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Fisheries, trade, and conservation of manta and devil rays in Peru

Stefany Rojas-Perea · Nidhi G. D'Costa · Keny Kanagusuku · Rosario Escobedo · Frida Rodríguez · Alejandra Mendoza · Rossana Maguiño · Renan Flores · Betty J. L. Laglbauer · Guy M. W. Stevens · Shaleyla Kelez

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Abstract The Mobulidae family comprises nine extant manta and devil ray (mobulid) species in the monogeneric genus *Mobula*, of which five occur in Peruvian waters. In this study, we assessed mobulid ray landings and trade along the coast of Peru by analysing historical captures, monitoring landing sites, and conducting interviews with fishers ($n=37$) and traders ($n=21$). A total of 7444.9 tons of mobulids were reported from 2000 to the end of 2023 in artisanal fisheries through data collected by the Marine Institute of Peru. Between 2013 and 2023, mean yearly mobulid ray landings for northern Peru were approximately 11,520 individuals (7414 M. *munkiana*, 3126 M. *mobular*, and 981 M. *thurstoni*) based on species-specific estimates of weight at maturity. This ranks Peru among the top mobulid fisheries globally. Of great concern was a 75.05% decline in mobulid ray landings between 2013 and 2023 relative to 2000–2012. Additionally, six key mobulid landing sites in the Tumbes and Piura region were monitored between April 2017 and February 2019, sampling 257 mobulid ray specimens for detailed morphometric data. In these surveys, the most abundant species was *M. mobular* ($n=156$, 60.7%), followed by *M. thurstoni* ($n=47$, 18.3%), *M. munkiana* ($n=24$, 9.3%), and *M. birostris* ($n=4$, 1.6%). Interviews suggest the highest mobulid landings occur during the warm season (December to May). Although *M. birostris* has been protected in Peruvian waters since 2016, and recent legislation extends protection to all mobulid species, this study reinforces that all mobulid species are globally threatened. Therefore, the

Rosario Escobedo sadly passed away in 2021.

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S. Rojas-Perea (✉) · N. G. D'Costa · R. Escobedo · B. J. L. Laglbauer · G. M. W. Stevens
The Manta Trust, Catemwood House, Norwood Lane, Corscombe, Dorset DT2 0NT, UK
e-mail: stefany@mantatrust.org

K. Kanagusuku
Área de Laboratorio de Ciencias Naturales, Universidad Científica del Sur, Lima, Peru

K. Kanagusuku
Carrera de Biología Marina, Universidad Científica del Sur, Lima, Peru

F. Rodríguez
Ministerio del Ambiente, Av. Antonio Miro Quesada 425, Magdalena del Mar, Lima, Peru

A. Mendoza · R. Maguiño · S. Kelez
ecOceánica, Copernico 179, San Borja, Lima, Peru

R. Maguiño
Asociación Peruana de Astrobiología, Calle Santa Cruz MZ A Lt 8 Las Flores de Villa, Lima, Peru

R. Flores
Instituto de Educación Superior Tecnológico Público Contralmirante Manuel Villar Olivera, Tumbes, Peru

large number of mobulid rays landed in Peru annually is a major concern and requires urgent attention by fisheries management authorities to determine the necessary regulations required to conserve these highly vulnerable species.

Keywords *Mobula* · Bycatch · Small-scale fisheries · Landings · Interviews

Introduction

The global population of sharks and rays (Subclass: Elasmobranchii) is facing an unprecedented extinction crisis, with over 75% of species threatened primarily due to overfishing (Dulvy et al. 2021). Among elasmobranchs, batoids (Batoidea, 633 spp.; Last et al. 2016), particularly mobulid rays and their relatives, are at severe risk (Dulvy et al. 2014; González-Pestana et al. 2022). In the Eastern Pacific, Peru plays a significant role in this crisis, ranking 15th globally in batoid landings and contributing 11% of worldwide landings between 2005 and 2011 (González-Pestana et al. 2022). Mobulid rays account for 28% of Peru's total batoid catch, with the majority of landings occurring along the northern coast, and gillnets are the primary fishing gear responsible for mobulid captures (González-Pestana et al. 2016; Alfaro-Cordova et al. 2017; González-Pestana 2022) .

The Mobulidae family comprises nine species within the genus *Mobula* (Couturier et al. 2012; White et al. 2018; Notarbartolo di Sciara et al. 2019; Hosegood et al. 2020). Five of these species have been recorded off Peru: the oceanic manta ray (*M. birostris*), the spinetail devil ray (*M. mobular*), Munk's pygmy devil ray (*M. munkiana*), the sicklefin devil ray (*M. tarapacana*), and the bentfin devil ray (*M. thurstoni*) (Chirichigno and Cornejo 2001; Cornejo et al. 2015; González-Pestana 2022). These species are particularly susceptible to overexploitation due to their slow growth, late sexual maturity, and low reproductive potential (Marshall and Bennett 2010; Dulvy et al. 2014; Stewart et al. 2018; Rambahiniarison et al. 2018). This vulnerability has led to significant population declines and indications of overfishing in landing hotspots worldwide (Moazzam 2018; Fernando and Stewart 2021; Carpenter et al. 2023; Carpenter 2023). However, long-term species-specific data remains scarce for most regions (Stewart et al. 2018).

The impact of fishing on mobulid populations is substantial. A study in northern Peru revealed that nearly 2000 mobulids were landed in Zorritos alone in 2015 in small-scale artisanal fisheries, with over 97% being immature spinetail devil rays (Alfaro-Cordova et al. 2017). Mobulid catches have been reported in both small-scale and industrial fisheries (Hall and Roman 2013; Alfaro-Shigueto et al. 2010; Alfaro-Cordova et al. 2017). The purse seine tuna fishery off Peru reported an average of more than 600 mobulids/year captured as bycatch between 1994 and 2009 (Hall and Roman 2013). Moreover, the vulnerability of mobulid rays is exacerbated by their habitat preferences. These zooplanktivorous rays aggregate to feed in the rich upwelling systems off the Peruvian coast (Alfaro-Cordova et al. 2017; Guirkinger et al. 2021; González-Pestana et al. 2022; González-Pestana 2022), which overlap with fishing grounds of other oceanic species (Jabado et al. 2023). This overlap results in large bycatch quantities, primarily by gillnets and other non-selective fishing gear (Croll et al. 2016; Stewart et al. 2017; Alfaro-Cordova et al. 2017; Guirkinger et al. 2021; González-Pestana et al. 2022; González-Pestana 2022). While the retention of mobulid rays in many fisheries is driven by the demand for their gill plates in the Asian medicinal trade, particularly in mainland China and Hong Kong (O'Malley et al. 2017; Palacios et al. 2024 in press), the situation in Peru is different. Here, mobulid rays are primarily retained for meat consumption, both fresh and dried, with no apparent commercialization of gill plates (Ayala and Romero 2016; Guirkinger et al. 2021; Alfaro-Cordova et al. 2017). Additionally, mobulid meat is used in traditional cuisine in the Lambayeque region of Peru (Rojas 2016).

Due to global concern over the extinction risk of mobulid rays caused by fishing pressure, the International Union for Conservation of Nature (IUCN) categorises *M. birostris*, *M. mobular*, *M. tarapacana*, and *M. thurstoni* as 'Endangered' and *M. munkiana* as 'Vulnerable' on the Red List of Threatened Species (IUCN 2024). In Peru, all mobulid ray species are subject to some level of protection derived from international and national agreements. Since 2014, all mobulid ray species have been listed in Appendices I and II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS), promoting conservation efforts in member states (CMS 2015). Additionally, since 2016, all mobulid ray species have been included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which requires Peru, as a member state, to ensure that international trade in these species is legal, sustainable, and traceable (CITES 2016). Regional efforts to reduce mobulid ray capture and promote their conservation have also been implemented. Peru, as a cooperating party of the Inter-American Tropical Tuna Commission (IATTC), is subject to Resolution C-15–04, adopted in 2015, which incorporates mobulid ray safe handling and release guidelines and retention bans in tuna fisheries. This resolution aims to minimise the impact of fishing activities on these species and promote their survival when incidentally caught. At the national level, Peru has implemented specific regulations for mobulid rays. Since 2016, *M. birostris* has been granted special protection status in Peru (Produce 2015). This measure prohibits the capture, retention, and commercialization of *M. birostris* throughout the year. Building on this initial protection, Peru has recently taken a more comprehensive approach to mobulid conservation. In 2024, the government amended the existing law to expand protection to all mobulid species (Produce 2024). This comprehensive regulation, scheduled for implementation in January 2025, marks a significant advancement in mobulid conservation in the country. However, concerns raised by fishing communities regarding potential livelihood impacts have cast uncertainty on the law's enforcement and long-term viability (Rojas pers. comm.).

Despite national and international measures, Peru continues to play a significant role in mobulid ray trade, particularly for meat consumption. The ongoing high levels of domestic consumption and potential cross-border trade with Ecuador highlight the challenges in implementing and enforcing regulations effectively. This situation is exacerbated by the non-selective nature of fishing gear, particularly gillnets, which often result in the incidental capture of mobulid rays (Palacios et al. 2024 in press; Zhou et al. 2024; Harris and Stevens 2024). Information regarding Peruvian mobulid ray populations is increasing but remains relatively scarce and limited in scope, e.g. fisheries monitoring has often been restricted to specific landing sites over relatively short study periods (Alfaro-Cordova et al. 2017), and species misidentifications are very common which generates a significant bias in official capture data (Rojas 2016; Alfaro-Cordova et al. 2017). Nonetheless, *M. mobular* appears to be the most abundant species in the fisheries, with a high percentage of immature individuals caught in artisanal landings (Alfaro-Cordova et al. 2017). Indeed, due to the high proportion (82%) of immature individuals recorded, a potential nursery area for *M. mobular* has been proposed in the Tumbes and Piura region in northern Peru (González-Pestana 2022). This area has also been officially recognised by the IUCN as an Important Shark and Ray Area (ISRA) since it functions as a reproductive area (Jabado et al. 2023). Moreover, 15% ($n=8$) of the documented *M. munkiana* caught in October 2015 in Zorritos were gravid females according to Rojas (2016). In the small-scale gillnet fishery in northern Peru, mobulid ray catches are considered opportunistic events, that is, their capture rates are high if one considers them a bycatch species, but relatively low for a target catch. Also, they are captured when the target species are scarce or during warm seasons (Alfaro- Cordova et al. 2017).

All previously mentioned factors contribute to a vulnerable environment for mobulids in Peru, making it necessary to expand our knowledge of their fisheries, trade, and associated effects on population status. Therefore, the present study aimed to characterise mobulid fisheries and trade in Peru. The three different information sources used to achieve these objectives were (1) official long-term landing data reported in seven regions, (2) focused landing surveys at six hotspots, and (3) interviews with fishers and traders from three localities. This study is expected to provide relevant information contributing to decision-making for the conservation of mobulid ray species in Peru and at a larger scale.

Methodology

Official public data

The Marine Institute of Peru (Instituto del Mar del Peru-IMARPE) has maintained a national landing monitoring system of artisanal fishing in the main landing sites since 1996 (Guevara-Carrasco and

Bertrand 2017). Even though total landings from the entire country are not registered, it is the largest sample in space and time available for all artisanal fisheries in Peru. Data was collected across 24 landing sites along the coastline and covers all key fisheries off northern Peru. IMARPE has undertaken regular monitoring of landings since 2000, and enumerator coverage has reportedly been stable since 2005 (R. Flores pers. comm.). However, in 2020–2021, COVID-19 may have affected fishing and data collection to some extent, which we could not account for in this study.

Through requests for access to public information by transparency law No. 27806, IMARPE (https://www.imarpe.gob.pe/imarpe/accesoinformacion) and the Ministry of Production (PRODUCE) (https://transparencia.produce.gob.pe/index.php/formularios-de-atencion-al-ciudadano/solicitud-de-acceso-a-la-informacion-publica) were contacted to provide statistics on mobulid landings from 2000 to the end of 2023. IMARPE provided two overlapping datasets on mobulid landings: one covering 2000–2019 and another spanning 2019–2023. For the year 2019, which appears in both datasets, there is a discrepancy in reported landings. The 2000–2019 dataset reported 344.8 tons, while the 2019–2023 dataset indicated 286.4 tons, a difference of 58.3 tons or 16.9% of the higher value. To address this inconsistency, landings for 2019 were averaged using both reported figures. Mean yearly mobulid ray landings in numbers of individuals were estimated from the total mobulid ray landings reported by IMARPE by weight (in kg), using average weight at maturity for each of the recorded species from 2013 to 2023. Mean DW at maturity (among males and females—Stevens et al. 2024) was used to estimate the weight at maturity using species-specific conversion formulas (Ehemann et al. 2017; Rambahiniarison et al. 2018). Mean yearly species-specific landings were then converted to a number of individuals using these estimated weights (*M. mobular*, 91.7 kg; *M. munkiana*, 9.4 kg; and *M. thurstoni*, 44.0 kg).

To examine mobulid landings and fisheries in Peru, landing data was analysed from the IMARPE (2024a, b) public database instead of PRODUCE due to better data disaggregation. PRODUCE aggregates all ray landings data without distinguishing the genus *Mobula* and lacks continuous, time-series-specific data for mobulids.

Opportunistic monitoring and interview data

Study area

The study focused on six key artisanal fishing ports in northern Peru—Puerto Pizarro, Zorritos, Acapulco, Cancas in Tumbes, and Mancora and Los Organos in Piura—critical for mobulid landings due to significant fishing activity (IMARPE 2015; Rojas 2016; Vera et al. 2021; Gonzalez-Pestana 2022). Site selection was informed by local research and the author's field experience, ensuring a contextually relevant approach. To complement the data on landings, semi-structured interviews were conducted with fishers and traders in Zorritos, Mancora, and Chiclayo (Lambayeque region) to gather their perceptions on mobulids and to explore the dynamics of this fishery within the value chain (Fig. 1).

Data collection

The sampling methodology for monitoring mobulid landings between April 2017 and February 2019 was opportunistic. While the sampling was not uniformly distributed across the year, with more coverage during the Austral winter than summer, sites were visited randomly during survey periods. During survey periods, random landing site surveys were complemented by notifications from local fishers about expected landings, which ensured that majority of total landings were captured on survey days at each site. However, this methodology may have also skewed data collection towards relatively larger fishing events of the Austral winter. Additionally, landings per survey day were estimated for each site, enabling comparison among sites.

The data collection process was comprehensive, including species identification based on morphological characteristics (Stevens et al. 2018), body size measurements (disc width, cm) from the tip of one pectoral fin to the other, sex, landing site, and fishing gear used. Because in most cases larger mobulid ray specimens were landed eviscerated and sectioned in half (with only pectoral fins and vertebral columns), DW was estimated by measuring each half of the body and doubling these measurements to estimate total DW. Also, it is important to note that according to fishers, approximately 20% of mobulid catches are discarded at sea to save

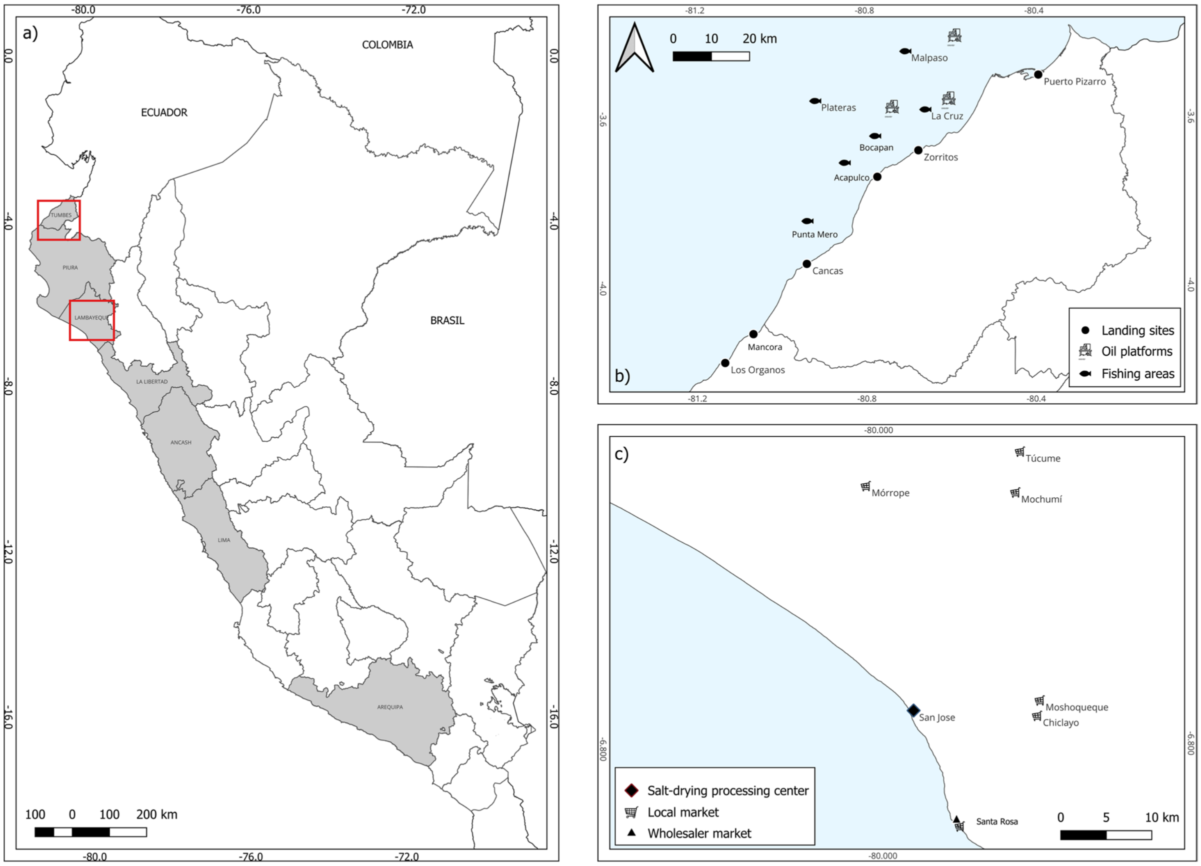

Fig. 1 Study area: **a** mobulid landing regions reported from IMARPE dataset. **b** Landing sites and fishing areas in Tumbes and Piura from this study; **c** meat salt-drying processing centre, wholesaler, and local distribution markets

space on vessels, with heads and viscera typically discarded. However, smaller individuals are often landed whole (Rojas, pers. comms.).

Fishers and traders interviews

Between June and July 2018, in-person semi-structured interviews were conducted with artisanal fishers and mobulid meat traders in Mancora, Zorritos, and Chiclayo to gather information on fishing practices, species-specific trends, and trade dynamics. Interviewers explained how the results would be used and shared, and that data would be de-identified. To conduct the interviews, the study utilised non-probability sampling techniques, such as convenience, opportunistic, and snowball sampling methods, as described in previous research (Jabado et al. 2015; Liao et al. 2019; Patankar 2019). To enhance data reliability, different questions were repeated strategically to confirm key data and to identify potential response biases. The questionnaires were designed to capture both qualitative and quantitative data through a variety of question types, including open-ended, closed-ended, and multiple-choice formats (Online Resource 1 and 2).

Interviews with fishers focused on fishing gear, target species, seasonal patterns, fishing locations, and perceptions of mobulid population trends, as well as historical changes in fishing practices and species abundance. For fishing areas, fishers identified locations by their common names; in some cases, GPS points were provided, while in others, locations were described based on their distance from the coast (Online Resource 1). Interviews with traders concentrated on trade practices, product types (e.g. meat, fins, gills), pricing, and market destinations, offering insights into the seasonality of mobulid product demand and the structure of local supply chains (Online Resource 2). Both questionnaires emphasised anonymity and voluntary participation, encouraging honesty and completeness in responses. Visual aids, such as species identification guides, were used to enhance the accuracy of reported species.

Data analysis

Official public data analysis

An exploratory analysis was conducted to compile and visualise data on mobulid landings from 2000 to the end of 2023. The raw dataset included monthly catch data according to six variables: regions ($n = 7$), landing sites ($n = 24$) (Supplemental Table 1), taxonomic group ($n = 1$, 'Peces'), common name ($n = 3$: manta diablo, manta de munk, diablo manta), scientific name ($n = 4$: *M. mobular*, *M. munkiana*, *M. thurstoni*, and *Mobula* spp.), and fishing gears ($n = 5$): gillnets, purse seines, harpoon, longlines, and others. It is noteworthy that an additional dataset from IMARPE (2018), reporting landings from 1996 to 2017 and that included some landings for *M. birostris* between 2014 to 2017, was available (Supplemental Table 2). However, this dataset was excluded from the analysis due to discrepancies in total counts and a lack of comprehensiveness across spatial and temporal scales.

Before 2013, all species caught were misreported as *M. thurstoni*, so in our analysis, all landings from 2000 through to the end of 2012 were collectively reported as *Mobula* spp. to best utilise this data in the study. Species-specific catch analyses were conducted across different regions and gear types over 11 years (2013–2023) to illustrate landing trends. Additionally, to assess the significance in seasonality of mobulid landings in Peru, a chi-squared test was performed on monthly landings of three different species (*M. mobular*, *M. munkiana*, *M. thurstoni*) throughout the study period (2013–2023). The seasons that were considered in the analysis are as follows: warm season (December to May) and cold season (June to November).

Opportunistic landing data analysis

Size distribution analyses were performed on mobulid landings data collected between 2017 and 2019. The frequency distributions of body sizes, measured as disc width (DW) in centimetres, were examined for *M. mobular*, *M. thurstoni*, and *M. munkiana*. Only *M. birostris* was not included in this analysis due to the small sample size of only 4 individuals recorded during the study period. These analyses were conducted separately for each species and stratified by sex to investigate sex-specific size patterns. Descriptive statistics, including mean, median, and range of DW, were calculated for each species-sex combination. In addition, to evaluate potential deviations from a 1:1 sex ratio in each species, a chi-square (χ^2) goodness-of-fit test was conducted. The null hypothesis posited that the sex ratio for each species did not significantly differ from parity. Observed frequencies of males and females were compared against expected frequencies derived from the hypothesised equal proportion. The significance level was set at $\alpha = 0.05$, with degrees of freedom (df) $= 1$ for each test. Additionally, to compare landings across sites, mobulid landings per survey day are reported for each site.

Interview data analysis

The analysis of interview data focused on three key aspects of the mobulid ray fishery and trade in northern Peru. Firstly, the seasonality of mobulid ray captures in Mancora and Zorritos was examined based on fisher interviews. Responses were aggregated to identify peak fishing periods and potential patterns in capture rates throughout the year. This qualitative data was used to complement and contextualise the quantitative landing data.

Secondly, the salt-drying process for mobulid ray meat was documented through a series of images capturing each step: (a) skin extraction, (b) cutting, (c) washing, (d) salting, and (e–f) sun drying. Interviews and these photos of the traditional preservation methods used in the region offer insights into the post-harvest handling and processing of mobulid ray meat.

Lastly, a descriptive analysis was conducted on the average prices of mobulid ray meat, categorised by processing method (fresh/dry), meat colour (white, pink, or black), and seasonality (high/low season). This analysis was performed separately for each landing site (Zorritos and Mancora) and market (San Jose, Chiclayo, Morrope, and Moshoqueque). Prices were converted from Peruvian soles (PEN) to U.S. dollars (USD) using the average nominal exchange rate published by the Central Reserve Bank of Peru for June 2018 (1 USD = 3.27 PEN) to facilitate comparisons across sites and seasons.

Results

Official public data analysis

Catch trends in gear types and across regions

A total of 7444.9 tons of mobulid rays were landed over 24 years (2000–2023) according to the IMARPE data, across all gear types. The highest landings were recorded in 2023 (635 tons, representing 8.5% of total landings recorded in the dataset), followed by 2006 (568 tons, 7.63%) and 2003 (543 tons, 7.29%) (Fig. 2a). Species-specific data between 2013 and 2023 indicated that *M. mobular* dominated landings across all gear types (3152 tons, 71.79%) (Fig. 2b), followed by *M. munkiana* (763 tons, 17.38%) and *M. thurstoni* (475 tons, 10.81%) (Fig. 2b–d). The average annual landings in number of individuals were 11,520 mobulid rays per year from 2013 to 2023. Species-specific estimates of annual landings in number of individuals were the highest in *M. munkiana* (7414 individuals/year, 64.36%), followed by *M. mobular* (3126 individuals/ year, 27.14%) and *M. thurstoni* (981 individuals/year, 8.52%).

Over this time period, gillnets were responsible for the majority of landings in *M. mobular* (87.23%) and *M. thurstoni* (79.68%). For *M. munkiana*, landings from gillnets (47.41%) represented a similar volume to landings from purse seines (44.29%) (Fig. 2c). Purse seines were also responsible for a considerable amount of *M. thurstoni* landings (13.17%) (Fig. 2d), while harpoons were the second most important gear type capturing *M. mobular* (9.31%) (Fig. 2b). From 2000 to 2012 when catches were not identified to the species-specific level, the majority of mobulid ray landings occurred in purse seines (*Mobula* spp.: 1975 tons, 64.67%) (Fig. 2a).

For the top three gear types (gillnets, purse seines, and harpoons), species-specific mobulid ray landing trends were observed between 2013 and 2023, totalling 3490 tons in gillnets (Fig. 3a), 472 tons in purse seines (Fig. 3b), and 302 tons on harpoons (Fig. 3c). *Mobula mobular* dominated gillnet (78.78%) and harpoon (96.93%, 294 tons) landings while *M. munkiana* dominated purse seine landings (71%, 338 tons) (Fig. 3a–c). While gillnets were the main gear responsible for *M. thurstoni* landings, harpoons also occasionally caught this species (2.64%, 8 tons). In addition, based on the analysis of purse seine landings from 2000 to 2023, distinct trends emerge between two defined periods: 2000–2012 (Fig. 2a) and 2013–2023 (Fig. 3b). The earlier period, spanning 2000 to 2012, exhibited a higher average annual landing of mobulid rays of approximately 150 tons, with notable peaks in 2003 (483 tons) and 2006 (453 tons). In contrast, the latter period from 2013 to 2023 (Fig. 3b) saw a significant decline in average annual landings to approximately 37.5 tons, reflecting a substantial decrease in landings of about 75.05% when compared with the period before species-specific identification began in Peru (2000–2012) (Figs. 2a and 3b).

Landing trends of mobulid species between 2000 and 2023 across seven regions in Peru (Ancash, Arequipa, La Libertad, Lambayeque, Lima, Piura, and Tumbes) were also analysed (Supplemental Table 3). For a more in-depth understanding at a species-specific level, trends were observed across the three regions that had the highest landings between 2013 and 2023: Tumbes, Piura, and La Libertad (Fig. 3d–f). The highest mobulid ray landings were recorded in Tumbes (1958 tons), followed by Piura (1486 tons) and La Libertad (36 tons). Across all three regions, *M. mobular* comprised the majority of the landings, representing 73.81% of total mobulid landings in Tumbes, 53.21% in Piura, and 94.71% in La Libertad. In Tumbes, *M. munkiana* represented 21.59% of mobulid landings, while 4.59% of landings were *M. thurstoni*. However, *M. thurstoni* was the second most-landed species after *M. mobular* in Piura (24.52%) and La Libertad (3.55%), and *M. munkiana* represented 22.26% of mobulid landings in Piura, and 1.72% in La Libertad.

Between 2000 and 2004, mobulid landings in Tumbes increased significantly from 0 to 17.5 tons, and the average annual growth was approximately 3.5 tons per year. In contrast, between 2005 and 2009, landings sharply decreased by about 83.9% overall, with an average yearly decrease of about 58.1 tons,

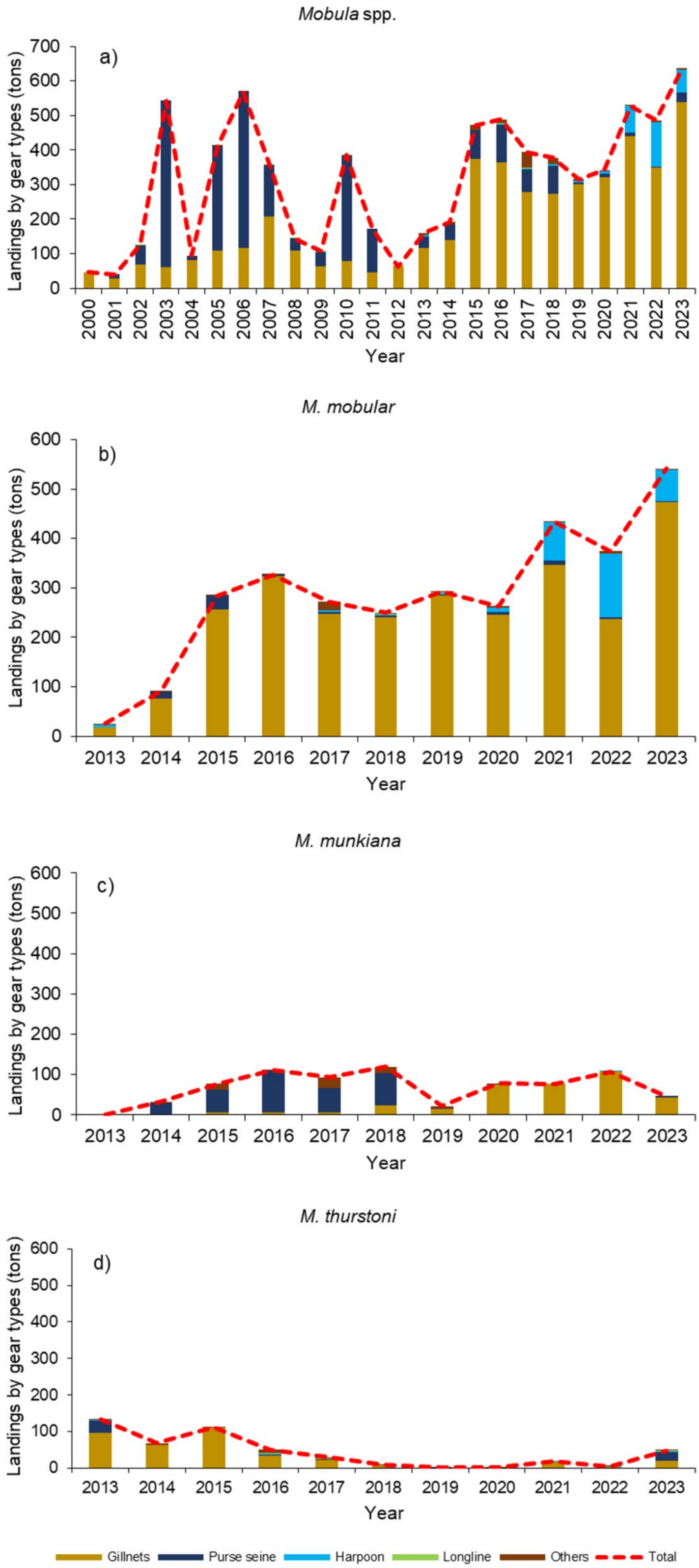

Fig. 2 **a** Total mobulid ray landings (tons) by gear type between 2000 and 2023 and gear used to catch *Mobula* spp., **b** *Mobula mobular* (2013–2023), **c** *Mobula munkiana* (2013–2023), and (**d**) *Mobula thurstoni* (2013–2023). The red trend line indicates the total catch amount for each mobulid species

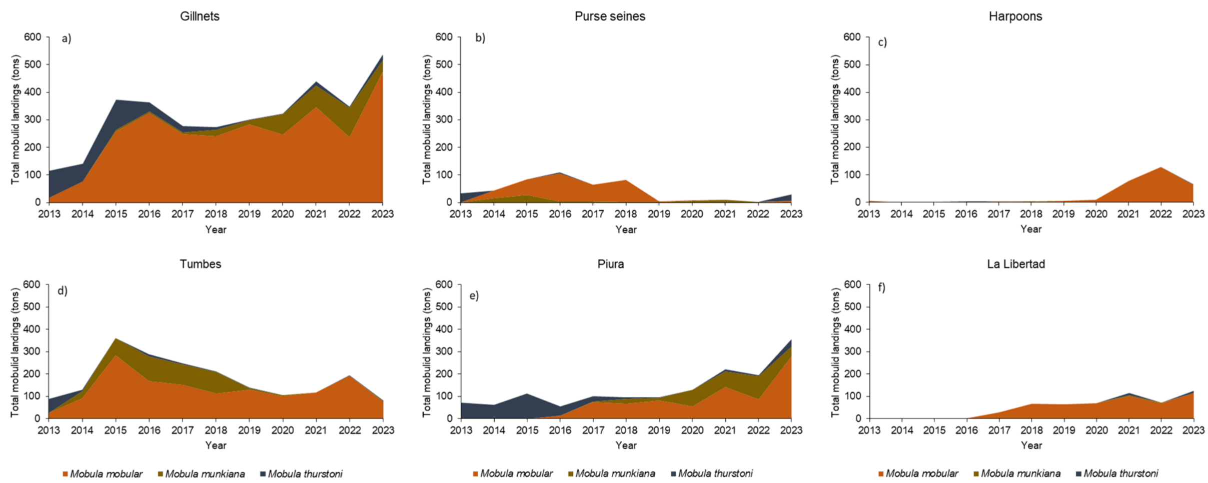

Fig.3 **a**–**c** Total mobulid landings (tons) between 2013 and 2023 in top three gears (gillnets, purse seines, and harpoons) at species-specific level; **d**–**f** total mobulid landings (tons) between 2013 and 2023 in top three regions (Tumbes, Piura, and La Libertad) at species-specific level

from 346 tons to 55.7 tons. The decline continued between 2010 and 2023, with landings decreasing by about 75.4% overall and an average annual decrease of approximately 17.5 tons. In Piura, landings increased significantly by 64.05%, with an annual growth of about 5.9 tons annually. However, there was a slight decline in mobulid landings of 23.9% (about 3.2 tons per year) between 2005 and 2009 and a substantial average annual increase of 21.2 tons from 2010 to 2023. It is important to note that there were no recorded mobulid ray landings in La Libertad before 2015, and the data shows a sharp increase starting from 2017 of 13.8 tons per year on average (Supplemental Table 3). Mobulid landings in Ancash, Lima, and Arequipa were inconsistent and of a low magnitude (Supplemental Table 3). It is also noteworthy that 51.8 tons of *M. birostris* were recorded in the 2000–2019 IMARPE dataset between 2014 and 2017 from two regions (Tumbes and Piura) (Supplemental Table 2). However, no *M. birostris* was reported in the 2000–2023 IMARPE dataset, which was considered for the study's public data analysis.

Seasonality trends in landings

Monthly landings over two different seasons (warm: Dec–May; cold: June–Nov) are shown in Fig. 4. There was no statistically significant difference in mobulid landings between the warm (December–May) and cold (June–November) seasons from 2013 to 2023 (χ^2 (2, 148) = 1.6189, P = 0.4451). However, it is important to note that the descriptive data indicates some seasonal patterns. Mobulid landings were generally higher in the warmer season (55.93%, 2434.5 tons). Additionally, when comparing monthly mobulid landings, March ranked highest (11.75%, 466.8 tons), followed by February (10.80%. 470.1 tons) and December (10.72%, 466.8 tons). Peak *M. mobular* landings were observed in March (423.5 tons). For *M. munkiana*, peak landings were observed in January (152.9 tons), while for *M. thurstoni*, they were observed in July (78.5 tons).

Opportunistic monitoring of landings

Overview of landed specimens

Data on species composition, fishing methods, morphometrics, and reproductive status were collected for 257 landed specimens from 2017 to 2019 in six landing sites in Peru (Table 1). Of these, 89.9% (n = 231) were identified at species level. One *M. birostris* and three *M. munkiana* gravid females were also observed. However, additional gravid mobulid ray specimens likely went unnoticed during our surveys since fishers generally discard viscera at sea. The gravid *M. birostris* had one foetus, and Cabanillas-Torpoco (2019) described morphometrics for

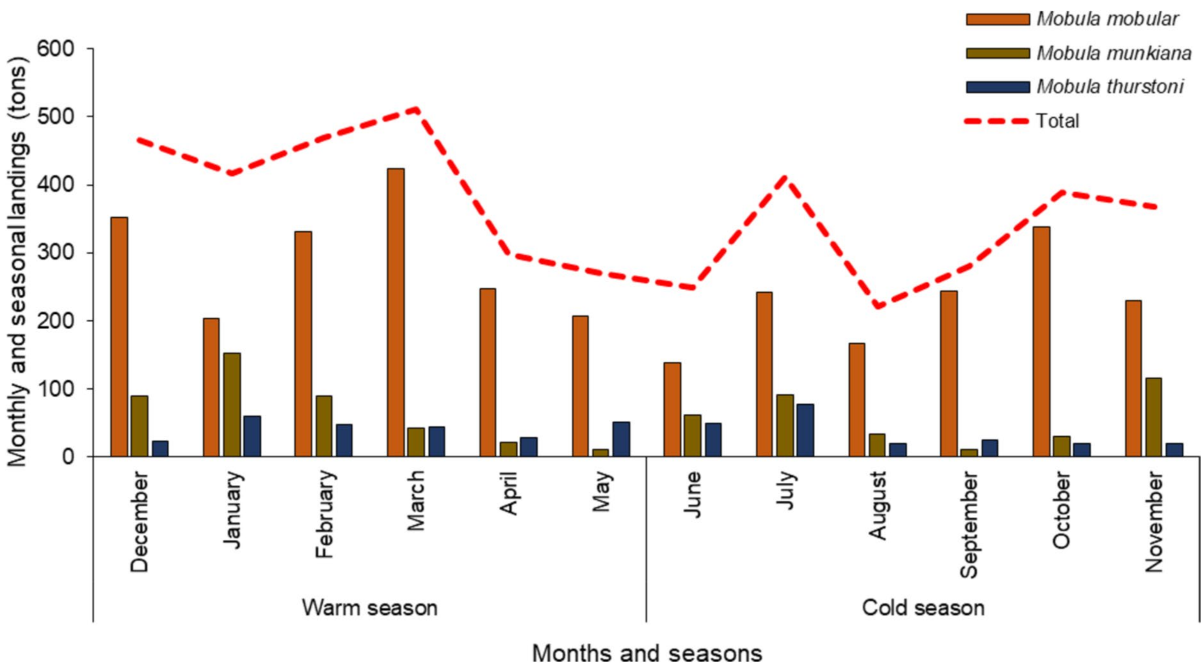

Fig. 4 Seasonal and monthly mobulid landings (tons) from 2013 (the year in which species-specific identification began) to 2023 at a species-specific level

Table 1 Number of mobulid rays sampled during the landing site surveys (2017–2019) by species and landing sites

Landing site	Region	Monitoring days	Sample size						Estimated landings per survey day
			M. birostris	*M. mobular*	*M. munkiana*	*M. thurstoni*	*Mobula* spp.	Total	
Puerto Pizarro	Tumbes	222	0	0	1	0	0	1	0.0045
Zorritos	Tumbes	21	1	71	14	3	20	109	5.19
Acapulco	Tumbes	34	2	38	7	4	6	57	1.68
Cancas	Tumbes	191	0	9	2	0	0	11	0.06
Mancora	Piura	38	1	36	0	40	0	77	2.03
Los Organos	Piura	18	0	2	0	0	0	2	0.11
	Total	524	4	156	24	47	26	257	0.49

this individual. Additionally, the gravid *M. munkiana* specimens each had one foetus, with sex and body sizes as follows: male of 31 cm disc width (DW), female of 34 cm DW, and male of 34.5 cm DW.

Across landing surveys, *M. mobular* was the most abundant species ($n=156$, 60.7%), followed by *M. thurstoni* ($n=47$, 18.3%), *M. munkiana* ($n=24$, 9.3%), and *M. birostris* ($n=4$, 1.6%) (Table 2). Sex ratios did not significantly differ from parity in *M. birostris* (1: 1; $\chi^2=0$, $P=1$), *M. munkiana* (10: 13; $\chi^2=0.39$, $P=0.53$), and *M. thurstoni* (10: 19; $\chi^2=2.79$, $P=0.09$). However, there were significantly more males than females in *M. mobular* (39: 60; $\chi^2=4.45$, $P<0.05$). Overall, there was a predominance of males (40%) over females (26.8%), with the sex of approximately one-third (33%) of mobulid rays remaining undetermined.

The data show differences in species composition and abundance across sites. Zorritos and Mancora had higher mobulid ray landings per survey

Table 2 Number of mobulid rays landed per species (*n*), mean disc width (DW), standard deviation (SD), and number of females (F), males (M), and unsexed individuals (U)

Species	*n*	DW	SD	F	M	U
M. birostris	4	364.67	257.66	1 (25.0%)	1 (25.0%)	2 (50.0%)
M. mobular	156	168.48	26.22	39 (25.0%)	60 (38.5%)	57 (36.5%)
M. munkiana	24	100.4 *	17.72	10 (42.8%)	13 (52.4%)	1(4.8%)
M. thurstoni	47	167.25	31.27	10 (21.3%)	19 (40.40%)	18 (38.3%)

*3 foetuses measurements for M. munkiana was excluded from calculating the mean DW

day relative to other sites and a higher species diversity, with *M. munkiana* particularly abundant in Zorritos (Table 1). Puerto Pizarro and Cancas had the fewest landings per survey day and a low species diversity (Table 1). Most landed individuals ($n = 190$) were captured using pelagic gillnets with a seven to eight-inch mesh ($n = 166$, 87.4%), followed by purse seine nets with a 1.5 to 3.5-inch mesh ($n = 16$, 8.4%), and coastal bottom gillnets ($n = 8$, 4.2%). At a specific-species level ($n = 140$), in pelagic gillnets, 79.2% of the catch was *M. mobular*, followed by *M. thurstoni* (17.8%), *M. munkiana* (2.1%) and *M. birostris* (0.7%). In coastal bottom gillnets, the catch was mainly composed of *M. mobular* (75%) and equal catch proportions for *M. birostris* (12.5%) and *M. munkiana* (12.5%). For purse seines, the catch was highest for *M munkiana* (87.5%), followed by *M. birostris* (87.5%) and *M. thurstoni* (6.25%).

Size frequency distribution

Disc width estimates obtained from mobulid rays landed eviscerated during surveys produced slightly overestimated DWs, which was apparent in 13 M. *thurstoni* specimens having an estimated DW above the maximum reported size for this species (189 cm DW for females and 177 cm DW for males—Stevens et al. 2024). For this reason, the proportions of juveniles are somewhat underestimated here, at least for *M. thurstoni* and *M. mobular*, but not in *M. munkiana* since this species was usually landed whole.

Species	n	DW	SD	F	M	U
M. birostris	4	364.67	257.66	1 (25.0%)	1 (25.0%)	2 (50.0%)
M. mobular	156	168.48	26.22	39 (25.0%)	60 (38.5%)	57 (36.5%)
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*3 fetuses measurements for *M. munkiana* was excluded from calculating the mean DW.

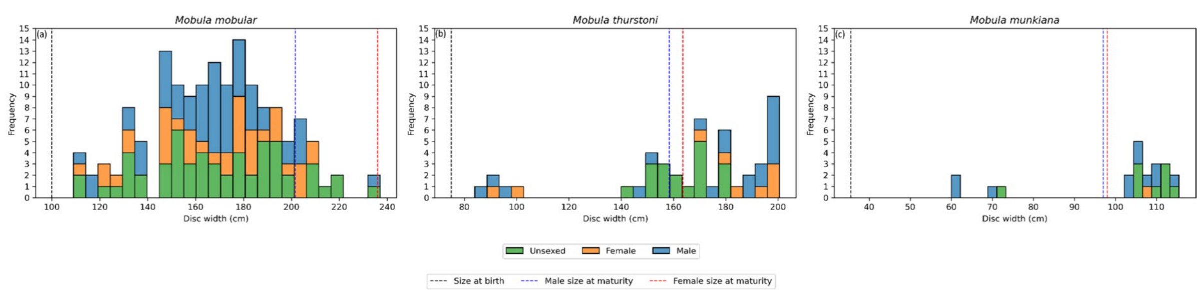

Fig. 5 a–c Size frequency distributions (disc width in cm) by sex were for *M. mobular*, *M. thurstoni*, and *M. munkiana* between 2017 and 2019. The vertical lines indicate the size at birth (black) and size at maturity for males (blue) and females (red) according to Stewart et al. (2018)

Nevertheless, size distributions in Fig. 5 provide important insight into the size composition of mobulid landings.

Mobula mobular body size ranged from 109 cm DW ($n=2$; one male and one female) to 237 cm DW (male), with most specimens measuring between 145 and 180 cm DW (Fig. 5). The majority of males (91.7%, $n=55$) and all females ($n=39$) were below the sizes at maturity (201.6 cm DW in males; 236.0 cm DW in females—Stewart et al. 2018). Overall, 92.3% ($n=140$) of the total *M. mobular* landings ($n=156$) were juveniles, with very few specimens (7.69%, $n=12$) exceeding the size at maturity (Fig. 5a and Table 2).

In *M. thurstoni*, body size ranged from 84 cm DW (male) to 200.6 cm DW (female), and most individuals measured 160–180 cm DW. Mature specimens (74.5%, $n=35$) dominated the landings for this species, comprising 19 males (78.9% above 158.4 cm DW) and ten females (80% above 163.6 cm DW) (Stewart et al. 2018). One-third of the specimens (25.5%, $n=12$) were below the size at maturity (Fig. 5b and Table 2).

In *M. munkiana*, body size ranged from 31 cm DW (male) to 115.5 cm DW (female), with most individuals measuring between 105 and 115 cm DW. Most specimens were mature ($n=24$), with equal proportions of males ($n=8$ above 97 cm DW) and females ($n=8$ above 98 cm DW) (Stewart et al. 2018). Three foetuses (below 35.5 cm DW) from 3 gravid females were excluded from the mean DW calculation (Table 2) and the size-frequency-distribution analysis (Fig. 5c).

Only four *M. birostris* specimens were recorded, measuring between 200 and 600 cm DW (not included in Fig. 5). Of these, two individuals were juveniles below 375 cm DW (one unsexed and one male), with the smallest recorded size at 207 cm DW for the male specimen. A gravid female measuring 662 cm DW was the largest specimen observed.

Interviews with fishers and traders

A total of 37 semi-structured interviews were conducted with artisanal fishers between June and July 2018 in Zorritos ($n=17$) and Mancora ($n=20$), targeting or opportunistically capturing mobulids. Fisher age ranged from 18 to 67 years, with an average age of 41.6 years and a mean fishing experience of 23.8 years (ranging from 4 to 53 years). Additionally, 21 interviews were conducted with traders involved in processing mobulid products. These interviews took place in Tumbes (Zorritos, $n=3$), Piura (Mancora, $n=3$), and Lambayeque (San Jose, $n=5$; Morrope, $n=2$; Moshoqueque, $n=4$; Chiclayo, $n=4$) (Fig. 1b, c).

Boats and fishing gear

The boats that capture mobulids in Mancora and Zorritos have a storage capacity of three to six tonnes. The main fishing gear used by fishers interviewed were gillnets (87%), followed by bottom longlines (8%) and purse seines (5%). Gillnets were further divided into pelagic gillnets (70%) and coastal gillnets (30%). The key difference between these gillnets lies in their size: coastal gillnets have a mesh size of 3 to 3.5 inches, while pelagic gillnets range from 7 to 8 inches. Additionally, coastal gillnets are primarily used within 5 nautical miles of the shore, whereas pelagic gillnets are deployed farther offshore.

According to interview data, pelagic gillnets are primarily used to target 'atún aleta amarilla' (Yellowfin tuna, *Thunnus albacares*), sharks such as 'tiburón martillo' (Smooth hammerhead, *Sphyrna zygaena*) and *Alopias* spp., as well as billfish like 'pez espada' (Swordfish, *Xiphias gladius*). In contrast, coastal gillnets are used to capture species including 'pámpano' (Paloma pompano, *Trachinotus paitensis*), 'sierra' (Pacific sierra, *Scomberomorus sierra*), and 'chiri' (Pacific harvestfish, *Peprilus medius*).

Species and seasonality

The fishers interviewed catch mobulid rays year-round (97%), with Mancora as a bycatch landing site and Zorritos as an opportunistic catch site for mobulid rays in the absence of other more desirable target species. Their responses showed that most mobulid ray captures occurred during the Austral Summer (December–March), although they persist throughout the year (Fig. 6). The majority of fishers interviewed (67%) mentioned that, compared to 10 years ago, the abundance of mobulid species is lower.

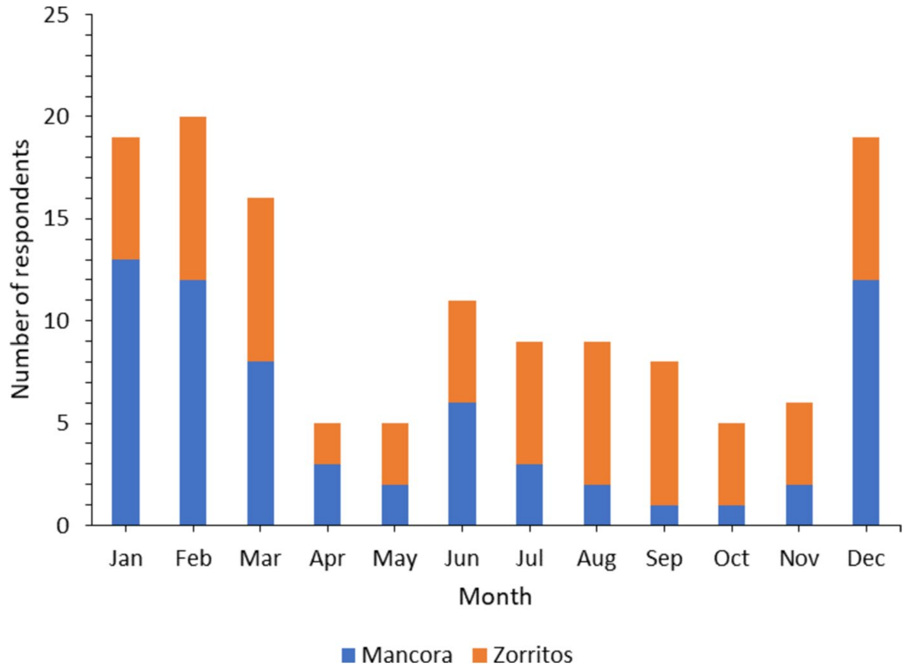

Fig. 6 Seasonality (warm season: Dec–May; cold season: Jun–Nov) of mobulid ray captures in Mancora and Zorritos based on fisher interviews

Fishing areas

Interactions with *M. birostris* are reported close to the oil platforms in Zorritos, La Cruz, and Puerto Pizarro, 2–7 miles from the coast (Fig. 1b). Moreover, Zorritos fishers pointed out that *M. mobular* is captured in front of Bocapan. Areas such as 'Las Plateras' and 'Malpaso' (Fig. 1b). Concurrently, those from Mancora indicated that Mancora, Punta Mero, and Acapulco are the main capture zones for *M. mobular* (Fig. 1b). No specific fishing grounds were reported for the remaining mobulid species, as they were usually recorded in the same areas as *M. mobular*.

Mobulid trade

Distribution and use

Mobulid rays are consumed domestically, with the Lambayeque Region being a key area of demand. Typically, only the pectoral fins are landed at fishing terminals across the country, while the heads, including gill plates, are discarded at sea during fishing trips to optimise storage space. Fresh mobulid meat is often landed on beaches, where it is sold directly to intermediary buyers and sellers, commonly known as traders.

For small landings (less than one tonne), traders distribute fresh mobulid meat to nearby local markets. For larger landings or in cases where there is no local demand, the meat is transported to the 'Empresa de Comercialización Mayorista de Productos Hidrobiológicos de Santa Rosa'-ECOMPHISA (Company of Wholesalers of Hydrobiological Products S.A.) in Santa Rosa (Lambayeque). According to traders, a small portion of the fresh meat is sold to local markets in Chiclayo, while the majority is purchased by salt-drying processors and transported to San José's Cove, which hosts the largest salt-drying processing centre in the country. The dried meat is then distributed to local markets in Lambayeque, including Mórrope, Mochumí, Moshoqueque, Túcume, Chiclayo, and Santa Rosa, as well as in Lima. It is widely used in traditional Peruvian dishes such as *tortilla de raya*, *guisado con papas*, and *ceviche* (Fig. 1c). It is essential to mention that according to interviews, *tortilla de raya* was initially prepared with Pacific guitarfish (*Pseudobatos planiceps*).

Salt-drying processing

San Jose's salt-drying processing centre is made up of 30 different modules (small processing centres where 5 to 6 workers process meat). Apart from mobulids, the workers also process other species, such as 'caballa' (chub mackerel, *Scomber japonicus*), 'raya águila peruana' (Peruvian eagle ray, *Myliobatis peruvianus*), 'pez guitarra' (Pacific guitarfish, *Pseudobatos planiceps*), and various shark species (mainly threshers, *Alopias* spp.).

The processing procedure of mobulid meat starts with gutting, removing pectoral fins from the carcass, and extracting skin (Fig. 7a). Thereafter, perpendicular (to the vertebral line) cuts are made on the pectoral fins, alternating between the dorsal and ventral sections (butterfly cuts) (Fig. 7b). The meat is then washed with seawater to remove excess blood (Fig. 7c) and liberally covered in salt for 24 h (Fig. 7d). This process removes excess water from the meat as the salt enters the tissue. Afterwards, the meat is washed to remove the excess salt, before drying begins (Fig. 7e, f). The sun drying of the pectoral fin meat can last from 3 to 7 days, depending on the weather. Therefore, for example, when a fresh mobulid, weighing 100 kg (complete individual including head), is processed, around 80% of the total body weight is utilised for human consumption. This translates to 80 kg of the mobulid being usable in its fresh form. However, the drying process significantly reduces the weight of the usable meat. Specifically, the 80 kg of fresh meat shrinks to 32 kg after drying, due to a 60% loss in weight. This dramatic reduction underscores the substantial impact that the drying process has on the overall yield of consumable meat. Other than the meat, the skin of mobulids is sometimes extracted and dried with other fish products to make fertilisers for plants (Fig. 7).

Meat value

Price differences in meat value (fresh or dried) were influenced by the meat colour (white, pink, or black) and varied between the high catch (April to November) or low catch (December to March) seasons. Meat prices also varied by location, with the lowest prices at Zorritos and Mancora, while in San Jose, the selling price was almost double. According to the interviewees, *M. mobular* is preferred for its white meat and enhanced flavour. *M. thurstoni* meat is classified as pink and *M. birostris* and *M. munkiana* as black meat. The average selling prices (USD/kg) of dry and fresh meat combined across high and low seasons are shown in Table 3. White meat had an average selling price of 2 USD for fresh meat and 5.1 USD for dry meat, pink meat was sold at 1 USD for fresh meat and 3.6 USD for dry meat, and black meat was sold at 0.9 USD for fresh meat and

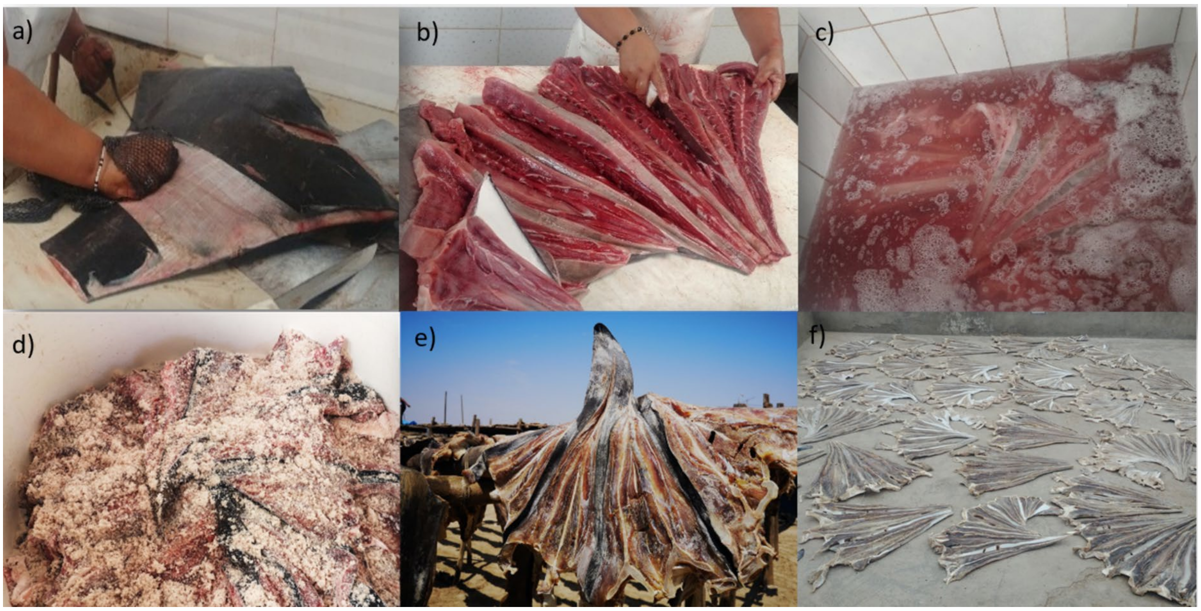

Fig. 7 Salt-drying processing of mobulid ray meat. **a** Skin extraction, (**b**) cutting, (**c**) washing, (**d**) salting, and (**e**, **f**) and sun drying

Table 3 The average price in USD for buying and selling mobulid ray meat (fresh/dry) by kilogram according to meat colour (white, pink, or black) and seasons (high/low) at each site. Landing sites: Zorritos and Mancora; markets: San Jose, Chiclayo, Morrope, and Moshoqueque

		White meat (*M. mobular*)		Pink meat (*M. thurstoni*)		Black meat (*M. birostris* and *M. munkiana*)	
Landing sites	Seasons	BP (USD)	SP (USD)	BP (USD)	SP (USD)	BP (USD)	SP (USD)
Zorritos	High season	*1.38*	*1.83*	*0.92*	*0.86*	*0.46*	*0.78*
	Low season	-	-	-	-	-	-
Mancora	High season	*0.95*	*2.08*	*0.52*	*1.19*	*0.28*	*1.08*
	Low season	-	-	-	-	-	-
San Jose	High season	*2.32*	**5.32**	*1.74*	**3.85**	*1.47*	**3.50**
	Low season	*0.95*	**3.70**	*0.98*	**2.54**	*0.49*	**2.31**
Chiclayo	High season	**4.89**	**6.12**	**4.34**	**4.59**	**3.30**	**4.17**
	Low season	**3.91**	**5.14**	**2.94**	**3.15**	**2.26**	**2.86**
Morrope	High season	**5.66**	**6.12**	**4.28**	**4.28**	**3.82**	**3.89**
	Low season	**3.98**	**4.28**	**3.67**	**3.06**	**2.60**	**2.78**
Moshoqueque	High season	**5.75**	**6.06**	**4.31**	**4.28**	**3.91**	**3.89**
	Low season	**3.98**	**4.37**	**3.79**	**3.18**	**2.84**	**2.89**

Keys: *BP* buying price, *SP* selling price, fresh meat (italicised), dry meat (bold). Conversion rate: 1USD = 3.27PEN, Central Reserve Bank of Peru, June 2018

3.3 USD for dry meat. These price variations reflect market preferences and highlight the economic value of mobulid meat, particularly in regions like San Jose where the processing and commercialization of dried meat are significant (Table 3).

Discussion

Peru's coastal waters are home to significant populations of mobulid rays, including oceanic manta rays (*M. birostris*) and four devil ray species (González-Pestana 2022; Alfaro-Cordova et al. 2017). This study comprehensively analyses mobulid landing trends, gear use, catch demographics, landing hotspots, seasonality, and trade and market pressures in Peru. By examining the spatial and temporal patterns of mobulid landings within Peruvian waters, the study identifies critical areas and periods of intense fishing activities. It delves into the types of fishing gear employed and their impacts on catch rates and bycatch. Additionally, the study assesses the demographic profiles of the caught individuals, including size, sex, and species composition for mobulid rays, aiming to inform sustainable management and conservation strategies for these vulnerable marine species in this region.

Landing trends in gear types and across regions

The persistently large number of mobulid rays landed in Peru is concerning given their endangered status worldwide. Recent studies have highlighted the magnitude of this issue, with González-Pestana (2022) reporting 270 mobulid individuals landed over 183 survey days, and Alfaro-Cordova et al. (2017) documenting 3673 individuals over 395 survey days. These findings translate to estimated annual catches of 539 and 3394 mobulid individuals in northern Peru (González-Pestana 2022 ; Alfaro-Cordova et al., 2017). However, this study suggests that the mean annual landings in northern Peru were 11,520 mobulid rays per year from 2013 to 2023, according to IMARPE data. This amount ranks Peru as one of the largest fisheries for mobulid rays globally, with annual landings above multiple mobulid fishery hotspots globally (Croll et al. 2016). Based on IMARPE data, total mobulid landings have generally increased in recent years, particularly in gillnet fisheries. However, trends differed across gears, and the absence of fishing effort data in the analysis could have obscured a decrease in mobulid ray catch per unit effort over time. This is supported by a notable reduction in mobulid landings by 75.05% from purse seine fisheries since 2013 (< 100 tons), with landings remaining low through 2022–2023 (318.74 tons). This decline could be due to several factors, including changes in fish stocks, regulatory measures, economic pressures, or environmental changes impacting fish availability or fishing practices. Nevertheless, similar declining trends in mobulid landings across their range suggest many populations are overfished (Moazzam 2018; Fernando & Stewart 2021; Venables et al. 2024).

In northern Peru, particularly in the Piura region which hosts the largest fishery community, gillnet fishing effort has generally increased over time. This increase is evident in the expansion of the small-scale fleet, with an 186% increase in the number of vessels and a 140% increase in fishers between 1996 and 2015 (González-Pestana et al. 2024). Additionally, the average length of gillnets has grown substantially, from 72–81 m in 1970 to 800–3300 m in 2005 (Alfaro-Shigueto et al. 2010). The extensive use of gillnets in Peru, with an estimated total length exceeding 100,000 km per year in 2010 (Alfaro-Shigueto et al. 2010), has likely increased since then. For instance, in Tumbes alone, there were around 749 gillnets used by fishers in 2018 (Castillo et al. 2018). This growth in fishing effort has been accompanied by technological improvements, resulting in larger fishing areas, longer fishing trips and reductions in the time spent searching for target species (De la Puente et al. 2020). Overall, the widespread use of gillnets, coupled with their effectiveness in mobulid entanglements and the targeting of various coastal species that share habitats with mobulid rays, significantly increases the chances of mobulid captures (Ayala and Romero 2016; Alfaro-Cordova et al. 2017). However, it is essential to note that specific, detailed data on fishing effort in northern regions, particularly for mobulid species, remains limited, hindering more comprehensive analysis (Alfaro-Shigueto et al. 2010; De la Puente et al. 2020; González-Pestana et al. 2024).

Peru plays a crucial role in the global crisis of batoid landings, ranking 15th worldwide and contributing 11% of global landings from 2005 to 2011 (Alfaro-Cordova et al. 2017; González-Pestana et al. 2022). Mobulid rays make up 28% of Peru's total batoid catch, with most landings occurring along the northern coast. Gillnets are the primary fishing gear responsible for mobulid captures in Peru (González-Pestana et al. 2016; Alfaro-Cordova et al. 2017; González-Pestana et al. 2022; González-Pestana 2022). Recent studies have provided more detailed insights into the distribution and environmental preferences of mobulid species in the eastern Pacific Ocean. Lezama-Ochoa et al. (2019a) analysed observer data from the tropical tuna purse-seine fishery, revealing spatial and temporal patterns in mobulid ray occurrences. Their findings showed that mobulid species, including the spinetail devil ray (*Mobula mobular*), are more frequently encountered in specific areas and seasons, which could inform conservation strategies. Furthermore, Lezama-Ochoa et al. (2019b) found that sea surface temperature, chlorophyll-a concentration, and bathymetry were significant factors influencing the spinetail devil ray's distribution in the eastern tropical Pacific. Building on this work, Lezama-Ochoa et al. (2020) employed a Bayesian modelling approach to predict the occurrence of *M. mobular*, providing a more robust understanding of the species' habitat preferences and potential distribution.

In addition, there is substantial evidence of IUU fishing in northern Peru, particularly in the Tumbes region (López de la Lama and de la Puente 2023). Of primary concern is that *M. birostris* was recorded in landing surveys but not reported in IMARPE data, suggesting that the fishing impacts on this species have persisted despite the prohibition on capturing *M. birostris* since 2016 (Produce 2011). A study by Guirkinger et al. (2021) supports these findings, with an estimated total annual interactions of 349 M. *birostris* in 2018 based on surveys conducted with artisanal fishers in Zorritos and Mancora. Moreover, illegal industrial and small-scale fishing continues to occur in this protected zone despite the 2011 prohibition of purse seines within the first 5 miles of the coast (Produce 2011). Numerous unregistered purse seiners and trawlers have been documented operating illegally within the 5-mile limit, using non-selective fishing gear and catching juvenile fish (López de la Lama and de la Puente 2023). This illegal activity likely results in significant unreported landings, including potential mobulid bycatch. Furthermore, gillnets have been observed to have both more frequent interactions and higher catch rates of mobulids compared to purse seines (Sarah Martin 2020). For example, studies from other regions, such as the Indian Ocean, have shown that gillnet fisheries are responsible for a significantly higher proportion of mobulid interactions (> 99%) compared to purse seine fisheries (0.1%) (Sara Martin 2020). This trend appears to be consistent with observations in Peru (Alfaro-Cordova et al. 2017).

Despite the opportunistic nature of mobulid captures reported in this study, consistent retention of mobulid rays in these fisheries suggests that realistic and practical incentives are needed to reduce mortality. In particular, enforcing national mobulid ray protections will require addressing post-capture mortality since most of the catch occurs in non-selective gear, and measures must be designed pragmatically and developed with active involvement from fishers, who are the primary stakeholders in this activity. Because fishers may also target mobulid ray aggregation sites when using non-selective gear, it is important to consider the socio-economic drivers of the fishery, such as the demand for mobulid meat regionally. Engaging fishers in the creation and implementation of these strategies not only ensures a more effective and adaptable approach but also promotes their cooperation and compliance. Also, a lack of effort data, declines in landing trends for certain gears and regions, and continued meat trade of highly vulnerable mobulid ray species combine to raise concerns for the survival of these species in Peruvian waters. Also, as mentioned before, besides the protection of *M. birostris* (Produce 2015), more is needed to ensure all mobulid ray populations are sustained regionally. Given the non-selective character of these fisheries, measures to prevent bycatch, retention and trade should be integrated into management plans.

Catch demographics

Based on size frequency distribution analysis, this study provides insights into the mobulid catch demographics in Peru. The body size distributions documented across the four mobulid species recorded indicate varied population structures. The study shows a wide range of body sizes in catches for *M. mobular*, which suggests that individuals of various life stages are being caught. Yet, the vast majority of specimens landed were immature (92.3%). The findings of this study align with and support the designation of northern Peru as an Important Shark and Ray Area (ISRA) by the IUCN, specifically recognising it as a crucial reproductive zone for the spinetail devil Ray (*Mobula mobular*) (Jabado et al. 2023). The presence of a majority of juveniles in our study is consistent with the characteristics of a nursery area. Additionally, the catch data for *M. mobular* indicates that both males and females are being caught in relatively equal proportions, which suggests no sex-specific segregation in the areas where fishing occurs (Lezama-Ochao et al. 2019a; Alfaro-Cordova et al. 2017; González-Pestana 2022; Carpenter 2023). Diverse size ranges, majority of juveniles, and balanced sex ratios support Gonzalez-Pestana's (2022) suggestion that northern Peru may serve as a potential nursery area for *M. mobular*. This corroborates the ISRA's identification of north Peru as one of the three most important habitats for *M. mobular* in the Eastern Pacific. Furthermore, the species' association with productive upwelling systems, of which Peru contains one of the largest aggregations, underscores the region's importance for *M. mobular*'s life cycle (Jabado et al. 2023).

For *M. thurstoni* and *M. munkiana*, more adults were landed relative to juvenile specimens, and intermediary life-stages were absent from each of their size distributions. This could indicate that the fishing activities primarily intercept specific life stages or size classes of these species (Lezama-Ochoa et al. 2019b; Alfaro-Cordova et al. 2017; González-Pestana 2022). Adults and juveniles of both species may use different habitats, with fishing activities primarily occurring in areas frequented by one age group. Also, different life stages might be present in the fishing areas at different times of the year. Moreover, the fishing methods used might be more effective at catching certain size classes of these species (Lezama-Ochoa et al. 2019b; Alfaro-Cordova et al. 2017; González-Pestana et al. 2022; González-Pestana 2022; Carpenter 2023). However, the skewed distribution of body sizes for adults in *M. munkiana* and *M. thurstoni* could also be a result of limited sampling or catch data for these species compared to *M. mobular*.

With very few data points ($n=4$), *M. birostris* displays no pattern as both large and small individuals were recorded. More extensive sampling is required to accurately determine the population structure. However, due to its catch prohibition since 2016 (Produce 2015), obtaining a reliable estimation of population structure is extremely challenging, as only illegal landings may occur which is often not reported. These illegal landings often take place at night, particularly when inspectors are not present, as fishermen seek to take advantage of market demand for the species to sell it clandestinely (Rojas pers. comms.). Although there were some landings reported in an earlier IMARPE dataset between 2014 and 2017

(Supplemental Table 2), since the protection of this species in 2016, landings were not reported in the latter datasets (2000–2023) received from IMARPE.

These findings highlight species-specific differences in population dynamics and emphasise the need for tailored conservation strategies to address the unique life history traits and maturity schedules of each species. The potential nursery area for *M. mobular* in northern Peru suggests that this region may be particularly important for the species' life cycle and population dynamics. For *M. thurstoni* and *M. munkiana*, the narrow size distributions in catches could indicate that certain life stages are more vulnerable to fishing pressure in Peru, which may have implications for population sustainability. To fully understand these patterns and their implications for mobulid conservation, further research would be needed to investigate habitat use, migration patterns, and the impacts of fishing practices on different life stages of these species in Peruvian waters.

Catch hotspots and seasonality

Northern Peru exhibits distinct seasonal patterns, evident in the distribution of species concerning sea-surface temperature and chlorophyll levels (Lezama-Ochoa et al. 2019b). The three most important landing sites (and their respective fishery areas) identified in this study (Tumbes, Piura, and La Libertad) overlap with important habitats for mobulid species, particularly the spinetail devil ray (*M. mobular*) (Jabado et al. 2023). Moreover, La Libertad and Piura are part of the Humboldt Current System and Transition Zone, a highly productive upwelling zone rich in zooplankton and small fish and are also in a temperature range preferred by mobulids (Francis and Jones 2017) thus hosting important feeding areas for mobulid rays (Lezama-Ochoa et al. 2019a, b; Alfaro-Cordova et al. 2017; González-Pestana 2022; Jabado et al. 2023). This is further supported by Coasaca-Céspedes et al. (2018), who conducted the only direct feeding study of mobulid rays in northern Peru. Their preliminary analysis of stomach contents revealed that mobulids in this region primarily feed on euphausiids and small teleost fishes, confirming the importance of the area's rich zooplankton communities for these species' dietary needs. These environmental factors could also contribute to more mobulid catch in the northern Peru regions, as this study shows. Also, fishers' interviews underscored Mancora as a primary catch site, supplemented by opportunistic catches in Zorritos during periods of low target species availability. This strategic identification of key areas and seasons is pivotal as it enables focused studies on mobulids in Peru, and crucial information for management, aligning closely with the oceanographic dynamics of the Eastern Pacific Ocean as elucidated by previous studies (Lezama-Ochoa et al. 2019b; Jabado et al. 2023).

Distinct seasonal trends in mobulid ray catches were observed, with peaks in March, February, and December accordingly, the austral summer, closely followed by a notable increase in July, consistent with findings from fishers' interviews indicating year-round catch activity, particularly during summer months. While *M. mobular* exhibited the highest landings in March, *M. munkiana* and *M. thurstoni* showed variations, with peak catches in January and July, respectively. These patterns align with the observed seasonality in mobulid ray fisheries, confirmed by a chi-square test indicating significant variation in landings across seasons. Also, this could be a result of experiencing intense upwelling currents during this period, creating nutrient-rich waters that attract filter-feeding species like mobulids (Fernando and Stewart 2021; Alfaro-Cordova et al. 2017; González-Pestana 2022). Additionally, the seasonal increase in productivity leads to larger feeding aggregations, making them more susceptible to capture (Fernando and Stewart 2021; Alfaro-Cordova et al. 2017; González-Pestana 2022). For *M. munkiana*, the highest catches in January, November, and July indicate a different pattern. This species may have specific migration patterns that bring them closer to the Peruvian coast during these months. Recent research by Palacios et al. (2023) on Munk's devil ray ecology in the Gulf of California and Mexican Pacific provides insights into the species' behaviour and vulnerability to fisheries. Their study revealed that *M. munkiana* exhibits seasonal reproductive patterns and uses specific coastal areas as critical habitats for courtship and mating. While the Gulf of California is geographically distinct from Peru, this research suggests that *M. munkiana* may have similar seasonal movements and habitat preferences in other parts of its range, potentially explaining the observed catch patterns in Peruvian waters. The peak catches in July, January, and May for *M. thurstoni* suggest a more complex pattern. This species may utilise different areas throughout the year, resulting in varied catch patterns. *M. thurstoni* might respond differently to seasonal changes in ocean currents and productivity compared to other mobulid species (Fernando and Stewart 2021; Alfaro-Cordova et al. 2017; González-Pestana 2022; Sarah Martin 2020). Notably, bycatch events often occur at oceanographic fronts, such as those off Peru in March for *M. mobular* and the Galapagos Islands in December for *M. thurstoni*, indicating specific hotspots of vulnerability (Lezama-Ochoa et al. 2019a, b). This comprehensive analysis sheds light on the temporal dynamics and geographic preferences driving mobulid ray fisheries in Peru.

Each mobulid species has unique life history traits, feeding preferences, and migration patterns, leading to different seasonal catch trends (Sarah Martin 2020; González-Pestana 2022). This is further supported by recent research on manta and devil ray aggregations, which highlights that mobulid species form seasonal aggregations ranging from a few to thousands of individuals, often linked to environmental factors, food abundance, critical habitats, and reproduction (Palacios et al. 2023). These aggregations facilitate key life history functions such as feeding, courtship, mating, predation avoidance, cleaning, and thermoregulation, which can vary among species and locations (Palacios et al. 2023). Furthermore, changes in fishing effort throughout the year may contribute to observed catch patterns (Carpenter et al. 2023; Carpenter 2023; Sarah Martin 2020; González-Pestana et al. 2022; González-Pestana 2022). For example, fishers might target different species or areas depending on the season. The Humboldt Current system experiences seasonal and interannual variability, which can affect the distribution and abundance of mobulid rays (Carpenter 2023; Sarah Martin 2020; González-Pestana 2022). In previous studies, fishers have reported that mobulid ray presence is correlated with krill abundance, which may vary seasonally and by species (Carpenter 2023). Different fishing methods may be more effective at catching certain species or size classes, contributing to observed catch patterns (IOTC 2020; González-Pestana 2022). It is important to note that these trends may be influenced by sampling biases or limitations in data collection methods (Sarah Martin 2020; González-Pestana 2022).

These species-specific seasonality trends highlight the need for tailored conservation and management strategies for each mobulid species in Peruvian waters. Further research is needed to better understand the drivers of these patterns and their implications for mobulid population dynamics and conservation.

Market pressures

Mobulid rays are commercialised in Peru primarily for national consumption, with evidence of illegal meat imports from Ecuador (Rojas, pers. comms.), where these species are protected (SRP 2010). Unlike other countries that utilise the gill plates, the trade appears to be restricted to meat (Croll et al. 2016; O'Malley et al. 2017; Palacios et al. 2024 in press). The salt-drying process for fish is used in Peru as an ancient practice and the warm and arid environment of mid-northern Peru is an ideal environment for this process, so fish can be preserved for months or up to a year (Turan 2015; González-Pestana et al. 2024). It is important to note that commercialization and consumption are concentrated in northern Peru, particularly in regions like Tumbes, Piura, and Lambayeque. These regions are especially significant for elasmobranchs, as they serve as key hubs for the trade and consumption of marine resources. This pattern has been observed for other species such as sharks (Lopez de la Lama et al. 2018; Grillo-Núñez and Gozzer-Wuest 2019) and guitarfish (González-Pestana et al. 2024).

Commercialising dry meat for traditional dishes has been a cultural practice in Peru for millennia (González-Pestana et. al 2024). Processors indicate that the Pacific guitarfish (*Pseudobatos planiceps*) has been regularly consumed as a cultural tradition in Lambayeque; this information is corroborated by Jimenez et al. (2024). However, a dramatic 98% decline in the Pacific guitarfish population in Peru, as González-Pestana et al. (2024) reported, has forced processors to seek alternative resources. The authors suggest that mobulid ray meat has likely emerged as a replacement for Pacific guitarfish, primarily due to its lower cost and availability. González Pestana et al. (2024) highlighted that Pacific guitarfish maintained an average price of approximately 1.5 USD, with a range of 0.4 and 4.4 USD per kilogram between 2014 and 2020. In contrast, as reported in this study, the average cost for mobulid ray fresh meat was notably lower, ranging between 0.78 and 2.08 USD (selling price in Zorritos and Mancora).

The cheapest meat is fresh and is consumed locally in the markets near landing sites. As the product moves further from the source of processing, the price per kg increases because of the costs of transportation and processing. Processing not only increases the shelf-life of the product, but it also improves the calorific value per kg through the drying process that removes much of the water from the meat, reducing the weight and volume which contribute to its storage and transportation (González-Pestana et. al 2024). The colour of the meat is also a determinant characteristic of the price. White meat (*M. mobular*) is considered the best quality because of its superior taste, resulting in a higher price, indicating a greater demand for this species (Alfaro-Cordova et al. 2017).

Study limitations

Despite the robust dataset and comprehensive approach, the study has several limitations. One significant area for improvement is the absence of detailed fishing effort data, which constrains the ability to fully understand the dynamics of mobulid ray landings and the impact of fishing intensity on these populations. Without this data, it is challenging to draw comprehensive conclusions about the sustainability of current fishing practices. Also, it is important to note that before 2013, all landed mobulid species were recorded as a single species, whereas from 2013 onwards, IMARPE began differentiating and reporting other mobulid species in their landing records. This change in species identification practices should be considered when interpreting trends in species-specific landings data, particularly for the period before and after 2013.

Sampling limitations also affect the study's findings. For example, the sample size for species like *M. birostris* is too small to draw reliable conclusions about population structure and trends. Additionally, while the study covers key regions and seasons, there may be gaps in data from less-studied areas or off-peak seasons that could provide a more complete picture. This lack of comprehensive coverage limits the overall robustness of the study's conclusions. While the study highlights the socio-economic importance of mobulid fisheries, it lacks a detailed analysis of the economic incentives and market forces driving the continued capture and trade of mobulid rays. A deeper understanding of these factors could provide valuable insights for developing more effective management strategies. Lastly, the study mentions evidence of illegal meat importation from Ecuador but does not quantify or explore this issue in depth. This gap limits the understanding of its impact on local mobulid populations and markets. Addressing these weaknesses through more comprehensive data collection, targeted research, and detailed analysis would enhance the understanding of mobulid ray fisheries and support the development of effective management and conservation strategies in Peru.

Future directions

Effective management of mobulid fisheries requires a multifaceted approach that integrates scientific research, policymaking, and stakeholder engagement (Roman and Hall 2022; Haque et al 2021). Guirkinger et al. (2021) emphasise the importance of addressing economic hardship, corruption, and low social influence to enhance fishers' compliance with fisheries legislation. Collaborative efforts between scientists, policymakers, and local communities are essential for implementing effective conservation measures and ensuring the long-term viability of mobulid fisheries in Peru. Moreover, the association of mobulid captures within nearshore waters and continental shelf regions underscores the need for habitat-focused conservation strategies (Ward-Paige et al. 2013; Stewart et al. 2018; Haque et al. 2021; Roman and Hall 2022). Understanding the interaction between oceanographic conditions, seasonality, and mobulid distributions, as highlighted by Lezama-Ochoa et al. (2019a, b), is crucial for identifying and protecting key habitats. Dynamic hotspots, such as those near coastal upwelling systems, necessitate proactive spatial and temporal protective management measures to mitigate fishing pressure and preserve critical habitats and the species that rely upon them (Lezama-Ochoa et al. 2019a, b; Roman and Hall 2022).

Prioritising research on reproduction and feeding zones, contaminants' impact, and population characteristics are critical for informing conservation measures (Stewart et al. 2018). Due to the apparent global fishing pressures on mobulid populations and their conservative life history traits, implementing fisheries management for these species is vital to protect their populations. Some conservation efforts are present in the region (both in artisanal and industrial fisheries), such as the protection of *M. birostris*, a bycatch registration and release programme in the industrial tuna fishery, and the awareness work carried out by local NGOs in coastal communities. However, dynamic spatial management measures based on habitat use hotspots and seasonal trends are vital for reducing mortality and ensuring the sustainability of mobulid populations (Haque et al. 2021; Roman and Hall 2022) in the eastern Pacific Ocean (Lezama-Ochoa et al.

2019a). By addressing these future directions, incorporating detailed research, and engaging stakeholders at all levels, it is possible to improve the conservation and sustainability of mobulid ray populations in Peru.

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Author contribution SR, KK, FR, and SK conceived and designed the study. SR, RE, RM, AM, and RF coordinated and carried out landings, market surveys, and interviews with fishers in Peru. SR, NGD, BL, RE, and SK analysed the data. SR, NGD, BL, GS, and SK wrote the paper with input from all co-authors.

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Data availability The landing and sampling datasets used during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All applicable national guidelines for sampling of organisms for the study have been followed. Informed consent was obtained from all individual participants included in the study.

Conflict of interest The authors have no relevant financial or non-financial interests to disclose. Dr. Guy Stevens is a Guest Editor on this Special Issue, but he was not involved in the peer review of this article and had no access to information regarding its peer review.

Deceased or incapacitated authors The authors have the legal approval of Rosario Escobedo's direct relative (mother) to include her as a co-author as her work is reflected in the manuscript.

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