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ORIGINAL ARTICLE

# The biogeography of group sizes in humpback dolphins (*Sousa* spp.)

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## Abstract

Humpback dolphins (*Sousa* spp.) are obligate shallow-water and resident species, and they typically live in fission–fusion societies composed of small-sized groups with changeable membership. However, we have scant knowledge of their behavioral ecology, starting with potential factors influencing inter-population variability of their group sizes. Here, we compiled a new global dataset of humpback dolphin group sizes based on 150 published records. Our data indicated an inter-specific consistency of group-living strategy among the 4 species in the *Sousa* genus, as these species preferred living in small-sized groups with a mean size of mostly no more than 10, a minimum size of single individual or small pairs, and a maximum size of several tens or ≈100. In addition, we clearly showed the geographic variations in group sizes of humpback dolphins at a global scale. We found that the geographic variations in humpback dolphin group sizes were primarily associated with the latitude, sea surface temperature, and abundance. To conclude, our findings provide insights into social dynamics and socioecological trade-offs of humpback dolphins, and help better understand how these resident animals adapted to their shallow-water habitats from the perspectives of biogeography and socioecology.

**Key words:** biogeography, geographic variations, group size, habitat, humpback dolphins, social dynamics, socioecology

## INTRODUCTION

Group-living is an adaptive strategy for many social animal species (Fortin & Fortin 2009; Markham *et al*. 2015). Individuals decide to join or leave a group based on benefit–cost trade-offs of being in the group, and thus group-living is the foundation for a range of added benefits (Jakob 2004; Kutsukake 2009). The group size is an important trait of gregarious animals (Alexander 1974; Parrish & Edelstein-Keshet 1999; Connor *et al*. 2000a). Changes in group size can determine how individuals allocate time, space, and resources within and between groups, and affect both an individual's fitness and the whole group's benefits (Gygax 2002a,b; Silk 2007).

Factors affecting group sizes of social animals are diverse and can operate at varied time and space scales (Sibly 1983; VanderWaal *et al*. 2009). In the societies of dolphins and whales, group sizes may vary among species and are associated with species diet, life history, and living environments (Gygax 2002b). For example,

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bottlenose dolphins (*Tursiops* spp.), one of the most studied cetaceans, showed a clear picture of the variability of group sizes within and between a variety of populations (Connor *et al*. 2000b). Some studies indicated that the size and composition of bottlenose dolphin groups might vary over time and space, which was primarily in response to changes in prey availability and predation pressure (Heithaus 2001a,b; Heithaus & Dill 2002), although many other factors such as demographic parameters (Lefebvre *et al*. 2003), life-history traits (Connor *et al*. 2000a; Gygax 2002b), behaviors (Bouveroux *et al*. 2018a), and human disturbances, can all have potential influences. Coastal areas of small, shallow bays, lagoons, and estuaries, where prey availability was predictable and predation pressure was low, typically host small-sized groups of bottlenose dolphins; however, large-sized groups were mostly found in offshore waters or pelagic habitats, where prey availability was hard to predict and predation pressure increases (Connor *et al*. 2000b; Gowans *et al*. 2007; Bouveroux *et al*. 2018a).

Societies of various dolphin species display a great diversity of social organization and grouping patterns (Gowans *et al*. 2007; Kutsukake 2009; Gowans 2019). Although socioecological factors affecting group sizes have been studied in some species like bottlenose dolphins (Bouveroux *et al*. 2018a), river dolphins (Santos & Rosso 2007; Gomez-Salazar *et al*. 2012), and killer whales (Baird & Dill 1996), there has been scant socioecological research on strictly inshore and resident species like humpback dolphins. In particular, previous studies on humpback dolphin social dynamics often focus on the sociality within a specific population while lacking an attention to the intra-specific variability of group sizes, and therefore may underrepresent more proximate socioecological factors influencing group sizes.

The *Sousa* spp. (i.e. humpback dolphins) is a unique genus in the Delphinoidea family, of which includes only obligate shallow-water delphinids, with wide distribution areas but restricted regional movements (Gowans *et al*. 2007; Li 2020). Humpback dolphins can be found in coastal waters of the eastern Atlantic, Indian, and western Pacific Oceans, with a tropical-to-temperate range between 35° South and 35° North (Jefferson & Curry 2015; Fig. 1a). To date, there are 4 recognized species with little overlap between their distribution ranges: the Atlantic humpback dolphin (*S. teuszii*), Indian Ocean humpback dolphin (*S. plumbea*), Indo-Pacific humpback dolphin (*S. chinensis*), and Australian humpback dolphin (*S. sahulensis*) (Jefferson & Rosenbaum 2014). Notably, all these 4 species strongly prefer inshore (distance to the nearby land <20 km) and shallow (depth <20–30 m) waters (Jefferson & Curry 2015). Furthermore, they are typically considered resident species without any indication of large-scale migration, because the ranges of their movements have been found generally less distant than 100–200 km (Jefferson & Curry 2015; Würsig *et al*. 2016; Li 2020).

Most humpback dolphin populations live in fission–fusion societies mainly composed of small-sized groups (about 10 or less individuals), of which the group membership changes often, so that most dyadic interactions are relatively short-lived (Karczmarski 1999; Parra *et al*. 2011; Dungan *et al*. 2012, 2016; Bouveroux *et al*. 2019; Hunt *et al*. 2019). There is however variability around this central tendency in social life, as solitary individuals are not uncommon, and large aggregations up to dozens or even 100 individuals have occasionally been recorded in some regions (Parsons 2004; Baldwin *et al*. 2004; Würsig *et al*. 2016). Although some previous studies have described such an intra-specific variability in the group sizes of humpback dolphins (Parsons 2004; Gowans *et al*. 2007; Würsig *et al*. 2016), so far we do not know what socioecological factors primarily influence geographic and inter-population variations in group sizes of humpback dolphins.

In this paper, we assumed that the humpback dolphins can maximize their group-living benefits by adjusting their group sizes within and between a variety of populations. By using available published records, we presented a clear picture of geographic variations in group sizes of humpback dolphins all over the world. We expected that the humpback dolphins could geographically vary their group sizes. In addition, we further hypothesized that some explanatory variables like demographics and habitat characteristics were possible to influence the group sizes of humpback dolphins, which might be an adaptation to different environments. This biogeographic study on humpback dolphins can provide foundational information to better understand social dynamics of these resident range-restricted animals, and establish a crucial baseline to reveal socioecological trade-offs of humpback dolphins for adapting to their inshore habitats.

## MATERIALS AND METHODS

### Data preparation

We searched electronic databases (Web of Science, ProQuest, Google Scholar, and CNKI) for combinations of the following keywords: "*Sousa*" or "humpback dolphin" or "hump-backed dolphin" and "group" or "group size" or "group characteristics" or "group

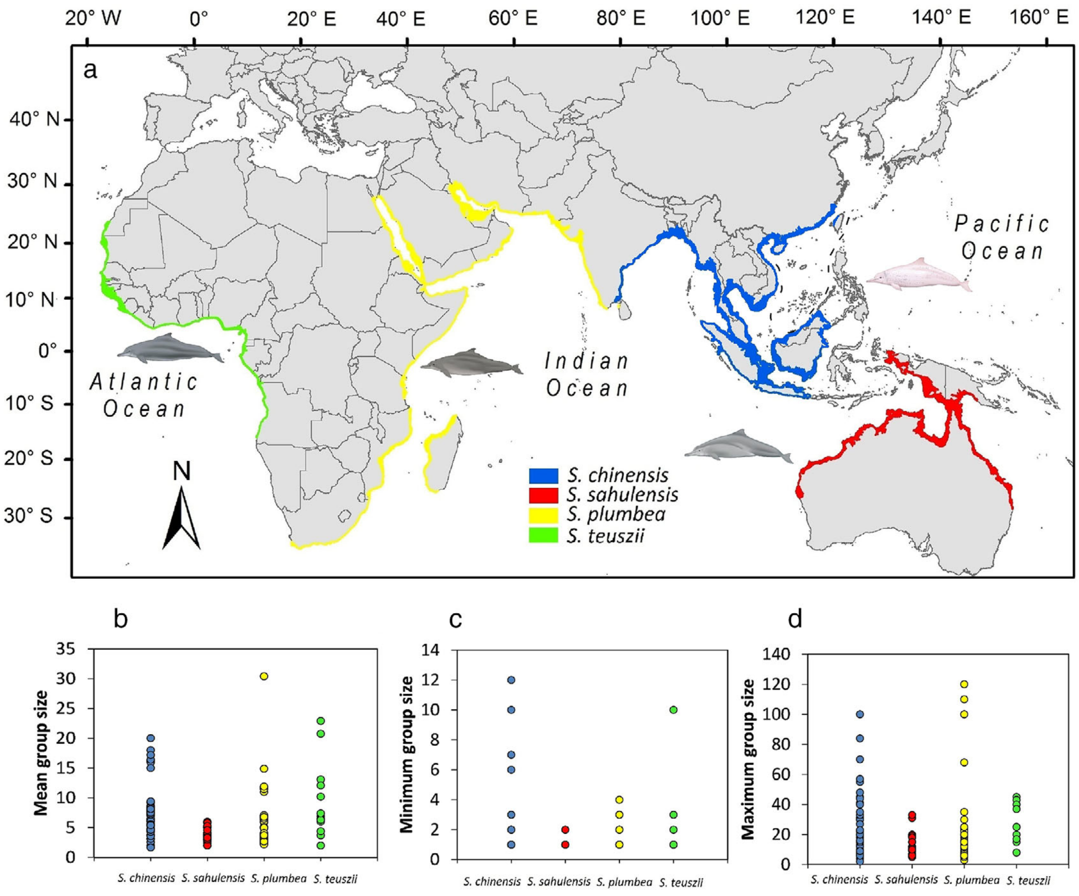


**Figure 1** (a) Global distribution ranges of humpback dolphins (*Sousa* spp.). Scatter plots of the (b) mean, (c) minimum, and (d) maximum group sizes of four *Sousa* species (Indo-Pacific humpback dolphin *S. chinensis*, Australian humpback dolphin *S. sahulensis*, Indian Ocean humpback dolphin *S. plumbea*, and Atlantic humpback dolphin *S. teuszii*). Distribution data on humpback dolphins were obtained from the International Union for Conservation of Nature's Red List of Threatened Species (http://www.iucnredlist.org/).

dynamics" or "social dynamics" or "school size" or "pod size" or "population" or "abundance" or "behavior". We manually examined relevant publications between 1970 and 2020, including journal papers, book chapters, theses, dissertations, conference papers, and investigation reports (Liu *et al*. 2020). We extracted useful information on group sizes of humpback dolphins from these publications (mean ± standard deviation/error, number of sampled groups, and range) with details of species, populations, survey area, survey period, sampled method, and reference (see Data S1, Supporting Information). In each sampled population, we selected 3 commonly documented indicators as response variables, that is, mean, minimum, and maximum group size (Gygax 2002a,b; Gomez-Salazar *et al*. 2012).

To explore biogeographic variations in group sizes of humpback dolphins, we selected 7 factors as explanatory variables including the species, abundance (population size), latitude, estuary, bay, island, and sea surface temperature (SST). For each sampled population, the species was determined according to the distribution ranges of humpback dolphins obtained from *The IUCN Red List of Threatened Species* (http://www.iucnredlist.org/). According to those systematic review articles on humpback dolphins (e.g. Braulik *et al*. 2015; Cerchio *et al*. 2015; Collins 2015; Jefferson & Curry 2015; Piwetz *et al*. 2015; Sutaria *et al*. 2015; Xu *et al*. 2015; Hanf *et al*. 2016; Jefferson & Smith 2016; Karczmarski *et al*. 2016), the abundance (population size) was categorized into an ordered scale: small (<100), medium (100–300), and large (>300). In addition, we extracted the location information (latitude, longitude) from the relevant publications with the help of Google Earth Pro (Google Inc. CA, USA). Based on the location

**Table 1** Response and explanatory variables included for the analysis in this study

| | Variable | Type | Description/Category | Source |
|---|---|---|---|---|
| Response | $G_{mean}$ | Scale | Mean group size | Publication review |
| | $G_{minimum}$ | Scale | Minimum group size | Publication review |
| | $G_{max}$ | Scale | Maximum group size | Publication review |
| Explanatory | Species | Categorical | Indo-Pacific humpback dolphin (*Sousa chinensis*), Australian humpback dolphin (*S. sahulensis*), Indian Ocean humpback dolphin (*S. plumbea*), and Atlantic humpback dolphin (*S. teuszii*) | *The IUCN Red List of Threatened Species* (http://www.iucnredlist.org/) |
| | Abundance | Ordinal | Small-sized population (<100 estimated individuals) Medium-sized population (100−300) Large-sized population (>300) | Publication review |
| | Latitude | Scale | Latitude (°) to South (−) or North (+) | Publication review and Google Earth |
| | Estuary | Binary | 0 (non-estuarine area)1 (estuarine area) | Global Estuary Database (https://data.unep-wcmc.org/datasets/23) |
| | Bay | Binary | 0 (highly enclosed or semi-enclosed bay or harbor with twisty coastlines) 1 (relatively open area with relatively straight coastlines) | Google Earth |
| | Island | Binary | 0 (adjacent to mainland, no island around) 1 (adjacent to an island or islands, surrounded by archipelagos) | Google Earth |
| | SST | Scale | Sea surface temperature (°C, mean annual sea surface temperature) | National Oceanic and Atmospheric Administration, USA (https://psl.noaa.gov/data/gridded/data.noaa.ersst.v5.html) |

information, we further determined and examined whether the habitat location of a particular population of humpback dolphins is characterized as estuary (0 estuarine; 1 non-estuarine), bay (0 no; 1 yes), and island (0 no; 1 yes). Data on SST from 2011 to 2015 (averaged by month) were achieved from the website of National Oceanic and Atmospheric Administration, USA (https://oceancolor.gsfc.nasa.gov/cgi/l3), and then were searched by location information. Details on description of response and explanatory variables are given in Table 1.

## Data analysis

First, we displayed variations in mean, minimum, and maximum group sizes among the 4 species of *Sousa* genus by using scatter plots. Second, based on all available records, we created several maps to show geographic variations in mean, minimum, and maximum group sizes of humpback dolphins. Third, to determine which explanatory variable was significant in affecting each response variable, we built and pruned the classification and regression trees (CARTs) for explaining the variations in mean, minimum, and maximum group sizes (De'ath & Fabricius 2000). Lastly, we fitted the relationship between each response variable and the most significant explanatory variable in CARTs via linear fitting and nonlinear polynomials fitting (quadratic and cubic). All the statistical analyses were conducted in R 3.5.1 (R Development Core Team 2018), and all the maps were created in ArcMap 10.1 (ESRI, Redlands, CA, USA).

## RESULTS

In total, we retrieved 150 published group size estimates of humpback dolphins all over the world from 147 relevant publications (Data S1, Supporting Information). Of these records, 59 were from *S. chinensis*, 29 were from *S. sahulensis*, 47 were from *S. plumbea*, and 14 were from *S. teuszii*. Based on these records, *S. sahulensis* had a much smaller range of the mean group size (2–5.1 individuals) than *S. chinensis* (2–20 individuals), *S. plumbea* (2.38–14.9 individuals), and *S. teuszii* (2–23 individuals) (Fig. 1b). A similar trend was also detected in the mimimum and maximum group sizes among species (Fig. 1c,d). The range of minimum group size of *S. sahulensis* (1–2 individuals) was narrower than that of *S. chinensis* (1–12 individuals), *S. plumbea* (1–4 individuals), and *S. teuszii* (1–10 individuals) (Fig. 1c). In addition, the range of maximum group size of *S. sahulensis* (5–31 individuals) was also narrower than that of *S. chinensis* (2–55 individuals), *S. plumbea* (5–110 individuals), and *S. teuszii* (8–45 individuals) (Fig. 1c).

Geographically, we showed the variability of mean, minimum, and maximum group sizes for humpback dolphins among a range of sampling locations (Fig. 2a–c). In the genus *Sousa*, the majority of populations generally formed small-sized groups with a mean size of mostly no more than 10, a minimum size of typically single individual or small pairs, and a maximum size of several tens or $\approx$100 (Fig. 2d–f). We also plotted variations in habitat features among different sampling sites (Fig. S1, Supporting Information). Our CARTs could illustrate 85.6%, 73.4%, and 74.8% of the total variations for the mean, minimum, and maximum group sizes, respectively (Fig. 3a–c). The mean group sizes were primarily explained by latitude, followed by SST (Fig. 3a). The minimum group sizes were mainly explained by SST (Fig. 3b). The maximum group sizes were primarily explained by latitude, followed by abundance and SST (Fig. 3c).

With the increase of latitude (from 35° South to 30° North), there was a weak positive impact of latitude on mean group sizes (Fig. 4a). Larger records of mean group sizes ($>$10 individuals) were mainly observed between 0° and 25° North (Fig. 4a). With the increase of SST (generally between 17 °C and 30 °C), there was a weak positive impact of SST on minimum group sizes (Fig. 4b). In addition, larger records of minimum group sizes (3–12 individuals) were primarily observed around 27 °C (Fig. 4b). The latitudinal impact on maximum group sizes was shown in Fig. 4c, and such a trend is very similar to Fig. 4a.

## DISCUSSION

In this study, there were 3 critical results from our analyses. First, based on all available records, we highlighted the social strategy of living in small-sized groups for humpback dolphins all over the world. Second, we showed the population-level variations in group sizes of humpback dolphin across different habitats. Third, we found that the humpback dolphin group sizes could be primarily explained by demographics and some habitat characteristics. These findings provide the necessary baseline information on which (1) to assess the sociality of humpback dolphins in the framework of dolphin fission–fusion dynamics, and (2) to better understand social dynamics and group-living trade-offs of these obligate shallow-water animals.

Our data showed an inter-specific consistency of grouping patterns among 4 humpback dolphin species in the *Sousa* spp., although the mean, minimum, and maximum group sizes of various species might differ in a series of sampling places. Based on 150 published records, we clearly indicated that humpback dolphins often lived in small-sized groups, typically including single individual, small pairs, and rarely middle-to-large aggregations of several tens or $\approx$100. Such grouping patterns were similar to some other inshore dolphin species inhabiting coastal and estuarine environments, but were different from those oceanic or pelagic species living in large groups/communities of several hundred or thousand members (Jefferson *et al*. 2011).

In dolphin societies, forming different sizes of groups is highly associated with fission–fusion social dynamics (Gowans *et al*. 2007; Parra *et al*. 2011). While all dolphin societies described to date can be called fission–fusion, they do not behave the same. As a fission–fusion species, humpback dolphins were characterized by medium fluidity in group sizes, indicating that they generally have both stable (preferred companionships) and fluid (casual acquaintances) associations (Chen *et al*. 2011; Dungan *et al*. 2012, 2016; Hunt *et al*. 2019). Consequently, group sizes of humpback dolphins are often dynamic, which can vary across space, time (specific times of day, season, and year), populations, and behaviors (Parsons 2004; Wang *et al*. 2016; Würsig *et al*. 2016). Regular medium-fluid and small-sized groups of humpback dolphins showed huge dissimilarity to highly stable and well-structured groups in resident killer whales (*Orcinus orca*) (Baird & Dill 1996; Parsons *et al*. 2009), low-fluid groups in Hector's dolphins (*Cephalorhynchus hectori*) (Jefferson *et al*. 2011), or high-fluid groups in spinner dolphins (*Stenella longirostris*) (Karczmarski *et al*. 2005). Such difference

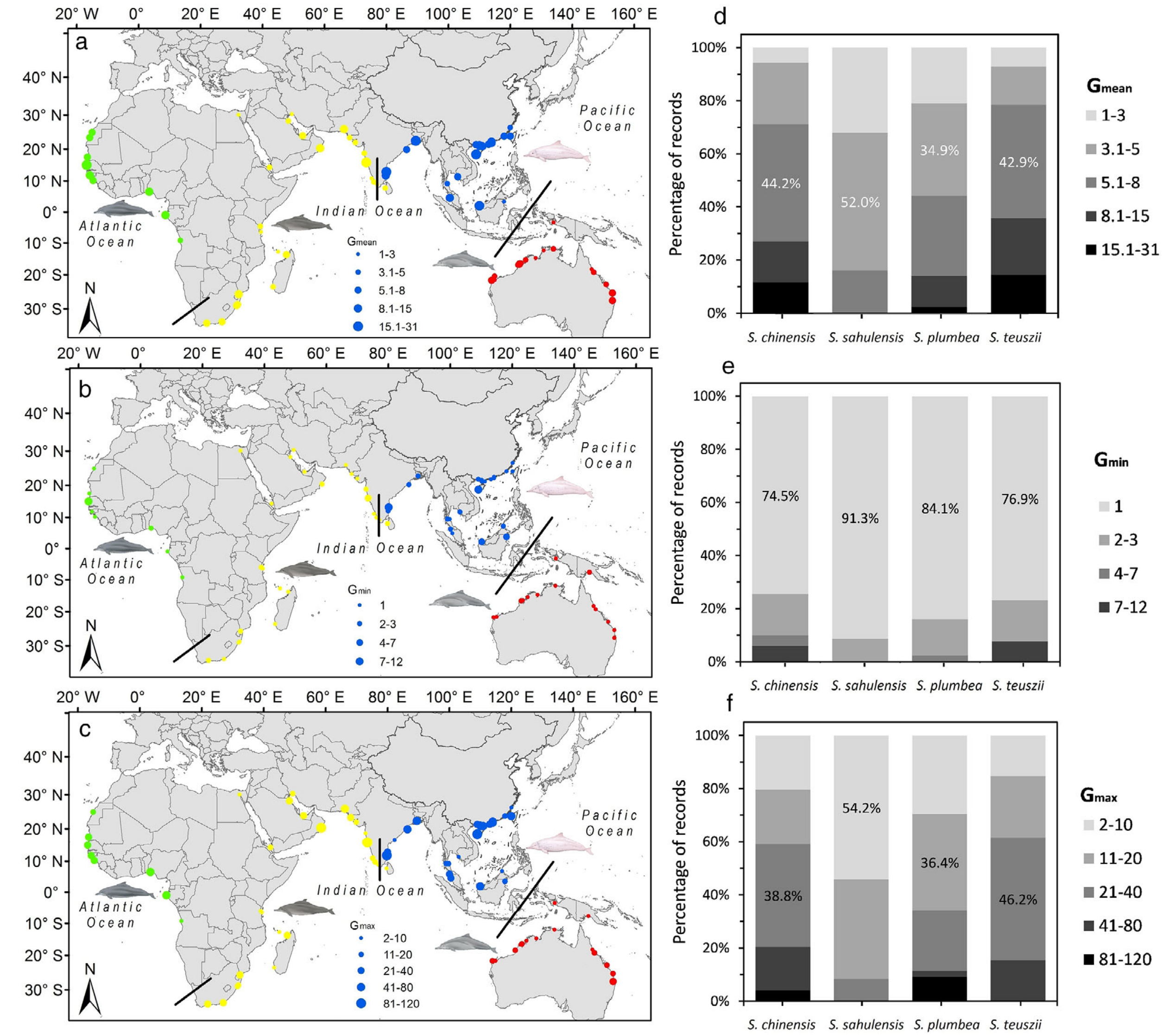


**Figure 2** Geographic variations in (a) mean, (b) minimum, and (c) maximum group sizes of humpback dolphins (blue: Indo-Pacific humpback dolphin *S. chinensis*, red: Australian humpback dolphin *S. sahulensis*, yellow: Indian Ocean humpback dolphin *S. plumbea*, and green: Atlantic humpback dolphin *S. teuszii*). Percentage of records of the (d) mean, (e) minimum, and (f) maximum group sizes of humpback dolphins varied among species.

between humpback dolphins and other dolphin species might be attributed to differences in species characteristics such as demographics, living environments, behaviors, diet, and residency patterns (Lusseau 2003; Gowans *et al*. 2007; Gowans 2019).

For the first time, we presented a clear picture to show geographic variations in group sizes for all 4 humpback dolphin species throughout the distribution ranges of *Sousa* genus. Such geographic variations might reflect a result of biogeographic differences in social dynamics and socioecological trade-offs between different humpback dolphin populations. The mean group sizes of humpback dolphins may closely correspond to the predicted optimal group sizes, as a result of their social and behavioral adaptations to specific ecological constraints (Aureli *et al*. 2008; Markham *et al*. 2015). Notably, our results showed that the larger records of mean group sizes (10–30 individuals) could be observed within the populations inhabiting waters between 0° and 25° North. For instance, the mean group size of humpback dolphins

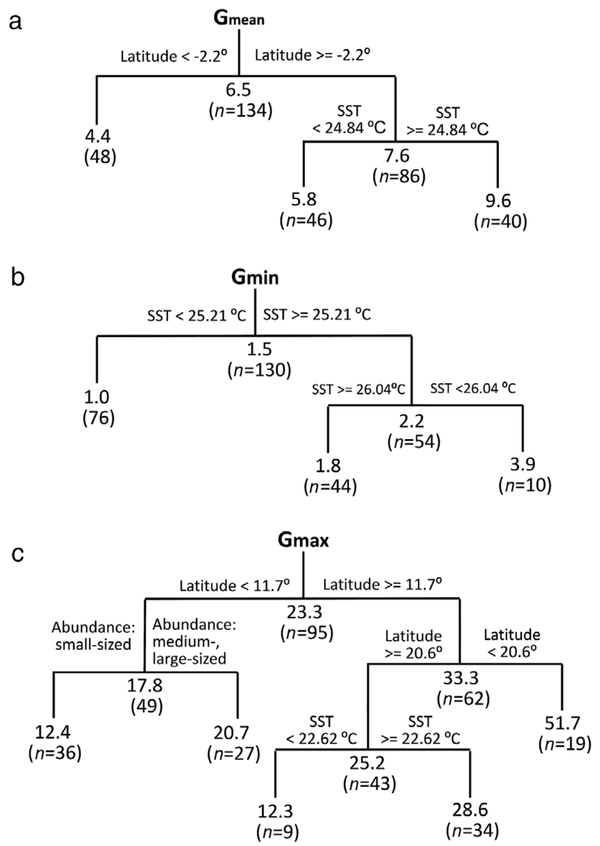


**Figure 3** Classification and regression trees (CARTs) of the (a) mean, (b) minimum, and (c) maximum group sizes of humpback dolphins. Each split was labeled with the explanatory variable and its requirements that determined the split. Each node was labeled with the mean value of response variable and number of observations in the bracket.

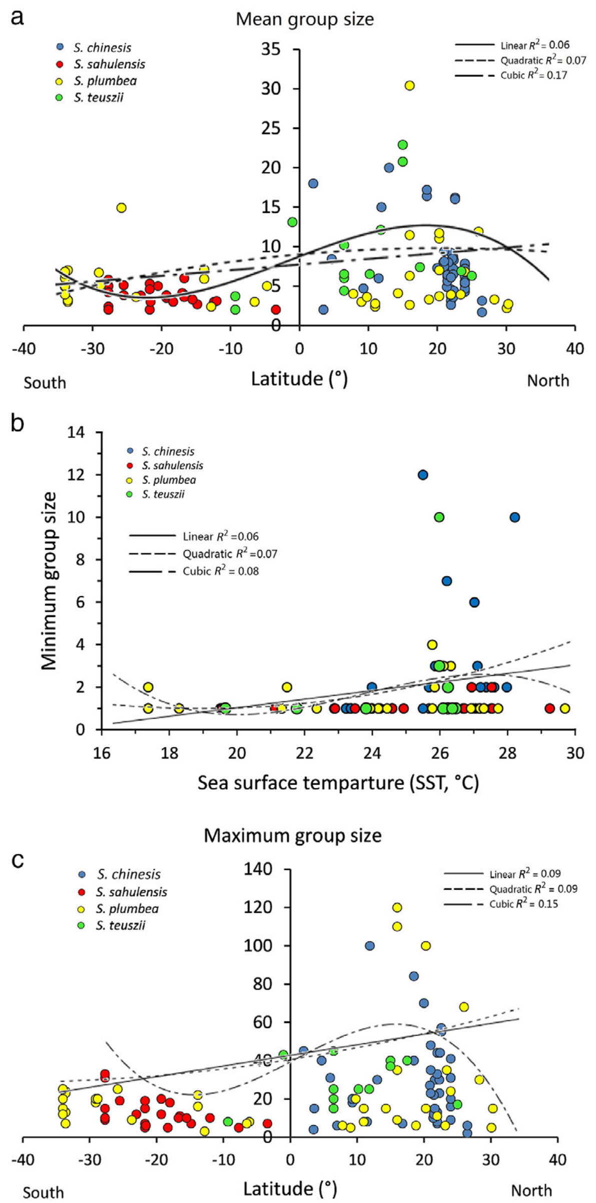


**Figure 4** (a) The latitudinal impact on the mean group sizes of humpback dolphins; (b) the impact of sea surface temperature (SST, °C, mean annual sea surface temperature) on the minimum group sizes of humpback dolphins; and (c) the latitudinal impact on the maximum group sizes of humpback dolphins.

documented in the waters southwest of Hainan Island, China, was 17.2 individuals (Liu *et al*. 2020), which was larger than values reported for many other regions (Parson 2004). Liu *et al*. (2020) suggested that such unique pattern may be a response to local environments where there are some small islands but no large estuarine systems in the region, which leads to patchy prey distribution in variable environments and thus resulting in larger groups for cooperative feeding.

A number of humpback dolphin populations tend to prefer turbid estuaries with river run-offs, while others reside in bays, harbors, lagoons, and waters near to reefs or islands without estuarine systems (Karczmarski 1999; Chen *et al*. 2009; Jefferson & Curry 2015). Although humpback dolphins regularly formed small groups with a mean group size <10 individuals, there were several larger records of mean group size within the population along the Chennai coast, Bangladesh (mean: 20 individuals; Muralidharan 2013), in the Kuching Bay (mean: 18 individuals; Poh *et al*. 2016), along the Sindhudurg Coast of Maharashtra, India (mean: 30.4 individuals; Smith *et al*. 2008), and in the Saloum Delta, Senegal (mean: 22.9 individuals; Van Waerebeek *et al*. 2004).

There is an estuarine system in some of these regions but none in others, suggesting a much more complex impact of other habitat characteristics (not estuarine) on humpback dolphin social dynamics. This is supported by our CARTs results because we found that the humpback dolphin group sizes could be primarily explained by latitude, SST, and abundance.

There are several rare records of large-sized groups with more than 50 humpback dolphins around the latitude of 20° North. This finding is further explained by inter-population differences in abundance and SST on the latitudinal gradient (Fig. 3c). For example, the humpback dolphin abundance in the Pearl River Estuary (22.3° North; Jefferson & Smith 2016), in the Sonmiani Bay, Pakistan (26° North; Kiani & Waerebeek 2015), in the Arabian Gulf, Oman (20.3° North; Baldwin *et al*. 2004), are much larger than those small populations in other regions, which thus provides more opportunities for supporting larger-sized feeding or breeding aggregations. In addition, SST may have an impact on the prey resources of humpback dolphins, and thus can influence the group sizes of humpback dolphins by enhancing cooperative feeding as well as reducing intra-group competition (Gowans *et al*. 2007; Bouveroux *et al*. 2018a).

Predation pressure and resource availability are generally considered 2 main ecological constraints driving the changes in dolphin group sizes over time and space (Heithaus 2001a,b; Heithaus & Dill 2002); however, potential ecological constraints behind the variability of dolphin group sizes are difficult to assess. Compared to oceanic species, most humpback dolphin populations are subject to relatively low predation pressure from apex predators (Dungan *et al*. 2012, 2016; Wang *et al*. 2016). The regions where there have been documented interactions of humpback dolphins with apex predators such as tiger sharks or killer whales only includes some waters of Australia and South Africa (Karczmarski 1999; Keith *et al*. 2002; Parra *et al*. 2004; Hanf *et al*. 2016), and this presents an obstacle to quantify predation pressure of a particular population and compare predation pressures across different populations.

We acknowledge that potential bias in group size data potentially came with different sampling methods (observer-based estimation vs. photo-identification, or land-based vs. boat-based vs. aircraft-based estimation), sample sizes, research teams, and survey periods. Nevertheless, we are confident of most, if not all, results and discussion reported here. To the best of our knowledge, this is the first biogeographic analysis of group size data on humpback dolphins. We do not take some other critical factors like environmental changes and human activities into our analysis, but they indeed disrupt social bonds and influence social parameters. For instance, the mean group size of humpback dolphins observed in the Algoa Bay, South Africa, has been confirmed to decrease from 7 in 1990s to 3 in 2010s, and such a trend was most likely due to the sharp increase of human-caused disturbance such as shipping, fishing, and entertainment in this region during the last several decades (Karczmarski 1999; Koper *et al*. 2016; Bouveroux *et al*. 2018b). Thus, additional research is warranted to better understand how humpback dolphins vary their group sizes and social dynamics in response to the increase of anthropogenic pressure in their shallow-water habitats.

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## SUPPLEMENTARY MATERIALS

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Data S1** A global dataset of group sizes of humpback dolphins (*Sousa* spp.) extracted from the relevant publications.

**Figure S1** Variations in explanatory variables of humpback dolphins among different sampling sites.

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