frontiers | Frontiers in Mammal Science

TYPE Original Research
PUBLISHED 15 January 2026
DOI 10.3389/fmamm.2025.1712553

The dolphin tap: assessing the ecosystem role of spinner dolphins in supplying nutrients to coral reefs in Maui Nui, Hawai'i

Grace L. Olson*, Shannon M. Barber-Meyer and Jens J. Currie

Pacific Whale Foundation, Wailuku, HI, United States

EDITED BY
Pedro Manoel Galetti Jr,
Federal University of São Carlos, Brazil

REVIEWED BY
Fabio Favoretto,
University of California, San Diego,
United States
Mariana C. Neves,
Laboratório de mamíferos aquáticos e
bioindicadores/UERJ, Brazil

*CORRESPONDENCE
Grace L. Olson
graceolson@pacificwhale.org

RECEIVED 24 September 2025
REVISED 10 December 2025
ACCEPTED 15 December 2025
PUBLISHED 15 January 2026

CITATION
Olson GL, Barber-Meyer SM and Currie JJ (2026) The dolphin tap: assessing the ecosystem role of spinner dolphins in supplying nutrients to coral reefs in Maui Nui, Hawai'i. *Front. Mamm. Sci.* 4:1712553. doi: 10.3389/fmamm.2025.1712553

Introduction: Considering the ecological functioning of small cetaceans is important for ecosystem-based management and conservation, including their potential role in transporting limiting nutrients across habitats. Spinner dolphins (*Stenella longirostris longirostris*) in Hawai'i forage nocturnally on mesopelagic prey offshore and, during the day, rest and avoid predators inshore. These predictable behavioral and spatial use patterns in the Maui Nui region suggest that spinner dolphins may transfer pelagic nutrients to inshore habitats, including shallow coral reefs - a mechanism we refer to as "the dolphin tap".

Methods: To assess the role of spinner dolphins as nutrient vectors, we quantified spinner dolphin spatial overlap with inshore and coral reef habitats in Maui Nui using vessel-based survey data collected from 2013–2022. We estimated nutrient deposition using standard metabolic models, spinner dolphin distribution and temporal overlap of dolphins with coral reef habitats.

Results and discussion: We determined spinner dolphin distribution from 51 encounters. We estimated that an individual spinner dolphin deposited 0.10 kg N day^{-1} (SD = 0.02) into the overall marine environment. Dolphins overlapped with coral reef habitat during 25 encounters and 28% (SD = 36%) of total sighting time. Using daytime-only observations, we estimated an individual spinner dolphin deposited between 0.01 kg N day^{-1} (SD = 0.02) and 0.02 kg N day^{-1} (SD = 0.03) over coral reefs, depending on the extent of nighttime deposition. Individual-level annual deposition values were extended to group (mean = 65.40 individuals, SD = 45.24) and population (594 individuals) levels to quantify nutrient deposition in the overall marine environment and to coral reef habitats. This naturally occurring nutrient input from pelagic foraging grounds to inshore habitats may enhance productivity and promote coral reef resilience and health. Our findings provide baseline estimates of nutrient deposition by spinner dolphins in Maui Nui, yet additional research and monitoring are needed to better understand the nutrient dynamics. As Maui Nui's coral reefs experience stress from warming oceans, this dolphin-mediated subsidy may become increasingly important for sustaining coral reef function. Protecting spinner dolphins is therefore essential to maintaining “the dolphin tap” nutrient pathway and supporting the health of Hawai‘i’s coral reef ecosystems.

KEYWORDS

ecosystem roles, foraging, metabolic rate, nutrient transfer, *Stenella longirostris longirostris*

Introduction

Spinner dolphins (*Stenella longirostris)* are an abundant, small odontocete species that is distributed throughout tropical and subtropical oceans worldwide (Perrin, 1998). In the Hawaiian Island archipelago, spinner dolphins (*S. l. longirostris*) are island-associated, inshore dolphins that are genetically distinct from other populations in the Pacific Ocean (Andrews et al., 2010). Spinner dolphins in Main Hawaiian Islands (MHI) waters exhibit a distinct diurnal pattern of resting and avoiding predators inshore during the day and foraging offshore at night (Norris and Dohl, 1980; Norris et al., 1994; Benoit-Bird and Au, 2003; Stack et al., 2020). The predictable use of inshore waters during the day in the MHI makes spinner dolphins highly susceptible to disturbances from tourism, including pressure from vessels that target dolphins for wildlife viewing and swim-with-dolphin opportunities (Tyne et al., 2018; Wiener et al., 2020). Spinner dolphins off Hawai‘i Island have one of the highest exposure rates to anthropogenic activities of all cetaceans and are exposed to human activities for >82% of the day (Tyne et al., 2018). Such human activities can cause spinner dolphins to be displaced from their preferred resting areas and may interrupt resting behavior (Tyne et al., 2014, 2017). In 2021, to minimize impacts of tourism, National Oceanic and Atmospheric Association (NOAA) implemented a 50-yard (43 meter) approach limit for humans and boats regarding spinner dolphins within two nautical miles of shore (NOAA, 86 FR 53818). Despite these protections, the proximity of spinner dolphins to the human-populated MHI brings additional anthropogenic-based threats of high concern for these island-associated populations of dolphins, due to their limited movements, distribution, and specialized behavior (e.g., Tyne et al., 2014, 2015; New et al., 2020).

Spinner dolphins in the MHI forage offshore at night on prey that are part of a mesopelagic boundary community of small fish, squid and shrimp that undergo a vertical and horizontal migration through the night and can be encountered as shallow as 100 meters (m) (Reid et al., 1991; Reid, 1994). Previous research found that spinner dolphins cooperatively hunt the high-density boundary prey community between 8 kilometers (km) and 1–1.5 km from the coast, diving to depths up to 150 m (Benoit-Bird and Au, 2003; Benoit-Bird, 2009). Through their role as a top marine predator, spinner dolphins can also serve as an ecosystem sentinel by exhibiting responses to ecosystem and environmental changes that can otherwise be difficult to observe (Hazen et al., 2019). The ecological roles that species can play may be more diverse than predator-prey dynamics and vary in the degree of contribution, where sometimes the ‘ecological importance’ of a species can lead to community or ecosystem level consequences with changes in abundance (Kiszka et al., 2015, 2022). However, there are gaps in our understanding of any additional roles spinner dolphins in MHI may have in maintaining marine ecosystem functioning (Kiszka et al., 2022), as most previous research on spinner dolphins in the MHI concentrated on other ecological factors like distribution and behavior (e.g., Norris and Dohl, 1980; Tyne et al., 2015).

Much of the extensive research on spinner dolphins within the MHI focused on the daily use of coastal waters and bays for resting by spinner dolphins off Hawai‘i Island and O‘ahu, where steep slopes equate to deeper foraging waters in close proximity to the islands (Norris and Dohl, 1980; Lammers, 2004; Tyne et al., 2015). These studies determined that spinner dolphin-preferred daytime resting habitat was shallow bays sheltered from wind, with sandy substrate that provided better visual detection of predators and was also near their nighttime foraging waters (Norris and Dohl, 1980; Tyne et al., 2015). More recent studies on the distribution of spinner dolphins in a different area of the MHI, the Maui Nui or 4-Islands region, including waters surrounding Maui, Lāna‘i, Moloka‘i, and Kaho‘olawe islands, determined that the dolphins utilized the area differently (Stack et al., 2020; McElligott and Lammers, 2021). The overall shallow bathymetry in the channels separating the four islands in Maui Nui and the leeward protection from wind provide suitable habitat for spinner dolphins to not only rest in protected bays, but also to utilize the relatively shallow channels for resting and traveling throughout the day (Stack et al., 2020; McElligott and Lammers, 2021).

In addition to the differences in habitat use by spinner dolphins between several of the MHI, research based on photo-identification data and genetic testing found low gene flow between island-associated spinner dolphins off islands that are separated by deep ocean channels (Andrews et al., 2010). Correspondingly, NOAA delineated these island-associated dolphins into five management stocks: Kaua‘i/Ni‘ihau stock, O‘ahu/4-islands stock, Hawai‘i stock, Pearl and Hermes Reef stock, and Midway Atoll/Kure stock (Andrews et al., 2010; Hill et al., 2010). Our study focused on dolphins included in the Oʻahu/4-islands stock, specifically those using waters in the Maui Nui region (Figure 1). The abundance estimate for spinner dolphins in the Oʻahu/4-islands stock is currently considered unknown due to a lack of updated data (Carretta et al., 2022). Within the Oʻahu/4-islands stock boundary, the most recent abundance estimate of spinner dolphins was from the island of Oʻahu and was 594 individuals (95% CI [360, 980]), using distance-sampling data collected between 2020 and 2022 (Lacey et al., 2025). This estimate is considered a constant estimate and does not account for seasonality (Lacey et al., 2025).

Despite the location of the MHI in the oligotrophic North Pacific Ocean, inshore waters utilized by stocks of island-associated spinner dolphins during the day also contain productive habitats, including coral reef communities (Grigg, 1988). Coral reef communities in the MHI mainly consist of shallow fringing reefs, with some pinnacle and patch reefs, that support a diverse ecosystem with many endemic species (Friedlander et al., 2005). The higher diversity and productivity found on coral reefs in the MHI are partially driven by the ‘island mass effect’ which results in a general increase in nearshore nutrient conditions from mechanisms such as upwelling, current mixing, and natural and anthropogenic nutrients influx (Grigg, 1988; Gove et al., 2016). Coral species worldwide and in the MHI can further thrive in otherwise nutrient-limited waters (i.e., nitrogen, phosphorus), by relying on a symbiotic relationship with the microalgae species zooxanthellae that uptake nutrients from the water column for primary production (Dubinsky and Jokiel, 1994). Productivity on coral reefs can also be supplemented by natural nutrient input from other species, as has been described for local coral reef communities off Oʻahu with populations of seabirds (Honig and Mahoney, 2016). Presently, the nutrient input connection between spinner dolphins and larger ecosystems in the MHI, including coral reef communities, remains unknown.

Based on their known diurnal behavioral patterns and regular use of inshore waters, spinners dolphins likely play a role in ecosystem functioning by facilitating the translocation of limiting nutrients from productive deep scattering layers where they forage to inshore habitats where they rest, resulting in increased inshore primary production (Kiszka et al., 2022). Several large whale species have been described as nutrient vectors, as they forage in deep water and release fecal plumes and urinate while at the surface due to a higher metabolism and decreased hydrostatic pressure in shallow waters (Kooyman et al., 1981; Katona and Whitehead, 1988). These waste releases can deposit significant amounts of nutrients in bioavailable forms (e.g., ammonium NH_4^+) in surface water environments which stimulate primary productivity, a process referred to as ‘the whale pump’ (Roman and McCarthy, 2010; Roman et al., 2014). However, there are limited data to confirm the pathway through smaller cetaceans, like spinner dolphins (Kiszka et al., 2022). Letessier et al. (2022) investigated the potential ecological role of spinner dolphins providing nutrients that may enrich primary productivity for coral growth in atoll lagoon reef systems, determining that an average local spinner dolphin group may contribute subsidies estimated at 1,294 kilograms (kg) of nitrogen annually (kg N year^{-1}) in the Maldives archipelago and 288 kg N year^{-1} in the Chagos archipelago (Letessier et al., 2022).

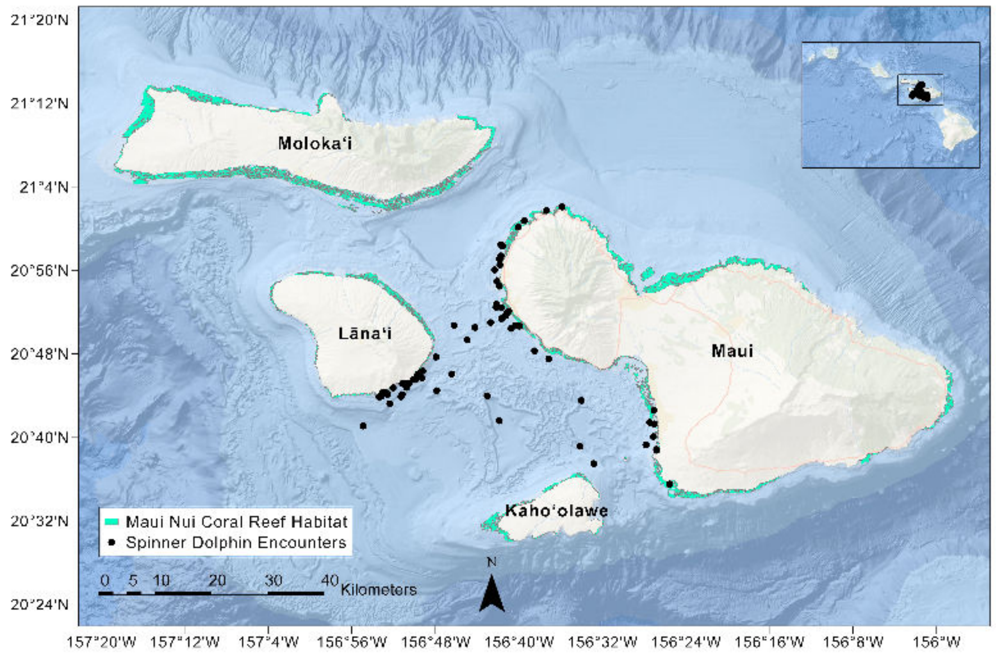

FIGURE 1
Location of spinner dolphin (*Stenella longirostris longirostris*) encounters analyzed from 2013–2022 and mapped coral reef habitat in the Maui Nui region, Hawaiʻi. Geospatial shapefile data for mapping coral reef habitat obtained from National Oceanic & Atmospheric Administration (NOAA), National Ocean Service (NOS) and National Centers for Coastal Ocean Science (NCCOS) project: Mapping of Benthic Habitat for the Main Eight Hawaiian Islands (Battista et al., 2007).

The prevalence of spinner dolphins and their predictable use of inshore regions in Maui Nui (Stack et al., 2020) with known coral reef habitats suggests that the dolphin population may contribute to the functioning of coral reef ecosystems via a mechanism we refer to as "the dolphin tap" by enhancing coral health through the deposition of limiting nutrients, such as nitrogen, that are needed for primary production (e.g., Shantz and Burkepile, 2014; Savage, 2019; Allgeier et al., 2020). To gain insight into the role of nearshore small cetaceans on ecosystems in a changing marine environment, we assessed the spatial use of spinner dolphins in Maui Nui and estimated nutrient deposition from dolphins transferred into the overall marine environment and to coral reefs via proportion of time they overlapped with coral reef habitat and standard metabolic models.

Methods

Study area

The study area consisted of waters surrounding the four islands of Maui, Lānaʻi, Kahoʻolawe, and Molokaʻi, known as the Maui Nui or 4-Islands region of Hawaiʻi. The area surveyed encompassed 7,186 square kilometers (km^2) and largely comprised leeward and shallow water channels, predominately less than 200 m in depth, which were once land bridges connecting the four islands (Grigg et al., 2002). Additionally, we surveyed the windward side of the Maui Nui islands and deeper offshore waters south of Maui, Lānaʻi, and Kahoʻolawe that range up to 2,992 m in depth (Figure 2). The bottom topography of the channels between the islands consists of ridge crests, basins, pinnacles and sand plains, with areas of live benthic cover, such as mesophotic coral and macroalgae also persisting at depths up to 130 m (Grigg et al., 2002; Kahng et al., 2016). The four islands of Maui Nui protect sections of coastline between the islands from large open ocean waves and provide ideal locations for coral reef development (Field et al., 2019). Within Maui Nui, the largest and most complex coral reefs in the MHI are found primarily in leeward shallow waters, as the most substantial reef accretion and coral growth occurs in depths < 30 m with low wave energy (Storlazzi et al., 2005; Field et al., 2019). Shallow water coral reef structure covered 258.91 km^2 throughout the Maui Nui region (Battista et al., 2007), representing 4% of our study area.

Data collection

We collected data from a 7.92 m research vessel from 7 February 2013 to 18 November 2022. A combination of systematic and nonsystematic research surveys (Stack et al., 2019) and line-transect methodologies (Currie et al., 2017) were used for multi-species cetacean surveys. While on surveys, a minimum of two observers (port and starboard) and the captain continuously scanned over a 180-degree field of vision to detect dolphins resulting in 360-degree coverage, while an additional crew member acted as a data recorder. We conducted on-effort surveys only when sea conditions were Beaufort Sea State 3 or less. During surveys, when dolphins were encountered, we initiated a focal follow to confirm the species, collected data on group size (number of animals, recorded as minimum, best, maximum estimations), group composition (estimated number of adults,

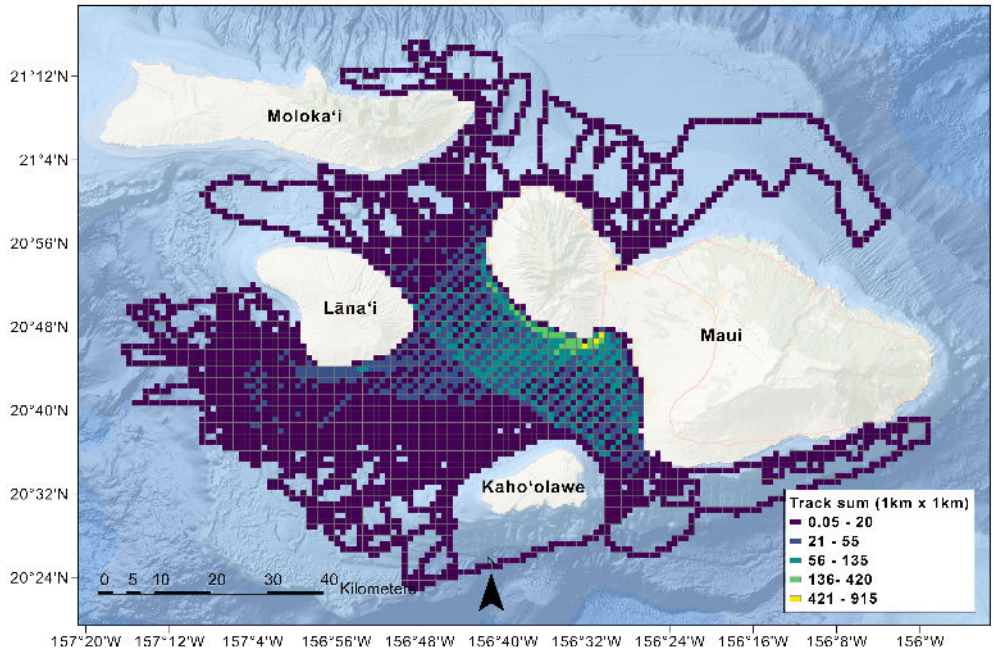

FIGURE 2
Map depicting the grid density (1 km x 1 km) of total km traveled per grid cell during vessel surveys from 2013–2022 in Maui Nui, Hawaiʻi.

sub-adults, and calves), and photo-identification data. At the start and the end of an encounter with a group of dolphins, we collected a waypoint using a Garmin GPSMAP78 handheld Global Positioning System (GPS) to represent the location (latitude and longitude) and the GPS further recorded a track of the vessel throughout the encounter, with vessel movements generally optimized for photo-identification. Additionally, from 2013–2016 we documented the group spread distance (m) for each spinner dolphin encounter, by estimating the farthest points visible of the group by eye. To maximize our sample for this analysis, we included both on- and off-effort encounter data. Off-effort encounters occurred during active encounters with another group or species, while transiting between line transects, or when weather conditions were not ideal.

Data analysis

Spinner dolphin distribution

We quality controlled the GPS tracks from the research vessel surveys and the waypoint locations of spinner dolphin encounters for location errors and corrected or removed errors as applicable. We examined locations of all encounters by effort type, to ensure that off-effort encounters reflected the same general spatial distribution as on-effort encounters. To visualize spatial variation in overall survey effort, we set 1 km x 1 km grid cells through the survey area and summed the vessel track distance (km) per grid cell. Then, using a custom R-script (R Core Team, 2024) we pulled track segments for duration of each spinner dolphin focal follow based on the start and end encounter waypoints. The track segments represented a proxy for spinner dolphin distribution and reflected time spent during each encounter with a group of dolphins. We imported the track segments of each encounter into ArcGIS (v. 10.8.2; ESRI 2021) using a WGS 1984 World Mercator projection and WGS 1984 datum.

Coral distribution

We obtained geospatial shapefile data for benthic habitat in the Maui Nui region from the National Oceanic & Atmospheric Administration (NOAA), National Ocean Service (NOS) and National Centers for Coastal Ocean Science (NCCOS) project: Mapping of Benthic Habitat for the Main Eight Hawaiian Islands (Battista et al., 2007). These data included classifications of the biological cover of nearshore habitat up to 30 m depth using satellite imagery and site ground validation, representing the region with a minimum mapping unit of 1 acre (4,046.86 m^2) (Battista et al., 2007). We imported the data into ArcGIS and edited the shapefile to delineate the presence of coral by selecting only structure features classified as 'coral reef and hardbottom', with biological covers of live coral greater than 10 percent. The resulting coral reef habitat shapefile represented colonized biological coastal habitat and consisted of areas of potential coral recruitment within our study area (Battista et al., 2007).

Dolphin-coral overlap

Our spatial analysis of the overlap of spinner dolphins with coral reef habitat included the waters off primarily leeward Maui and Lāna'i, where the majority of our surveys were conducted (Figure 2). The coral reef and hardbottom structures of the coral reef habitat covered 129.34 km^2 along the shoreline of Maui and Lāna'i islands. To assess the spatial overlap of spinner dolphin groups with coral reef habitat, we overlaid the vessel track segments from both on and off-effort 2013–2022 spinner dolphin encounters on the coral reef habitat shapefile in ArcGIS (Figure 3). Our vessel's location was not an exact representation of the location of all dolphins in the group. Therefore, to aid in the estimation of whether the group passed over coral reef habitat, we centered a buffer on the vessel track segment that was derived from the group spread distances estimated during 2013–2016 as noted above. We considered the buffered track a proxy for dolphin location during our encounters. To quantify uncertainty around the group spread distances, we performed 100,000 bootstrap iterations to generate a group spread distribution. We assessed the sensitivity of our overall results to the buffer distance by applying 3 distinct buffer distance values representing the 25%, 50%, and 75% quartiles of the bootstrapped distribution. We then tallied the minutes (min) for each encounter when the buffered vessel tracks intersected with the mapped coral reef habitat using the GPS timestamps to calculate overlap duration. We divided this "time over coral" by the total time for each encounter to calculate an overlap proportion for each encounter. We calculated these overlap proportions for all encounters for each of the 3 buffered track distances (i.e., the values from the 25%, 50%, and 75% quartiles).

Spinner dolphin estimated nutrient deposition

To estimate nutrient deposition of spinner dolphins into the overall marine environment in Maui Nui, we approximated the daily prey consumption using standard metabolic theory scaled by species as per Letessier et al. (2022). It is important to note that there are no direct measurements for the field metabolic rate of spinner dolphins, or the assimilation efficiency and nitrogen content in prey consumed in the spinner dolphins' diet in Hawai'i. Therefore, we used previously published values of the most similar information available (Table 1), incorporating and propagating error where possible via a Monte Carlo simulation using 100,000 iterations (Annan, 1997).

We used a spinner dolphin mass (M) of 58.5 kg for spinner dolphins in Hawai'i (as seen in Norris and Dohl, 1980) to calculate basal metabolic rate (BMR) with the following equation (Kleiber, 1975):

$$\mathrm{BMR} = 293.1\mathrm{M}^{0.75}$$

As BMR represents only the minimum amount of energy an organism needs to sustain life while at rest, we also calculated the field metabolic rate (FMR) to account for the higher metabolic requirements of marine mammals needed for energy expenditure

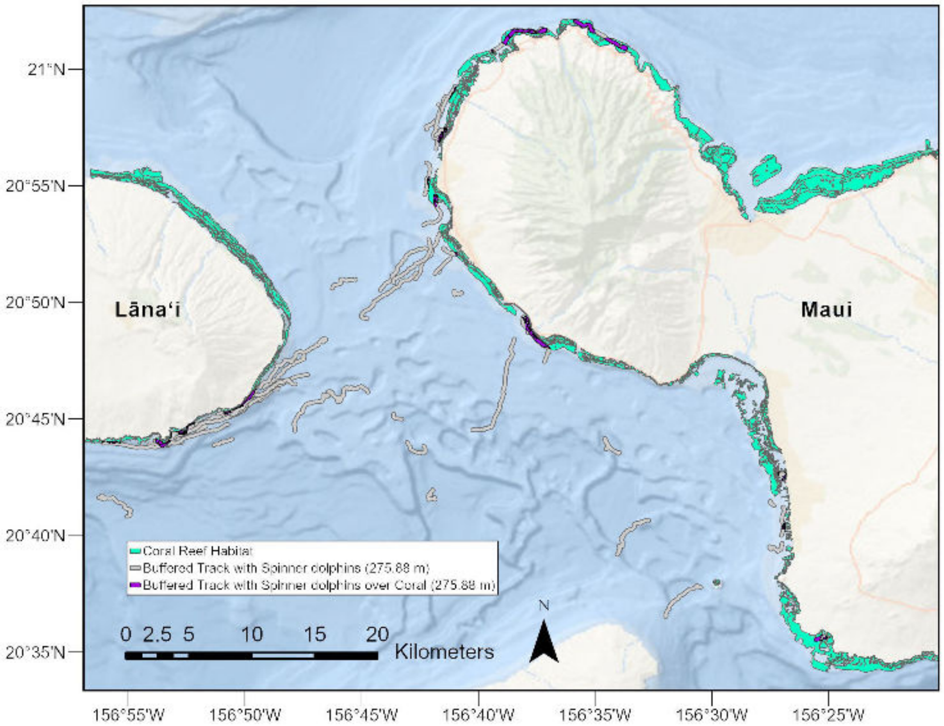

FIGURE 3
Subset of study area around Maui and Lāna'i with spinner dolphin (*Stenella longirostris longirostris*) and coral reef habitat overlap represented by buffered vessel tracks (275.88 m) from spinner dolphin encounters analyzed from 2013 – 2022. Geospatial shapefile data for mapping coral reef habitat obtained from National Oceanic & Atmospheric Administration (NOAA), National Ocean Service (NOS) and National Centers for Coastal Ocean Science (NCCOS) project: Mapping of Benthic Habitat for the Main Eight Hawaiian Islands (Battista et al., 2007).

and additional energy required to move and survive (Noren and Rosen, 2023). For each iteration, a BMR multiplier was sampled from a Normal distribution with mean = 3.52 and SD = 0.62 (Noren and Rosen, 2023). This sampled value was then multiplied by the BMR to calculate the FMR for that iteration, allowing for the propagation of uncertainty into the subsequent deposition calculations. The average daily (24-hr) ration (ADR) (kg day^{-1}) of spinner dolphin prey consumption was then estimated by converting the energy requirements of FMR to the wet weight of prey items (Barlow et al., 2008). In the calculations for the ADR (see equation below), the energy densities for spinner dolphin prey items were based on the literature and set to be 3900 kJ kg^{-1} for crustaceans and 5450 kJ kg^{-1} for squid and fish (Leaper and Lavigne, 2007). For ADR, the proportion of crustaceans in the diet of spinner dolphins (Z) was set as 7% (Dolar et al., 2003) and included an assimilation efficiency of 80% (Leaper and Lavigne, 2007).

$$\text{ADR} = \frac{FMR}{(0.8[3,900(Z) + 5,450(1 - Z)])}$$

From the ADR, we estimated daily (24-hr) nitrogen deposition into the overall marine environment per spinner dolphin (N_{dep}), utilizing the typical proportion of nitrogen (N_{prey}; set at 2.5%; Boyd, 1999) in the prey consumed by dolphins, of which 80% is metabolized and therefore may be egested (N_{met}; set at 80%; Gaskin, 1982).

$$N_{dep} = (\text{ADR})(N_{prey})\,(N_{met})$$

The metabolic nutrient deposition calculations in the overall marine environment were on a 24-hr scale, and all estimates were considered for adult spinner dolphins, assuming all individuals deposited at the same rate, without costs from reproduction or growth. To determine the annual nitrogen deposition (N_{depY}) for an individual spinner dolphin into the overall marine environment, we multiplied the daily 24-hr estimate by 365 days (Table 2). We similarly calculated nitrogen deposited annually (N_{depY}) into the marine environment by a spinner dolphin group for each of the iterations by multiplying the annual deposition of an individual dolphin estimate by a group size sampled from a log-Normal distribution (derived from natural-scale mean = 65.40 and SD = 45.24) to enforce non-negativity and to account for positive skew in the observed data (Table 2). Due to the absence of population level estimates of spinner dolphins in the O'ahu/4-islands stock or within the Maui Nui region of the stock where our study occurred, we illustrated annual nutrient deposition on a population level into the overall marine environment by utilizing spinner dolphin population data collected from part of the stock's known distribution. For this illustrative population-level example, we multiplied the annual individual nutrient deposition estimate by the distance-sampling point estimate of spinner dolphin abundance from around the island of O'ahu, 594 individuals (95% CI [360, 980]) (Lacey et al., 2025) (Table 2). Given distance-sampling often

TABLE 1 Parameters used for estimating spinner dolphin (*Stenella longirostris longirostris*) nitrogen input in Maui Nui, Hawai'i.

Parameter	Unit	Equation	Value (SD)	Citation
Body size spinner dolphin adult in Hawai'i (M)	kg	NA	58.5 (N/A)	Middle range of mass adult spinner dolphins 55–62 kg (Norris and Dohl, 1980)
Basal metabolic rate (BMR)		BMR= 293.1 M $^{0.75}$	6,199.87 (N/A)	(Kleiber, 1975)
Field metabolic rate (FMR)		BMR x (metabolic multiplier)	21,826.69 (3,845.15)	Multiplier rate = 3.52 (SD = 0.62) (Noren and Rosen, 2023)
Proportion crustaceans in diet (Z)	%	NA	7 (N/A)	(Dolar et al., 2003)
Average daily ration (ADR) (Adjusted for assimilation efficiency 80%)	kg wet weight d^{-1}	$\mathrm{ADR} = \frac{FMR}{(0.8[3,900(Z) + 5,450(1 - Z)])}$ $Z = 0.007$ *3900 kJ kg^{-1} for crustaceans* *5450 kJ kg $^{-1}$ for fish and squid*	5.02 (0.88)	(Leaper and Lavigne, 2007)
Proportion nitrogen in prey N_{prey}	%	NA	2.5 (N/A)	(Gaskin, 1982)
Proportion nitrogen metabolized N_{met}	%	NA	80 (N/A)	(Boyd, 1999)
Daily nitrogen deposited per spinner dolphin N_{dep}	kg N d^{-1}	(ADR) (0.8) (0.025)	0.10 (0.02)	Letessier et al., 2022

results in wide confidence intervals (e.g., Bradford et al., 2021), we elected not to incorporate the distance-sampling study error into our deposition calculation for this illustrative example, instead relying on the point estimate for scaling up nutrient deposition.

We then estimated individual spinner dolphin daily nitrogen deposition (mean, SD) over coral reef habitat, by first multiplying the 24-hr (N_{dep}) value for the overall marine environment by 0.5 to account for our surveys occurring during daytime only (12-hr), when spinner dolphins are known to utilize inshore habitat for resting and socializing (e.g., Norris and Dohl, 1980; Norris et al., 1994). We then multiplied that result for each iteration by an overlap proportion sampled from a zero-inflated Beta distribution (Ospina and Ferrari, 2010) based on the overlap proportions from each of the encounters calculated for each buffered track distance. The 12-hr daytime result represented our "low" estimate nitrogen deposition (N_{corLow}) that would occur during a 24-hr period (i.e., a "daily" rate), assuming no additional deposition occurred during nighttime. We followed this same procedure to calculate a "mid" estimate ($N_{corMid)}$ if the daytime overlap deposition rate extended to ¼ of the nighttime hours (i.e., 15-hr total) but multiplied the 24-hr value by 0.625 (instead of 0.5). The same method was used for our "high" estimate ($N_{corHigh)}$ but multiplied by 0.75 (i.e., 18-hr total; the daytime rate extended through ½ of the nighttime hours). We considered these example estimates of the probable range of nutrient deposition from spinner dolphins. Since behavioral observations show that spinner dolphins typically forage offshore during the night (Norris and Dohl, 1980; Benoit-Bird and Au, 2003), the true 24-hr deposition rate over coral reef habitat would be less than extending the 12-hr deposition rate for 24-hr. We similarly scaled the deposition estimates over coral reef habitat up to annual deposition per spinner dolphin, annual deposition per spinner dolphin group, and annual deposition at a population level, as per above (Table 2).

Results

Survey effort

From 7 February 2013 to 18 November 2022, we traveled 57,300 km across 429 dolphin surveys. During that time, we encountered 51 spinner dolphin groups in the focal area of our study (Figure 3). We found no clear spatial differences based on encounter type, of which 34 encounters were on-effort and 17 were off-effort. The best group size estimates ranged from 3 to 200 animals, and the mean group size was 65.4 (SD = 45.24) individuals. Over the ten-year study, encounter times with spinner dolphins ranged from 3 mins to 98 mins, and averaged 41 mins. When pooling encounter dates across years, spinner dolphin encounters occurred in all months of the year (Figure 4). Using the group spread data from 15 encounters during 2013– 2016, we determined the median of the bootstrapped group spread mean was 275.88 m (SD = 46.66) (25% quartile of mean distribution = 245.29 m; 75% quartile of mean distribution = 308.24 m). Given the similarities in results across these three group spread distances, below we report only the results of the 50% (275.88 m) quartile, with the 25% and 75% quartile results available in Supplementary Materials (Supplementary Tables S1, S2; Supplementary Figures S1, S2).

Spatial analysis of spinner dolphin distribution and overlap with coral reef habitat

We analyzed GPS tracks from 51 spinner dolphin encounters totaling 1,339 min during daytime (12-hr) when dolphins could be visually sighted (720 mins/day). Most encounters occurred either in the channel between the islands of Maui and Lānaʻi or were concentrated on the southeast Lānaʻi and west Maui coast. When determining the spatial overlap of spinner dolphins and coral reef using the 275.88 m buffered track, we found 25 spinner dolphin encounters overlapped coral reef habitat around Maui and Lānaʻi (Figure 5). At this buffer distance, spinner dolphin time over coral reef habitat ranged from 1–60 min, over 28% (SD = 36%) of the total time we observed spinner dolphin groups.

Spinner dolphin estimated nitrogen deposition

Using the metabolic calculations for FMR and ADR (see Table 1) we estimated that an individual spinner dolphin in Maui Nui deposited a daily mean of 0.10 (SD = 0.02) kg N day^{-1} (24-hr) and an annual mean of 36.62 (SD = 6.45) kg N year^{-1} into the overall marine environment (Table 2). The mean annual estimated nitrogen deposition into the marine environment was 2,397.34 (SD = 1,734.17) kg N year^{-1} from a group of spinner dolphins in Maui Nui and was 21,750.84 (SD = 3,831.79) kg N year^{-1} when scaled up to the illustrative population.

Using daytime-only observations (i.e., 12-hr deposition rate) as the low estimate for spinner dolphin coral reef overlap with the 275.88 m buffered on the track, the mean daily deposition of

TABLE 2 Calculations for spinner dolphin (*Stenella longirostris longirostris*) nitrogen input in Maui Nui, Hawaiʻi.

24-hour scale	Spinner dolphin individual daily	Spinner dolphin individual annual	Spinner dolphin group annual average group size = 65.40 (SD = 45.24) individuals	Spinner dolphin population annual O'ahu population estimate 594 (Lacey et al., 2025)
Equations	N_{dep}	(N_{dep}) (365) = N_{depY}	(N_{depY}) (group size) =	(N_{depY}) (594) =
Estimated nitrogen deposited in the overall marine environment Mean (SD)	0.10 (0.02) kg N day^{-1}	36.62 (6.45) kg N year^{-1}	2,397.34 (1,734.17) kg N year^{-1}	21,750.84 (3,831.79) kg N year^{-1}
Low estimate of nitrogen deposited over coral reef N_{corLow} Mean (SD) Low 24-hr deposition; no nighttime deposition 12-hr deposition = 24-hr rate x (0.5) x coral overlap proportion	(N_{dep}) (0.5) (coral overlap proportion) =N_{corLow}	(N_{corLow}) (365) = $N_{corYLow}$	($N_{corYLow}$) (group size) =	($N_{corYLow}$) (594) =
	0.01 (0.02) kg N day^{-1}	5.19 (6.83) kg N year^{-1}	340.12 (591.95) kg N year^{-1}	3,081.60 (4,058.07) kg N year^{-1}
Mid estimate of nitrogen deposited over coral reef N_{corMid} Mean (SD) Mid 24-hr deposition; nighttime deposition at daytime rate during ¼ of night 15-hr total deposition = 24-hr rate x (0.625) x coral overlap proportion	($Ndep$) (0.625) (coral overlap proportion) = N_{corMid}	(N_{corMax}) (365) = $N_{corYMid}$	($N_{corYMid}$) (group size) =	($N_{corYMid}$) (594) =
	0.02 (0.02) kg N day^{-1}	6.48 (8.54) kg N year^{-1}	425.15 (739.94) kg N year^{-1}	3,852.00 (5.072. 59) kg N year^{-1}
High estimate of nitrogen deposited over coral reef $N_{corHigh}$ Mean (SD) High 24-hr deposition; nighttime deposition at daytime rate during 1/2 of night 18-hr total deposition = 24-hr rate x (0.75) x coral overlap proportion	(N_{dep}) (0.75)(coral overlap proportion) = $N_{corHigh}$	(N_{corUp}) (365) = $N_{corYHigh}$	($N_{corYHigh}$) (group size) =	($N_{corYHigh}$) (594) =
	0.02 (0.03) kg N day^{-1}	7.78 (10.25) kg N year^{-1}	510.20 (887.93) kg N year^{-1}	4,622.40 (6,087.11) kg N year^{-1}

Spinner dolphin nitrogen deposition over coral reef habitat was estimated based on the overlap of coral and the buffered vessel tracks (buffer distance = 275.88 m; 50% quartile of the bootstrapped group spread distribution).

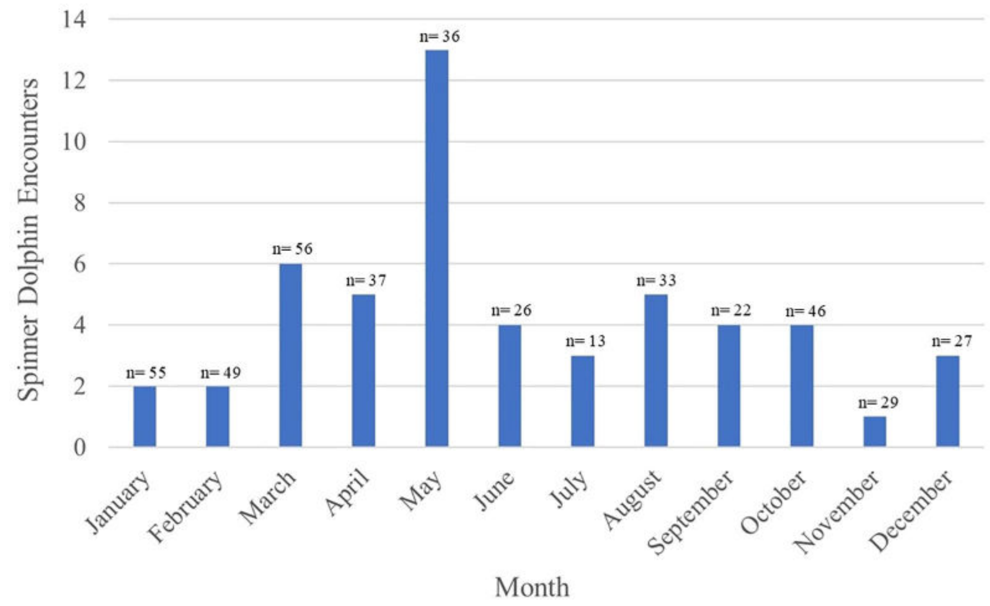

FIGURE 4
Monthly count of spinner dolphin (*Stenella longirostris longirostris*) encounters analyzed from Maui Nui region (n= number of surveys per month), pooled across years from surveys conducted during 2013 – 2022.

nitrogen from a single spinner dolphin over coral reef habitat around Maui and Lānaʻi was 0.01 (SD = 0.02) kg N day^{-1} and 5.19 (SD = 6.83) kg N year^{-1} (Table 2). The low (12-hr) rate estimation for annual deposition from a spinner dolphin group over coral reef habitat with the same buffer distance was 340.12 (SD = 591.95) kg N year^{-1} and the deposition at a population level was 3,081.60 (SD = 4,058.07) kg N year^{-1}. The estimates for individual spinner dolphin deposition over coral reef habitat extending into nighttime hours (N_{corMid}) and ($N_{corHigh}$) were 0.02 kg N day^{-1} (SD = 0.02) and 0.02 kg N day^{-1} (SD = 0.03), respectively. The annual estimates for an individual spinner dolphin over coral reef were 6.48 kg N year^{-1} (SD = 8.54) at the mid estimate and 7.78 kg N year^{-1} (SD = 10.25) at the high estimate. We estimated a group of spinner dolphins would annually deposit 425.15 kg N year^{-1} (SD = 739.94) at the mid estimate and 510.20 kg N year^{-1} (SD = 887.93) for a high estimate. The population level mid estimate for spinner dolphin nutrient deposition over coral reef was 3,852.00 kg N year^{-1} (SD = 5,072.59) and the high estimate was 4,622.40 kg N year^{-1} (SD = 6,087.10) (Table 2). See Supplementary Material for nutrient deposition based on 25% (245.29 m; Supplementary Table S1, Supplementary Figure S1) and 75% (308.24 m; Supplementary Table S2; Supplementary Figure S2) quartile buffered track distances.

Discussion

In this study we assessed the potential for spinner dolphins to contribute nutrients into the marine environment including over the coral reef habitats around the islands of Maui and Lānaʻi using spatial and temporal overlap with coral reefs and estimates of nitrogen deposition based on standard metabolic models. Based on their spatial and temporal distribution in Maui Nui, we found that a spinner dolphin may deposit an estimated 36.62 (SD = 6.45) kg N year^{-1} into the marine environment. This provides a pathway for spinner dolphins to serve as a nutrient vector when overlapping with coral reef habitats, with a low estimate nutrient deposition from an individual dolphin over coral reefs of 5.19 (SD = 6.83) kg N year^{-1}.

The spatial distribution of spinner dolphins in this study aligns with previous studies in the Maui Nui region (Stack et al., 2020; McElligott and Lammers, 2021) indicating the use of a variety of habitats that differ from the other MHI (Norris and Dohl, 1980; Lammers, 2004; Tyne et al., 2015). In this study, all spinner dolphin encounters occurred in the inshore waters in the channels and along the coasts of Maui and Lānaʻi, where any pelagic nutrient inputs from spinner dolphins into the overall marine environment would bring benefits through the promotion of primary production from phytoplankton biomass (Gove et al., 2016). Further, spinner dolphins' use of the inshore Maui Nui basin channels also overlaps with large areas of other biological benthic cover, including mesophotic reefs and macroalgae assemblages, at depths > 30 m that cannot be mapped by satellites (Battista et al., 2007; Kahng et al., 2016). These ecologically important communities were not considered here, yet likely could also be supported by nutrients transported by spinner dolphins (Kahng et al., 2016), since the density and consistency of marine mammal fecal plumes vary and can be dispersed by either floating or sinking in the water column (Parsons et al., 2003). Additional trophic connections between spinner dolphins and reef fish were

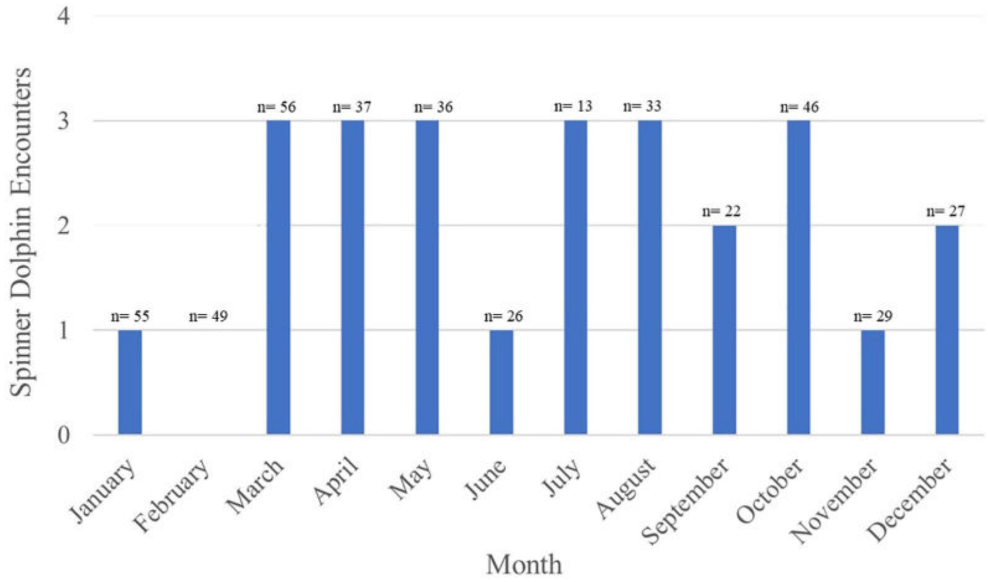

FIGURE 5
Monthly count of spinner dolphin (*Stenella longirostris longirostris*) encounters analyzed that overlapped coral reef habitat at buffered vessel tracks (275.88 m) around the islands Maui and Lāna’i (n= number of surveys per month), pooled across years from surveys conducted during 2013 – 2022.

described in Brazil, where fish associate with dolphins to opportunistically feed on their waste (Sazima et al., 2003), and if similar behavior occurred here, it could enhance nutrient transfer.

In this study, we further document that spinner dolphins in the Maui Nui region use coral reef habitat for up to 28% of their observed daytime hours (using the 50% quartile buffered track overlap with coral reef habitat). In McElligott and Lammers (2021), spinner dolphin acoustic activity was also detected over coral reef habitat at half of their passive acoustic sites located around Maui and Lāna’i. The protected nature of the leeward waters and channels between the four islands of Maui Nui likely influence both spinner dolphin and coral reef distribution and their overlap (Field et al., 2019; Stack et al., 2020; McElligott and Lammers, 2021). In this area, the main climatic and oceanographic factors influencing local marine ecosystems are wave activity, the predominant trade-winds, and local circulation patterns (e.g., Storlazzi et al., 2017; Field et al., 2019). For coral reefs here, the proximity of the four islands can decrease flushing, as well as provide protection from large wave activity, resulting in increased exposure and retention of materials (Storlazzi et al., 2017). Additionally, local circulation patterns provide connectivity for biological material from one island of the region to another, such as the movement of coral larvae or nutrients from Maui to Moloka‘i (Storlazzi et al., 2017). While the exact fate of nutrients transported by spinner dolphins remains unknown, our findings indicate that spinner dolphins in Maui Nui spend a considerable amount of time over biological habitats inshore where they may be a source of pelagic nutrients.

We estimated the amount of daily nutrient deposition from an individual spinner dolphin into the overall marine environment in Maui Nui to be 0.10 (SD = 0.02) kg N day^{-1} (24-hr). Similar to ‘the whale pump’, several other studies demonstrated that spinner dolphins could mediate the transport of nutrients through their foraging on the deep-scattering prey layer and daily deposition within surface waters (Letessier et al., 2022; Woodstock et al., 2023), a mechanism we refer to as “the dolphin tap”. In the Gulf of Mexico, the estimated daily nitrogen deposited from an individual spinner dolphin (0.005 kg N day^{-1}) from their foraging depths to the oligotrophic surface waters (Woodstock et al., 2023), was lower than our 24-hr estimate of deposition into the overall marine environment. When compared to island-associated spinner dolphins in the Indian Ocean, our nutrient deposition per individual into the overall marine environment was higher than the estimate in the Chagos and Maldives archipelagos (0.0654 kg N day^{-1}) (Letessier et al., 2022). However, our low estimate that a spinner dolphin would deposit (5.19 kg N year^{-1}) when over coral reefs around the islands of Maui and Lāna’i was lower than the annual estimation over coral reefs in Chagos and Maldives archipelagos (23.9 kg N year^{-1}). The differences in estimations are likely influenced by the extent of coral coverage within the coral reef ecosystems, where Letessier et al. (2022) considered any visual or acoustic observations throughout both archipelagos in the Indian Ocean to be over coral. In Maui Nui, the coral reef habitat encompassed only 4% of our survey area and we only tallied sightings overlapping with coral reefs around Maui and Lāna‘i as over coral. The coral reef habitats off Moloka‘i, and Kaho‘olawe were not included in this analysis, but these areas should be considered in future research for a more complete understanding of the local spinner dolphin nutrient input throughout all of Maui Nui. Additionally, our low estimate nutrient deposition represented daytime only spinner dolphin nutrient contribution to coral reef communities, with the mid and high estimates extending deposition partially into nighttime. The true value of nutrients deposited likely is encapsulated within this range, given previous behavioral data found spinner dolphins are not over inshore coral reefs as often during nighttime hours (Norris and Dohl, 1980; Norris et al., 1994; Stack et al., 2020; Benoit-Bird and Au, 2003). Our results represent baseline estimates of the potential natural nutrient transfer from pelagic sources by spinner dolphins to coral reefs off human-populated islands in the Maui Nui region.

Our low nutrient deposition estimate indicated that a spinner dolphin group could supply an additional 340.12 (SD = 591.95) kg N year^{-1} from pelagic sources over coral reef habitats around Maui and Lānaʻi. There is increasing evidence that nutrient input from animal-derived sources (e.g., ammonium) enhances coral reef growth and health, while increases in human-mediated nutrients (e.g., nitrate) tend to decrease coral growth (e.g., Shantz and Burkepile, 2014; Savage, 2019; Allgeier et al., 2020). This highlights the potential importance and benefit of pelagic-sourced natural nutrient inputs for coral reefs from spinner dolphins found around the islands of Maui Nui. It is worth noting that the mapped coral reef habitat used for assessing spinner dolphin overlap in this analysis was based on prior spatial data and may not represent the current state of coral reef coverage around Maui and Lānaʻi. While this may have resulted in an over or under-estimate of coral reef-dolphin overlap for our analysis, the habitat data we used represented the largest and most comprehensive spatial data available for coral reefs in MHI. More recent, less extensive monitoring of coral reef sites around the island of Maui found changes in coral coverage with some locations showing evidence of decline and others coral reef tracts increasing in coral cover over time (Sparks et al., 2015; Maynard et al., 2019). Unfortunately, changes to coral reefs from the impacts of ocean warming and bleaching events also occurred in the Hawaiian archipelago during our study (Field et al., 2019). Such bleaching events have been increasing in frequency and severity since 1980 (Hughes et al., 2018), with mass coral reef bleaching events occurring in the MHI in 2014, 2015, and 2019 (Rodgers et al., 2017; Winston et al., 2022). Despite the uncertainty in the contemporary state of coral cover in Maui Nui, several studies have shown that natural nutrients from animals can potentially decrease the susceptibility of coral bleaching and promote recovery after bleaching events by providing optimal ratios of nutrients needed for maintaining mutualism between coral and symbiotic algae (Burkepile et al., 2020; Benkwitt et al., 2023). Since the number of animals available to serve as nutrient vectors directly scales to the amount of natural nutrients deposited (Subalusky and Post, 2019), it is important to consider the population level benefits of this nutrient pathway. Our illustrative population level nutrient deposition low estimate over coral reefs was 3,081.60 (SD = 4,058.07) kg N year^{-1}, and represented only animals from part of the stock boundary around Oʻahu. To best interpret the results for spinner dolphin nutrient deposition over coral reefs in Maui Nui, an updated location specific abundance estimate would be necessary, but our example estimate provides insight into the amount of nutrients that could be transferred at a population level. These findings indicate that the natural nutrient contributions from a group and population of spinner dolphins may be of critical consequence in promoting coral reef resistance from future climate-related disturbances (e.g. Burkepile et al., 2020; Benkwitt et al., 2023).

The health and physiology of coral reefs benefit from high concentrations of natural nutrient supplementation that are episodic and short in nature (van Der Zande et al., 2021), indicating that the punctuated spatial and temporal nature of spinner dolphin nutrient subsidies could be further advantageous for coral reefs around Maui and Lānaʻi. Spinner dolphins in Maui Nui are known to move through the inshore region, with individuals traveling between the four islands (Stack et al., 2020). These movement patterns likely promote nutrient dispersal to different coral reef communities throughout the region with brief influxes of nitrogen when spinner dolphins overlap with coral reef habitat. The non-continuous daytime use of spatial areas by spinner dolphins is further evidenced by our unpublished observational data collected from daytime shore-based surveys of Hulopo'e Bay located on Lānaʻi, where shallow coral reefs are also found. Our shore surveys found spinner dolphins present in the Hulopoʻe Bay during 62 of 124 surveys, averaging an hour of time observed in the bay per use, representing 62% of the time we surveyed the bay (4,250 total minutes dolphins were observed/6,844 total daytime minutes surveyed). Such nutrient deposition dynamics, which support coral reef health, are contrary to the larger influx and continuous deposition of excess nutrients from anthropogenic sources that can cause eutrophication and threaten coral reef health (e.g., Burkepile et al., 2013; Shantz and Burkepile, 2014; Allgeier et al., 2017; van Der Zande et al., 2021). There is an increasing concern for coral reef loss, evidenced by declining health of coral reefs in the MHI in recent decades, mainly due to land-based pollution, sedimentation and overfishing (e.g., Sparks et al., 2015; Field et al., 2019). Within our study area, coral reef systems around the island of Maui are in close proximity to larger human population centers, and have increasingly experienced high macroalgae blooms as the result of pollutants, excess anthropogenic nutrient runoff, and overfishin (Field et al., 2019).

This study fills a gap in knowledge on an additional role of spinner dolphins in ecosystem functioning and highlights the importance of spinner dolphins in transporting limited nutrients to inshore waters and coral reef habitats around Maui and Lānaʻi. Our results suggest that through their role as natural nutrient vectors that promote coral reef health, spinner dolphins in the MHI provide ecosystem services that can supply substantial value to the human population through economic and environmental benefits (e.g., Cook et al., 2020). The roles of spinner dolphins in maintaining natural coral reef functioning is highly beneficial for humans, and the overall value will likely increase over time due to the growing threats to coral reefs and overall marine ecosystems, as coral reefs are one of the most profitable marine ecosystems (e.g., Mehvar et al., 2018). Previous studies have also described tourism as an additional economic benefit that spinner dolphins in the MHI provide for humans. For example, in 2013, commercial tourism based on wild dolphins in Hawaiʻi generated an estimated $102 million/year (Wiener et al., 2020). However, popularity and demand of these activities may negatively impact dolphins, which could lead to population decrease or shift of habitat use during daytime resting (Tyne et al., 2018; Stack et al., 2020). Given their proximity to human-populated areas, spinner dolphins are additionally sensitive to other anthropogenic-based threats, such as marine debris (Currie et al., 2017), entanglement (Bradford and Lyman, 2015, 2018), and noise pollution (Heenehan et al., 2017). While no studies have described the impacts of climate change on spinner dolphins, this threat is likely of high concern as well, especially for island-associated stocks that have limited opportunities to adapt to changing conditions, given their small populations, and restricted geographic distribution (Lettrich et al., 2023). The extent of impact that these threats potentially have on spinner dolphins in Maui Nui remains unknown but warrants further attention. Spinner dolphins serve as a sentinel species in the Maui Nui region through their role as a top predator and can provide insight into ecosystem functioning and future changes (Hazen et al., 2019). Therefore, it is imperative for effective management efforts to consider the larger ecological roles of dolphins to help guide ecosystem-based conservation strategies (e.g., Hazen et al., 2019; Kiszka et al., 2022).

With increasing environmental changes, naturally-sourced nutrients translocated by spinner dolphins may provide increased resilience and resistance of coral reefs to climate change stressors (e.g., Benkwitt et al., 2023). This relationship suggests that if adverse impacts to spinner dolphin populations or changes in their habitat use occur, coral reefs around Maui and Lānaʻi could suffer from lack of beneficial natural nutrient sources (e.g., Burkepile et al., 2013). Healthy coral reefs worldwide and in MHI promote biodiversity and provide essential ecosystem services for humans through economic benefits, protections of coastal infrastructures, food resources and cultural value (Field et al., 2019). Specifically, in the MHI, coral reef habitats were estimated to bring $360 million/year into the local economy (Cesar and van Beukering, 2004). These factors highlight the significance of enhancing natural ecosystem functioning to promote resilience and recovery for coral reefs from future disturbances for both ecological purposes (e.g., Graham et al., 2018; Benkwitt et al., 2023) and additional human benefits (Field et al., 2019). This is of increased importance in the wake of the recent fires on the island of Maui, which were likely intensified due to drought-like conditions influenced by climate change (Lee and Freitas, 2025). Wildfire events may negatively impact local dolphin populations and coral reef habitats through influx of ash, debris and other chemicals into the water, along with algal blooms and food chain disruptions (e.g. Santori et al., 2023). Future conservation efforts should consider the connection between spinner dolphins and coral reef communities with an aim towards a more cohesive ecosystem level approach to management.

Conclusion and future research

Our results add to the nascent body of knowledge on the role of small cetaceans in nutrient transfer and provide baseline data for the specific ecological role that spinner dolphins may play as “the dolphin tap” nutrient vector between pelagic nutrient sources and inshore coral reef habitats in the Maui Nui region. This information is beneficial to decision-makers and managers working to preserve productivity and functioning of ecosystems, especially under ecological stressors like changing environmental conditions (Kiszka et al., 2022). Due to the uncertainty inherent in our baseline analysis, additional research is necessary to better define the magnitude and implications of the natural dynamics between spinner dolphins and marine habitats in Maui Nui. Updated abundance estimates for the Oʻahu/4-islands stock and the other MHI stocks are needed to better understand their nutrient transfer dynamics and if their ecological role may be impacted by changing populations of spinner dolphins. Further, the metabolic models used for estimating nutrient deposition would be improved with subspecies-specific parameters for spinner dolphins in Hawaiʻi. Finally, within the context of rapidly changing environments, it is important to continue monitoring coral reef health and assess other nutrient pathways, including anthropogenic influx, to Maui Nui coral reefs to guide conservation-based management on a larger ecosystem scale.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by the National Oceanic and Atmospheric Administration as part of the permitting process. This research was conducted under NMFS LOC 18101 and NMFS MMPA/ESA Permit No. 21321. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

GO: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing, Investigation. SB-M: Conceptualization, Formal analysis, Investigation, Project administration, Supervision, Writing – review & editing. JC: Funding acquisition, Investigation, Project administration, Supervision, Writing – review & editing.

Funding

The author(s) declared that financial support was received for work and/or its publication. We thank the members and supporters of Pacific Whale Foundation (PWF) for providing funding for this study.

Acknowledgments

We thank the members and supporters of Pacific Whale Foundation (PWF) for providing funding for this study. Our sincere gratitude goes out to the many research volunteers, interns and staff that contributed to the data collection and processing of our long-term dolphin studies. We especially thank PWF volunteer, Nicolas Brilliande, who collected the shore-based spinner dolphin survey data from Hulopoʻe Bay, Lānaʻi. This research was carried out under NMFS LOC 18101 and NMFS MMPA/ESA Permit No. 21321 issued to Pacific Whale Foundation.

Conflict of interest

The authors declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author SB-M declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmamm.2025.1712553/full#supplementary-material

References

Allgeier, J. E., Andskog, M. A., Hensel, E., Appaldo, R., Layman, C., and Kemp, D. W. (2020). Rewiring coral: Anthropogenic nutrients shift diverse coral–symbiont nutrient and carbon interactions toward symbiotic algal dominance. *Glob. Change Biol.* 26, 5588–5601. doi: 10.1111/gcb.15230

Allgeier, J. E., Burkepile, D. E., and Layman, C. A. (2017). Animal pee in the sea: consumer-mediated nutrient dynamics in the world's changing oceans. *Glob. Change Biol.* 23, 2166–2178. doi: 10.1111/gcb.13625

Andrews, K. R., Karczmarski, L., Au, W. W. L., Rickards, S. H., Vanderlip, C. A., Bowen, B. W., et al. (2010). Rolling stones and stable homes: social structure, habitat diversity and population genetics of the Hawaiian spinner dolphin (*Stenella longirostris*):Genetic Structure of the Hawaiian Spinner Dolphin. *Mol. Ecol.* 19, 732–748. doi: 10.1111/j.1365-294X.2010.04521.x

Annan, J. D. (1997). On repeated parameter sampling in Monte Carlo simulations. *Ecol. Model.* 97, 111–115. doi: 10.1016/S0304-3800(96)00080-4

Barlow, J., Kahru, M., and Mitchell, B. (2008). Cetacean biomass, prey consumption, and primary production requirements in the California Current ecosystem. *Mar. Ecol. Prog. Ser.* 371, 285–295. doi: 10.3354/meps07695

Battista, T. A., Costa, B. M., and Anderson, S. M. (2007). *Shallow-water benthic habitats of the main eight Hawaiian Islands (U.S. Dept. of Commer).* (Silver Spring, Md.: NOAA Tech. Memo. NOS NCCOS 61). Available online at: https://products.coastalscience.noaa.gov/collections/benthic/e97hawaii/data2007.aspx (Accessed January 15, 2024).

Benkwitt, C. E., D'Angelo, C., Dunn, R. E., Gunn, R. L., Healing, S., Mardones, M. L., et al. (2023). Seabirds boost coral reef resilience. *Sci. Adv.* 9, eadj0390. doi: 10.1126/sciadv.adj0390

Benoit-Bird, K. J., and Au, W. W. L. (2003). Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. *Behav. Ecol. Sociobiol.* 53, 364–373. doi: 10.1007/s00265-003-0585-4

Benoit-Bird, K. J., and Au, W. W. L. (2009). Phonation behavior of cooperatively foraging spinner dolphins. *J. Acoust. Soc Am.* 125, 539–546. doi: 10.1121/1.2967477

Boyd, I. L. (2009). Reproduction in marine mammals. In *Biology of marine mammals* ed. J. E. III Reynolds and S. A. Rommel (Smithsonian Institution Press), 218–286.

Bradford, A. L., and Lyman, E. G. (2015). *Injury determinations for humpback whales and other cetaceans reported to NOAA response networks in the Hawaiian Islands during 2007–2012 (U.S. Dept. Commer.)* (NOAA Tech. Memo. NOAA-TM-NMFS-PIFSC-45). doi: 10.7289/V5TX3CB1

Bradford, A. L., and Lyman, E. G. (2018). *Injury Determinations for Humpback Whales and Other Cetaceans Reported to NOAA Response Networks in the Hawaiian Islands During 2013–2016 (U.S. Dept. Commer.)* (NOAA Tech. Memo. NMFS-PIFSC-75). doi: 10.25923/7N69-JH50

Bradford, A. L., Oleson, E. M., Forney, K. A., Moore, J. E., and Barlow, J. (2021). *Line-transect abundance estimates of cetaceans in US waters around the Hawaiian Islands in 2002, 2010, and 2017 (U.S. Dept. of Commer.)* (NOAA Tech Memo. NMFS-PIFSC-115). doi: 10.25923/daz4-kw84

Burkepile, D. E., Allgeier, J. E., Shantz, A. A., Pritchard, C. E., Lemoine, N. P., Bhatti, L. H., et al. (2013). Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. *Sci. Rep.* 3, 1493. doi: 10.1038/srep01493

Burkepile, D. E., Shantz, A. A., Adam, T. C., Munsterman, K. S., Speare, K. E., Ladd, M. C., et al. (2020). Nitrogen identity drives differential impacts of nutrients on coral bleaching and mortality. *Ecosyst.* 23, 798–811. doi: 10.1007/s10021-019-00433-2

Carretta, J. V., Oleson, E. M., Forney, K. A., Bradford, A. L., Yano, K., et al. (2022). *Spinner Dolphin: (*Stenella longirostris longirostris*): Hawaiian Islands Stock Complex- Hawaii Island, Oahu/4-islands, Kauai/Niihau, Pearl & Hermes Reef, Midway Atoll/Kure, Hawaii Pelagic (revised 3/2019). U.S. Pacific marine mammal stock assessments U.S. Depart. of Commer.* (NOAA Tech. Memo. NMFS-SWFSC-684). doi: 10.25923/aqdn-f357

Cesar, H., and van Beukering, P. (2004). Economic valuation of the coral reefs of Hawaii. *Pac. Sci.* 58, 231–242. doi: 10.1353/psc.2004.0014

Cook, D., Malinauskaite, L., Davíðsdóttir, B., Ögmundardóttir, H., and Roman, J. (2020). Reflections on the ecosystem services of whales and valuing their contribution to human well-being. *Ocean Coast. Manage.* 186, 105100. doi: 10.1016/j.ocecoaman.2020.105100

Currie, J. J., Stack, S. H., McCordic, J. A., and Kaufman, G. D. (2017). Quantifying the risk that marine debris poses to cetaceans in coastal waters of the 4-island region of Maui. *Mar. pollut. Bull.* 121, 69–77. doi: 10.1016/j.marpolbul.2017.05.031

Dolar, M. L. L., Walker, W. A., Kooyman, G. L., and Perrin, W. F. (2003). Corporative feeding ecology of spinner dolphins (*Stenella longirostris*) and Fraser's dolphins (*Lagenodelphis hosei*) in the Sulu Sea. *Mar. Mammal Sci.* 19, 1–19. doi: 10.1111/j.1748-7692.2003.tb01089.x

Dubinsky, Z., and Jokiel, P. L. (1994). Ratio of energy and nutrient fluxes regulates symbiosis between zooxanthellae and corals. *Pac. Sci.* 48, 313–324.

Field, M. E., Storlazzi, C. D., Gibbs, A. E., D'Antonio, N. L., and Cochran, S. A. (2019). The major coral reefs of Maui Nui, Hawaiʻi—Distribution, physical characteristics, oceanographic controls, and environmental threats. *U.S. Geological Survey.* 1–71. doi: 10.3133/ofr20191019

Friedlander, A., Aeby, G., Brown, E., Clark, A., Coles, S., Dollar, S., et al. (2005). Silver Sprin, MD.: NOAA Tech Memo NOS NCCOS 11. Available online at: https://repository.library.noaa.gov/view/noaa/17792/noaa_17792_DS1.pdf (Accessed March 5, 2024).

Gaskin, D. E. (1982). *The Ecology of Whales and Dolphins* (London: Heinemann), 459.

Gove, J. M., McManus, M. A., Neuheimer, A. B., Polovina, J. J., Drazen, J. C., Smith, C. R., et al. (2016). Near-island biological hotspots in barren ocean basins. *Nat. Commun.* 7, 10581. doi: 10.1038/ncomms10581

Graham, N. A. J., Wilson, S. K., Carr, P., Hoey, A. S., and Jennings, S. (2018). Seabirds enhance coral reef productivity in the absence of invasive rats. *Nature* 559, 250–253. doi: 10.1038/s41586-018-0202-3

Grigg, R., Grossman, E., Earle, S., Gittings, S., Lott, D., and McDonough, J. (2002). Drowned reefs and antecedent karst topography, Au'au Channel, S.E. Hawaiian Islands. *Coral Reefs* 21, 73–82. doi: 10.1007/s00338-001-0203-8

Grigg, R. W. (1988). Paleoceanography of coral reefs in the Hawaiian-Emperor chain. *Science* 240, 1737–1743. doi: 10.1126/science.240.4860.1737

Hazen, E. L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M. G., Savoca, M. S., et al. (2019). Marine top predators as climate and ecosystem sentinels. *Front. Ecol. Environ.* 17, 565–574. doi: 10.1002/fee.2125

Heenehan, H. L., Van Parijs, S. M., Bejder, L., Tyne, J. A., and Johnston, D. W. (2017). Using acoustics to prioritize management decisions to protect coastal dolphins: A case study using Hawaiian spinner dolphins. *Mar. Policy* 75, 84–90. doi: 10.1016/j.marpol.2016.10.015

Hill, M. C., Oleson, E. M., and Andrews, K. (2010). *New Island-Associated Stocks for Hawaiian Spinner Dolphins (Stenella longirostris longirostris): Rationale and New Stock Boundaries* (Honolulu, HI: Pacific Islands Fish. Sci. Cent., Natl. Mar. Fish. Serv.).

Honig, S. E., and Mahoney, B. (2016). Evidence of seabird guano enrichment on a coral reef in Oahu, Hawaii. *Mar. Bio* 163, 22. doi: 10.1007/s00227-015-2808-4

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., et al. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science.* 359, 80–83. doi: 10.1126/science.aan8048

Kahng, S., Copus, J. M., and Wagner, D. (2016). "Mesophotic Coral Ecosystems," in *Marine Animal Forests*. Eds. S. Rossi, L. Bramanti, A. Gori and C. Orejas (Springer International Publishing, Cham), 1–22. doi: 10.1007/978-3-319-17001-5_4-1

Katona, S., and Whitehead, H. (1988). Are cetacea ecologically important? *Oceanogr. Mar. Biol. Annu. Rev.* 26, 553–568.

Kiszka, J., Heithaus, M., and Wirsing, A. (2015). Behavioural drivers of the ecological roles and importance of marine mammals. *Mar. Ecol. Prog. Ser.* 523, 267–281. doi: 10.3354/meps11180

Kiszka, J. J., Woodstock, M. S., and Heithaus, M. R. (2022). Functional roles and ecological importance of small cetaceans in aquatic ecosystems. *Front. Mar. Sci.* 9. doi: 10.3389/fmars.2022.803173

Kleiber, M. (1975). *The fire of life. An introduction to animal energetics* (Huntington, NY: R.E. Kreiger Publishing 658 Co), 453.

Kooyman, G. L., Castellini, M. A., and Davis, R. W. (1981). Physiology of diving in marine mammals. *Annu. Rev. Physiol.* 43 , 343–356. doi: 10.1146/annurev.ph.43.030181.002015

Lacey, C., Hill, M. C., Bradford, A. L., Oleson, E. M., Vivier, F., Pacini, A. F., et al. (2025). Circum-island line-transect abundance estimates of spinner dolphins around O'ahu, hawai'i. *Mar. Mammal Sci.* 42, e70055. doi: 10.1111/mms.70055

Lammers, M. O. (2004). Occurrence and behavior of hawaiian spinner dolphins (*Stenella longirostris*) along oahu's leeward and south shores. *Aquat. Mamm.* 30, 237–250. doi: 10.1578/AM.30.2.2004.237

Leaper, R., and Lavigne, D. (2007). How much do large whales eat? *J. Cetacean Res. Manag* 9, 179–188. doi: 10.47536/jcrm.v9i3.666

Lee, A. M., and Freitas, V. M. P. (2025). Climate change and the lāhainā Wildfires: raising global awareness as native hawaiians. *Hawai'i J. Health Soc. Welfare* 84, 62–68. doi: 10.62547/IKLJ7422

Letessier, T. B., Johnston, J., Delarue, J., Martin, B., and Anderson, R. C. (2022). Spinner dolphin residency in tropical atoll lagoons: Diurnal presence, seasonal variability and implications for nutrient dynamics. *J. Zool.* 318, 10–22. doi: 10.1111/jzo.13000

Lettrich, M. D., Asaro, M. J., Borggaard, D. L., Dick, D. M., Griffis, R. B., Litz, J. A., et al. (2023). Vulnerability to climate change of United States marine mammal stocks in the western North Atlantic, Gulf of Mexico, and Caribbean. *PloS One* 18, e0290643. doi: 10.1371/journal.pone.0290643

Maynard, J., Conklin, E., Minton, D., Williams, G. J., Tracey, D., Amimoto, R., et al. (2019). *Assessing the Resilience of Leeward Maui Reefs to Help Design a Resilient Managed Area Network.* (U.S. Dept Commer.). NOAA Tech. Memo. CRCP 33, 40.

McElligott, M. M., and Lammers, M. O. (2021). Investigating spinner dolphin (*Stenella longirostris*) occurrence and acoustic activity in the maui nui region. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.703818

Mehvar, S., Filatova, T., Dastgheib, A., De Ruyter van Steveninck, E., and Ranasinghe, R. (2018). Quantifying economic value of coastal ecosystem services: a review. *J. Mar. Sci. Eng.* 6, 5. doi: 10.3390/jmse6010005

New, L., Lusseau, D., and Harcourt, R. (2020). Dolphins and boats: when is a disturbance, disturbing? *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00353

Noren, S. R., and Rosen, D. A. S. (2023). What are the metabolic rates of marine mammals and what factors impact this value: A review. *Conserv. Physiol.* 11, coad077. doi: 10.1093/conphys/coad077

Norris, K. S., and Dohl, T. P. (1980). Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fish. Bull.* 77, 821–849.

Norris, K. S., Wells, R. S., Würsig, B., and Würsig, M. (1994). *The hawaiian spinner dolphin* (Berkeley, CA: University of California Press).

Ospina, R., and Ferrari, S. L. (2010). Inflated beta distributions. *Stat. papers* 51, 111–126. doi: 10.1007/s00362-008-0125-4

Parsons, K. M., Durban, J. W., and Claridge, D. E. (2003). Comparing two alternative methods for sampling small cetaceans for molecular analysis. *Mar. Mammal Sci.* 19, 224–231. doi: 10.1111/j.1748-7692.2003.tb01104.x

Perrin, W. F. (1998). *'Stenella longirostris.' Mamm species.* 1–7 doi: 10.2307/3504456

R Core Team. (2024). *R: A Language and Environment for Statistical Computing.* (Vienna, Austria: R Foundation for Statistical Computing). Available online at: https://www.R-project.org/ (Accessed January 30, 2024).

Reid, S. B. (1994). *Spatial structure of the mesopelagic fish community in the Hawaiian boundary region* (Honolulu, HI: University of Hawaii).

Reid, S. B., Hirota, J., Young, R. E., and Hallacher, L. E. (1991). Mesopelagic boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Mar. Biol.* 109, 427–440. doi: 10.1007/BF01313508

Rodgers, K. S., Bahr, K. D., Jokiel, P. L., and Richards Donà, A. (2017). Patterns of bleaching and mortality following widespread warming events in 2014 and 2015 at the Hanauma Bay Nature Preserve, Hawai'i. *PeerJ* 5, e3355. doi: 10.7717/peerj.3355

Roman, J., Estes, J. A., Morissette, L., Smith, C., Costa, D., McCarthy, J., et al. (2014). Whales as marine ecosystem engineers. *Front. Ecol. Environ.* 12, 377–385. doi: 10.1890/130220

Roman, J., and McCarthy, J. J. (2010). The whale pump: marine mammals enhance primary productivity in a coastal basin. *PloS One* 5, e13255. doi: 10.1371/journal.pone.0013255

Santori, C., Rowe, S., and Smyth, C. (2023). *The impacts of the 2019–20 wildfires on marine species and ecosystems.* Australia's Megafires: Biodiversity Impacts and Lessons from 2019–2020 (Melbourne, Australia: CISRO Publishing), 78.

Savage, C. (2019). Seabird nutrients are assimilated by corals and enhance coral growth rates. *Sci. Rep.* 9, 4284. doi: 10.1038/s41598-019-41030-6

Sazima, I., Sazima, C., and Silva, J. M. (2003). The cetacean offal connection: feces and vomits of spinner dolphins as a food source for reef fishes. *Bull. Mar. Sci.* 72, 151–160.

Shantz, A. A., and Burkepile, D. E. (2014). Context-dependent effects of nutrient loading on the coral–algal mutualism. *Ecology* 95, 1995–2005. doi: 10.1890/13-1407.1

Sparks, R., Stone, K., White, D., Ross, M., and Williams, I. (2015). Maui and lanai monitoring report. *Department Land Natural Resour. Division Aquat. Resour.* (Wailuku, Hawai'i: Maui Office) 1–42.

Stack, S. H., Currie, J. J., McCordic, J. A., and Olson, G. L. (2019). Incidence of odontocetes with dorsal fin collapse in maui nui, hawaii. *Aquat. Mamm.* 45, 257–269. doi: 10.1578/AM.45.3.2019.257

Stack, S. H., Olson, G. L., Neamtu, V., Machernis, A. F., Baird, R. W., and Currie, J. J. (2020). Identifying spinner dolphin *Stenella longirostris longirostris* movement and behavioral patterns to inform conservation strategies in Maui Nui, Hawai'i. *Mar. Ecol. Prog. Ser.* 644, 187–197. doi: 10.3354/meps13347

Storlazzi, C. D., Brown, E. K., Field, M. E., Rodgers, K., and Jokiel, P. L. (2005). A model for wave control on coral breakage and species distribution in the Hawaiian Islands. *Coral Reefs* 24, 43–55. doi: 10.1007/s00338-004-0430-x

Storlazzi, C. D., van Ormondt, M., Chen, Y.-L., and Elias, E. P. L. (2017). Modeling fine-scale coral larval dispersal and interisland connectivity to help designate mutually-supporting coral reef marine protected areas: insights from maui nui, hawaii. *Front. Mar. Sci.* 4. doi: 10.3389/fmars.2017.00381

Subalusky, A. L., and Post, D. M. (2019). Context dependency of animal resource subsidies. *Biol. Rev.* 94, 517–538. doi: 10.1111/brv.12465

Tyne, J. A., Christiansen, F., Heenehan, H. L., Johnston, D. W., and Bejder, L. (2018). Chronic exposure of Hawaii Island spinner dolphins (*Stenella longirostris*) to human activities. *R. Soc Open Sci.* 5, 171506. doi: 10.1098/rsos.171506

Tyne, J. A., Johnston, D. W., Christiansen, F., and Bejder, L. (2017). Temporally and spatially partitioned behaviours of spinner dolphins: Implications for resilience to human disturbance. *R. Soc Open Sci.* 4, 160626. doi: 10.1098/rsos.160626

Tyne, J. A., Johnston, D. W., Rankin, R., Loneragan, N. R., and Bejder, L. (2015). The importance of spinner dolphin (*Stenella longirostris*) resting habitat: implications for management. *J. Appl. Ecol.* 52, 621–630. doi: 10.1111/1365-2664.12434

Tyne, J. A., Pollock, K. H., Johnston, D. W., and Bejder, L. (2014). Abundance and survival rates of the hawai'i island associated spinner dolphin (*Stenella longirostris*) stock. *PloS One* 9, e86132. doi: 10.1371/journal.pone.0086132

van Der Zande, R. M., Mulders, Y. R., Bender-Champ, D., Hoegh-Guldberg, O., and Dove, S. (2021). Asymmetric physiological response of a reef-building coral to pulsed versus continuous addition of inorganic nutrients. *Sci. Rep.* 11, 13165. doi: 10.1038/s41598-021-92276-y

Wiener, C., Bejder, L., Johnston, D., Fawcett, L., and Wilkinson, P. (2020). Cashing in on spinners: revenue estimates of wild dolphin-swim tourism in the hawaiian islands. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00660

Winston, M., Oliver, T., Couch, C., Donovan, M. K., Asner, G. P., Conklin, E., et al. (2022). Coral taxonomy and local stressors drive bleaching prevalence across the Hawaiian Archipelago in 2019. *PloS One* 17, e0269068. doi: 10.1371/journal.pone.0269068

Woodstock, M. S., Kiszka, J. J., Ramírez-León, M. R., Sutton, T. T., Fennel, K., Wang, B., et al. (2023). Cetacean-mediated vertical nitrogen transport in the oceanic realm. *Limnol. Oceanogr.* 9999, 1–16. doi: 10.1002/lno.12433