such as Important Marine Mammal Areas (IMMA) could provide valuable input on marine mammals while providing strategic conservation measures for these species (Important Marine Mammal Areas [IMMA], 2023). In addition, IMMA serves as a complement to helpful and useful conservation tools such as Key Biodiversity Areas (KBA), which identify nature's most critical and important sites, and Ecologically or Biologically Significant Marine Areas (EBSAs), which identify special areas that are required for a healthy ecosystem.

Occurrence and distribution of bottlenose dolphins in the southwest of La Gomera may be responding not only to natural but anthropogenic drivers of change. Dolphins in this area are particularly vulnerable to anthropogenic pressures especially from maritime traffic, including whale watching tourism, leading dolphins to change their behavior, being vulnerable to vessel strikes, while being exposed to organic and underwater pollution. Despite significant criticism on whale watching activities, it represents only a fraction of threats marine mammals are exposed around the world, such as bycatch (Ritter, 2012) and a small number of whale watching

providers are essential to collaborate with scientific research while contributing to public awareness and education. Nevertheless, precautionary principles and measures to prevent decline should be taken, such as limiting activities or closure of the area for all activities that are not research related during the summer, when the density of bottlenose dolphins is higher and breeding and calving season take place. In addition, actions to mitigate existing threats are also fundamental. As bottlenose dolphins are a highly mobile species and tend to travel between islands, an extension of the current SAC is recommended to include offshore waters and the area between La Gomera and Tenerife where they are increasingly exposed to vessel collisions. Zones where speed is limited and only certain activities are allowed, should be implemented, and controlled, especially in areas of high occurrence of cetaceans and in shallower areas. In addition, the continual monitoring of the resident populations, as well as analyses that enable connections to population trends in this area, are essential to contribute to their conservation.

The present study comprised 26 years of data, offering new insights about bottlenose dolphins' distribution and grouping behavior in these waters. Long-term studies monitoring bottlenose dolphins, such as summarized here in the southwest waters off La Gomera, are essential tools to scientists to understand the factors influencing dolphin populations on spatial and temporal scales. Proper management and conservation efforts for marine mammals require the understanding of their ecology, distribution, genetics, and responses to environmental and anthropogenic pressures. To protect this species and identify areas of connectivity, it is crucial to address gaps in knowledge, such as migration patterns, diet, and population trends. Integrating new technologies like unmanned aerial vehicles (UAV) or satellite telemetry, along with the continuing use of photo-IDs, can provide useful information to overcome these knowledge gaps. Further collaboration among the scientific community, local government, whale-watching operators and non-governmental institutions is vital. By coming together to collect data, analyze existing datasets, and publish findings, they can actively contribute to conservation efforts and develop projects aimed at protecting the species.

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Appendix

Appendix A

Table 9: Cetacean species documented in La Gomera (1995-2020), current status according to Canary Islands Catalogue, EU Habitats Directive, and IUCN Red List.

Canary Islands ¹ Directive ² List ³ 1 Atlantic Spotted dolphin - Annex IV Least Control	ncern
1 Atlantic Spotted dolphin - Annex IV Least Con	ncern
(Stenella frontalis)	
2 Blainville's beaked whale - Annex IV Least Con	ncern
(Mesoplodon densirostris)	
3 Blue whale (<i>Balaenoptera</i> Vulnerable/ Annex IV Endanger	red
musculus) special protection	
4 Bottlenose dolphin (<i>Tursiops</i> Vulnerable/ Annex II Least Con	ncern
truncatus) special protection	
5 Bryde's whale (<i>Balaenoptera</i> - Annex IV Least Con	ncern
6 Short-beaked common dolphin Of special interest Annex IV Least Con	ncern
(Delphinus delphis) (Annex VI)	
7Cuvier's beaked whale (Ziphius)-Annex IVLeast Con	ncern
cavirostris)	
8 False killer whale (<i>Pseudorca</i> - Annex IV Near	
crassidens) Threatened	ed
9 Fin whale (Balaenoptera Vulnerable/ Annex IV Vulnerable	le
physalus) special protection	
10Fraser's dolphin-Annex IVLeast Control	ncern
(Lagenodelphis hosei)	
11Gervais' beaked whale-Annex IVLeast Control	ncern
(Mesoplodon europaeus)	
12 Humpback whale (Megaptera Of special interest Annex IV Least Con	ncern
novaeangliae) (Annex VI)	
13Minke whale (Balaenoptera-Annex IVLeast Con	ncern
acutorostrata)	
14Northern bottlenose whale-Annex IVNear	
(Hyperoodon ampullatus) Threatened	ed

15	Northern right whale	In danger of	Annex IV	Critically
	(Eubalaena glacialis)	extinction/ special protection		Endangered
16	Orca (Orcinus orca)	Of special interest (Annex VI)	Annex IV	Data Deficient
17	Pygmy sperm whale (<i>Kogia breviceps</i>)	Of special interest (Annex VI)	Annex IV	Least Concern
18	Risso's dolphin (<i>Grampus</i> griseus)	Of special interest (Annex VI)	Annex IV	Least Concern
19	Rough-Toothed dolphin (Steno bredanensis)	-	Annex IV	Least Concern
20	Sei whale (<i>Balaenoptera borealis</i>)	Vulnerable/ special protection	Annex IV	Endangered
21	Short-finned pilot whale (<i>Globicephala macrorhynchus</i>)	Vulnerable/ special protection	Annex IV	Least Concern
22	Sperm whale (<i>Physeter macrocephalus</i>)	Vulnerable (Annex II)	Annex IV	Vulnerable
23	Striped dolphin (Stenella coeruleoalba)	Of special interest (Annex VI)	Annex IV	Least Concern

1. Canary Islands protected species:

Annex II: Vulnerable species.

Annex VI: Species included in the category of special interest in the state catalog affected by the paragraph 4 of the single transitional provision (Gobierno de Canarias, 2010)

2. EU Habitats Directive:

Annex II: Species of community interest whose conservation requires the designation of Special Areas of Conservation.

Annex IV: Animal and plant species of community interest in need of strict protection (European Environmental Agency, 2007).

3. Source: IUCN Red List, 2022b

Appendix B

* see DEFINITIONS

SIGHTING FORM Ascención Oceano (other)			
DATE: Skipper: Data recorded by:			
START of trip: END of trip: Wind/seastate:			
SIGHTING DURATION: from until Photos taken Y N			
POSITION: N . W 17. (at beginning of sighting) N . W 17. (at end of sighting)			
DISTANCE to nearest coast: nm O Estimation without GPS			
SPECIES: Pilot Bottlenose Rough-toothed Spotted Common Striped Other:			
NUMBER of animals: Juveniles*: Y N Calves*: Y N Newborns*: Y N			
BEHAVIOUR*: RESTING TRAVELLING MILLING FORAGE/FEEDING DIVE SOCIAL MIXED UNKNOWN Subgroups*: Y N			
GROUP STRUCTURE*: widely dispersed dispersed loose tight			
REACTION (group)*: AVOIDANCENO RESPONSEPROXIMITYINTERACTIONUNKNOWN			
Frequent behaviours of individuals (e.g. tailslaps, leaps, bowriding, etc.):			
Recognizable animals (please describe):			
OTHER SPECIES: Pilot Bottlenose Rough-toothed Spotted Common Striped Pardelas Gulls Other:			
Other boats present: (which ones?)			
NOTES:			

Figure 19: Sighting form used to collect data on boat surveys.

Appendix C



Figure 20: Pearsons correlation plot between environmental variables. Blue: positive correlations. Red: negative correlations. Color intensity and the size of the circle are proportional to the correlation coefficients. Numbers on the right and the legend color show the correlation coefficients and the corresponding colors.

Appendix D



Figure 21: Number of bottlenose dolphin sightings recorded at different distances to coast during the study period in the coastal waters southwest off La Gomera. X axis: distance to coast (in meters). Y axis: number of sightings (n = 3111).



Figure 22: Number of bottlenose dolphin sightings recorded at different bathymetry during the study period in the coastal waters southwest off La Gomera. X axis: bathymetry (in meters). Y axis: number of sightings (n = 2862).



Figure 23: Number of bottlenose dolphin sightings recorded at different benthic slope during the study period in the coastal waters southwest off La Gomera. X axis: number of sightings (n = 3199). Y axis: benthic slope (in degrees).

Appendix E

April - August	-8.790265 (0.0000)*
April - July	-8.209599 (0.0000)*
April - June	-4.414940 (0.0000)*
April - May	-3.554719 (0.0002)*
April - November	-2.659949 (0.0039)*
April - September	-6.608084 (0.0000)*
August - December	5.857281 (0.0000)*
August - February	5.687290 (0.0000)*
August - January	7.512919 (0.0000)*
August - June	2.857546 (0.0021)*
August - March	9.467567 (0.0000)*
August - May	4.399945 (0.0000)*
August - November	5.011754 (0.0000)*
August - October	6.560670 (0.0000)*
December - July	-5.560348 (0.0000)*
December - June	-2.936100 (0.0017)*
December - May	-2.121456 (0.0169)*
December - September	-4.480354 (0.0000)*
February - July	-5.373496 (0.0000)*
February - June	-2.644492 (0.0041)*

Table 10: List of pairwise comparisons per month, only showing significant differences. Values: Z statistic (p-value).

February - March	2.209465 (0.0136)*
February - September	-4.244050 (0.0000)*
January - July	-7.139776 (0.0000)*
January - June	-4.189703 (0.0000)*
January - May	-3.411997 (0.0003)*
January - November	-2.681374 (0.0037)*
January - September	-5.925299 (0.0000)*
July - June	2.600461 (0.0047)*
July - March	8.929981 (0.0000)*
July - May	4.054262 (0.0000)*
July - November	4.663948 (0.0000)*
July - October	6.108763 (0.0000)*
June - March	5.317931 (0.0000)*
June - October	2.752506 (0.0030)*
March - May	-4.558567 (0.0000)*
March - November	-3.690398 (0.0001)*
March - October	-2.919396 (0.0018)*
March - September	-7.426507 (0.0000)*
May - September	-2.790648 (0.0026)*
November - September	-3.422638 (0.0003)*
October - September	-4.690556 (0.0000)*

Table 11: List of pairwise comparisons per year, only showing significant differences. Values: Z statistic (p-value)

1996 - 1998	4.807049 (0.0000)*
1997 - 1998	3.337762 (0.0004)*
1997 - 1999	-2.470053 (0.0068)*
1998 - 1999	-5.898914 (0.0000)*
1997 - 2000	-2.455041 (0.0070)*
1998 - 2000	-6.244459 (0.0000)*
1996 - 2001	2.055676 (0.0199)*
1998 - 2001	-3.566354 (0.0002)*
1999 - 2001	3.174558 (0.0008)*
2000 - 2001	3.350435 (0.0004)*

1996 - 2002	-2.358423 (0.0092)*
1997 - 2002	-4.163611 (0.0000)*
1998 - 2002	-7.612473 (0.0000)*
2000 - 2002	-2.331322 (0.0099)*
2001 - 2002	-5.222737 (0.0000)*
1995 - 2003	-2.320823 (0.0101)*
1996 - 2003	-4.364300 (0.0000)*
1997 - 2003	-6.410189 (0.0000)*
1998 - 2003	-10.05851 (0.0000)*
1999 - 2003	-3.926720 (0.0000)*
2000 - 2003	-5.066621 (0.0000)*

2001 - 2003	-8.266204 (0.0000)*
2002 - 2003	-2.069266 (0.0193)*
1996 - 2004	-2.222583 (0.0131)*
1997 - 2004	-4.042126 (0.0000)*
1998 - 2004	-7.524585 (0.0000)*
2000 - 2004	-2.166957 (0.0151)*
2001 - 2004	-5.101275 (0.0000)*
2003 - 2004	2.299080 (0.0108)*
1997 - 2005	-2.824819 (0.0024)*
1998 - 2005	-6.223058 (0.0000)*
2001 - 2005	-3.581502 (0.0002)*
2003 - 2005	3.443314 (0.0003)*
1997 - 2006	-3.601361 (0.0002)*
1998 - 2006	-7.348354 (0.0000)*
2001 - 2006	-4.769581 (0.0000)*
2003 - 2006	3.596812 (0.0002)*
1998 - 2007	-3.813696 (0.0001)*
1999 - 2007	2.839862 (0.0023)*
2000 - 2007	2.950962 (0.0016)*
2002 - 2007	4.855182 (0.0000)*
2003 - 2007	7.799092 (0.0000)*
2004 - 2007	4.729379 (0.0000)*
2005 - 2007	3.246117 (0.0006)*
2006 - 2007	4.351289 (0.0000)*
1998 - 2008	-3.911203 (0.0000)*
2002 - 2008	3.591529 (0.0002)*
2003 - 2008	5.811989 (0.0000)*
2004 - 2008	3.463668 (0.0003)*
2005 - 2008	2.257286 (0.0120)*
2006 - 2008	2.973733 (0.0015)*
1996 - 2009	-2.324712 (0.0100)*
1997 - 2009	-4.229584 (0.0000)*
1998 - 2009	-7.840131 (0.0000)*
2000 - 2009	-2.327552 (0.0100)*
2001 - 2009	-5.440603 (0.0000)*
2003 - 2009	2.447585 (0.0072)*
2007 - 2009	-5.038035 (0.0000)*
2008 - 2009	-3.629022 (0.0001)*
1996 - 2010	2.496594 (0.0063)*
1998 - 2010	-3.009819 (0.0013)*

1999 - 2010	3.624947 (0.0001)*
2000 - 2010	3.850964 (0.0001)*
2002 - 2010	5.626868 (0.0000)*
2003 - 2010	8.588902 (0.0000)*
2004 - 2010	5.512130 (0.0000)*
2005 - 2010	4.018344 (0.0000)*
2006 - 2010	5.219314 (0.0000)*
2009 - 2010	5.855152 (0.0000)*
1996 - 2011	2.003234 (0.0226)*
1998 - 2011	-3.637671 (0.0001)*
1999 - 2011	3.122229 (0.0009)*
2000 - 2011	3.292811 (0.0005)*
2002 - 2011	5.178594 (0.0000)*
2003 - 2011	8.238344 (0.0000)*
2004 - 2011	5.056283 (0.0000)*
2005 - 2011	3.531238 (0.0002)*
2006 - 2011	4.720431 (0.0000)*
2009 - 2011	5.396218 (0.0000)*
1998 - 2012	-3.921466 (0.0000)*
1999 - 2012	2.719340 (0.0033)*
2000 - 2012	2.810001 (0.0025)*
2002 - 2012	4.730430 (0.0000)*
2003 - 2012	7.656609 (0.0000)*
2004 - 2012	4.602975 (0.0000)*
2005 - 2012	3.126578 (0.0009)*
2006 - 2012	4.210017 (0.0000)*
2009 - 2012	4.903691 (0.0000)*
1998 - 2013	-5.346771 (0.0000)*
2001 - 2013	-2.213124 (0.0134)*
2002 - 2013	3.319126 (0.0005)*
2003 - 2013	6.174301 (0.0000)*
2004 - 2013	3.169740 (0.0008)*
2006 - 2013	2.599453 (0.0047)*
2009 - 2013	3.395108 (0.0003)*
2010 - 2013	-2.750806 (0.0030)*
2011 - 2013	-2.149159 (0.0158)*
1998 - 2014	-3.867652 (0.0001)*
1999 - 2014	2.562496 (0.0052)*
2000 - 2014	2.606900 (0.0046)*
2002 - 2014	4.490631 (0.0000)*

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2012 - 2016-3.203800 (0.0007)*2014 - 2016-2.947939 (0.0016)*2015 - 2016-2.327012 (0.0100)*1998 - 2017-5.300180 (0.0000)*2001 - 2017-2.178380 (0.0147)*2002 - 20173.290758 (0.0005)*2003 - 20176.096217 (0.0000)*2004 - 20173.142094 (0.0008)*2006 - 20172.571345 (0.0051)*2009 - 20173.360483 (0.0004)*2010 - 2017-2.711912 (0.0033)*2011 - 2017-2.114866 (0.0172)*1998 - 2018-3.837825 (0.0001)*	2011 - 2016	-3.750555 (0.0001)*
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2002 - 20173.290758 (0.0005)*2003 - 20176.096217 (0.0000)*2004 - 20173.142094 (0.0008)*2006 - 20172.571345 (0.0051)*2009 - 20173.360483 (0.0004)*2010 - 2017-2.711912 (0.0033)*2011 - 2017-2.114866 (0.0172)*1998 - 2018-3.837825 (0.0001)*	2001 - 2017	-2.178380 (0.0147)*
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2011 - 2017 -2.114866 (0.0172)* 1998 - 2018 -3.837825 (0.0001)*	2010 - 2017	-2.711912 (0.0033)*
1998 - 2018 -3.837825 (0.0001)*	2011 - 2017	-2.114866 (0.0172)*
	1998 - 2018	-3.837825 (0.0001)*

1999 - 2018	2.727105 (0.0032)*
2000 - 2018	2.810110 (0.0025)*
2002 - 2018	4.707594 (0.0000)*
2003 - 2018	7.563939 (0.0000)*
2004 - 2018	4.580848 (0.0000)*
2005 - 2018	3.129079 (0.0009)*
2006 - 2018	4.183811 (0.0000)*
2009 - 2018	4.870573 (0.0000)*
2016 - 2018	3.189657 (0.0007)*
1996 - 2019	2.703761 (0.0034)*
1998 - 2019	-2.950902 (0.0016)*
1999 - 2019	3.899283 (0.0000)*
2000 - 2019	4.207560 (0.0000)*
2002 - 2019	5.986239 (0.0000)*
2003 - 2019	9.170862 (0.0000)*
2004 - 2019	5.874911 (0.0000)*
2005 - 2019	4.302168 (0.0000)*
2006 - 2019	5.639407 (0.0000)*
2009 - 2019	6.268968 (0.0000)*
2013 - 2019	3.053498 (0.0011)*
2015 - 2019	2.776547 (0.0027)*
2016 - 2019	4.760207 (0.0000)*
2017 - 2019	3.007578 (0.0013)*
1996 - 2020	2.817768 (0.0024)*
1999 - 2020	3.434286 (0.0003)*
2000 - 2020	3.407744 (0.0003)*
2002 - 2020	4.553662 (0.0000)*
2003 - 2020	5.889705 (0.0000)*
2004 - 2020	4.466320 (0.0000)*
2005 - 2020	3.674150 (0.0001)*
2006 - 2020	4.129703 (0.0000)*
2008 - 2020	2.126001 (0.0168)*
2009 - 2020	4.554805 (0.0000)*
2013 - 2020	2.830383 (0.0023)*
2015 - 2020	2.613578 (0.0045)*
2016 - 2020	3.545652 (0.0002)*
2017 - 2020	2.817242 (0.0024)*

Appendix F



Figure 24: Mean bottlenose dolphin group size across the years (2000-2020) at different sea surface temperature recorded during this 2000-2020 in the coast waters southwest off La Gomera.

Appendix G

DIVE - FORAGE/FEEDING	-3.942874 (0.0000)*
DIVE - MILLING	-1.999088 (0.0228)*
FORAGE/FEEDING - MILLING	3.995546 (0.0000)*
DIVE - MIXED	-4.472903 (0.0000)*
MILLING - MIXED	-4.044200 (0.0000)*
DIVE - RESTING	-3.150465 (0.0008)*
MILLING - RESTING	-2.171812 (0.0149)*
MIXED - RESTING	2.409103 (0.0080)*
DIVE - SOCIAL	-3.968228 (0.0000)*
MILLING - SOCIAL	-3.876157 (0.0001)*
FORAGE/FEEDING - TRAVELLING	7.344556 (0.0000)*
MIXED - TRAVELLING	5.356445 (0.0000)*
RESTING - TRAVELLING	4.084048 (0.0000)*
SOCIAL - TRAVELLING	6.667587 (0.0000)*

Table 12: List of pairwise comparisons between group behavior, only showing significant differences. Values: Z statistic (p-value).