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Research Article

Diving pattern and behavioral response to vessel traffic of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Xiamen, China: implications for conservation

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Abstract

Marine mammals have evolved sophisticated diving strategies to balance foraging efficiency with the avoidance of disturbances, a challenge that is particularly acute in coastal environments heavily influenced by human activities. The Indo-Pacific humpback dolphin (*Sousa chinensis*), inhabiting Xiamen Bay, China, is among the species most vulnerable to such pressure. Despite this, knowledge of its diving behavior and sensitivity to vessel traffic remains limited. In this study, a total of 4,408 dives of Indo-Pacific humpback dolphins were recorded, with a mean duration of 20.41 ± 1.77 s. Within the same age group, no significant differences in dive duration were found between traveling and foraging behaviors. However, comparisons across age classes revealed that subadults and adults consistently executed longer dives than juveniles, reflecting an ontogenetic progression in diving capacity. Furthermore, the dolphins demonstrated pronounced negative behavioral responses to speedboats and vessels operating at distances less than 100 m, underscoring marine traffic as a substantial source of disturbance. Based on these findings, it is recommended that vessels maintain a minimum buffer zone of 100 m, comply with a strict 10-knot speed limit, and adopt proactive avoidance practices when transiting through dolphin habitats.

Key words: Anthropogenic disturbance, behavior, conservation management, dive, Indo-Pacific humpback dolphin, vessel traffic

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Introduction

Cetaceans are fully aquatic mammals that rely on surfacing to obtain oxygen, a physiological necessity that directly shapes their diving behavior (Kramer 1988). Within marine mammal research, the concept of “diving” has been interpreted in two main ways: some studies restrict its definition to diving intervals alone (Leatherwood and Ljungblad 1979; Mate et al. 1994; Mate et al. 1995), whereas others include both dive duration and depth, thereby encompassing the broader underwater behavior of these species (Martin and Smith 1992; Westgate et al. 1995). Historically, observations of cetacean diving patterns were collected opportunistically during fishing expeditions (Gray and Flower 1882; Heezen 1957). With technological advances such as satellite telemetry and depth recorders,

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however, researchers have gained the ability to monitor diving profiles and movement patterns accurately (Scott and Chivers 2009; Rasmussen et al. 2013).

Body size has long been considered a key factor influencing dive duration, with early studies generally reporting a positive relationship between the two (Noren and Williams 2000; Marino et al. 2006). However, exceptions are evident, particularly among odontocetes (Ridgway et al. 2019). For instance, the pygmy sperm whale *Kogia breviceps* (average length 2.05 m) can perform dives exceeding 30 min. In comparison, the considerably larger killer whale, *Orcinus orca* (average length 5.82 m), typically restricts its dives to about 10 min (Ridgway et al. 2019). Diving capacity is also influenced by physiological development. In juvenile cetaceans, blood oxygen storage and diving capacity are not fully developed but gradually improve with age and body size (Noren and Williams 2000; Noren et al. 2002). Bottlenose dolphins (*Tursiops truncatus*), for instance, achieve near-adult levels of blood oxygen reserves by approximately 3 years of age (Noren et al. 2002).

Beyond foraging or physiological constraints, diving behavior also functions as a response mechanism to environmental pressures. In the presence of vessel traffic, bottlenose dolphins have been observed to increase swimming speeds, alter directional movements, synchronize breathing, and significantly prolong dive durations, reflecting an adaptive response to disturbance (Janik and Thompson 1996; Nowacek et al. 2001; Hastie et al. 2003; Lusseau 2003).

The Indo-Pacific humpback dolphin (*Sousa chinensis*) is distributed across the southeastern coast of China, throughout Southeast Asia, and along the coastal margins of the Bay of Bengal, extending to the coast of Odisha, India (Jefferson and Rosenbaum 2014). Several populations, particularly those in Xiamen Bay, the eastern Taiwan Strait, and the waters around Hong Kong, face intense anthropogenic threats (Jefferson 2000; Ng and Leung 2003; Chen et al. 2008; Dungan et al. 2011; Jefferson and Smith 2016). These regions are characterized by rapid industrial development, frequent vessel collisions, and heavy marine traffic (Jefferson 2000; Ng and Leung 2003; Araújo et al. 2014; Chen et al. 2018).

Xiamen Bay, in particular, represents a critical habitat for *S. chinensis* (Chen et al. 2008; Chen et al. 2011). However, it is also subject to intense human activity, including large-scale cargo transportation, extensive fishing operations, and routine channel dredging, resulting in persistently high levels of vessel traffic (Wang et al. 2015; Chen et al. 2018). Although cetacean diving behavior and responses to vessel disturbance have been documented elsewhere, studies focusing on *S. chinensis* have primarily been restricted to the waters of Hong Kong (Ng and Leung 2003). Thus, the present study aimed to examine the diving patterns of *S. chinensis* and assess their behavioral responses to vessel traffic in Xiamen Bay. These findings will contribute to a more comprehensive understanding of the species' behavioral ecology and provide crucial insights to inform conservation and management strategies for the local population.

Materials and methods

Study area and data collection

Xiamen waters represent a dynamic environment shaped by the interaction of river discharge and tidal exchange. The Beixi and Xixi Rivers, two principal tributaries of the Jiulongjiang River, deliver substantial volumes of freshwater and sediment

into the bay, while the currents of the Taiwan Strait govern tidal motion. The region experiences an irregular semi-diurnal tidal cycle, with an average tidal range of 4.08 m (Zuo et al. 2014). The sediment composition in the area is diverse, encompassing eight distinct types, although it is predominantly characterized by the accumulation of fine particulate matter (Zuo et al. 2016). Xiamen Port Channel is among the busiest maritime hubs in China, accommodating over 1,000 vessel transits daily. The western sector of the bay is home to more than 10 terminals that regularly service ferries and cargo ships. Ferry activity is particularly concentrated along the route connecting the mainland with Gulangyu Island, where vessel frequency averages approximately five ships every 20 minutes (Lu et al. 2024).

Boat-based surveys were conducted between 2017 and 2019 across four regions: Xiamen Bay, Zhangzhou, Quanzhou, and Kinmen (Fig. 1a). Weather permitting, the survey vessel navigated along predetermined transect lines designed to encompass as much of the Indo-Pacific humpback dolphin habitat as possible (Fig. 1a). During each survey, a minimum of two experienced observers were stationed at the bow of the vessel. Using either the naked eye or 10×50 mm binoculars, each observer scanned a 100° field of view in opposite directions. To minimize fatigue, observer roles were rotated every 30 min, and scheduled rest breaks were implemented every 3 hours.

Upon dolphin encounters, individuals were photographed using a digital camera (Canon EOS 1Dx Mark II with a 28–300 mm zoom lens, Japan). Simultaneously, to ensure reliable behavioral classification, a video camera (Sony FS5K, Japan) was employed to record dolphin activity for subsequent laboratory analysis. In this study, diving duration was defined as the time elapsed from the end of one surfacing event to the start of the next (Fig. 1b). Diving behavior was monitored through continuous sampling, with dive durations measured using a handheld stopwatch. For large groups, it was impossible to accurately track multiple individuals simultaneously (especially more than 10 individuals). A strategy involving sequential processing and video-based supplementation was employed. Observations of a focal individual were terminated if the animal was lost from view or if the tracking period exceeded 30 minutes, after which the survey vessel returned to the transect line to resume data collection.

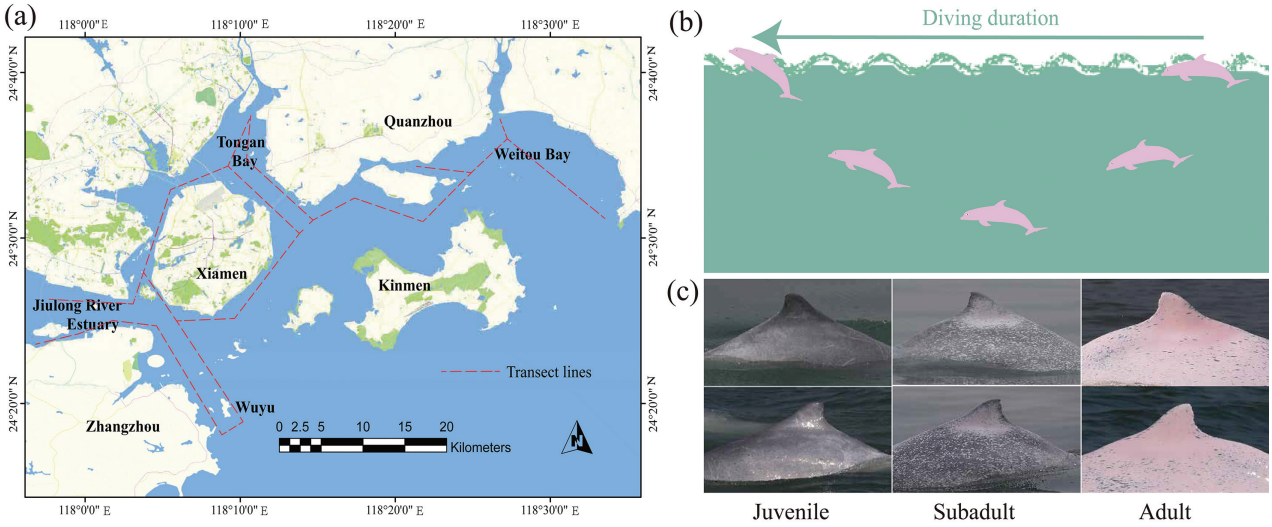

Figure 1. a. Study area in Xiamen Bay and its adjacent waters; **b.** Schematic diagram of the diving duration; **c.** Three age classes of Indo-Pacific humpback dolphins.

Age classification

Individuals were assigned to age classes based on body size and skin coloration, both of which undergo progressive changes with growth. In general, dolphin coloration develops through three broad stages. Newborns are typically dark gray to nearly black. Within a few months, their pigmentation begins to lighten, black spots gradually appear, and the skin takes on a whitish tone. Eventually, mature individuals are predominantly white, with relatively few black markings. While previous studies have proposed six detailed categories—unspotted calves, unspotted juveniles, mottled, speckled, spotted adults, and unspotted adults (Jefferson and Leatherwood 1997; Jefferson et al. 2012)—the present study employed a simplified scheme comprising three age classes: juvenile, subadult, and adult (Fig. 1c). This approach was adopted to minimize ambiguity and reduce overlap between intermediate categories.

Behavioral response

Building on previous studies, dolphin behaviors were categorized into two primary classes for analysis: traveling and foraging (Parsons 1998; Van Parijs and Corkeron 2001; Steiner 2011) (Table 1). Although further behavioral states were observed, only these two categories were included in the analyses. Because individual dolphins within the same group may respond differently to similar environmental stimuli, such as the presence of vessels (Shane 1990), behavioral data were recorded at the individual rather than the group level (Ng and Leung 2003) (Table 1). All behavioral responses were documented in real time during field surveys. To minimize disturbance, the survey vessel maintained a minimum distance of 100 m from the dolphins whenever possible. The study considered three common vessel types operating in Xiamen Bay: speedboats, fishing vessels, and cargo ships. When a vessel approached within 500 m of a dolphin, it was assumed that the animal's behavior could be influenced, and its response was recorded accordingly. The distance between the dolphins and the boat was estimated by referring to buoys and other floating objects near the dolphins. When no reference objects were available, these estimates were conducted by observers using the naked eye. In such cases, to prevent additional interference, the survey vessel either remained stationary or switched off its engines during observation. Once the dolphin had clearly moved away from the research vessel, the engine was restarted to resume tracking.

Table 1. Descriptions of behaviors observed and responses to vessels in Indo-Pacific humpback dolphins.

Behavior	Description
Traveling	Regular movement in one direction. Dolphins came together to breathe at regular intervals (sometimes long, sometimes short).
Foraging	Dolphins came to breathe separately at irregular intervals, with some long dives. Fish chasing, hitting the water surface, and changes in the general direction are often observed.
Synchronous breathing	Two or more dolphins surfaced and entered the water at the same time.
Positive	Actively approaching the vessel or boat-chasing afterwards.
Negative	Actively moving away from the vessel, i.e., boat-avoidance or fleeing away.
Neutral	No observable change in behavior; continue to perform ongoing activities.

Statistical analyses

All results are expressed as mean ± standard error (SE) and were analyzed using SPSS software (version 26). Before conducting statistical tests, data were assessed for normality and homogeneity of variance. Separate chi-square tests of independence were conducted to assess the associations between dolphin behavioral responses and (1) vessel type and (2) vessel distance category. Statistical significance was set at $P < 0.05$ for all analyses.

Results

Survey summary

Between 2017 and 2019, a total of 181 survey days were completed, generating 52,092 minutes of effective observation effort. During this period, Indo-Pacific humpback dolphins were tracked for 5,319 minutes, yielding 4,408 recorded dives. Furthermore, 3,469 individual dives and 939 synchronous breathing events were recorded. Of these, 893 dives occurred during traveling behavior, while 1,843 were associated with foraging behavior (Table 2).

With respect to age classification, 171 dives were attributed to juveniles, 751 to subadults, and 2,547 to adults (Table 2). When behavioral categories were further analyzed within age groups, juveniles showed 113 traveling events and 56 foraging events; subadults recorded 265 traveling events and 301 foraging events; and adults performed 476 traveling events alongside 1,475 foraging events (Table 2).

Diving pattern

Across all 4,408 recorded dives, the mean dive duration was 20.41 ± 1.77 s, with the majority of dives lasting less than 20 s. For both individual and syn-

Table 2. Summary of Indo-Pacific humpback dolphin dive durations.

	N	Mean ± SE (s)	*P* value
One individual	3469	20.36 ± 0.49	0.707
Synchronous breathing	939	20.56 ± 0.91	
Traveling	893	24.96 ± 1.12	0.315
Foraging	1843	21.31 ± 0.16	
Juvenile in traveling	113	15.92 ± 1.14	0.363
Juvenile in foraging	56	15.85 ± 1.34	
Subadult in traveling	265	24.48 ± 1.96	0.046
Subadult in foraging	301	19.89 ± 1.19	
Adult in traveling	476	21.75 ± 1.44	0.082
Adult in foraging	1475	21.28 ± 0.71	
Juvenile	171	15.43 ± 0.85	0.073
Subadult	751	20.54 ± 0.96	
Adult	2547	20.64 ± 0.62	
Juvenile in traveling	113	15.92 ± 1.14	0.015
Subadult in traveling	265	24.48 ± 1.96	
Adult in traveling	476	21.75 ± 1.44	
Juvenile in foraging	56	15.85 ± 1.34	0.654
Subadult in foraging	301	19.89 ± 1.19	
Adult in foraging	1475	21.28 ± 0.71	

N, number; SE, standard error.

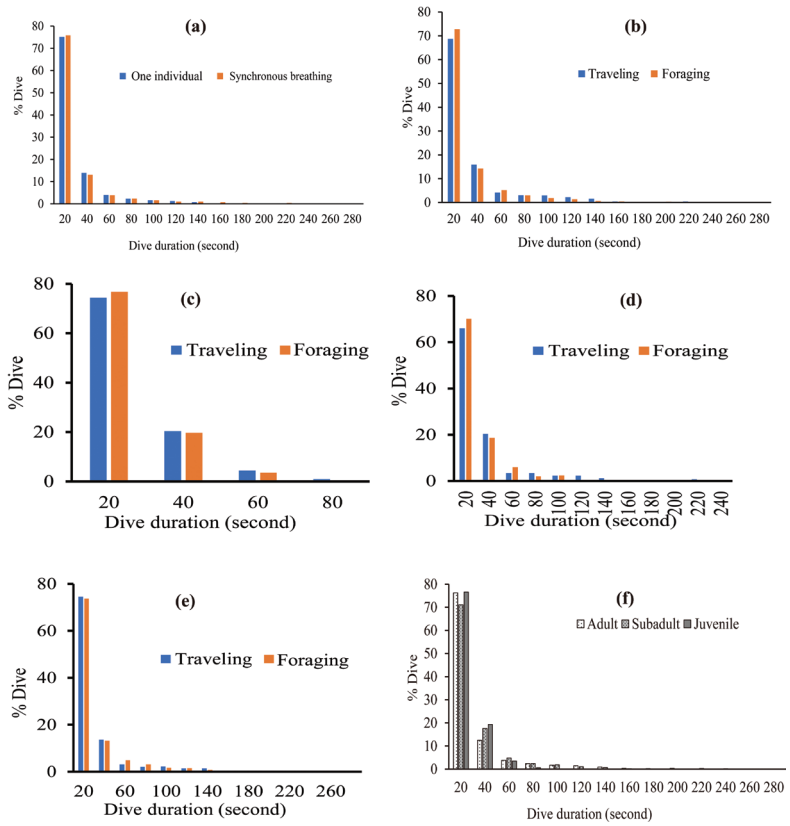

Figure 2. Histogram showing the percentage distribution of dive durations: **a.** Different dive modes; **b.** Different behavioral categories; **c.** Juvenile behavior; **d.** Subadult behavior; **e.** Adult behavior; **f.** Different age classes regardless of behavior.

chronous diving events, 75.14% and 75.83% of dives, respectively, were under 20 s (Fig. 2a). The mean durations for individual and synchronous dives were 20.36 ± 0.49 s and 20.56 ± 0.91 s, showing no significant difference between the two (Mann–Whitney *U* test, $Z = -0.376$, $P = 0.707$) (Fig. 3a; Table 2).

When examined by behavioral category, mean dive durations were 24.96 ± 1.12 s during traveling and 21.31 ± 0.61 s during foraging. This difference was not statistically significant (Mann–Whitney *U* test, $Z = -1.004$, $P = 0.315$) (Fig. 3b; Table 2). However, a large proportion of dives remained short, with 68.76% of traveling dives and 72.76% of foraging dives lasting less than 20 s (Fig. 2b).

Analysis of dive durations by age group revealed that juveniles primarily performed short dives. Specifically, 74.34% of traveling dives and 76.78% of foraging dives were shorter than 20 s (Fig. 2c). The mean durations were 15.92 ± 1.14 s for traveling and 15.85 ± 1.34 s for foraging, with no significant difference between the two behavioral categories (Mann–Whitney *U* test, $Z = -0.910$, $P = 0.363$) (Table 2).

Among subadults, 66.04% of traveling dives and 70.10% of foraging dives lasted less than 20 s (Fig. 2d). Mean durations were 24.48 ± 1.96 s during traveling and 19.89 ± 1.19 s during foraging, with dive duration during foraging significantly shorter than during traveling (*t*-test, $t = 1.998$, $P = 0.046 < 0.05$) (Table 2).

For adults, 74.58% of traveling dives and 73.69% of foraging dives were under 20 s (Fig. 2e). Mean dive durations were 21.75 ± 1.44 s for traveling and 21.28 ± 0.71 s for foraging, with no significant difference detected between the two (Mann–Whitney *U* test, $Z = -1.739$, $P = 0.082$) (Table 2).

When behavior was not taken into account, 76.61% of juvenile dives, 71.11% of subadult dives, and 76.24% of adult dives lasted less than 20 s (Fig. 2f). Mean

dive durations for the three age groups were 15.43 ± 0.85 s for juveniles, 20.54 ± 0.95 s for subadults, and 20.64 ± 0.62 s for adults. These differences were not statistically significant (Kruskal–Wallis test, $H = 5.221$, $P = 0.073$) (Fig. 3c).

When analyzed by both behavior and age, juveniles showed significantly shorter dive durations than subadults during travel (Kruskal–Wallis test, $H = 8.426$, $P = 0.015$) (Table 2). For foraging dives, however, no significant differences were detected among age groups (Kruskal–Wallis test, $H = 0.848$, $P = 0.654$) (Table 2).

Overall, an interactive effect of age and behavior on dive duration was observed when both variables were considered simultaneously (Fig. 3d).

Response to vessel traffic

During the study, 197 instances of dolphin responses to vessels were documented. Chi-square analysis revealed a significant association between dolphin responses and vessel type ($\chi^2 = 17.684$, $P = 0.001$). In most encounters, dolphins displayed neutral responses, maintaining their ongoing behavior despite the presence of the vessel. Speedboats elicited the highest rate of negative responses (68.18%) among all vessel types and typically involved abrupt directional changes or deep-diving behavior. Conversely, positive responses were rare across all vessel types (Fig. 4a).

Dolphin responses also varied significantly with vessel distance ($\chi^2 = 15.263$, $P = 0.004$). Positive responses occurred only when vessels approached within 200 m, while no negative responses were observed at distances greater than 200 m (Fig. 4b).

Discussion

The development of diving behavior in Indo-Pacific humpback dolphins

Previous research on marine mammals, including bottlenose dolphins (*Tursiops truncatus*) (Miketa et al. 2018), harbor seals *Phoca vitulina* (Bowen et al. 1999), New Zealand fur seals *Arctocephalus forsteri* (Baylis et al. 2005), and humpback whales *Megaptera novaeangliae* (Cartwright and Sullivan 2009), has consistently demonstrated that diving ability is closely linked to age. This relationship is primarily attributed to age-related increases in oxygen storage and carrying capacity, which enable longer dives as individuals approach adulthood. Our findings align with this pattern: Indo-Pacific humpback dolphins (*Sousa chinensis*) in Xiamen showed a clear age-dependent gradient in dive performance. Subadults (20.54 s) and adults (20.64 s) had significantly longer dive durations than juveniles (15.43 s), indicating physiological advancement with age. Interestingly, the mean dive duration observed in Xiamen dolphins (20.41 s) was comparable to that of the Hong Kong population (20.89 s), as recorded through land-based observations. The similarity in dive durations between Xiamen and Hong Kong suggests potential common underlying mechanisms, although the influence of environmental covariates requires further investigation.

Bottlenose dolphins typically achieve adult-like oxygen storage capacity around 3 years of age, coinciding with weaning (Mann et al. 2000; Noren and Williams 2000; Noren et al. 2002). Indo-Pacific humpback dolphins are weaned at approximately 4 years (Jefferson et al. 2012), and the comparable dive dura-

tions between subadults and adults in our study suggest that oxygen reserves may already reach near-adult levels by this stage. Before weaning, many young cetaceans begin practicing independent foraging through brief separations from their mothers (Guinet and Bouvier 1995; Gannon et al. 1997; Barbara 1999). In Shark Bay, bottlenose dolphin calves start foraging in shallow waters by 3 months of age, gradually shifting to deeper and more demanding dives as their capacity matures (Barbara 1999; Mann and Sargeant 2003; Foroughirad and Mann 2013; Miketa et al. 2018). Similarly, in the Xiamen population, juvenile dolphins showed shorter mean dive durations during foraging (15.85 s) compared with subadults

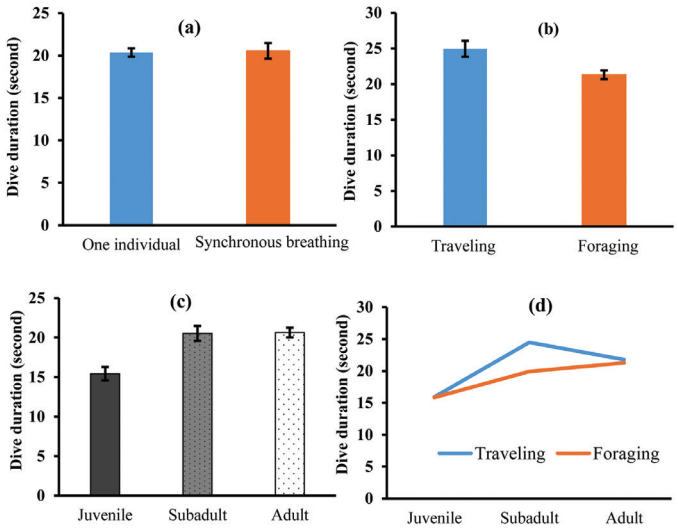

Figure 3. a. Differences in dive duration between individual and synchronous breathing; **b.** Differences in dive duration between traveling and foraging behaviors; **c.** Differences in dive durations among age classes; **d.** Interaction effects between age and behavior on dive duration.

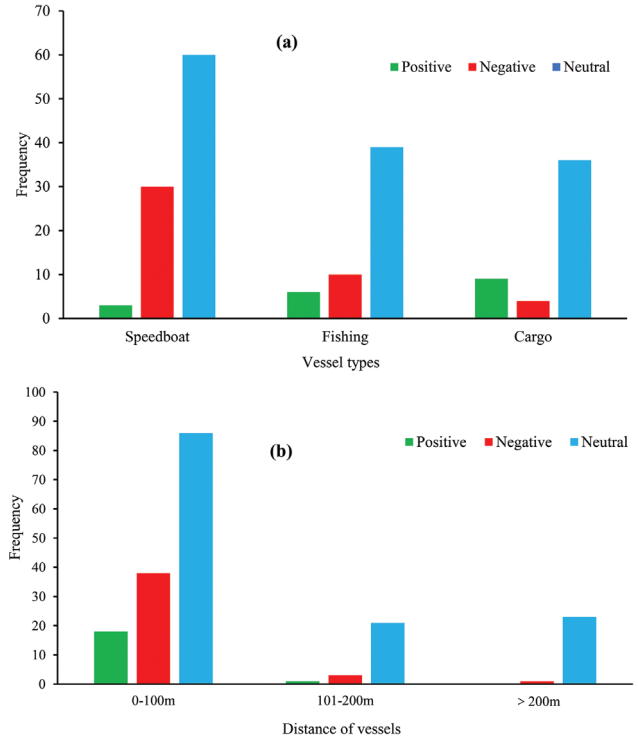

Figure 4. a. Dolphin responses to different vessel types; **b.** Dolphin responses at varying distances from vessels.

(19.89 s) and adults (21.29 s). The subadults exhibited shorter dive durations during foraging (19.89 s) compared with traveling (24.48 s). While the underlying causes require further investigation, we speculate that this pattern may reflect an age-specific trade-off between attention and foraging efficiency. Comparable observations were reported in the Hong Kong population, where younger dolphins displayed more exploratory behaviors than adults (Ng and Leung 2003).

Overall, the diving behavior of Indo-Pacific humpback dolphins in Xiamen shows strong age dependence, influenced by both physiological development and behavioral adaptation. These findings reinforce the broader understanding that maturation of oxygen storage capacity and experiential learning underpin the ontogeny of diving skills in cetaceans.

Response to vessel traffic

Heavy vessel traffic, particularly from high-speed boats, has emerged as a significant factor influencing the survival and behavior of cetaceans (Ng and Leung 2003; Chen et al. 2020; Koroza and Evans 2022). Although alterations in dive duration are often interpreted as behavioral responses to external disturbances (Würsig 1978), such measures must be applied cautiously. For example, in the Hong Kong humpback dolphin population, no significant differences in dive durations were observed among responses to vessel presence categorized as positive, neutral, or ambiguous (Ng and Leung 2003). Likewise, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) did not show clear differences in dive duration regardless of vessel proximity (Seuront and Cribb 2011). In light of these observations, the present study primarily evaluated the effects of vessel traffic on humpback dolphins through direct behavioral responses rather than changes in dive time. Distinct from some other cetacean populations, the humpback dolphins in Xiamen Bay did not display positive responses toward fishing vessels. Interactions between dolphins and fishing boats are relatively common, often arising from competition over shared resources, and in some cases may even prove advantageous for dolphins (Parsons 1998; Jia et al. 1999). For instance, in Hong Kong waters, dolphins were more frequently associated with double-trawl fishing vessels than with single-trawl or gillnet boats (Ng and Leung 2003). Two key factors likely explain the different response patterns observed in Xiamen. First, fishery resources in Xiamen Bay appear to be limited, as reflected by the absence of large fish aggregations during the survey period, reducing both competitive and mutualistic interactions between dolphins and fishermen. Second, the fishing vessels operating in this region were exclusively small-scale gillnetters, which are generally less attractive to dolphins—a trend similarly noted in the Hong Kong population.

The proximity of vessels had a pronounced effect on the behavior of dolphins. As vessels drew closer, dolphins were less likely to continue along their original trajectory and more likely to show avoidance responses, including abrupt directional changes and deep dives (Steckenreuter et al. 2011). The threshold distance that triggers such responses varies across cetacean species. For instance, bottlenose dolphins generally avoid vessels within 100 m (Nowacek et al. 2001; Lemon et al. 2006; Steckenreuter et al. 2011), whereas Hong Kong humpback dolphins frequently display negative responses at distances up to 500 m (Ng and Leung 2003). The Xiamen humpback dolphins demonstrated comparable sensitivity, showing a significant increase in avoidance behavior when vessels were within

100 m. Beyond eliciting evasive maneuvers, vessel traffic can also interfere with vital activities such as feeding and resting behaviors, which are critical for individual health, reproductive success, and long-term population viability (Gregory and Rowden 2001; Constantine et al. 2004). Previous work has shown that bottlenose dolphins substantially reduced feeding and resting when dolphin-watching boats approached within 50 m (Steckenreuter et al. 2011). Although this study did not quantify the impacts of vessels on feeding or resting in Xiamen humpback dolphins, disruptions to resting behavior were documented during field surveys.

Conservation implications

The Indo-Pacific humpback dolphins in Xiamen demonstrated complex behavioral strategies in response to vessel traffic. However, negative reactions accounted for only 22% of all documented responses, suggesting that dolphins do not consistently show proactive avoidance when vessels are present. Even within 100 m, only 27% of individuals exhibited clear avoidance behaviors, substantially increasing the risk of direct collisions or injuries, particularly from high-speed vessels. To mitigate these risks, vessel operators should maintain a minimum distance of 100 m from dolphins and strictly limit speeds to no more than 10 knots in their vicinity. In comparison, stronger law enforcement is required to ensure compliance with protective regulations. Furthermore, coordinated conservation efforts across regional jurisdictions, including Xiamen, Zhangzhou, Quanzhou, and Kinmen, are critical to safeguarding this endangered species.

Limitations of the study

Due to the behavioral diversity of Indo-Pacific humpback dolphins, some degree of observational error may have occurred during behavioral recording. Moreover, the potential influence of vessel noise and speed on dolphin responses was not quantified or systematically analyzed in this study. It is also important to note that neutral responses should not be interpreted as evidence of adaptation to vessel activities. Their long-term consequences remain uncertain and warrant further investigation, particularly regarding potential interference with acoustic communication and the disruption of essential behaviors such as resting.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Study conception and design were performed by Yi Lu and Guang Yang. Data collection and analysis were performed by Yi Lu, Haojie Zhou, Haizhou Li, and Xinrong Xu. The first draft of the manuscript was written by Yi Lu and Guang Yang, and all authors commented on previous versions of the manuscript. All authors read and approved the final version.

Data availability

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

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