THERYA, 2025, Vol. 16(3):409-426 DOI:10.12933/therya-25-6205 ISSN 2007-3364

Trophic ecology of marine mammals in the Mexican Pacific Ocean: Prey diversity, network structure, and overlap with fisheries

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During the 20th century, interaction between marine mammals and fisheries pervaded all Mexican seas and fishing activities, with severe impacts for both fishermen and mammals, generating the need to investigate these animals' trophic ecology to better manage the country's fisheries. Aimed to characterize the trophic ecology of marine mammal fauna in the Mexican Pacific Ocean and their interaction with fisheries, here we built a network for the diet similarity of marine mammals and examined its modularity to identify trophic guilds and analyze its relationship with trophic level, prey diversity, and trophic overlap with fisheries. We reviewed literature and data in our group to identify and validate for comparison, 380 prey species of 40 marine mammal species from the Mexican Pacific Ocean. We determined a similarity matrix between marine mammal diets that depended on the diversity and ingested amount of 8 prey types. From this matrix, we built a non-directional and weighted network, with mammal species being the nodes, and diet similarities the edges. We examined modularity and other network traits in relation to mammals' trophic level, prey richness, and overlap with fisheries. We identified 5 network modules of marine mammals that we defined as trophic guilds, being I) planktophagic, II) ichthyophagic, III) teuthophagic of low trophic level, IV) teuthophagic of high trophic level, and V) sarcophagic. We observed a wide variation among mammals for their weighted degrees (added pairwise similarities), prey richness, and trophic levels that combine differentially known diets and diets with different prey diversities. Inverse relationships between prey richness and weighted degree at the species level, and between trophic level and weighted degree at the guild level, indicate that Mexican Pacific marine mammals belong to two trophic systems –surface and deep waters– mainly structured by competitive exclusion, which is stronger at higher trophic levels. Marine mammals with greater trophic overlap with fisheries in the Mexican Pacific Ocean occur in guilds I and II, principally *Phocoena sinus*, *Zalophus californianus*, *Tursiops truncatus*, and *Delphinus bairdii*.

Key words: Competitive exclusion; Functional group; Network modularity; Trophic guild; Trophic system

Durante el siglo XX, la interacción entre mamíferos marinos y pesquerías se extendió a todos los mares mexicanos y actividades pesqueras con impactos severos para ambos, pescadores y mamíferos, generando la necesidad de investigar la ecología trófica de estos animales para desarrollar una mejor gestión de los recursos pesqueros del país. Para caracterizar la ecología trófica de la mastofauna marina del Pacífico Mexicano y su interacción con las pesquerías, aquí construimos una red de similitud en la dieta de mamíferos marinos, examinando su modularidad para identificar gremios tróficos y analizar su relación con el nivel trófico, la diversidad de presas y el traslape trófico con las pesquerías. Revisamos literatura y datos de nuestro grupo para identificar y validar para comparación, 380 especies presa de 40 especies de mamíferos marinos del Pacífico Mexicano. Determinamos una matriz de similitud entre las dietas de los mamíferos marinos, dependiente de la diversidad y la cantidad ingerida de 8 tipos de presas, con la que construimos una red no direccional con pesos, siendo las especies de mamíferos los nodos y sus similitudes las aristas. Examinamos la modularidad y otros atributos de la red en relación con el nivel trófico de los mamíferos, la riqueza de sus presas y su traslape con pesquerías. Identificamos 5 módulos en la red de mamíferos marinos que definimos como gremios tróficos, siendo éstos: I) planctófagos, II) ictiófagos, III) teutófagos de bajo nivel trófico, IV) teutófagos de alto nivel trófico y V) sarcófagos. Observamos una amplia variación entre los mamíferos en sus grados ponderados (la suma de sus similitudes pareadas), riquezas de presas y niveles tróficos, lo cual combina dietas diferencialmente conocidas y dietas que en realidad tienen diferentes diversidades de presas. Relaciones inversas entre la riqueza de presas y el grado ponderado a nivel de especies, así como entre el nivel trófico y el grado ponderado a nivel de gremio, indican que los mamíferos marinos del Pacífico Mexicano pertenecen a dos sistemas tróficos, –aguas superficiales y profundas–, mayormente estructurados por exclusión competitiva que es más fuerte en altos niveles tróficos. Los mamíferos marinos de mayor traslape trófico con las pesquerías en el Pacífico Mexicano son de los gremios I y II, principalmente *Phocoena sinus*, *Zalophus californianus*, *Tursiops truncatus* y *Delphinus bairdii*.

Palabras clave: Exclusión competitiva; Gremio trófico; Grupo funcional; Modularidad de redes; Sistema trófico

Most marine mammals are highly vulnerable to the ongoing environmental deterioration as they inhabit broad geographic distributions in which they travel long distances and are impacted by different human activities with complex effects on their health, foraging, reproduction, and dispersion (Katona and Whitehead 1988; Harwood 2001; Acevedo-Whitehouse and Duffus 2009; Smith *et al.* 2009). Marine mammal ecology is sensitive to shifts in the oceans, making their foraging and reproduction reflect changes in marine food webs, and their movements also reflect changes in large-scale biophysical signals. For these reasons, research on marine mammals focuses on inferring changes in the structure and function of marine ecosystems from them, under the concept of sentinel species (Ross 2000; Aguirre and Tabor 2004; Moore 2008; Bossart 2011; Moore and Kuletz 2019).

Marine mammals have medium to high trophic levels and consume large amounts of food, which importantly contribute to the flows of matter and energy in the oceans. They transport nutrients from deep to shallow waters, and their long-distance movements are relevant to horizontally spread fertilizing materials across the oceans, all of which stimulates primary productivity (Gaskin 1982; Katona and Whitehead 1988; Papale and Giacoma 2025). Especially large cetaceans have recently been recognized as being of great importance to the global dynamics of carbon (Roman *et al.* 2014; Pearson *et al.* 2023). However, the high trophic levels and high metabolic rates of marine mammals also make them assimilate large amounts of pollutants, which are involved in severe physiological failures, especially immunological and reproductive, indicating that such pollutants also affect other species in the marine trophic webs (*e.g.*, Aguilar *et al.* 1987, 1999; Reijnders 1988; Jefferson *et al.* 2006). Another important ecological trait of marine mammals is their high trophic plasticity by which these animals can adapt to diverse environmental changes, but by which they also negatively interact with the varied and intensive human activities at sea nowadays, especially fisheries (Nemoto 1970; Gaskin 1982; Northridge 1985, 1991, 2009a, b; Northridge and Hoffman 1999; Fertl, 2009; Plagányi and Butterworth 2009). Interactions between marine mammals and fisheries have occurred for centuries. Still, since the mid-20th century, fisheries drastically intensified and underwent technological revolutions, leading to profound changes in marine ecosystems, including high mortalities of marine mammals and other amniotes worldwide. The interaction between marine mammals and fisheries is a complex and dynamic problem that results in the annual death of several hundred thousand individuals and inflicts dreadful wounds on many thousands more. This problem has worsened during the 21st century, with gillnets accounting for 84% and 98% of fisheries-caused mortality of odontocetes and pinnipeds, respectively (Anderson 2001; DeMaster *et al.* 2001; Read *et al.* 2006; Northridge 2009a, b; Reeves *et al.* 2013; Sonne *et al.* 2024). Gillnets are now the greatest risk for the imminent extinction of the vaquita (*Phocoena sinus*) and another 12 units in critical risk of 5 small cetacean species (D'Agrosa *et al.* 2000; Rojas-Bracho *et al.* 2006; Jaramillo-Legorreta *et al.* 2017; Brownell Jr. *et al.* 2019).

Since the 19th century, several marine mammal conservation issues in Mexico have become important nationally and internationally, involving management, economy, politics, and social welfare. Such issues currently include interaction with fisheries, physical, chemical, and biological pollution, collisions with ships, interaction with touristic activities, habitat deterioration, and the synergisms of these impacts with climate change (Aurioles 1993; Arellano-Peralta and Medrano-González 2013, 2015; Heckel *et al.* 2020). Between 46 and 50 marine mammal species inhabit the Mexican Pacific Ocean, some of which have been economically, politically, or socially important throughout history. The Mexican Pacific Ocean encloses the oceanographic and biogeographic transition between the Eastern Tropical Pacific and the Northeastern Pacific, and thus exhibits species with different biogeographic and environmental affinities (Ballance *et al.* 2006; Medrano González *et al.* 2008; Medrano González and Urbán Ramírez 2019; Heckel *et al.* 2020), as well as one of the very few endemic marine mammals in the world: the vaquita.

Knowledge on marine mammal foraging accelerated throughout the 1980s when the collapse of several fisheries favored culling campaigns against diverse marine mammals, urging the need to assess interactions between fisheries and marine mammals and their impacts on both (Northridge 1985, 1991; Kaschner and Pauly 2005). Data on marine mammals feeding in Mexico have been obtained through direct observation (*e. g.*, Gendron and Urban 1993; Sánchez-Pacheco *et al.* 2001), examination of feces (*e. g.*, Bautista Vega 2000, 2002; Porras Peters 2004) and stomach contents (*e. g.*, Pérez-Cortés Moreno *et al.* 1996), analysis of fatty acids content (*e. g.*, Nolasco Soto 2003; López Montalvo 2005, 2012; Rueda Flores 2007; Traconis Corres 2010) and stable isotope proportions for different elements (*e. g.*, Gendron *et al.* 2001; Jaume Schinkel 2004; Porras-Peters *et al.* 2008; Elorriaga-Verplancken *et al.* 2013; Busquets-Vass *et al.* 2021), molecular scatology (Jiménez Pinedo 2010; Guerrero de la Rosa 2014), and metagenomics (Brassea-Pérez *et al.* 2019). These and other studies have examined the relationship of marine mammals with the abundance of their prey in the context of environmental variation (*e. g.*, Gendron Laniel 1990; Gendron and Urban 1993; García Rodríguez 1999; Jaquet and Gendron 2002; Porras-Peters *et al.* 2008). Nonetheless, not much research in Mexico has treated marine mammal trophic ecology at the community level, or on a non-local scale, *i. e.*, mesoscale.

In this work, we compile and compare the prey diversity of 40 marine mammal species from the Mexican Pacific Ocean. We built a network, with nodes being mammal species and edges their pairwise diet-similarities, to examine its modularity, weighted degree of connections, trophic level, and prey diversity, to identify trophic guilds and their relationships. We also examine diet similarities to examine the species' propensity for competition and interaction with fisheries.

Materials and methods

Diet data. We thoroughly reviewed literature and data from our group not reported in literature (Sánchez Arias 1992; Unpublished observations of author LMG), to identify 380 prey species taken by 8 mysticetes, 27 odontocetes, and 5 pinnipeds from the Mexican Pacific Ocean (Table 1; Figure S1; Supplementary Excel file). Prey compilation and validation are updated until September 2021. Since diet diversity is highly underestimated (Pauly *et al.* 1998; Trites 2019), we assumed that species or genera listed as prey in other regions are also taken in the Mexican Pacific Ocean if they are present there. This decision could cause a few false positives which surely

Table 1. Prey diversity (richness; PR), trophic level (TLMP), weighted degree (WD), and prey overlap with fisheries (%; POF) in the diet network of 40 marine mammal species from the Mexican Pacific Ocean.

Species	Acronym	Guild	PR	TLMP	WD	POF
Eubalaena japonica	Ejap	I	6	3.20	24.2	0.0
Balaenoptera musculus	Bmus	I	8	3.21	24.2	0.0
Eschrichtius robustus	Erob	I	3	3.28	24.6	0.0
Megaptera novaeangliae	Mnov	I	9	3.61	25.6	22.2
Balaenoptera borealis	Bbor	I	12	3.29	25.0	33.3
Balaenoptera physalus	Bphy	I	12	3.34	25.1	41.7
Balaenoptera edeni	Bede	I	7	3.37	26.2	42.9
Balaenoptera acutorostrata	Bacu	I	3	3.41	26.0	66.7
Steno bredanensis	Sbre	II	7	4.13	27.0	14.3
Delphinus delphis	Ddel	II	56	4.25	20.6	17.9
Phocoenoides dalli	Pdal	II	28	4.16	25.3	21.4
Phoca vitulina richardii	Pvit	II	27	3.98	22.8	22.2
Aethalodelphis obliquidens	Lobl	II	38	4.08	23.3	23.7
Arctocephalus townsendi	Aobl	II	35	3.86	23.4	25.7
Delphinus bairdii	Dbai	II	27	4.19	24.2	37.0
Arctocephalus galapagoensis	Agal	II	8	4.08	27.8	37.5
Tursiops truncatus	Ttru	II	56	4.20	18.6	39.3
Zalophus californianus	Zcal	II	102	4.05	10.1	42.2
Mesoplodon carlhubbsi	Mcar	III	8	4.20	26.7	0.0
Mesoplodon stejnegeri	Mste	III	2	4.20	27.2	0.0
Mesoplodon peruvianus	Mper	III	1	4.20	28.3	0.0
Berardius bairdii	Bbai	III	11	4.24	27.3	0.0
Mesoplodon densirostris	Mden	III	6	4.37	27.6	0.0
Feresa attenuata	Fatt	III	3	4.65	27.8	0.0
Lissodelphis borealis	Lbor	III	15	4.21	26.5	6.7
Peponocephala electra	Pele	III	6	4.42	27.7	16.7
Mirounga angustirostris	Mang	III	49	4.21	20.4	18.4
Phocoena sinus	Psin	III	20	4.09	24.6	45.0
Kogia breviceps	Kbre	IV	56	4.35	19.9	0.0
Lagenodelphis hosei	Lhos	IV	56	4.22	18.9	1.8
Grampus griseus	Ggri	IV	30	4.33	24.3	3.3
Stenella longirostris	Slon	IV	56	4.32	19.6	3.6
Kogia sima	Ksim	IV	28	4.43	24.1	3.6
Ziphius cavirostris	Zcav	IV	26	4.43	25.4	3.8
Stenella attenuata	Satt	IV	62	4.14	19.0	4.8
Stenella coeruleoalba	Scoe	IV	37	4.22	23.6	5.4
Globicephala macrorhynchus	Gmac	IV	28	4.33	25.6	7.1
Physeter macrocephalus	Pmac	IV	39	4.44	22.5	10.3
Orcinus orca	Oorc	V	59	4.53	16.0	8.5
Pseudorca crassidens	Pcra	V	20	4.56	24.3	15.0

are much less than the false negatives under the assumption that marine mammals do not take in Mexican waters preys that take elsewhere. We have thus included the Galapagos fur seal (*Arctocephalus galapagoensis*) in our analysis as it has been sighted in the Mexican Pacific Ocean repeatedly for more than 2 decades, and its diet includes items recorded in this region. We have not included the Galapagos sea lion (*Zalophus wollebaeki*), the Steller sea lion (*Eumetopias jubatus*), or the Southern elephant seal (*Mirounga leonina*) as they were recently registered in Mexican waters, apparently associated with unusual environmental variation (Gallo-Reynoso *et al.* 2020; Elorriaga-Verplancken *et al.* 2022; Barba-Acuña *et al.* 2024), and as we are not aware yet of these species feeding in the region.

Prey were grouped in 8 sets following Pauly *et al.* (1998) as benthic invertebrates (BI), large zooplankton (LZ), small cephalopods, mainly squid (SS), large cephalopods (LS), small pelagic fish (SP), mesopelagic fish (MP), miscellaneous fish (MF), and marine amniotes (HV in the Pauly *et al.* terminology). To properly compare diets that have been described with different taxonomic classifications and prey names along several years, we validated and updated prey identity and occurrence in the Mexican Pacific for the mammals studied by consulting the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), the World Register of Marine Species (WoRMS, http://www.marinespecies.org/), and several expert researchers at the *Instituto de Ciencias del Mar y Limnología* and *Instituto de Biología, Universidad Nacional Autónoma de México*.

Comparison of diet compositions. We determined a diet similarity index for pairwise comparisons (S_{ij}) between the 40 marine mammal species, looking to build a network with marine mammals as nodes and their similarity comparisons as edges. Our similarity index is based on the mass composition of the 8 prey types by Pauly *et al.* (1998), with slight modifications to the biomass fraction due to the absence or presence of prey types not identified by these authors on marine mammals from the Mexican Pacific Ocean. For Mexican Pacific mammals not in the Pauly *et al.* list, we defined their biomass fractions by averaging the fractions in listed marine mammals with the same foraging habits, distribution in the Eastern Pacific Ocean or adjacent regions, and belonging to the same genus or subfamily. Therefore, we estimated the biomass fractions of *Pseudorca crassidens* as the mean of *Orcinus orca* and *Feresa attenuata*, and the fractions of *Mesoplodon peruvianus* (East Tropical Pacific) as the average of *Mesoplodon densirostris* (tropical and subtropical oceans worldwide), *Mesoplodon layardii* (Southern Ocean), *Mesoplodon hectori* (Southern Ocean), *Mesoplodon stejnegeri* (North Pacific Ocean), and *Mesoplodon carlhubbsi* (Northeastern Pacific Ocean). Our similarity index also compares the number of shared prey species within each prey type. Diet similarity between the 40 marine mammal species analyzed is thus defined as follows:

$$S_{ij}=\Big(\sum_{x=1}^{8}[(R_{xi} \cap R_{xj})/(R_{xi} \cup R_{xj})] + [1\text{-}abs(f_{xi} - f_{xj})]\Big)/8$$

where x indicates the 8 prey types described by Pauly *et al.*, $R_{xi} \cap R_{xj}$ are the prey species of type x shared by mammals i and j, $R_{xi} \cup R_{xj}$ are the total prey species taken by both predators, and f_{xi} y f_{xj} are the biomass fractions that prey type x represents in mammals i and j. Notice that the occurrence of a prey species in two marine mammals contributes to their similarity, but the absence of a prey species in two mammal species does not. Adding and not multiplying the similarity factors of biomass fractions and shared species allows detection of a degree of similarity when there are no shared prey species, which might occur in poorly known diets. For the network analysis, our index design also avoids artificial modules created by diets with very few prey species, as Benavidez Gómez (2016) observed in her classification by cluster analysis based on shared prey only. We calculated the similarity matrix among the 40 marine mammal species in the format of an adjacency list, by developing the program DIETSIM in the LAZARUS Integrated Development Environment (https://www.lazarus-ide.org/; available upon request).

Network analysis. We determined the trophic level for each marine mammal species following equation 1 in Pauly *et al*. (1998), based on prey biomass fractions with the modifications described above for Mexican Pacific marine mammals. We used the program GEPHI 0.10 (https://gephi.org/) to build a network with marine mammals as nodes and their similarity comparisons as edges with weight and no direction for the similarity matrix having $(40^2-40)/2 = 780$ pairwise comparisons between all species. Notice that in such a network, nodes are all connected, even if their similarity could be zero. We used GEPHI to determine network attributes such as average degree, with and without weight, density, diameter, transitivity, nodes' degree with and without weight, and nodes' centrality. A node's degree is the sum of its connections (pairwise comparisons) in the network; a weighted connection is a pairwise similarity value –S_{ij}– as described above. See Menczer *et al.* (2020) for an introduction to network analysis.

We examined modularity with resolution 0.95, which better reproduced the cluster analysis of prey diversity by Benavidez Gómez (2016) that yielded the traditional marine mammal guilds: planktophagic, ichthyophagic, teuthophagic, and sarcophagic. Statistical significance of modularity was tested by the Erdös-Renyi procedure, which consists of randomly permuting edges and calculating modularity for each shuffle to build a random distribution of connections between nodes, which was then compared against actual modularity. A total of 1000 edge shuffles were made with the program SHUFFLEDAT developed in the LAZARUS Integrated Development Environment (available upon request), calculating raw modularity with equation 1 in Blondel *et al.* (2008), which is the one used by GEPHI. Statistical significance of modularity was accepted if its actual value was greater than the top 5% of its randomized distribution. We have termed statistically significant modules as trophic guilds.

Marine mammal species were accommodated in the network following modularity and trophic level; edges were plotted with thickness proportional to their weight and the color of the destination module. Marine mammal diets, organized by trophic guilds (network modules), were described with the biomass fractions of the 8 prey types, uniformly subdivided by prey species within each type. To know the position of each marine mammal on the scales of prey richness, weighted degree, and trophic level, and thus to identify species groupings and scale relationships, we examined the cumulative distributions of such scales, distinguishing trophic guilds. We particularly examined the relationship between the nodes' weighted degree and trophic level by marine mammal species and trophic guild.

Trophic overlap with fisheries. We consulted the Mexican National Fisheries Chart (Diario Oficial de la Federación 2012), which lists 298 species exploited by five fishery types: shrimp, squid, cartilaginous fish, minor pelagic fish, and finfish. We examined the trophic overlap between these fisheries and marine mammal diets in terms of shared species, looking to provide a minimum approach for the increasing problems of competition and operational interaction between marine mammals and fisheries worldwide that cause bycatch, depredation of fishing gear, and other ecosystemic impacts that are poorly understood biologically and socially (Jusufovski *et al.* 2019; Jog *et al.* 2022).

Results

Diet composition and trophic guilds. We registered 380 prey species that were validated to compare the diets of 40 marine mammals from the Mexican Pacific Ocean for 1062 trophic relationships in total. Taxonomically, such prey are 21 crustaceans, 74 cephalopods, 3 tunicates, 246 fish, 3 turtles, 5 birds, and 28 mammals. Per ecological type, prey are: BI, 9; LZ, 20; SS, 58; LS, 11; SP, 17; MP, 67; MF, 162; and HV, 36 (Supplementary file). Similarity between marine mammal diets varied from 0.02 between *Zalophus californianus* and *O. orca*, to 0.95 between *Balaenoptera physalus* and *Balaenoptera borealis*. Since the network is completely connected, its density, diameter, and average length are 1. Among nodes, the clustering coefficient is 1 for all; all have unweighted degree 39, all have eccentricity 1, all have centralities 1 (closeness, harmonic closeness, betweenness, and eigen), and all are part of 741 triangles. The average weighted degree was 23.77, ranging from 10.05 for *Z. californianus* (the least connected in the network) to 28.28 for *M. peruvianus*. Modularity after resolution 0.95 was 0.005 with raw calculation of 0.015 using equation 1 in Blondel *et al* (2008). The random distribution of edges in 1000 shuffles yielded a total raw-modularity interval of -0.006 – 0.008 for actual modularity be statistically significant with $p < 0.001$. Trophic level ranged from 3.20 in *Eubalaena japonica* to 4.65 in *Feresa attenuata* (Table 1; Figures 1, 2). Mind that trophic levels are not biased by very few prey species in the diet because the trophic level is calculated from the prey types' biomass fraction, not prey richness (Pauly *et al.* 1998).

GEPHI identified five marine mammal modules that were already identified by Benavidez Gómez (2016) from a cluster analysis based only on the species richness. However, those modules and clusters are not equal in terms of species assignments. We call these modules trophic guilds that, beyond their diet composition, are also distinguished by their trophic level and mean weighted degree. Such guilds, ordered by increasing trophic level, are:

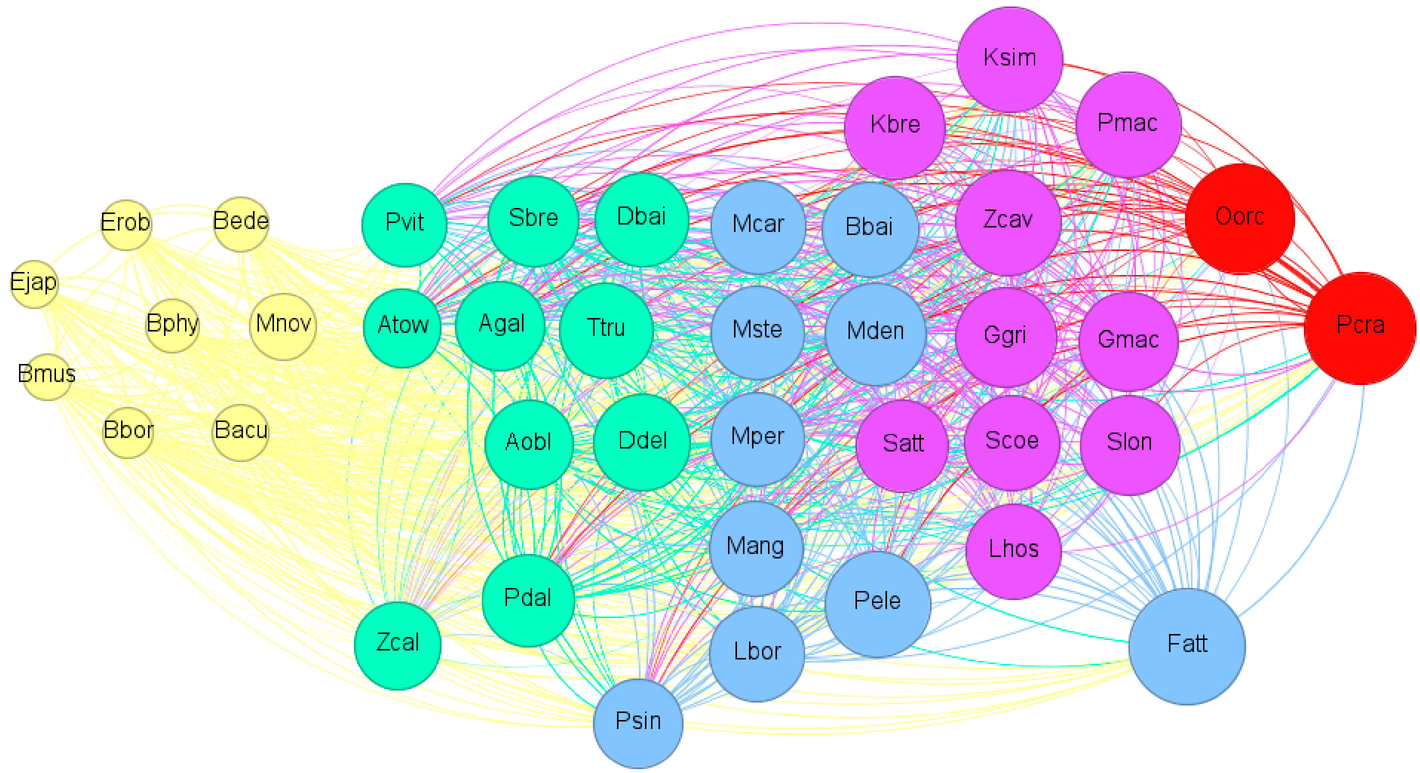

Figure 1. Network of diet similarities (edges) among 40 marine mammal species from the Mexican Pacific Ocean (nodes). Node colors correspond to the 5 modules identified by GEPHI, and their size to trophic level. The network is also oriented rightwards in parallel to the trophic level. Edge colors match the modules that GEPHI identified as their destinations, and their thickness to diet similarity. The network shows only the edges with similarity equal to or larger than 0.5, which is the lowest level at which all nodes are connected. The acronyms for marine mammal identities are formed by the first character of the genus and the first 3 characters of the species names.

I) mainly planktophagic, II) mainly ichthyophagic, III) mainly teuthophagic of low trophic level, IV) mainly teuthophagic of high trophic level, and V) mainly sarcophagic. Guild I includes eight mysticete species (*E. japonica, Balaenoptera musculus, Eschrichtius robustus, B. borealis, B. physalus, Balaenoptera edeni, Balaenoptera acutorostrata*, and *Megaptera novaeangliae*). Guild II is formed by four pinniped and six odontocete species (*Arctocephalus townsendi, Phoca vitulina richardii, Z. californianus, Aethalodelphis obliquidens, A. galapagoensis, Steno bredanensis, Phocoenoides dalli, Delphinus bairdii*, *Tursiops truncatus*, and *Delphinus delphis*). Guild III accounts for one phocid and nine odontocete species (*Phocoena sinus, M. carlhubbsi, M. stejnegeri, M. peruvianus, Mirounga angustirostris, Lissodelphis borealis, Berardius bairdii, M. densirostris, Peponocephala electra*, and *F. attenuata*). Guild IV contains 10 odontocete species (*Stenella attenuata, Lagenodelphis hosei, Stenella coeruleoalba, Stenella longirostris, Grampus griseus, Globicephala macrorhynchus, Kogia breviceps, Kogia sima, Ziphius cavirostris*, and *Physeter macrocephalus*). Guild V includes two delphinids (*O. orca* and *P. crassidens*; Table 1; Figures 1, 3).

Prey richness and diet similarities. Prey richness varied from 1 for *M. peruvianus* to 102 for *Z. californianus*, which combines different knowledge and actual prey diversity variation among the marine mammals studied. The cumulative profile of marine mammal species with reference to prey richness showed discontinuities and asymptotes defining 3 general sets (Figure 4). The first set includes 20 mammal species with 1 – 20 different prey items, the second set is formed by 11 mammal species with 26 – 39 preys, and the third set contains 9 mammal species with 49 – 102 preys. These groups seemingly correspond to marine mammals with poorly known, partially known, and well-known diets, as well as to mammals with really few (*e.g.*, mysticetes) and several prey items (*e.g.*, the California sea lion). Most Mexican Pacific mammals with few prey species after validation (richness < 20), include the false killer whale, and several species from guilds I and III, *i. e.*, several mysticetes that feed mainly in cold-temperate waters of the North Pacific Ocean or in the Eastern Tropical Pacific, and low trophic level teuthophagous, mainly beaked whales, about which there is little biological information. Guilds I and III also include a few poorly known pelagic dolphins, and the Galapagos fur seal, which has been registered repeatedly in Mexican waters for 2 decades (Aurioles-Gamboa *et al.* 2004; Medrano González *et al.* 2008; Tamayo-Millán *et al.* 2021), but whose diet is known for its regular distribution off Mexican waters (Clarke and Trillmich 1980; Dellinger and Trillmich 1999). Mammals with better-known diets (richness ≥ 26) are mainly in guilds II and IV, and include the killer whale from Guild V (richness = 59; Figure 4).

The cumulative profile of marine mammal species concerning weighted degree exhibited discontinuities defining 4 groups (Figure 5). *Z. californianus* alone composes the first set with weight 10.05; *O. orca*, also alone, composes the second set with weight 16.03. Seven species

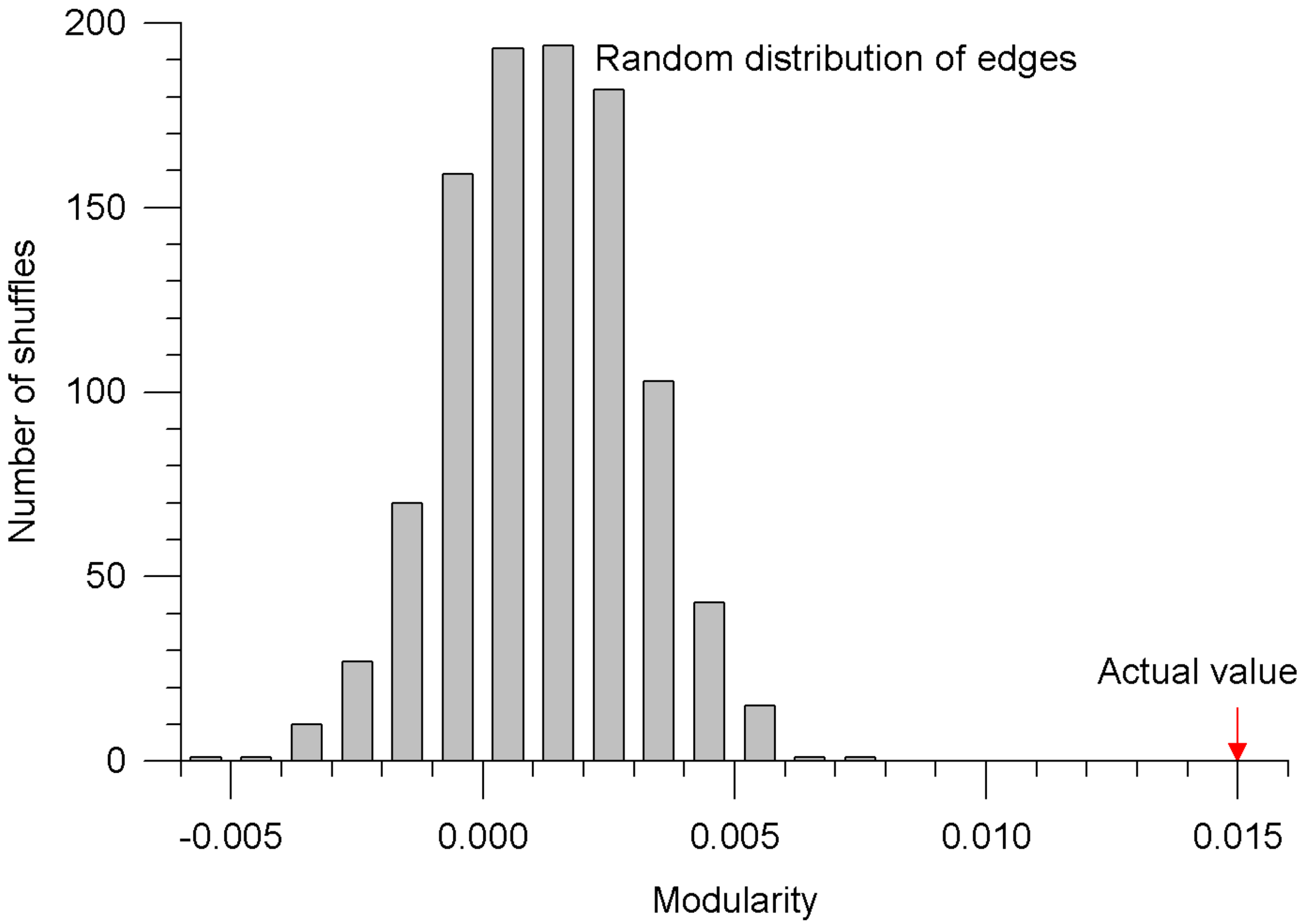

Figure 2. Actual raw-modularity (red arrow) for the network of diet similarities among 40 marine mammals from the Mexican Pacific Ocean and its statistical distribution after 1000 random permutations of the similarity connections between them (gray bars).

are included in the third set with weighted degrees 18.58 – 20.55, 4 from guild IV, 2 from guild II, and 1 from guild III. The fourth set is composed by 31 species with weighted degree varying in the range 22.48 – 28.28, with 8 out of 10 species from guild III being in the highest weight range, *M. peruvianus* in the top (Figure 5).

These results indicate that ordinations for the distributions of prey richness and weighted degree of the 40 marine mammals studied are inversely related. When both attributes were directly compared, an inverse relationship was indeed observed (Figure 6) with a high linear regression coefficient (-0.875) and slope of -0.152. *M. peruvianus* had the lowest prey richness and the highest weighted degree, whereas *Z. californianus* had the highest prey richness and the lowest weighted degree. *O. orca* appeared apart with a slightly lower prey richness and a higher weighted degree compared to *Z. californianus*. Marine mammals with low prey richness and high weighted degree were mainly in guilds I and III, whilst guilds II and IV occurred in the range of high prey richness and low weighted degree (Figure 6).

Trophic level and diet similarities. The cumulative profile of marine mammal species in trophic level exhibited discontinuities defining 4 general groups (Figure 7). The first group is formed only by trophic guild I in the trophic level range 3.2 – 3.6, well below the other guilds. Guilds II, III, and IV overlapped in the second group, with most species of guild II around trophic level 4.1, most species of guild III around trophic level 4.2, and guild IV species in subgroups around trophic levels 4.2, 4.3, and sperm whales by 4.45. The third group was composed only of guild V around trophic level 4.55. Only *F. attenuata* from guild III is in the fourth group with the highest trophic level of 4.65 (Figure 7).

Trophic guilds exhibited increasing trophic level from I to V (Figure 3), with the following means and standard deviations: I, 3.34 ± 0.13; II, 4.10 ± 0.12; III, 4.28 ± 0.16; IV, 4.32 ± 0.10; and V, 4.55 ± 0.02. The relationship between trophic level and weighted degree at the species level seemed inverse. Still, the linear regression index was very low (-0.013) since most species in guild III had high values of both trophic level and weighted degree (not shown). Trophic level and weighted degree showed a better-defined relationship at the guild level, with a linear regression coefficient of -0.279 and a slope of -2.83, with guild I having the lower average trophic level and higher average weighted degree, whilst guild V has the higher average trophic level and lower average weighted degree (Figure 8).

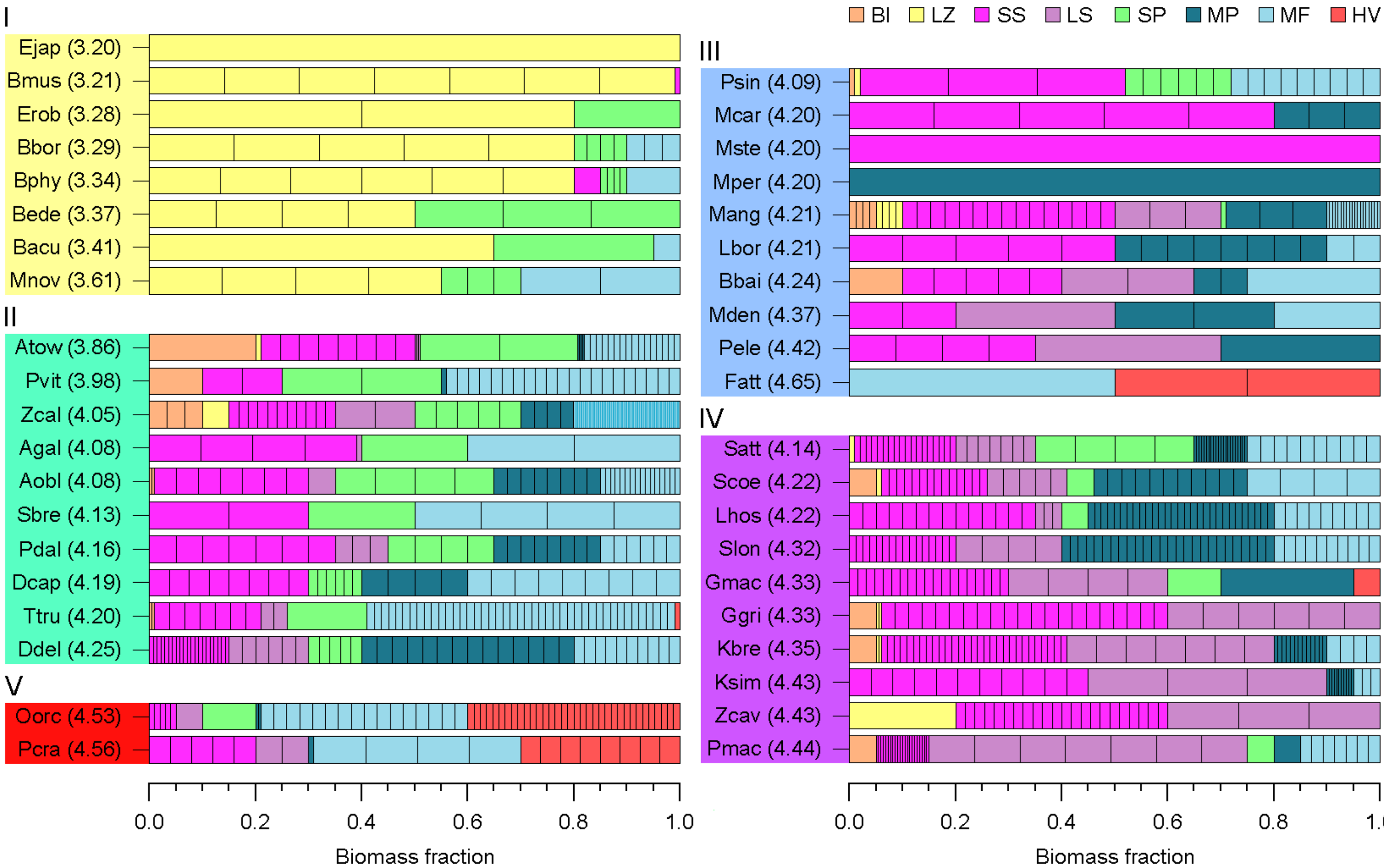

Figure 3. Diet composition of 40 marine mammal species from the Mexican Pacific Ocean. Mammals are grouped in the trophic guilds identified by the modularity analysis and are indicated by Roman numbers. Species are identified by acronyms as in Figure 1. Numbers in parentheses indicate the species' trophic level calculated in the Mexican Pacific Ocean. Bar colors indicate the biomass fraction of the 8 prey types defined by Pauly *et al.* (1998) and are subdivided equally among the prey type's species.

We found no relationship between prey richness and trophic level at the species or guild level. Average prey richness per guild is: I, 7.5 ± 3.5 (SD); II, 38.4 ± 27.8; III, 12.1 ± 14.3; IV, 41.8 ± 14.2; and V, 39.5 ± 27.7. Only within guilds III and IV do the species exhibit an apparent negative relationship between prey richness and trophic level, with r^2 = -0.122 and *r*2 = -0.374, respectively.

Trophic overlap with fisheries. Of the 298 species subjected to fisheries according to the Mexican National Fisheries Chart, 70 are also consumed by Mexican Pacific marine mammals (23.5%) and represent 180 of the 1062 trophic relationships in total (16.9%) validated for the 40 marine mammals and their 380 prey species examined here. 9 species exhibit trophic overlap over 30% of species in their diets shared with fisheries, including 4 mysticetes: *B. acutorostrata* with 2 preys shared with fisheries out of 3 in its diet (2/3 = 66.7%), *B. edeni* (3/7 =42.9%), *B. physalus* (5/12 = 41.7%), and *B. borealis* (4/12 = 33.3 %). The highest trophic overlaps with fisheries among odontocetes are: *P. sinus* (9/20 = 45.0%), *T. truncatus* (22/56 = 39.3%), and *D. bairdii* (10/27 = 37.0%). For pinnipeds, higher trophic overlaps are for *Z. californianus* (43/102 = 42.2%) and *A. galapagoensis* (3/8 = 37.5%). *B. musculus*, *E. robustus*, *E. japonica*, *F. attenuata*, *B. bairdii*, *M. carlhubbsi*, *M. stejnegeri*, *M. densirostris*, *M. peruvianus*, and *K. breviceps* showed no prey shared with fisheries in the Mexican Pacific Ocean (Table 1). Among guilds, higher trophic overlaps with fisheries are, on average: I, 25.8% ± 24.7 (SD); II, 28.1 ± 9.9; III, 8.7 ± 14.7; IV, 4.4 ± 2.8; and V, 11.7 ± 4.6 (Table S1). For fishery type, trophic overlaps with marine mammals are: minor pelagic fish (7/12 = 58.3%), finfish (56/228 = 24.6%), cartilaginous fish (6/52 = 11.5%), squid (1/1 = 100%), and shrimp (0/5 = 0.0%; Table S2).

Discussion

It is well recognized that marine mammals' diets are poorly and differentially known across species, time, and space (Trites 2019). Here, we compiled and validated 380 prey species to properly compare 40 marine mammal species from the Mexican Pacific Ocean. Validation of prey identities and geographic distributions after reviewing literature and our data implies that prey accounts here are in general lower, than the partial accounts in the literature treating marine mammals from the Mexican Pacific Ocean. Variation of prey richness (1 – 102) appears thus to result from differential knowledge of diets and actual prey diversity variation among species. We buffered the incomplete data in diet diversity by adding the similarity factors of biomass fractions and shared species, to minimize errors on similarity and thus network connections by diets with few validated prey items.

Mexican Pacific mammals with few validated prey species include poorly known species, mainly ziphiids and pelagic delphinids, but also well-known species such as

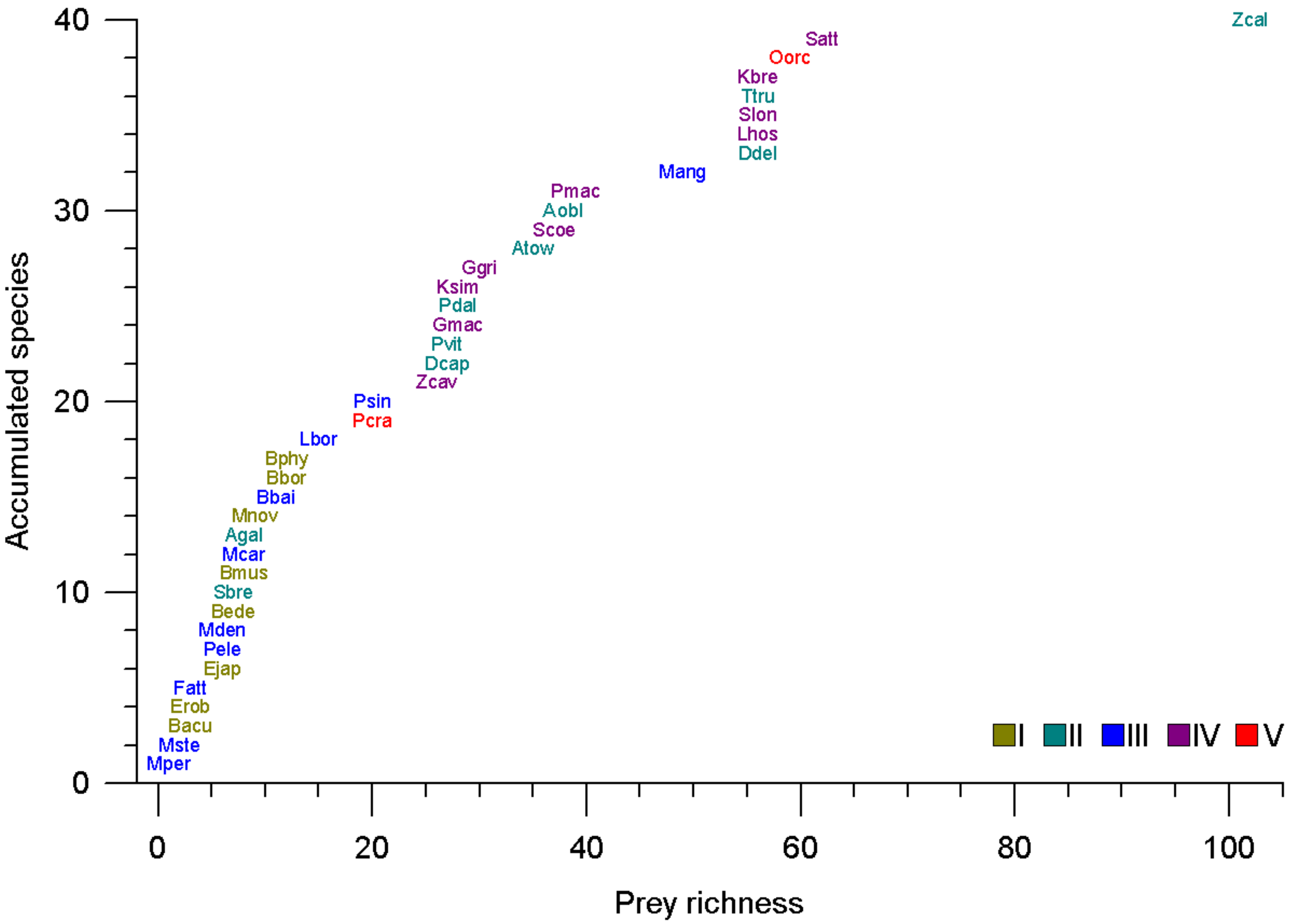

Figure 4. Cumulative distribution of prey richness for 40 marine mammals from the Mexican Pacific Ocean. Identity acronyms are as in Figure 1, and their colors correspond to the trophic guilds also in Figure 1.

the vaquita of which we validated for comparison 20 out of ca. 30 reported species, mysticetes that feed mainly in cold-temperate waters or in the Eastern Tropical Pacific, and the Galapagos fur seal, whose known diet is off Mexican waters. Average prey richness *ca*. 40 has been registered for guilds II, IV, and V, whilst guild I exhibited 7 – 8 prey, and guild III 12 prey. Prey richness appears thus underestimated in guild III, mainly by the few regional data for *M. peruvianus*, *M. stejnegeri*, *M. densirostris*, *F. attenuata*, and *P. electra*. *F. attenuata* is outstanding for it exhibits the highest trophic level among the studied mammals while pertaining to guild III (low trophic-level teuthophagous). First, such a high trophic level results from the higher biomass fraction of amniotes in the *F. attenuata* diet registered in the Mexican Pacific (*D. delphis* and *S. attenuata*), together with the fish *Merluccius* spp. that belong to the fish type with the highest trophic level (Sekiguchi *et al.* 1992; Perrin 2009). Second, to our knowledge, the diet of *F. attenuata* shows no published records of birds, large cephalopods, or small pelagic fish in the Mexican Pacific Ocean, causing us to overestimate the regional trophic level to 4.65 instead of the world value 4.4 by Pauly *et al.* (1998). Third, the diet of *F. attenuata* is in guild III, apparently because of artificial similarities with the diets of other poorly known mammals. The average and standard deviation of similarity between *F. attenuata* and other mammals in guild III was 0.82 ± 0.09, whilst similarity with guild II was 0.66 ± 0.15 and with guild V was 0.69 ± 0.16.

Because of the pairwise comparisons among marine mammal species, our network for diet similarities is all connected, exhibiting variation only in attributes dependent on weighted degree, besides prey richness and trophic level, which are not intrinsic network properties. The modularity analysis showed 5 statistically significant modules that we defined as trophic guilds and that very much correspond to the guilds identified by Benavidez Gómez (2016) from a cluster analysis of prey diversity that did not account for prey type biomass as we did here. Notice that we identified guilds by modules emerging from the trophic network. Such modules apparently assemble species that overlap their ecological niches, as using the same environmental resources in a similar way irrespective of their taxonomic position, as guilds are defined by Simberloff and Dayan (1991). Whether such guilds are generic in marine mammal trophic networks beyond the Mexican Pacific Ocean is uncertain, though we suspect that they might be, given that diet-biomass partition among the eight prey types should be similar at least in tropical and subtropical seas, as indicated by

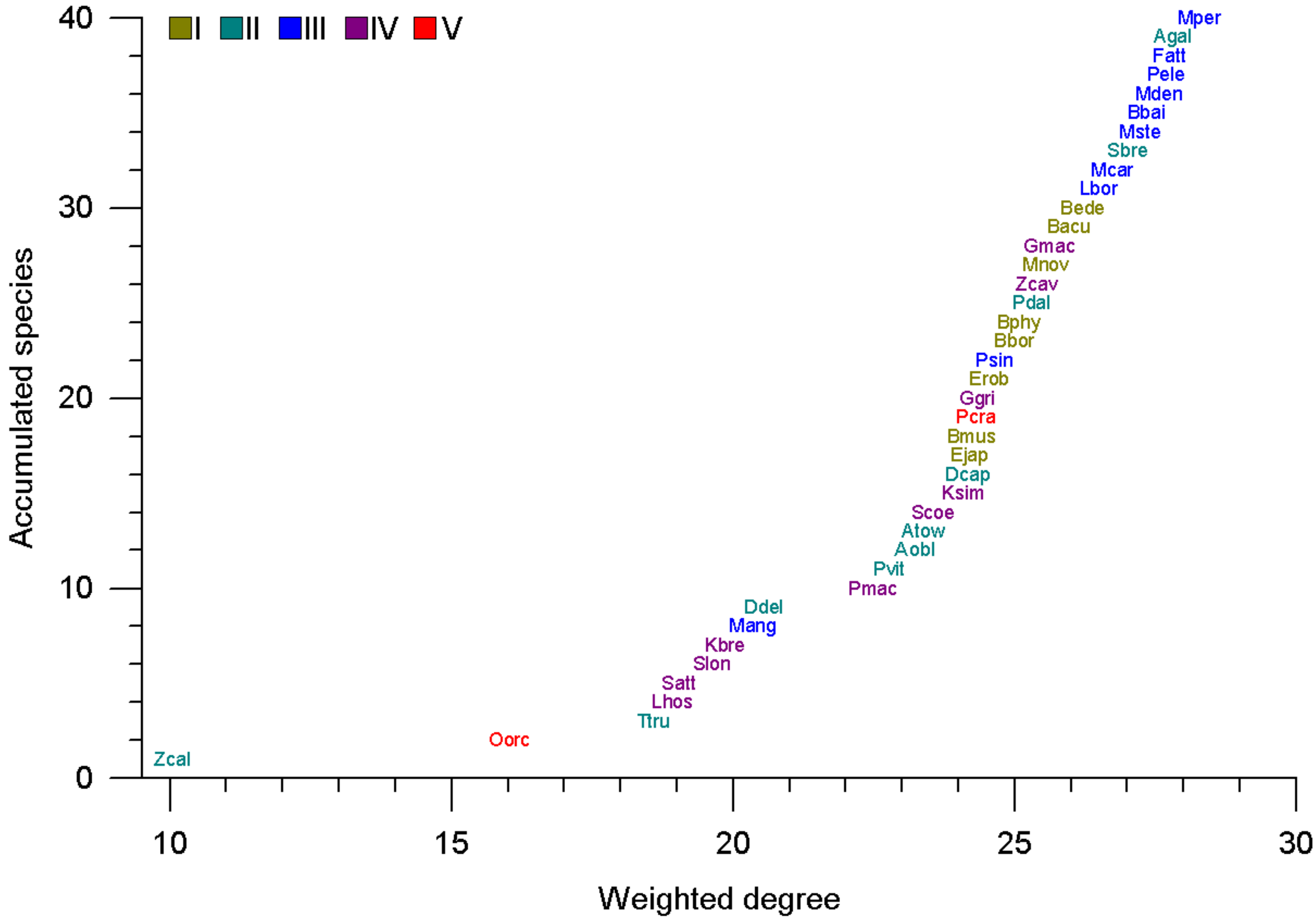

Figure 5. Cumulative distribution of the weighted degree for 40 marine mammals from the Mexican Pacific Ocean. Identity acronyms are as in Figure 1, and their colors correspond to the trophic guilds also in Figure 1.

the minor corrections done for the Mexican Pacific Ocean from the Pauly *et al.* (1998) data.

Despite the incomplete diet data, we determined a clear negative relationship between weighted degree and prey richness at the level of mammal species that results from the term in the similarity definition for which increasing prey richness of a mammal species conveys greater increments in the denominator, decreasing thus similarity which is the network's weighted degree; this does not depend from underestimations of prey richness for some species. This means that taking more prey species decreases the chances of not sharing such prey, *i. e.*, that prey richness of Mexican Pacific marine mammals is determined by competitive exclusion. For deviations in the prey richness vs weighted degree relationship, *Z. californianus*, *O. orca*, and the 8 mysticetes, especially *E. japonica*, exhibited the most negative residuals, *i. e.*, a weighted degree lower than expected from prey richness. Slightly positive residuals, *i. e.*, weighted degree higher than expected from prey richness, were observed for *A. galapagoensis*, *G. macrorhynchus*, *S. coeruleoalba*, and *D. delphis*. This means that the diets of *Z. californianus*, *O. orca*, and the 8 mysticetes are more unique among Mexican Pacific mammals in general, and these species indeed stand out among the other in several of the data comparisons, *e. g.*, the lowest pairwise diet similarity is between *Z. californianus* and *O. orca*. On the other hand, the diets of *A. galapagoensis*, *G. macrorhynchus*, *S. coeruleoalba*, and *D. delphis* share more prey items with other mammals. Larger negative residuals are greater than larger positive residuals, meaning that marine mammals may have unique diets rather than similar ones.

The average trophic level increases with guild ordination from I to V, paralleling a general decrease in guilds' average weighted degree. Guild III (low trophic level teuthophagous) had a trophic level slightly lower than guild IV (high trophic level teuthophagous). Still, guild III exhibited the highest average weighted degree, suggesting that this species group may be part of a different trophic system that permits greater trophic overlap –as indicated by diet similarity and thereon weighted degree– among the mammal species on it. However, if guild III prey richness is underestimated, as discussed above, increasing its prey richness could decrease its average weighted degree for a better fit of its relationship with trophic level, for perhaps integrating guilds III and IV as one, and possibly moving *F. attenuata* to guild V. If marine mammals from the surface ecosystem, segregate in guilds with clearly different trophic levels, marine mammals in the deep might too conform

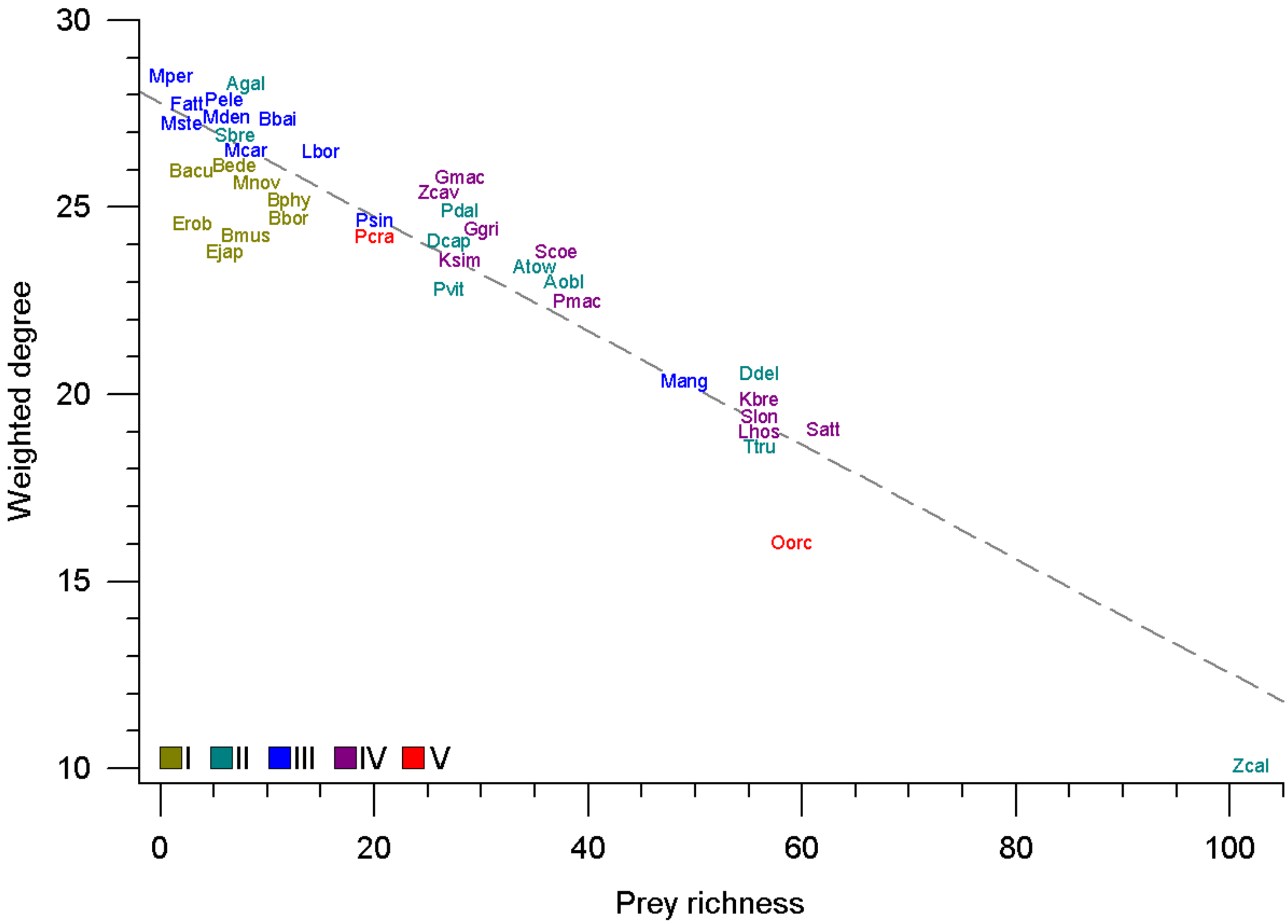

Figure 6. Relationship between prey richness and weighted degree for 40 marine mammals from the Mexican Pacific Ocean. Identity acronyms are as in Figure 1, and their colors correspond to the trophic guilds also in Figure 1. The dashed line indicates regression with parameters slope, -0.152; ordinate, 27.79; and r_2, -0.875.

guilds differentiated by trophic level, although maybe not so apart, exactly as Figure 8 shows. Independent of whether guilds III and IV are the same one or not, teuthophagous marine mammals indeed belong to a trophic system of deep waters different than that of guilds I, II, and V, which feed mainly in surface waters. We cannot define such trophic systems as different webs, as we do not know how much their trophic connections are separated, nor what their trophic bases are. A degree of trophic overlap between deep-water and surface-water marine mammals exists at least because teuthophagous mammals feed in part in surface waters when they are there for breathing. Another indication of different trophic systems for surface- and deep-water marine mammals comes from their different responses in distribution and occurrence to environmental variation, as observed by Arroyo Sánchez (2023) in the Gulf of California during the summer of years 2012 – 2019, which included two La Niña events (2012, 2017) and one strong El Niño event (2015 – 2016).

Over the statement that lower trophic levels have larger available biomass for feeding, the inverse relationship between average trophic level and weighted degree for marine mammals in the Mexican Pacific Ocean suggests stronger competitive exclusion at higher trophic levels and therefore lesser trophic overlap among mammal species, part of which is given by higher prey richness.

The Mexican Pacific is a region of high biodiversity and high marine productivity for which seasonal (*e. g.*, winds regime) and annual variations (*e. g.*, El Niño/La Niña) are important. The region's high productivity sustains an abundant, diverse, and singular marine mammal fauna with different biogeographic and ecological affinities (Rosales-Nanduca *et al.* 2011) by which species distributions and abundances fluctuate due to lowly known combinations of species plasticity and preferences, environmental variation, and anthropic impacts (Fiedler and Reilly 1994; Reilly and Fiedler 1994; Ballance *et al.* 2006; Fiedler *et al.* 2017). Human impacts on the Mexican Pacific ecosystems are not among the largest worldwide (Halpern *et al.* 2008, 2015), but exhibit concerning trends in some regions, including synergic effects of climate change (the anthropogenic warming of the ocean and atmosphere; Gates 1993) over anthropic impacts to marine mammals, especially by fisheries (Escobar Briones *et al.* 2015).

Largest diet similarities, *i.e.*, trophic overlaps, (0.90 – 0.95) occurred between mysticetes that feed mainly in the

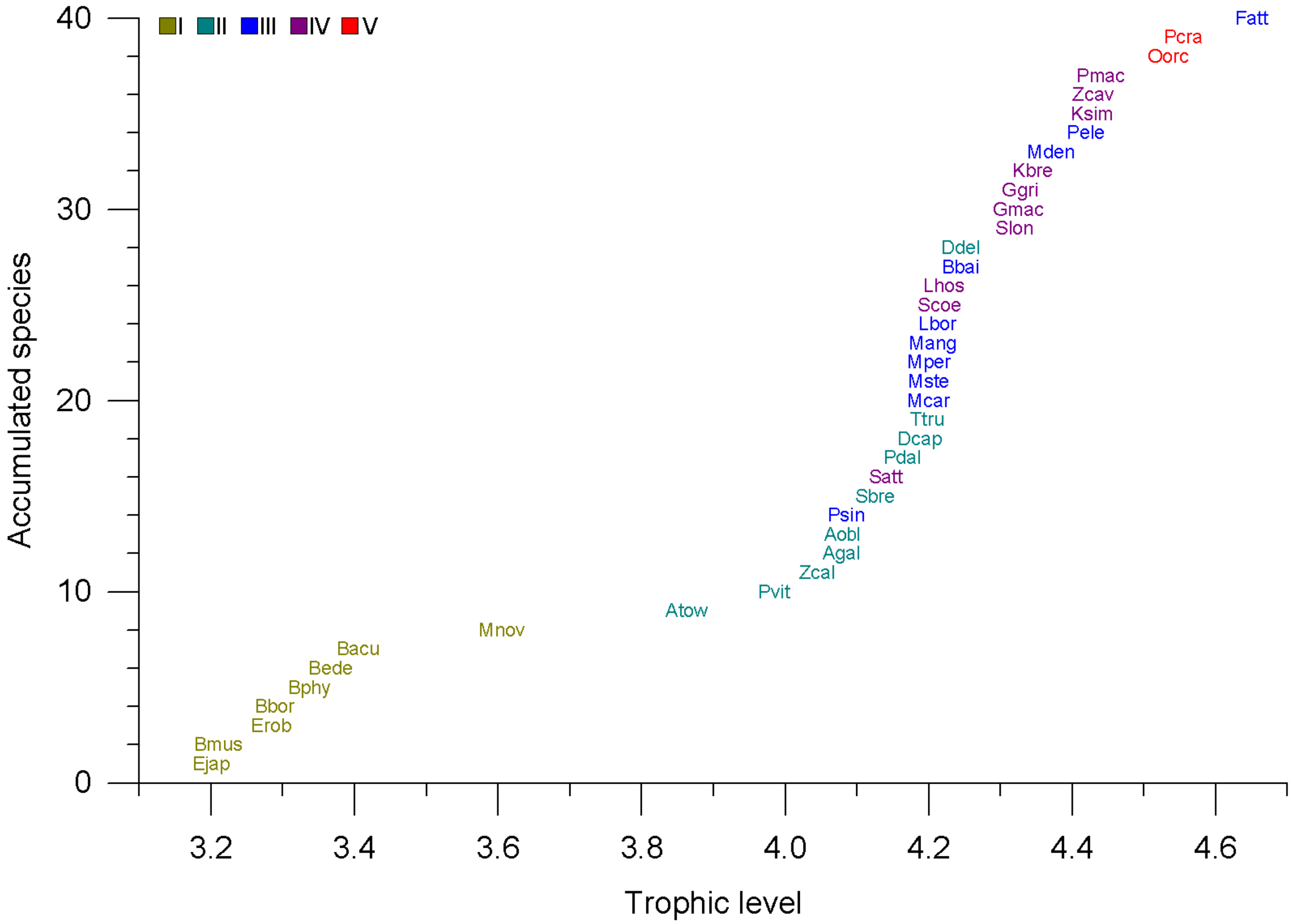

Figure 7. Cumulative distribution of the trophic level for 40 marine mammals from the Mexican Pacific Ocean. Identity acronyms are as in Figure 1, and their colors correspond to the trophic guilds also in Figure 1.

productive temperate and cold waters of the North Pacific or in the Eastern Tropical Pacific with different patterns of spatial and seasonal occurrence, as well as between *Mesoplodon* species, whose regional diet diversities seem quite incomplete and whose geographic distributions are separated by the California Stream, *e. g.*, *M. stejnegeri* vs *M. peruvianus*, or *M. carlhubbsi* vs *M. peruvianus*. Apparent geographic and seasonal overlap between mysticetes for feeding in Mexican waters occurs in the Gulf of California, which is a region of extraordinarily high productivity that sustains a diverse and abundant marine mammal fauna, outstanding at global level (Schipper *et al.* 2008; Arellano-Peralta and Medrano-González 2013, 2015). Therefore, the potential for competition between marine mammals should be assessed considering their geographic and seasonal distributions.

Trophic overlap between marine mammals and fisheries regarding shared species implicates operational and potential competitive interactions as well as operational interactions not mediated by shared prey, such as the tuna purse-seine fishery. Arellano-Peralta and Medrano-González (2015) reviewed published operational interactions between *T. truncatus* and five fisheries, *G. macrorhynchus* and five fisheries, as well as 12 marine mammal species and four fisheries, as the most relevant among others. The 12 referred species are: *Z. californianus*, *D. delphis*, *D. bairdii*, *S. attenuata*, *S. longirostris*, *S. coeruleoalba*, *A. obliquidens*, *G. griseus*, *Z. cavirostris*, *M. densirostris*, *M. peruvianus*, *P. macrocephalus*, and *K. sima*. Fisheries interacting with more mammal species are finfish (25), cartilaginous fish (17), shrimp (16), and minor pelagic fish (14). Given the incompleteness of diet data, trophic overlaps with fisheries are underestimated here. In our data, marine mammals with greater trophic overlap with fisheries in the Mexican Pacific Ocean occur in guilds I and II (surface water), mainly *P. sinus*, *Z. californianus*, *T. truncatus*, and *D. bairdii*. Together with *G. macrorhynchus*, these four species appeared as the most frequent in remains with indication of anthropogenic death along Mexican coasts (Zavala-González *et al.* 1994). Morant *et al.* (2025) have identified high values for potential feeding sites of marine mammals in the Gulf of California and the Pacific coast of the Baja California Peninsula, whilst Benavidez Gómez (2016) identified both, high values of marine mammal foraging and interaction with fisheries in these regions.

High trophic overlaps with fisheries also occur in *B. edeni*, *B. physalus*, and *B. borealis* that feed importantly in Mexican waters over 7 – 12 prey, of which the Pacific sardine (*Sardinops sagax*) and Northern anchovy (*Engraulis mordax*)

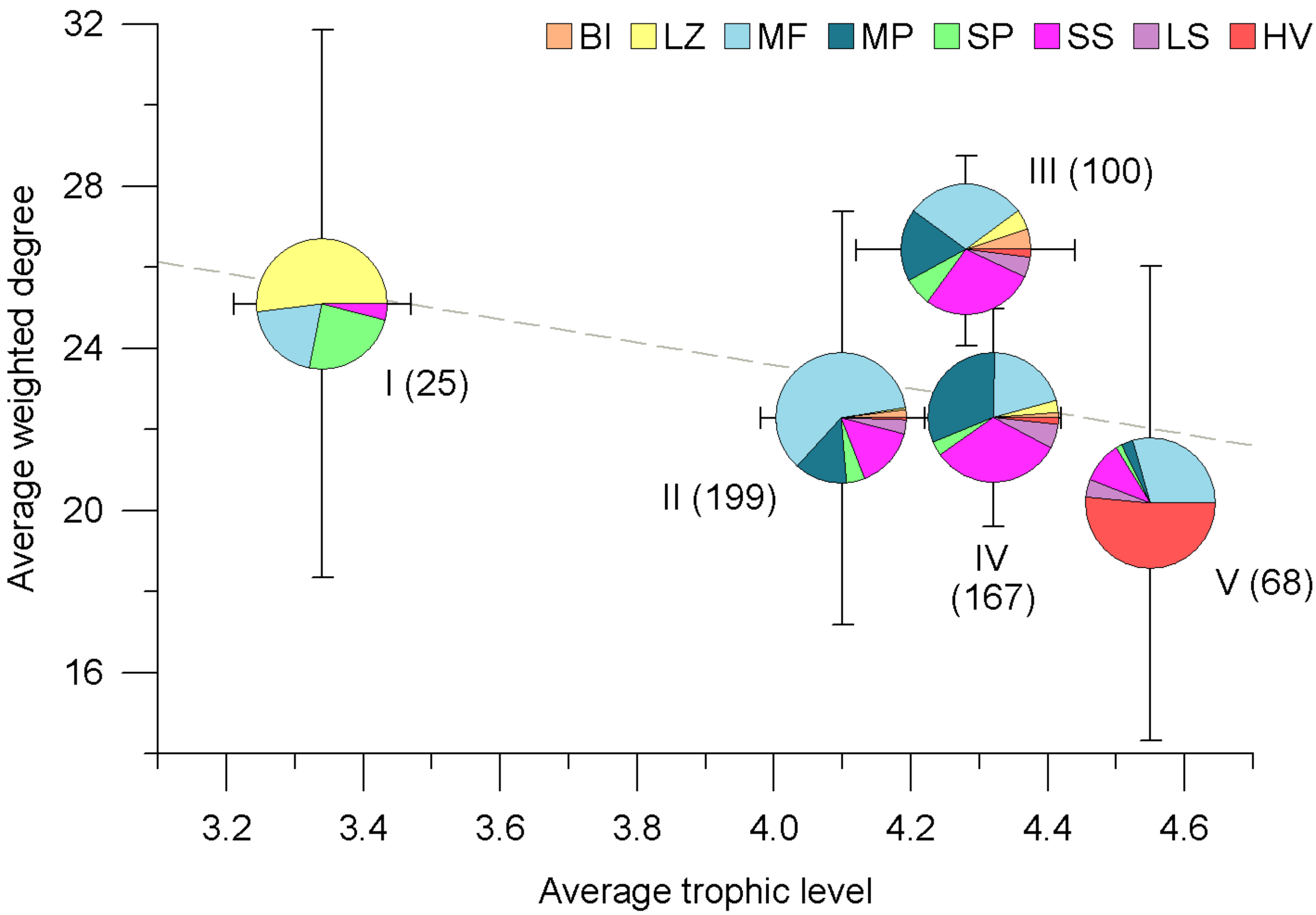

Figure 8. Relationship between average trophic level and average weighted degree among the 5 trophic guilds identified for marine mammals from the Mexican Pacific Ocean. Variation intervals indicate standard deviation among guild species. Guild identity and total prey richness in parentheses are indicated near the pies, which depict the richness of the 8 prey types.

are important food items in the Gulf of California and Pacific coast of Baja California (Tershy 1992). In the Eastern North Pacific, *Balaenoptera* whales are known to entangle only in offshore drift nets for sharks and swordfish, especially *B. acutorostrata*, though this is underestimated (Barlow *et al.* 1997; Reeves *et al.* 2013). Mysticetes are neither attracted to settings for minor pelagic fish (Morales-Bojórquez *et al.* 2021). Interaction between fisheries and *Balaenoptera* whales could occur by competition for minor pelagic fish that are subjected to large fluctuations associated with El Niño/La Niña oscillation; however, such variation in the Gulf of California seems not to affect the functional relationships of the pelagic trophic system (Del Monte-Luna *et al.* 2011; Velarde *et al.* 2013). For these reasons, we now consider that the high trophic overlap between *Balaenoptera* whales and fisheries in the Mexican Pacific is potentially relevant. Minor pelagic fishery appears important anyway for small cetaceans and pinnipeds, with 7 shared species among 12 fished in total, together with the finfish fishery, with 56 shared species among 228 fished.

An ultimate network analysis still shall wait for several diets to get sufficient data, as well as variation values for biomass fractions and prey diversities across space and time. Beyond the data constraints discussed above, our network analysis proved being useful for detecting marine mammal community structure in the Mexican Pacific Ocean over the patterns of diet diversity, diet similarity, and trophic level, which subsequently need examination for their relation with the spatial and temporal segregation between species. In summary, marine mammals from the Mexican Pacific Ocean compose 4 – 5 trophic guilds of at least 2 trophic systems, mainly structured by competitive exclusion over the regional biodiversity that these mammals feed on. How trophic relationships among marine mammals can be determined in their geographic distributions, and their responses to environmental variation, as well as how exclusion relationships are affected by human activities in the sea, principally fisheries, appear as relevant issues to investigate after the early attempt by Benavidez Gómez (2016). Under the principle of investigating marine mammals as indicators of marine ecosystems' condition, *i. e.*, as sentinels, getting actual data straight from the sea is the most necessary work to do nowadays.

Acknowledgements

We thank L. A. Pérez for her contribution compiling diet data, Z. Castillo, H. Espinosa, M. Hermoso, and B. Urbano for their expert advice on prey species validation, G. Heckel for her

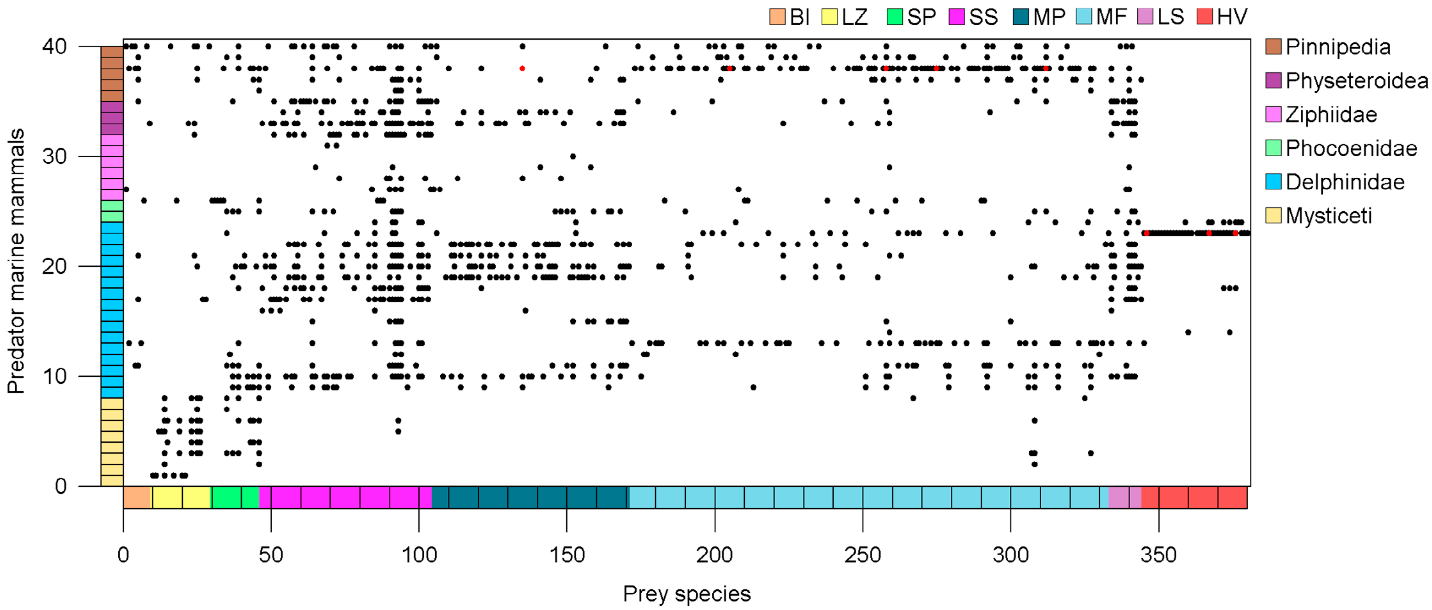

Figure S1. Graphic table of the validated 380 prey items taken by 40 marine mammal species for 1062 trophic relationships in the Mexican Pacific Ocean. Prey type abbreviations are defined in the Methods section. The 8 red points indicate trophic relationships from our group not recorded in the literature for the region.

generous and valuable review of manuscript, as well as J. P. Gallo, A. Gracia, E. Martínez, and J. J. Zúñiga for their review of the seedling work by Benavidez Gómez (2016). We very much thank two anonymous reviewers for their strong, positive, and enriching review. This work is entirely academic, did not receive any financial support, and we declare it as not having any conflict of interest or personal relationships that could have influenced its contents. We also declare that generative artificial intelligence was not used for conducting the investigation or elaborating this paper.

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Associated editor: Miguel Ángel León Tapia
Submitted: May 28, 2025; Reviewed: August 27, 2025
Accepted: September 24, 2025; Published on line: September 30, 2025

Supplementary material

This article contains Supplementary Material or Data Files, which can be downloaded from the journal website.