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REVIEW, CONCEPT, AND SYNTHESIS

Historical mass strandings of jumbo squid (*Dosidicus gigas*) in the Eastern Pacific Ocean: patterns and possible causes

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Abstract
Mass stranding events of different taxonomic groups are periodic in certain coastal regions worldwide, but the underlying causes for these occurrences are not yet fully understood. In the Eastern Pacific Ocean (EPO), the most frequent and documented mass strandings correspond to the jumbo squid *Dosidicus gigas*, but the different hypotheses proposed to explain this phenomenon fail to predict it. Here, we assembled a database with historical stranding occurrences from the nineteenth century to 2022, highlighting the dramatic increase in strandings since the year 2000 along the EPO. The most common regions for jumbo squid strandings in the northern hemisphere are USA and Mexico, whereas in the southern hemisphere these events have mostly occurred in Chile. In both hemispheres the strandings are frequent in summer months. Although we assessed different hypothetical causes (e.g., post-spawning mortality, high temperatures, toxins from harmful algal blooms, human disturbance), we did not find enough evidence to support any of them. Besides, the need to experimentally test the plausible cause(s), we also discuss an alternative ecophysiological hypothesis associated with upwelling shadows and the species' diel migratory behavior, highlighting the importance of stranding events as key components of global nutrient cycles.

Keywords Mortality · *Dosidicus gigas* · Pacific Ocean · Physiology · Upwelling shadow

Introduction

Mass stranding events of several marine taxonomic groups (e.g., marine mammals, fishes, turtles, crustaceans, cephalopods, cnidarians) have been registered more frequently in recent decades along the coast of the Eastern Pacific Ocean (EPO) (Chong et al. 2005; Hernández-Miranda et al. 2010, 2017; Häussermann et al. 2017; Alvarado-Rybak et al. 2019; Sepúlveda 2022). In the Southeastern Pacific, only a handful of these strandings (fishes and whales) have been studied in detail (Ahumada and Arcos 1976; Jara 1992; Hernández-Miranda et al. 2010, 2017; Häussermann et al. 2017). In general, the causes for most strandings remain uncertain (Hernández-Miranda et al.

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2010). Yet, it has been proposed that environmental factors promoting marine organisms (fishes, cephalopods and mammals) to the beach are related to: (i) changes in coastal currents, (ii) increased occurrence of harmful algal blooms (HABs, red tides), (iii) drastic changes in oxygen levels, and (iv) industrial waste (Schwabe 1951; Ahumada and Arcos 1976; Clement 1988; Jara 1992; Berg 1999; Fallesen et al. 2000; Wannamaker and Rice 2000; Peterson et al. 2003; Grantham et al. 2004; Hernandez-Miranda et al. 2010; Häussermann et al. 2017; Sepúlveda 2022). Other studies have also argued that the reproductive status of semelparous species (fishes and cephalopods), the escape behavior from predators, and diseases, could be other causes of mass strandings (Wilhelm 1954; Sklar and Browder 1998; Murphy and Rodhouse 1999; Crockford et al. 2005).

One of the most remarkable mass strandings along EPO, in terms of number of specimens, are those recorded for the jumbo squid *Dosidicus gigas* (D'Orbigny 1835) (Fig. 1). This squid inhabits the EPO, from southern Chile to Alaska, since its geographic range has greatly expanded (polewards) over the last decades (Cosgrove 2005; Keyl et al. 2008; Ibáñez et al. 2015). The squid range expansion has been accompanied by increased mass strandings along the California coast (Zeidberg and Robison 2007), a similar pattern to that detected at the southern end of *D. gigas* distribution range in Chile (Chong et al. 2005; Ibáñez et al. 2015).

There are several possible causes to explain the historic strandings of jumbo squid (Schneider 1930; Wilhelm 1930, 1954; Nesis 1983; Hatfield and Hochberg 2006). Therefore, the main goals of this review are to: (i) construct a comprehensive historical record of mass strandings of *D. gigas* along the EPO, and (ii) revisit possible causes (and similarities) and discuss alternative hypothesis linked to squid's ecophysiological limits.

Materials and methods

To obtain all records of jumbo squid strandings, we made an exhaustive review of the literature (papers, books, technical reports, theses) and digital media (newspapers, blogs, webpages, social media). Most of these records correspond to gray literature that was compiled mainly by authors C.M. Ibáñez and G. Bazzino during the last 20 years (2002-2022). To organize the data, we include location, coordinates, and date of the jumbo squid strandings. In addition, data on body size and a number of squids stranded were included when possible. The frequency of strandings was calculated by country and seasons (summer, autumn, winter, and spring). Since most stranding events occurred in the Gulf of Arauco from 2001 to 2019, we downloaded monthly sea surface temperature (SST, °C) data from NOAA to calculate thermal anomalies and explore a possible relation between jumbo squid strandings with upwelling shadows.

Results

Historical records

The database created in this study includes 81 records of jumbo squid mass strandings from the 19th century (Table S1) without any evident periodicity; however, the number of events has increased in all major regional areas along the EPO since the year 2000 (Table S1, Figs. 2A, B), except off Central America where no strandings have been documented. Moreover, the strandings occurred mainly during summer and spring in all areas (Fig. 2C). Considering that major regions include several specific locations, particularities of such strandings events will be discussed below.

A) Northeast Pacific Ocean (Pacific coast of USA and Canada)

There are 23 records of jumbo squid strandings in Northeast Pacific from 1892 to 2012 (Table S1). Jumbo squid strandings on the coast of California are known since 1892 on the beaches of the Monterey Peninsula after big storms (Berry 1912; Clark and Phillips 1936). Large numbers of squids were also fished very close to shore from the Newport wharf in 1934–1936 (MacGinitie and MacGinitie 1949), suggesting that *D. gigas* was very abundant on the coast of California during the 1930s, but the species left the region in the following years. Some studies proposed that jumbo squid mass strandings may occur approximately every 35–40 years during the grunion (*Leuresthes tenuis*) breeding months (Kerstitch 1989; Martin and Kuck 1991), becoming stranded on Southern California beaches at least twice in the 1970s (Straus 1977; Kerstitch 1989). Hochberg and Gordon (1980) hypothesized that these strandings occurred because the jumbo squid pursue the California grunions that move near shore to spawn.

Other mass strandings of jumbo squid were reported in June 1990 in northern Baja California (Sánchez-Juárez 1991) and at beaches of southern California in August 1990 (Dana Point and Laguna Beach; Martin and Kuck 1991). According to Mazzilo et al. (2011) and local media attention, the frequency (and range) of the strandings had spiked over the first decade of the 21st century along the west coast of the USA and Canada. The most frequent strandings recorded in this century occurred during

Fig. 1 Pictures of *Dosidicus gigas* strandings along the Eastern Pacific Ocean. **A** Bahia Inglesa, Chile 2018, **B** Coliumo, Chile 2003, **C** Loreto, Mexico 2008, **D** Mexico

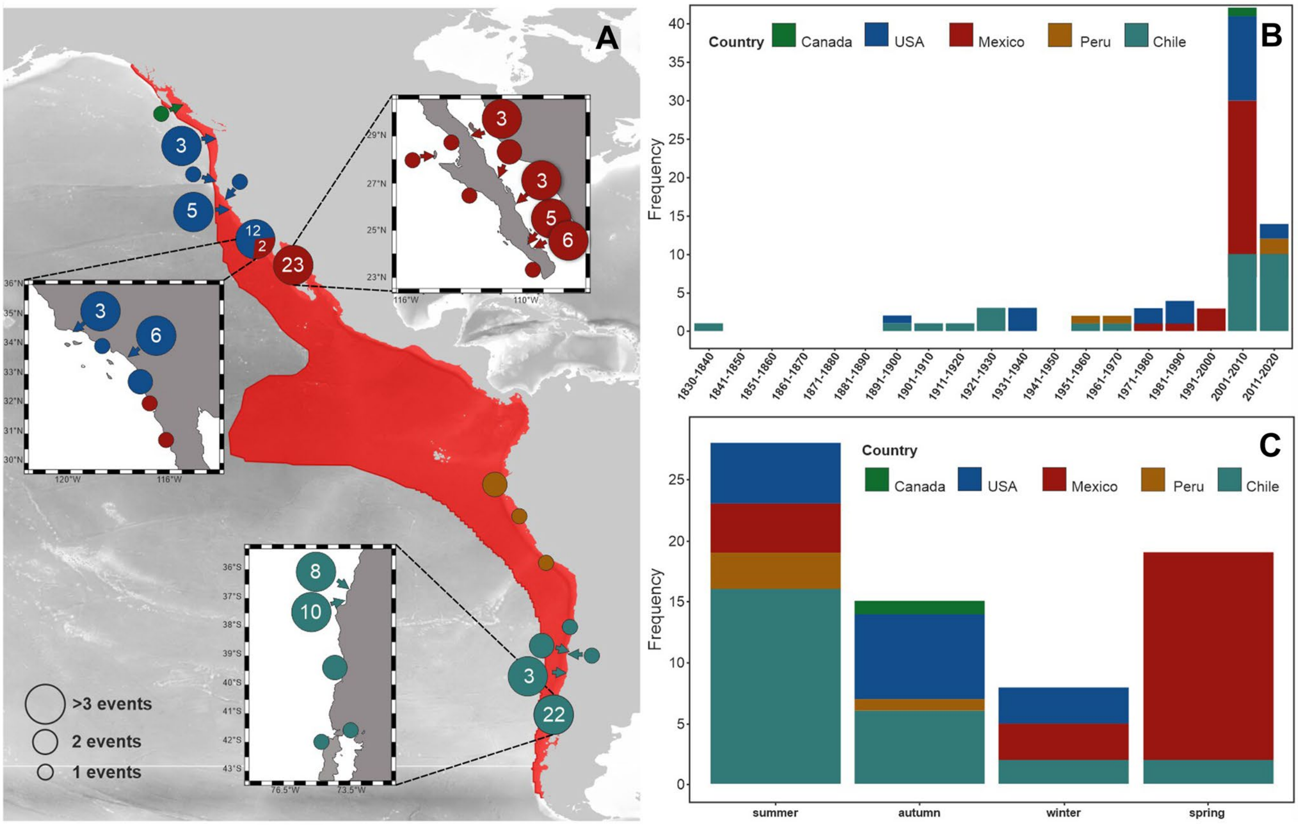

Fig. 2 Updated records of mass strandings of *Dosidicus gigas* along the Eastern Pacific Ocean, where: **A** geographic locations of events (red polygon represents the geographic distribution of *D. gigas*), **B** temporal records (1890–202219) in different countries, and **C** seasonal trends of mass strandings by country

boreal summer (June to August) between 2002 and 2012 (Table S1, Fig. 2, Fig. S1).

B) Eastern tropical Pacific Ocean (Gulf of California and Mexican Pacific)

There are 25 records of jumbo squid strandings in the Eastern Tropical Pacific from 1980 to 2008 (Table S1). The first documented stranding of *D. gigas* in the Gulf of California was in 1980 at La Paz Bay (Baja California Sur, Mexico; Table S1). However, some of the most experienced fishermen from La Paz Bay argued about the occurrence of previous strandings in the region, yet no documented evidence was found. No other records were found until 1990 and 1992, and new records appeared again in June 2002 and 2004 at Balandra beach, near La Paz region. According to local people, most of the events occurred during summer; nonetheless, in 2005 the events occurred during boreal winter months (January-April) on the Pacific coast of the Baja California peninsula (near Ensenada, Isla Cedros, and San Quintin) (Table S1, Fig. 1, Fig. 2, Fig. S2). These events evidenced some seasonality, being more frequent during boreal summer (June to August), especially inside the Gulf of California in Los Angeles Bay, Coronado Island and other islands near Loreto area, and La Paz Bay. To date, there are no stranding records on the other coast of the Gulf of California off Sonora and Sinaloa.

C) Southeast Pacific Ocean (Peruvian and Chilean coast)

There are 33 records of jumbo squid strandings in the Southeastern Pacific from 1830 to 2020 (Table S1). The mass strandings off the coast of Chile have been reported since the 19th century when the French naturalist Alcide d'Orbigny published his observations from 1830 (d'Orbigny 1835). Subsequently, Schneider described events that occurred in February 1895 and 1916 at Concepcion Bay (Schneider 1930). The best-documented events occurred in 1930 in Concepcion Bay, as Schneider (1930) and Wilhelm (1930, 1954) reported the occurrence of strandings and proposed some biological and environmental causes of the events in Concepcion Bay during the years 1895, 1916, and 1930.

Mass mortalities on the coast of Coquimbo (before 1970) caused great sanitary problems as the animals quickly decomposed producing a strong unpleasant odour (Schmiede and Acuña 1992). From 2002 to 2005, several strandings were also reported from Antofagasta to Puerto Montt (22–41° S), being most frequent near Talcahuano around 36° S (see Arancibia et al. 2007). Several stranding events occurred at Coliumo Bay and Santa María Island ~ 37°S between February to May 2003 (Chong et al. 2005) (Table S1, Fig. 1, Fig. 2, Fig. S3). The most recent mass strandings have been recorded in (i) Santa María Island and Gulf of Arauco on January 2016 and March 2018, respectively, (ii) Bahia Inglesa and Caldera on February 2019 (< 40 mm mantle length [ML]), and (iii) Coquimbo on March 2019 (32–40 mm ML).

On the Peruvian coast, the strandings have been less frequent and less documented than in Chile, occurring principally during austral summer. The most recent events were recorded during February 2019 and in June 2020. However, these records consisted of a few specimens (< 10) and were not comparable with the strandings in Mexico or Chile.

Discussion

Hypothetical causes

Reproductive cycle

As many cephalopod species, *D. gigas* dies at the end of the spawning period (Nesis 1970, 1996; Rocha et al. 2001). Therefore, the strandings could represent the end of the life cycle when post-spawning mortality is high. Males seem to die soon after mating while females perish after the spawning event (Nesis 1970, 1983). However, in several events the stranded specimens of *D. gigas* were small or medium-sized and sexually immature, with no evidence of spawning, which may provide empirical background to reject this hypothesis (Schneider 1930; Wilhelm 1954; O'Sullivan et al. 1983; Nolan et al. 1998; Chong et al. 2005).

Toxins

During the strandings, squids swim actively to the beach, suggesting some neurological damage associated with the exposure to toxins or domoic acid (DA) during the occurrence of Harmful Algal Blooms (HABs). In fact, red tides (namely paralytic shellfish poisoning, PSP) have been proposed as potentially responsible for mass strandings of *D. gigas* in California and Canada (Brongersma-Sanders 1957; Gilly 2005; Braid et al. 2011; Mazzilo et al. 2011). In California, periods with high concentrations of DA coincide with the mass deaths of squid. However, Gilly (2005) was unable to detect domoic acid in the squids stranded along Monterey Bay. In Canada, the main preys of *D. gigas* are *Sardinops sagax* (sardine) and *Clupea pallasii* (herring), which are known to constitute key DA vectors, and consequently assumed to be the cause of squid death (Jester et al. 2009; Work et al. 1993; Gulland et al. 2002). However, the concentrations of DA found in squids were always below regulatory levels for human consumption and cannot be implicated as the cause of death of the stranded squids (Braid et al. 2011; Mazzillo et al. 2011). In Chile, red tides are common in southern locations where the stranding events have not been recorded (40°S-56°S) (Villarroel 2004), with the areas of higher frequency of HAB not closely matching those of the stranding events. Therefore, there is no solid evidence to link marine toxins and squid mass mortalities.

Coastal environmental processes

Historical records suggest some common patterns in the occurrence of jumbo squid strandings (Fig. 2), at least in some geographic regions (Gulf of California and Southern Chile) and especially in enclosed systems during summer (Table S1). Therefore, the topography is another element to consider, as 50% of the strandings recorded have occurred in shallow bays or coves, whereas others occurred in islands near to the coast (e.g., Santa Maria Island, Coronado Island, Table S1).

Regarding the possible role of coastal environmental processes, the mass stranding of the squid *Martialia hyadesii* in New Zealand was assumed to be linked to sudden wind changes (affecting the water surface condition), which ultimately led to squid disorientation (O'Sullivan et al. 1983). A similar finding was reported on the coast of Uruguay, where many pelagic octopod *Argonauta nodosus* beached due to changes in the direction and intensity of prevailing winds, which also led to the advection of warm oceanic waters to the coast (Demicheli et al. 2006). In the case of fish strandings (i.e., *Aphos porosus*, *Prolatilus jugularis*, *Strangomera bentincki*, *Genypterus chilensis*) in southern Chile, it has been proposed that the entry of the Equatorial Sub-Surface Waters (ESSW) added very low levels of dissolved oxygen in Concepcion and Coliumo Bays (due to an event of intense upwelling), affecting a large part of the fish populations within this coastal ecosystem (Ahumada and Arcos 1976; Jara 1992; Hernández-Miranda et al. 2010). Curiously, during fish mass strandings there were no jumbo squids strandings around the Coliumo or Concepcion Bays. Interesting is the description made by Wilhelm (1954) about the state of the bays during *D. gigas* mass strandings in southern Chile. "One of the phenomena that often precedes jumbo squid mortality in Concepcion Bay is the sudden change in the color of the sea, which in summer takes on a pale green or milky green color" (Wilhelm 1954). This color change in the sea is an effect of the hypoxic event (see Fig. 1 in Hernández-Miranda et al. 2017). Hypoxic events reduce the oxygen concentration from 6 to < 0.5 (mL L^{-1}) and could be the cause of these strandings since the significant increase in the 21st century could be reflecting an environmental change in the species habitat (maybe related to climate change: higher SST, shoaling of the oxygen minimum zone OMZ, acidification of the ocean).

Throughout the summer months, when coastal upwelling is more frequent in Chile, and upwelling shadow events often occur inside bays or gulfs (Marin et al. 2003, Piñones et al. 2007; Letelier et al. 2009; Wong et al. 2021). Water temperatures in normal conditions at the Gulf of Arauco range between 14 to 15 °C in summer, whereas it can be reduced to 12 °C during upwelling events. During the development of upwelling relaxation events, sea surface temperature usually increases at a local scale (Graham and Largier 1997). During upwelling shadow events in the Gulf of Arauco, water temperature can increase to 16–18 °C. In Chile, as these events frequently occur within shallow systems, they eventually co-occur with hypoxic events as a result of the entrance of oxygen-deficient waters from the continental slope (OMZs, Helly and Levin 2004) into the continental shelf (Giesecke and González 2004; Sobarzo et al. 2007). These conditions have previously produced fish and invertebrate mortality in southern Chile (Hernández-Miranda et al. 2010, 2012, 2017; Sepúlveda 2022) and could be potentially responsible for the strandings of *D. gigas* when they are foraging inside the bays (Ibáñez et al. 2008; Bruno et al. 2021).

Ecophysiological challenges during upwelling shadow events in shallow-water bays

Based on the above scenarios, a conceptual ecophysiological hypothesis could also be proposed to explain the jumbo squid strandings, at least for south Pacific waters. In this specific context, it would be plausible to expect that warmer waters (18–25 °C) with low oxygen content (< 0.5 mL L^{-1}) may enter shallow bays after several days of intense upwelling during summer. Under such conditions (i.e., the triple threat) the squid could suffocate, lose orientation, diminish their swimming abilities, to finally being swept by the currents towards the beach resulting in mass mortality (Fig. 3). Jumbo squids experience physiological suppression under hypoxic conditions (1% oxygen) (Seibel et al. 2014), which are higher than the low oxygen content (< 0.5 mL L^{-1}) in shallow bays in Chile (Hernández-Miranda et al. 2017). Although *D. gigas* regulate their metabolism according to temperature (Seibel and Birk 2022) probably the low oxygen content and for temperature in upwelling shadow events could drown squid. This hypothesis could be evaluated in the Gulf of Arauco, Chile, as corresponds to a location with unique geomorphological features that promotes intense upwelling shadows (Wong et al. 2021), but also to the location with more records of jumbo squid strandings (Fig. 2). In fact, thermal anomalies in the Gulf of Arauco (Fig. 4) during 2003–2004 and 2016–2018 coincides with *D. gigas* mass strandings, principally at Santa María Island (Table S1).

Since several hypoxic events have been reported in the northern hemisphere (Mexico and USA) (Lechuga-Devéze et al. 2001; Low et al. 2021) and upwelling shadows are

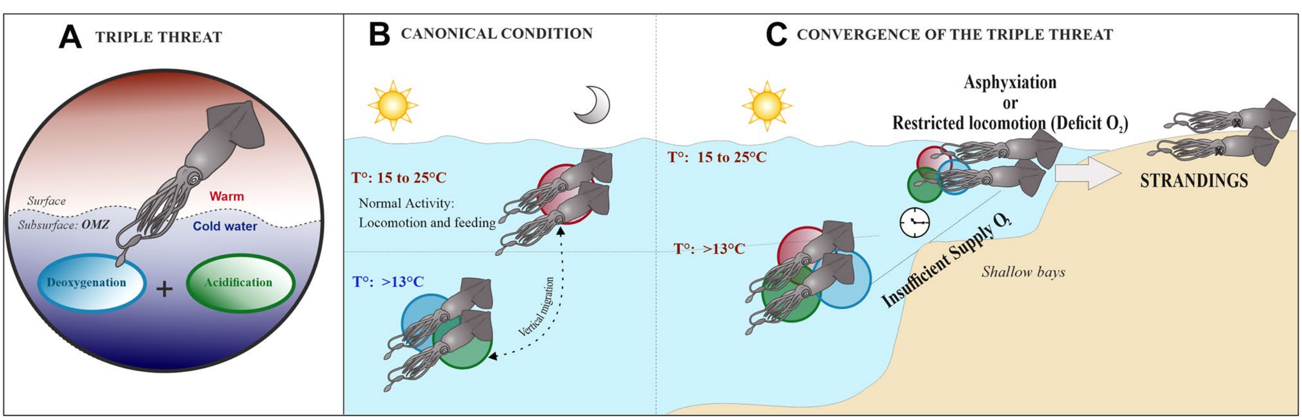

Fig. 3 Conceptual model on the physiological hypothesis of *Dosidicus gigas* strandings, where: **A** description of the general environmental challenges associated with the life history of *D. gigas*, including the temperature of the surface and subsurface water layers and the conditions found in the oxygen minimum zone (OMZ). **B** The canonical conditions experienced by *D. gigas* through behavioral (i.e. daily vertical migration, locomotion, feeding) and environmental (i.e. temperature ranges) components. **C** The convergence of the triple threat and the physiological consequences (e.g. metabolic suppression, alternative anaerobic pathways) due to the limited oxygen conditions during high-temperature periods, ending with the strandings of *D. gigas*. The clock represents the limited time that biological strategies can be supported in this condition

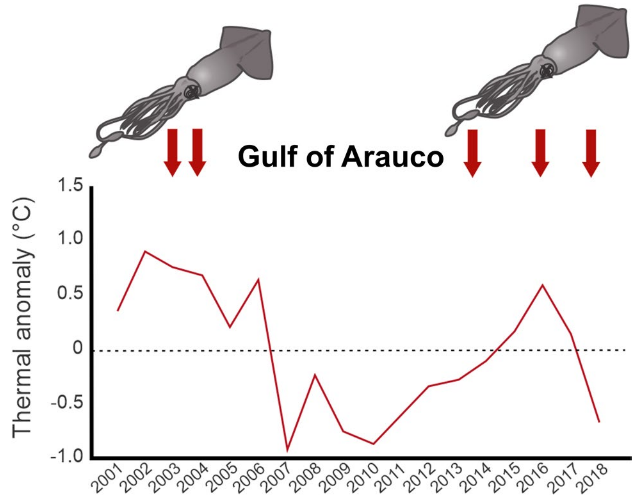

Fig. 4 Thermal anomalies and strandings (red arrows) of *Dosidicus gigas* in the Gulf of Arauco, Chile

common in bays where squid strandings are frequent (Fig. 2) (Graham et al. 1992; Graham and Largier 1997; Grantham et al. 2004), we suggest that those events could be one of the major responsibilities of jumbo squid strandings. Accordingly, occurrences of jumbo squid strandings have not been recorded in embayment places in the tropical Pacific without upwelling events (e.g., Ecuador, Colombia, Panama).

Conclusions

Along the extended geographic range of *Dosidicus gigas* within the EPO, the largest and best-documented strandings are those occurring on the Chilean coast during spring–summer near Concepcion (~36°S) (d'Orbigny 1835; Wilhelm 1954), in the Gulf of California, and on the Pacific coast off California during summer (June) (see also Markaida 2001). At a large geographic scale, the relationship between periods of high squid abundances and subsequent strandings has been observed in both hemispheres (see Schmiede and Acuña 1992; Fernández and Vásquez 1995; Markaida 2001; Rocha and Vega 2003), suggesting a possible density-dependent mechanism. Changes in water masses (i.e., oxygen and temperature) within shallow water bays seem a plausible hypothesis to be evaluated, yet further research still needs to be carried out via field and laboratory experiments. To be able to elucidate the causes of mass squid strandings, we suggest that when a stranding of jumbo squid (or of other marine organisms) occurs, environmental variables (e.g., oxygen, temperature) need to be recorded and the stranded specimens measured, sexed, as well as examined for tissue anomalies and spawning signals. It would also be desirable to take samples of muscle tissue, gills, and hemocyanin (blood) for future biochemical and genetic studies to explore signals of oxygen choking.

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Authors' contribution CMI and GAB: Conceptualization, Compiled data, Methodology, Writing—original draft. MAG: Conceptualization and Writing—review & editing. GSS: Conceptualization, Formal analysis, and Writing—review & editing. RR: Conceptualization and Writing—review & editing, SAC: Conceptualization and Writing—review & editing.

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Data availability All data of this article is in supplementary files.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval This study did not need ethical approval since is based on literature review.

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