

**A trait-based assessment of the functional diversity of marine Cetacea in the Canadian
Offshore Pacific Bioregion**

by

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**We acknowledge and respect the ləkʷəŋən peoples on whose traditional territory the
university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical
relationships with the land continue to this day.**

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Abstract

The identification of biodiversity hotspots is a critical step in the protection and conservation of wildlife, and the ecosystems they depend upon. Recently, the identification of numerous highly diverse benthic seafloor and seamount habitats in the Canadian Offshore Pacific Bioregion (OPB) has prompted the establishment of large marine protected areas (MPAs) which target the protection of these sensitive benthic habitats. This region has high productivity due to eddy associated upwelling of nutrients, and contains numerous unique environments, including the continental slope, cold water seamounts, hydrothermal vents, and the open ocean. Elevated productivity supports a number of Cetacea species, which take advantage of seasonal windows of productivity. Cetaceans provide ecological functions related to nutrient transfer (e.g., the whale pump), food web processes (e.g, suppression of lower trophic levels), and the creation of unique seafloor habitats (i.e., whale falls). Despite the functional importance of these species, present conservation measures in the OPB and its associated MPAs do not legislate protections targeting the surface waters Cetacea species depend on. Here, I assess whether the OPB hosts a functionally diverse subset of the global marine Cetacea species pool through comparative analyses based on the global functional space of Cetacea spp., using seven traits related to species roles in food web processes and nutrient cycling. I also identify unique features of the species found in the OPB by comparing their trait distribution to the global Cetacea species pool. The OPB hosts 28% of the known marine Cetacea species but encompasses 70% of the global marine cetacean functional space. The functional dispersion and functional redundancy of the OPB mirrors values obtained from randomly subsampling the global species pool, indicating that the region is a representative sample of functional diversity present in the global species pool. Species using the OPB are distinguished by increased body sizes, likely due to the increased richness of large-bodied, baleen feeding Mysticeti species. The functional roles of large bodied

species are fundamental for ecosystem health and stability, but are being eroded around the world as human activities continue to down-size the populations of the largest megafauna on Earth. Thus, the OPB is critical for protecting a high proportion of the global cetacean functional diversity, and the ecological roles of large cetaceans.

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Introduction

A core aim of conservation biology is to protect the biodiversity of our planet and restore ecosystems and wild communities impacted by anthropogenic disturbance. Critical to this objective is the identification of expanses of our planet which host a high biodiversity, coined as biodiversity hotspots (Myers, 1988). Since the original description of biological hotspots by Myers (1988), which focused almost exclusively on the species level diversity of endemic plant species, conservation biologists have expanded the search for hotspots across both terrestrial and marine realms, and to animal communities. Biodiversity is commonly assessed as species richness and composition - i.e., the relative abundances of species. Enhanced species diversity has been linked to increased stability and resistance of ecosystems to perturbation from climatic events (Yachi and Loreau, 1999; Tilman *et al.*, 2001; Polley *et al.*, 2013; Isbell *et al.*, 2015), as well as greater recovery outcomes for ecosystems undergoing management efforts (Williams *et al.*, 2017). However, it is also increasingly recognized that in addition to species richness and abundances, the range of ecological roles which species play in the environment significantly shapes ecosystem processes (Yachi and Loreau, 1999; Diaz & Cabido, 2001; Polley *et al.*, 2013; Tilman *et al.*, 2001; Stuart-Smith *et al.*, 2013). Functional diversity refers to the range and variety of functions which organisms provide in their ecosystems, which includes how an organism influences ecosystem structure, species/community composition, and processes like nutrient transfer and food web dynamics (Diaz and Cabido, 2001; Tavares *et al.*, 2019). Thus, functional diversity is a key additional facet of biodiversity assessment.

Functional diversity can identify biodiversity hotspots, alongside species diversity (Tilman *et al.*, 2001; Stuart Smith *et al.*, 2013). Moreover, functional diversity can be incorporated into

frameworks to evaluate species and ecosystem level vulnerability and identify differences in how taxa shape the functions of ecosystems between regions (Albouy *et al.*, 2017; Richards *et al.*, 2021; Alfaro-Lucas *et al.*, 2024). Functional diversity is estimated from species traits, which includes the behavioural, physiological, and morphological characteristics of an organism (Diaz and Cabido, 2001; reviewed in Tavares *et al.*, 2019). Through the use of functional diversity indices, one can obtain a more comprehensive assessment of how the roles of different species influence their environments, identifying commonalities and differences within and between different taxa (reviewed in Tavares *et al.*, 2019). By using species traits as a proxy, it is possible to approximate the functional roles of species in hard to access and remote environments, complementing existing species diversity analyses (Tavares *et al.*, 2019).

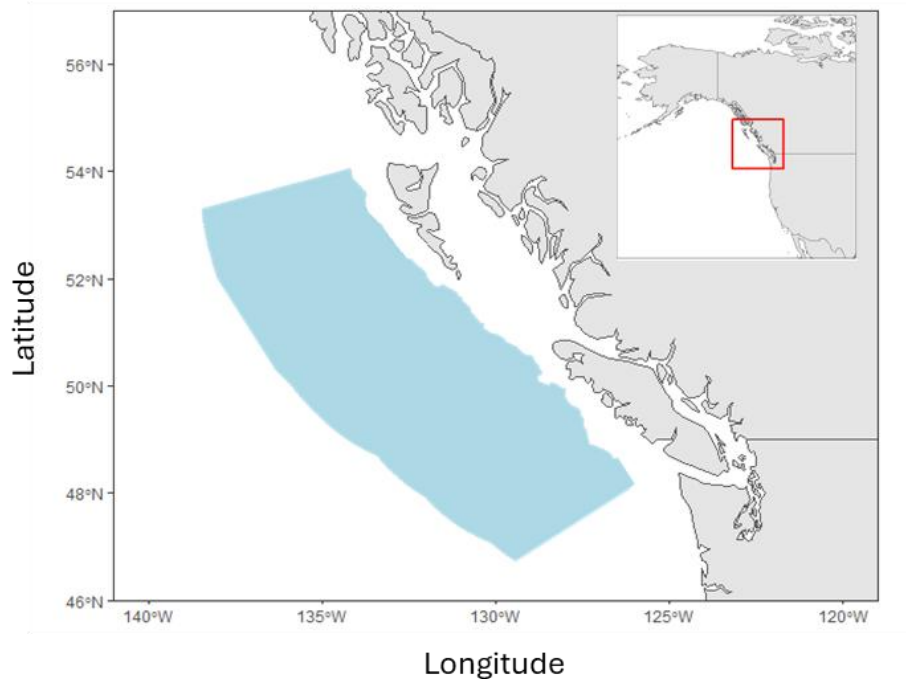


Figure 1. The geographic setting of the Offshore Pacific Bioregion (OPB; light blue polygon) in the NE Pacific. The polygon of the OPB was obtained from a publicly available DFO shapefile dataset (DFO, 2016).

The Offshore Pacific Bioregion (OPB) has become an area of extensive research and biodiversity assessment and is increasingly being recognized as a hotspot for biodiversity (Ban *et al.*, 2016; traitORS, 2024). Extending from the continental shelf break to the edges of the Pacific Canadian Exclusive Economic Zone (Figure 1), this temperate cold water region (Mackas *et al.*, 2007; Payne *et al.*, 2012) encompasses a wide variety of habitats including: the continental slope, cold water seamounts, hydrothermal vents, and open water pelagic communities (reviewed in Ban *et al.*, 2016). Such a diverse array of habitats contributes to many different biological communities with highly variable species composition (reviewed in Ban *et al.*, 2016). This region is a highly productive system, hosting high biomasses of phytoplankton and zooplankton over the span of the seasonal cycle (Rudjakov *et al.*, 1995; Robinson *et al.*, 2010; Pata *et al.*, 2022). High primary and secondary productivity is made possible by sustained elevated surface nutrient concentrations (Anderson *et al.*, 1969), supplied by localized deep water upwelling created by seamount associated eddies (Dower *et al.*, 1992; Comeau *et al.*, 1995) and the Haida eddy which carries nutrient rich coastal waters into the offshore region (Whitney and Robert, 2002). Presently, it is recognized that many of the habitats in the region host great biomasses and biodiversity, including a highly speciose zooplankton assemblage (Pata *et al.*, 2022), thousands of invertebrate and fish species, and large megafaunal vertebrate species (reviewed in Ban *et al.*, 2016). In many of the seamount and hydrothermal vent habitats, it has been noted that high quantities of endemic species are present (reviewed in Ban *et al.*, 2016), warranting increased protection of this region.

A positive development in the conservation of this region has been the establishment of marine protected areas (MPAs) across many of the major habitats of the region. There are presently

three MPAs within the OPB: the Endeavor Hydrothermal Vents MPA (97 km²), the SGáan Kínghlas-Bowie Seamount MPA (6103 km²), and the Tang.gwan – Һačxwiqak – Tsigis (ThT) MPA (133 017 km²), which is the most recent addition in June of 2024 (DFO, 2024). These MPAs are actively protecting the unique seafloor communities and overlying water column of the region and aim to conserve the highly unique benthic biodiversity (DFO, 2024; Oceans Act, 2024). Present conservation measures across these MPAs are focused on the seafloor and deep water column communities, including restrictions on deep water commercial fishing and activities which would cause disturbances to wildlife of the seafloor and deep water column (Oceans Act, 2024). However, conservation measures which protect the surface water communities are not as strongly regulated for these regions (i.e., there are no additional limitations on shipping and commercial fishing of surface waters [0-500m] is still permitted in the majority of the ThT MPA; Oceans Act, 2024). Thus, much of the surface pelagic community of the region is still exposed to significant anthropogenic threats such as boat traffic and entanglement from fishing gear, especially in the case of marine megafauna like cetaceans which need to access the ocean-air interface where these impacts are strongest (Ramp *et al.*, 2021; Nisi *et al.*, 2024).

Marine mammals are a highly functionally diverse marine megafaunal clade (Albouy *et al.*, 2017; Pimiento *et al.*, 2020). In the OPB, it is the Cetacea (whales, dolphins and porpoises) that drive the marine mammalian species diversity, making up over 80% of the marine mammals species in the region (Alfaro-Lucas *et al.* [unpublished data]; reviewed in Ban *et al.*, 2016). Cetaceans provide numerous ecological services to their ecosystems, especially as it relates to food web dynamics and nutrient cycling, with key ecological roles due to their large body sizes

(Estes *et al.*, 1998; Roman and McCarthy, 2010; Savoca *et al.*, 2020; Towner *et al.*, 2022). Here we explore three key roles. First, due to the tendency of Cetacea spp. to feed in waters below the surface mixed layer while defecating near the surface, these animals link the nutrient cycle of the surface ocean and deep waters, increasing the nutrients available for photosynthetic activity in surface waters (Roman and McCarthy, 2010; Lavery *et al.*, 2010; Savoca *et al.*, 2020). For instance, whale defecate represents a major source of limiting nutrients like iron to the surface waters of iron-depleted regions like the Southern Ocean (1.2×10^3 tonnes of iron yr^{-1} from Mysticeti spp. [baleen whales] alone; Savoca *et al.*, 2020), and is expected to increase the localized primary production and carbon sequestration within core feeding grounds (Savoca *et al.*, 2020; Lavery *et al.*, 2010). As the NE Pacific is a region where primary productivity is iron limited (Maldonado *et al.*, 1999), whales and dolphins could represent a key driver of localized primary production. Upon death, cetaceans contribute significantly to biodiversity in the deep, food poor regions of the ocean, with carcasses creating islands of biodiversity known as whale falls on the seafloor (Lundsten *et al.*, 2010). Thus, these large-bodied animals also contribute to sequestration of carbon in the deep ocean, a sink which has been severely reduced by an estimated order of magnitude post-commercial whaling (Pershing *et al.*, 2010).

Second, many Cetacea spp. represent the terminal links in food webs and can exert a significant amount of top down pressure on food webs (Estes *et al.*, 1998; Savoca *et al.*, 2020; Towner *et al.*, 2022). For example, the estimated historic krill biomass consumed by Mysticeti spp. in the Antarctic is greater pre-whaling than the estimated standing stock of Antarctic krill is today, suggesting that the largest cetaceans must have played a significant role in suppression of zooplankton stocks in the region (Savoca *et al.*, 2020). Even at very low population sizes,

cetaceans can completely restructure their communities. A well known example of this is trophic cascades observed in Aleutian Islands kelp forest ecosystem, which could have been accomplished by as little as four individual *Orcinus orca* suppressing sea otter populations in the region (Estes *et al.*, 1998). More recently an elasmobranch predator abundance shift off the South African coast was linked to the actions of just two individual *O. orca* (Towner *et al.*, 2022). Third, some cetaceans can play critical roles in sediment resuspension during benthic feeding (Johnson & Nelson, 1984; reviewed in Kiszka *et al.*, 2015, 2022) and indirectly increasing the feeding efficiency of other organisms through means like bait ball formation, which benefits other macrofaunal fish and seabird species (reviewed in Kiszka *et al.*, 2015, 2022).

Given the essential role of Cetacea spp. in shaping ecosystem dynamics at both local and broader geographic scales, safeguarding the functional diversity of this clade is crucial—particularly as many populations continue to recover from the lasting effects of commercial whaling and ongoing human-induced disturbances worldwide (Pershing *et al.*, 2010; Alter *et al.*, 2007; Whitehead & Shin, 2022). Yet, despite recent efforts to understand the diversity and ecological roles of organisms in the OPB, the full extent of functional biodiversity of Cetacea in the region remains a critical knowledge gap. Current protective measures in the OPB are focussed primarily on the benthic hydrothermal vent and seamount ecosystems, meaning surface dependent pelagic clades like Cetacea may be under protected by current MPAs, along with the functional roles they perform. Thus, it is pertinent to identify if the functional diversity of the OPB Cetacea community represents a global hotspot for the clade, so that we can identify if expanded measures to protect Cetacea spp. should be implemented in the region. Protective measures

designed for Cetacea spp. in the OPB could indirectly provide wide sweeping protections for numerous other surface and pelagic species in the region such as seabirds and large pelagic fish (reviewed in Ban *et al.*, 2016). The Canadian Pacific is known to host elevated marine mammal functional diversity compared to the global average, but this assessment does not consider Cetacea functional diversity independently from other marine mammal taxa which are less common in offshore environments due to their terrestrial dependencies (Albouy *et al.*, 2017).

The overarching goal of this research is to quantify how the variability in cetacean functional diversity within the OPB compares with the global species pool. Specifically, I will 1) quantify the global marine Cetacea functional trait space; 2) test whether the OPB emerges as a hotspot of Cetacea functional diversity; and 3) identify if the OPB community is unique in relation to species composition, or any specific traits compared to the global species pool. I hypothesize that OPB will emerge as a Cetacea functional hotspot for functions related to nutrient transfer and food web processes due to the highly seasonal biomass and diversity of both small zooplankton and large prey species in the region (Rudjakov *et al.*, 1995; Robinson *et al.*, 2010, Pata *et al.* 2022; reviewed in Ban *et al.*, 2016). High productivity will promote a greater variety of predation strategies dictating where and how a species obtains food, resulting in differing functional roles. I further hypothesize that species with increased body sizes will be overrepresented in the region as an adaptation to the cold water temperatures of the region and the high prey biomass which can sustain the energetic requirements of increased body sizes (Gearty *et al.*, 2018).

Methods

Species lists

A global species list of 88 marine Cetacea spp. was downloaded from the International Union for the Conservation of Nature (IUCN) on November 25, 2024 (IUCN, 2024; Appendix 1). The IUCN identifies marine Cetacea as species having part of their known range within the marine realm, therefore river dolphins with no known oceanic populations were not included in the species list. To ensure that the scientific names provided by the IUCN were consistent with currently accepted nomenclature for each species, the species names were updated to align with the World Cetacea Database (Fordyce and Perrin, 2025).

A presence-absence list of Cetacea spp. occupying the OPB was obtained from the traitORS offshore research synthesis project (traitORS, 2024; Appendix 1). This list was compiled from geospatial databases like the Ocean Biodiversity Information System (OBIS, 2024) and the Global Biodiversity Information Facility (GBIF, 2024), technical documents from the Department of Fisheries and Oceans Canada (DFO), and the expert inputs of marine mammalogists at the DFO (Alfaro-Lucas, personal communication).

Trait database

For each of the 88 marine Cetacea species, I compiled and scored eight traits relating to a species' functional roles in nutrient transfer, food web processes, and biodiversity promotion (Table 1). Traits were scored based on an extensive review of existing scientific literature and databases and described aspects of species morphology and behaviour. For each trait, I also

assigned a confidence score in the trait value (high or low). High confidence in a trait value indicates that there was at least one reliable scientific reference directly pertaining to the species, while low confidence indicates traits for which trait designation was speculative in the literature, or for which a species trait was inferred from the known traits of closely related species. To be included in the functional diversity and individual trait analyses, a given trait had to have high confidence in the assigned value for over 80% of the global species pool. Based on this criterion, the migration trait was dropped from statistical analyses (79.5% high confidence), therefore seven traits were used for all analyses.

1) Quantifying the global marine cetacean functional trait space

I assessed if the selected number of traits would allow for redundancy in the trait combination of species in the global species pool to be maintained. The number of traits used in functional diversity analysis is an important consideration, as the number of traits used can significantly influence the magnitude of functional diversity indices (Zhang *et al.*, 2021). Incorporating too many traits into a functional diversity analysis results in the redundancy of trait combinations between species being lost, which approximates species diversity instead of functional diversity in extreme cases (Petchey & Gordon, 2002). An objective of my study was to observe the redundancy of traits among OPB cetaceans, as the redundancy of traits can influence the stability of an ecosystem (Yachi & Loreau, 1999; Diaz & Cabido, 2001). I found that the incorporation of seven traits in functional diversity analyses maintained trait redundancy between species (See Results), and thus I used all seven traits for subsequent analyses. Continuous traits (i.e., maximum length, maximum mass, mass to length ratio) were grouped as ordinal categorical variables for the functional diversity and redundancy analyses but were maintained as continuous

traits during the individual trait assessments. This shift from continuous to categorical variables was aligned with the objective of maintaining trait redundancy in the functional diversity analysis. If left in the continuous format, each species would have a unique trait combination based on the continuous traits alone, and trait redundancy would be masked (Table 1).

Table 1. A description of the traits scored for functional diversity analyses and the percent high confidence associated with each trait.

Trait	Trait Description	Categories	Description of Individual Categories	% High Confidence	Functions and services related to trait (from Tavares <i>et al.</i> , 2019)
Maximum Length	Maximum reliably measured body length of a mature adult specimen in meters.	Small	Maximum body length of species is less than 5 m	98.9	Nutrient storage, cycling and transport, biodiversity promotion, food provisioning. Is also known to approximate the life span of cetaceans (Buddhachat <i>et al.</i> , 2021).
		Medium	Maximum body length of the species is between 5 and 9.99 m		
		Large	Maximum body length of the species is between 10 and 14.99 m		
		Very Large	Maximum body length of the species is greater than or equal to 15 m		
Maximum Body Mass	Maximum recorded body mass of a mature adult in kilograms.	Small	Maximum body mass between 10 and 99.9 kg	94.3	Nutrient storage, cycling and transport, genetic biodiversity promotion, food provisioning.
		Medium	Maximum body mass between 100 and 999.9 kg		
		Large	Maximum body mass between 1000 and 9999.9 kg		
		Very Large	Maximum body mass between 10000 kg		
Mass/Length Ratio	The ratio of the maximum mass of the species to the maximum length in kilograms per meter.	Low	Maximum body mass/length ratio between 10 and 99.9kg/m	93.2	Nutrient storage and transport. Thermal insulation or blubber content is likely best approximated by this trait.
		Medium	Maximum body mass/length ratio between 100 and 999.9kg/m		
		High	Maximum body mass/length ratio between 1000 and 9999.9kg/m		
Dentition	The type of hard feeding structure displayed by the organism.	Long Bristled Baleen	Baleen bristles longer than 2m	100	Directly related to the feeding strategy of cetaceans. Influences nutrient Storage and impacts trophodynamic processes.
		Short Bristled Baleen	Baleen bristles shorter than 2m		
		Functional Calcareous Teeth	Possesses calcareous teeth which are utilized in prey capture/consumption		
		Non-Functional Calcareous Teeth	Reduced calcareous teeth which are not utilized in prey capture (suction feeders)		
Average Group Size	The average size of pod in which an individual of the species is regularly observed.	Solitary	Average pod size less than 2	97.7	Nutrient storage, ecosystem engineering via excretion, influence on primary production rates. Influences biodiversity promotion and the overall stability of ecosystems.
		Small	Average pod size between 2-4.9		
		Small-Medium	Average pod size between 5-9.9		
		Medium	Average pod size between 10-19.9		
		Medium-Large	Average pod size between 20-50		
Large	Average pod size greater than 50				

Trait	Trait Description	Categories	Description of Individual Categories	% High Confidence	Functions and services related to trait (from Tavares <i>et al.</i> , 2019)
Migratory Behaviour	The presence or absence of a significant (100's of kilometers or more) shift in the home range or spatial distribution of a species which occurs in a regular seasonal cycle.	Migratory	Species which undergo a temporally regular seasonal shift between home ranges or a regular seasonal distribution pattern shift.	79.5	Nutrient storage, nutrient cycling, can shape communities by transporting species long distances. Can lead to species contributing significantly to otherwise energy poor food webs.
		Mixed	Species where a significant population level variation in seasonal migratory behaviour and residency is observed		
		Non-Migratory	Species which demonstrate high rates of site specific residency or nomadic behaviours which have no discernable seasonal pattern.		
Diving Depth	The maximum depth in which a mature adult has been recorded/reliably estimated while diving.	epipelagic	Remains in shallow waters (0-200m)	85.2	Trophodynamic regulation, and transport of nutrients across density boundaries in the ocean. Links directly to the whale pump (Roman and McCarthy, 2010).
		upper mesopelagic	Can dive into upper mesopelagic (201-500m)		
		lower mesopelagic	Can dive into the lower mesopelagic (501-1000m)		
		bathypelagic	Can dive into the bathypelagic (>1000m)		
Prey Choice	The prey type which makes up the greatest net proportion of the total diet of the species.	Zooplankton	Includes copepods, euphausiids, and other common zooplanktonic species	97.7	Trophodynamic maintenance, and control of pest, or invasive species. Greatly influences where trophic pressure is applied in the food web.
		Non-Cephalopod Invertebrates	Includes benthic and pelagic macroinvertebrates, minus cephalopods		
		Cephalopods	Includes squid, octopi, and other cephalopod molluscs		
		Fish	Any combination of fish species making up most of the diet		
		High Vertebrates	Consumption of primarily tetrapod prey (e.g., marine mammals)		

Dissimilarity Matrix and Principal Coordinate Analysis

To quantify the functional space of Cetacea in the OPB and the global species pool, I ordinated the 88 marine Cetacea species based on the seven previously described traits with a Principal Coordinate Analysis (PCoA). PCoA is an ordination technique which condenses multidimensional data (i.e., seven species traits) into fewer dimensions explaining as much of the variation as possible (Laliberté & Legendre, 2010). The PCoA axes were created using a dissimilarity matrix, which was generated from pairwise functional distances calculated by Gower's dissimilarity index (Gower, 1971) using the “func.dist” function in the mFD R package

(Magneville *et al.*, 2015). I used Gower's dissimilarity as it is the dissimilarity index which can robustly accommodate the presence of categorical, or mixed categorical and continuous variables in the species-trait data frame (Gower, 1971; Laliberté & Legendre, 2010). Ultimately, the dissimilarity matrix is structured as an array of values between zero and one which specify how similar each species is to each other species, with smaller values indicating two species are more alike in trait composition.

Nine PCoA axes were generated using the “quality.fspaces” function (mFD package: Magneville *et al.*, 2015) whereby the first axis explained the most variation between species, and subsequent axes (ranked by relative eigenvalue) each explaining less of the total variation between species. The mean absolute deviation (MAD) calculated by the “quality.fspaces” function (mFD package: Magneville *et al.*, 2015) was used to determine how many PCoA axes would be optimal for use in subsequent analyses. Using the number of axes at which MAD is minimized ensures that the maximum amount of variation is explained over the fewest dimensions possible, producing the most accurate functional space possible (Magneville *et al.*, 2015). Based on PCoA axis three having the lowest mean absolute deviation of all plotted axes (MAD=0.034), it was determined that the first three principal coordinate axes would create the optimal functional space for the global Cetacea species pool. Additionally, the “traits.faxes.cor” function (mFD package: Magneville *et al.*, 2015) was used to run Kruskal-Wallis tests which assessed which of the seven traits were significantly contributing to the position of species along each of the PCoA axes (Appendix 2).

2) Test whether the OPB emerges as a hotspot of Cetacea functional diversity

To determine if the functional diversity of the OPB cetacean community was greater than would be predicted from the global Cetacea species pool, two functional indices were considered: the functional dispersion (FDis) and functional redundancy (FRed). FDis is a metric of alpha functional diversity calculated as the mean distance in the global functional space between each species and the centroid of the community's functional space. It is a measure of the dissimilarity of species traits, or more simply, how spread apart the species are in the functional space (Laliberté & Legendre, 2010). Increased functional dispersion indicates an increased diversity of functional roles in a community (Laliberté & Legendre, 2010) and thus a community with an exceptionally high FDis would be considered a functional hotspot. Functional redundancy (FRed) is the average number of species per unique trait combination (or functional entity) in the functional space (Magneville *et al.*, 2015). It can act as an estimate of the resilience of the community, as the loss of a species in a community with elevated FRed is less likely to result in a functional entity being lost compared to a low FRed community. Both functional dispersion and functional redundancy were calculated for the OPB community utilizing the “alpha.fd.multidim” and “alpha.fd.fe” functions in the mFD package respectively (Magneville *et al.*, 2015). The “alpha.fd.multidim” function additionally calculated the functional richness of the OPB as well, which indicates the proportion of the functional spaces convex hull hypervolume which is occupied by the OPB (Magneville *et al.*, 2015).

I used randomization tests to compare the OPB community to the global species pool. Using the “randomizeMatrix” function from the R package “picante” (Kembel *et al.*, 2010), a random community of 25 Cetacea spp. (equal to the species richness of the OPB) was selected from the

global species pool. This process was repeated until 1000 random communities were created. For each of these Cetacea spp. assemblages, the functional dispersion and functional redundancy were calculated, producing a null distribution of each functional index. The null distributions represent the expected frequency of FDis and FRed one would obtain from random assemblages of the global Cetacea species pool which are equally speciose as the OPB. The position of observed values can be compared to the null distributions, which depict the likelihood of obtaining a given magnitude of FDis or FRed at random from the global species pool. The standard effect size (SES) of the OPB community was then calculated for each functional diversity index using Equation 1. A standard effect size greater than 1.96 or less than -1.96 indicates that the observed value for the OPB is significantly different from what would be predicted from the global species pool alone (Gotelli and McCabe, 2002).

$$(1) \quad \text{SES} = \frac{\text{Observed Value}_{\text{OPB}} - \text{Mean}_{\text{Null}}}{\text{Standard Deviation}_{\text{Null}}}$$

3) Identify if the OPB community is unique in relation to species composition, or any specific traits compared to the global species pool.

Mysticeti species richness

I conducted a randomization test to determine if the proportional richness of Mysticeti spp. in the OPB (baleen whales) was non random from the global species pool. This was accomplished by generating random assemblages of 25 cetaceans from the global species pool using the “sample” function in R (Core R Team, 2023) and calculating the proportional richness of Mysticeti for

each assemblage. This was repeated to generate 1000 random assemblages, producing a null distribution of the expected species richness of Mysticeti from the global Cetacea species pool. The standard effect size (SES) of the observed OPB proportional Mysticeti richness was then calculated via equation 1.

Unique Species

Unique species possess a combination of trait values that are not shared by any other species in the global pool. This implies that the functional roles of this species would be different from all other species in the global pool, and that the loss of this species is equivalent to the loss of a functional entity. To determine if the frequency of unique species in the OPB differed compared to what one would expect from the global species pool, I used the “uniqueness” function in the “funrar” R package (Grenié *et al.*, 2017) to calculate the Uniqueness (U_i) value of each species based on the previously constructed dissimilarity matrix. Uniqueness describes the functional distance of a given species to its nearest neighbour in the functional space (Grenié *et al.*, 2017). A Uniqueness of zero indicates that a species shares a unique trait combination with at least one other species, or in other words that there is no distance between the target species and its nearest neighbour in the functional space. Any Uniqueness greater than one indicates that a given species’ trait combination is unique from all other species in the global species pool, with greater magnitudes of U_i indicating greater separation in the functional space from other species. By calculating the Uniqueness for each species in the global pool, I was able to identify species which demonstrate high functional separation from all other species in the OPB, or in other words, species with high Uniqueness index. By counting the number species in which $U_i > 0$, I established how many unique species there are in the global and OPB cetacean communities.

To establish whether the number of unique Cetacea species in the OPB was significantly different compared to the global species pool, I used a randomization testing procedure where 25 species (number of cetacean species in the OPB species pool) were randomly selected from the global pool utilizing the “sample” function in R [version 4.3.2] (Core R Team, 2023), and the number of species where $U_i > 0$ was counted. This was repeated for 1000 permutations, producing a null distribution of unique species counts. The standard effect size (SES) of the OPB community was then calculated using equation 1.

Individual Trait Analyses

To quantify whether the distributions of the seven scored traits differed significantly between the OPB community and the global species pool, each trait was assessed independently. For the three continuous traits (maximum length, maximum mass, and mass to length ratio), the mean of each trait was calculated for the OPB community. Mean values of each trait were also calculated for 1000 randomly sampled communities of 25 cetaceans to construct a null distribution of the means of each trait. The SES of each trait was then calculated using equation 1. For categorical traits (dentition, average group size, maximum diving depth, and prey choice), Fisher's exact probability test was used to compare the species counts for each trait in the OPB to the species trait counts of the global species pool. Trait frequencies were obtained for the OPB and global species pools by multiplying the Community Weighted Means of each trait (calculated by the “functcomp” function in the “FD” R package; Laliberté *et al.*, 2014), by the number of species in each species pool (25 spp. and 88 spp., respectively). These frequencies were imputed in the “fisher.test” function in R (Core R Team, 2023) to compare the expected values of the global species pool against the observed OPB species pool.

All analyses were conducted with R version 4.3.2 (R Core Team, 2023) and are available at https://github.com/MatthewATTuck/Cetacean_Functional_Diversity.

Results

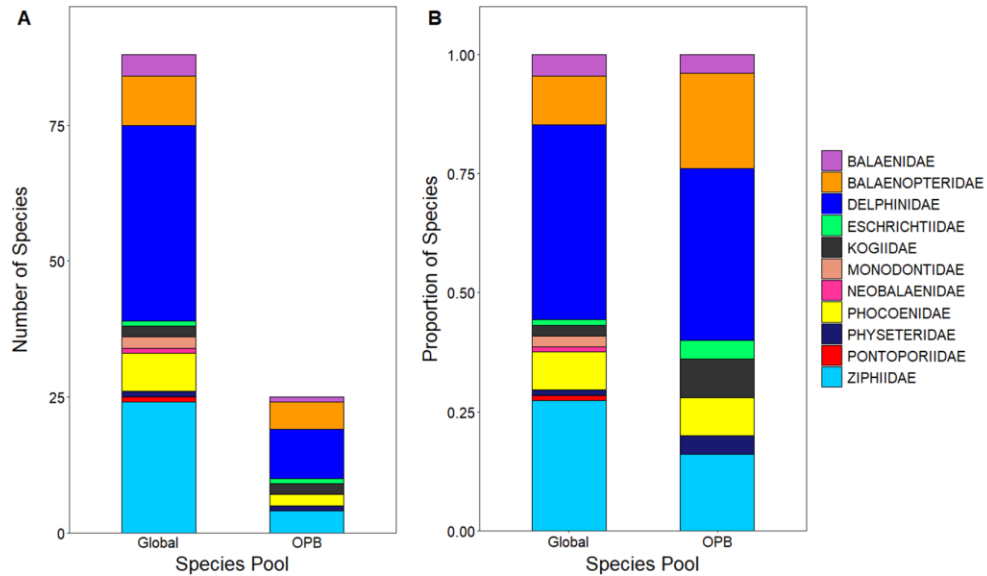


Figure 2. Stacked bar plots depicting the species counts (A) and proportional abundance (B) of marine cetaceans in the global species pool (N=88 spp.) and the Offshore Pacific Bioregion (N=25 spp.). The family names are listed in vertical order of appearance in the chart in the legend (right).

Species Proportions

The OPB region hosts 25 cetacean species, representing approximately 28% of the total marine cetacean species pool. These 25 species were distributed across eight of the eleven known cetacean families (Figure 2). Absent families were the Monodontidae (beluga and narwhal), Neobalaenidae (pygmy right whales), and Pontoporiidae (river dolphins), which are species poor in the marine realm (2, 1, and 1 species, respectively). The proportional richness of Balaenopterid whales was almost twice as great in the OPB than in the global cetacean species pool (0.2 and 0.11 respectively), and overall, baleen whales (Mysticeti) were proportionally more abundant in the OPB than in the global cetacean species pool (0.28 and 0.17 respectively).

Functional Space

Species occupying the OPB span across the majority of the global marine Cetacea functional space (Figure 3). The convex hull volume of the OPB is nearly 70% of the convex hull volume of the global species pool, and the species of the OPB are well distributed over the functional space (Figure 3). The 88 species in the global cetacean species pool divide into 56 functional entities. Most functional entities were populated by only one or two species (50 functional entities), and the maximum number of species in a functional entity was nine. This functional entity was comprised of members of the family Ziphiidae (beaked whales). Of the 56 functional entities, 21 were populated by species in the OPB community. There were two distinct clusters of functional entities produced by PCoA 1 and PCoA 2 (Figure 3), reflecting a separation of the Mysticeti and Odontoceti whales in the functional space. The area of the functional space occupied by Mysticeti is more constrained than what is observed in the Odontocetes. 41.7% of the Mysticeti functional entities include OPB species (5 of 12 species), while 36.4 % of the Odontoceti functional entities included OPB species (16 of 44 species).

PCoA 1 explained 62.76% of the total variation across traits. Moving towards increasing values of PCoA 1, there is a transition from less gregarious, large body sized cetaceans which feed primarily on zooplankton and cephalopods (e.g., baleen whales and beaked whales), to smaller body sized cetaceans which are primarily preying on fish species, and which are highly gregarious like oceanic dolphins and porpoises (Figure 4). PCoA 2 explained 31.32% of the total trait variation. As you move towards increased values of PCoA 2, we see a transition from solitary, shallow diving species with baleen dentition to deeper diving species with calcareous teeth, and gregarious tendencies (Figure 4). PCoA 3 explains the smallest amount of variation of

the three axes (8.85%). As PCoA 3 increases, there is a transition from more gregarious species to less gregarious species (Appendix 3). For both PCoA 1 and PCoA 2, all seven traits contributed significantly to species ordination along the axis (Kruskal-Wallis test, $p \leq 0.05$; Appendix 2), while for PCoA 3, maximum length and prey choice did not explain the location of a species on the axis (Kruskal-Wallis test, $p=0.1335$ and $p=0.5423$ respectively; Appendix 2; Appendix 3).

Functional Dispersion (FDis)

The observed functional dispersion of the OPB cetacean community was greater than the functional dispersion of the global species pool ($FDis_{OPB}$ [25 spp.] = 0.76, $FDis_{Global}$ [88 spp.] = 0.74). Although the functional diversity of the OPB was slightly greater than the mean of the null distribution of functional dispersion (mean $FDis_{null} = 0.73$, sd $FDis_{null} = 0.04$, $FDis_{OPB} = 0.76$), the SES of this difference was small ($SES_{FDis} = 0.58$). This suggests that the functional diversity of the OPB is typical of the average functional diversity you would expect for 25 species drawn at random from the species pool (Figure 5).

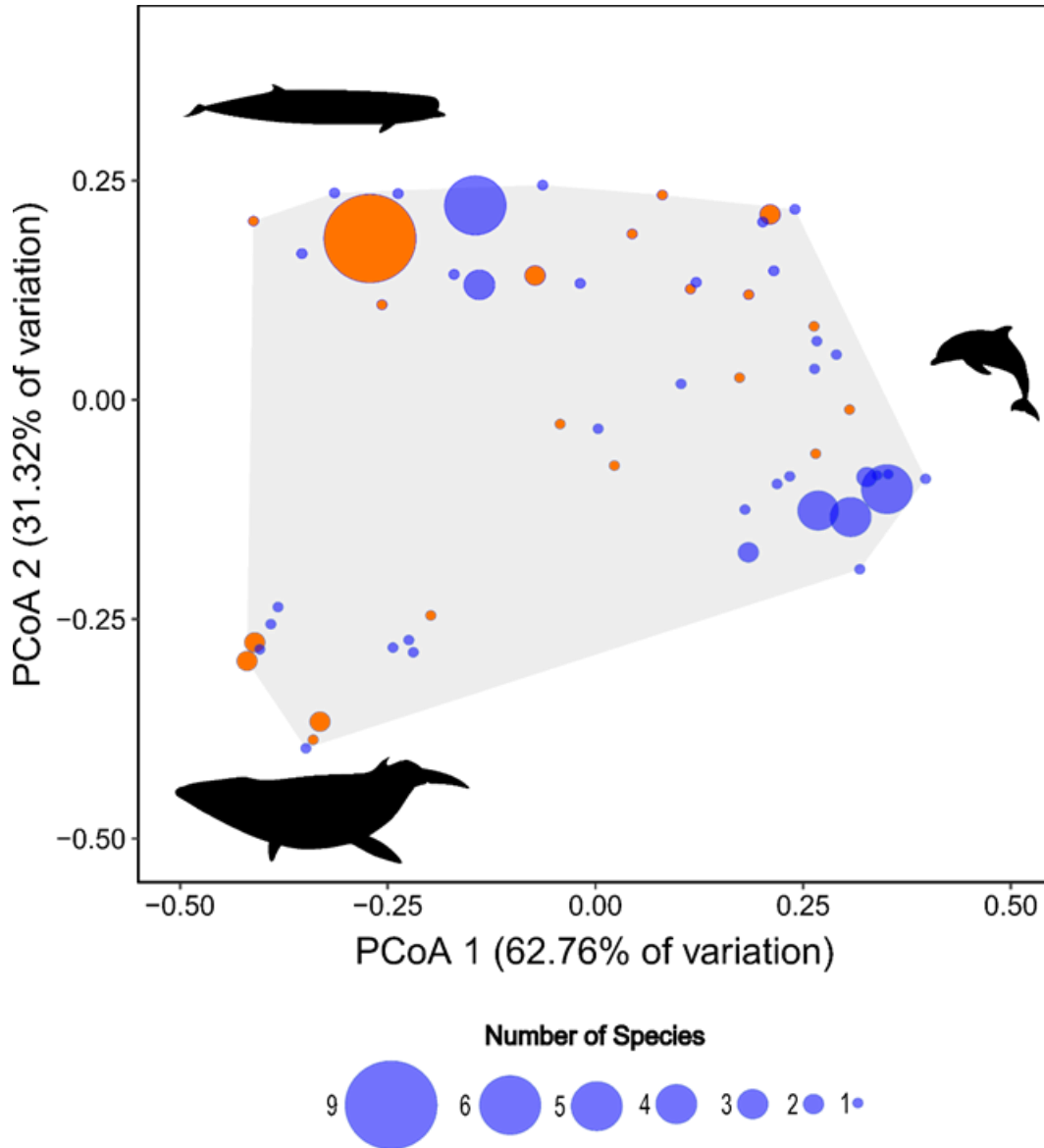


Figure 3. The global functional space of Cetacea as plotted out by PCoA axes. PCoA 1 and PCoA 2 explain the most variation of all PCoA axes. Each of the 56 individual points in the functional space represents a functional entity, with the number of species per functional entity indicated by the size of the point. Orange points represent functional entities populated by at least one species present in the OPB ($n=21$), while blue points indicate that none of the associated species are observed within the OPB ($n=36$). The grey background polygon represents the convex hull area of the global functional space. Silhouettes indicate the families which are associated with each region of the global functional space (bottom left = Mysticeti, top left = Ziphiidae and other large Odontocetes, center right = oceanic dolphins and porpoise). Silhouettes were obtained from Phylopic (<https://www.phylopic.org/>; T. Michael Keeseey, 2023) using the “rphylopic” package in R (Gearty and Jones, 2023). Silhouettes accreditation: Micheal Day, 2019 (CC0 1.0).

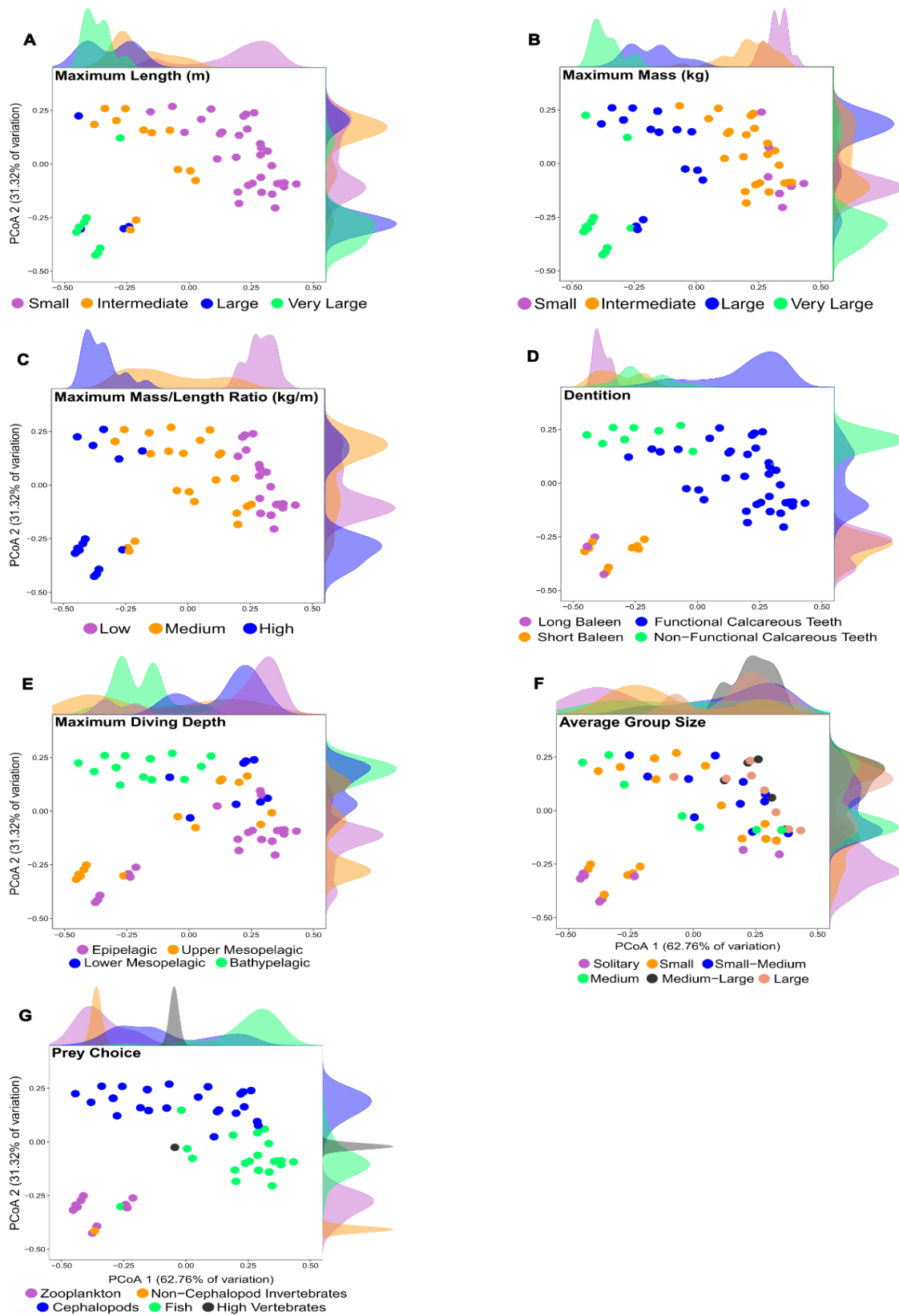


Figure 4. The distribution of species traits across the global functional space of marine Cetacea spp. as plotted by PCoA 1 and PCoA 2. Traits described include: maximum length (A), maximum mass (B), the mass to length ratio (C), dentition (D), maximum diving depth (E), average group size (F) and prey choice (G). Density plots on the periphery are included to visualize how traits were distributed across each principal coordinate axis.

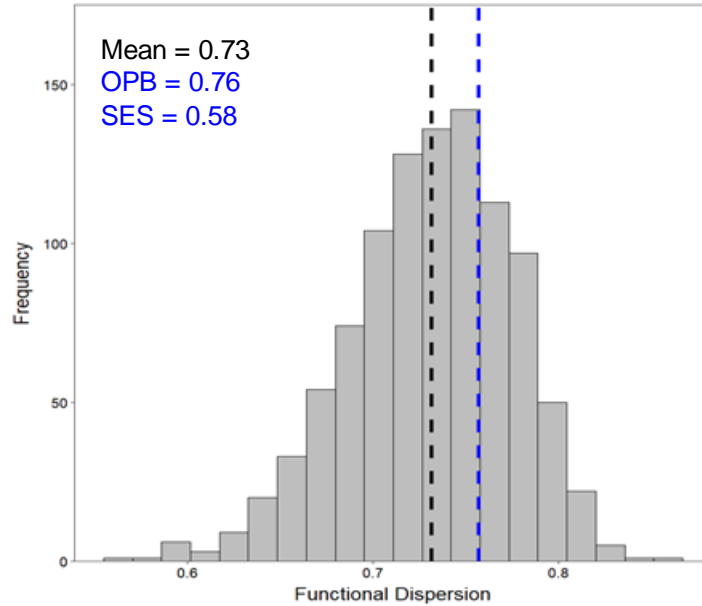


Figure 5. The null distribution of functional dispersion (FDis) generated by randomization testing of the global Cetacea species pool. Each of the 1000 observations in the null distribution represents the FDis of a random selection of 25 Cetacea spp. from the global species pool. The black dashed line is the mean of the null distribution (mean $FDis_{null} = 0.73$) while the blue dashed line represents the observed FRed of the OPB Cetacea community ($FDis_{OPB} = 0.76$). The SES of the OPB Cetacea community was statistically similar to a random assemblage of the global species pool ($SES_{OPB} = 0.58$).

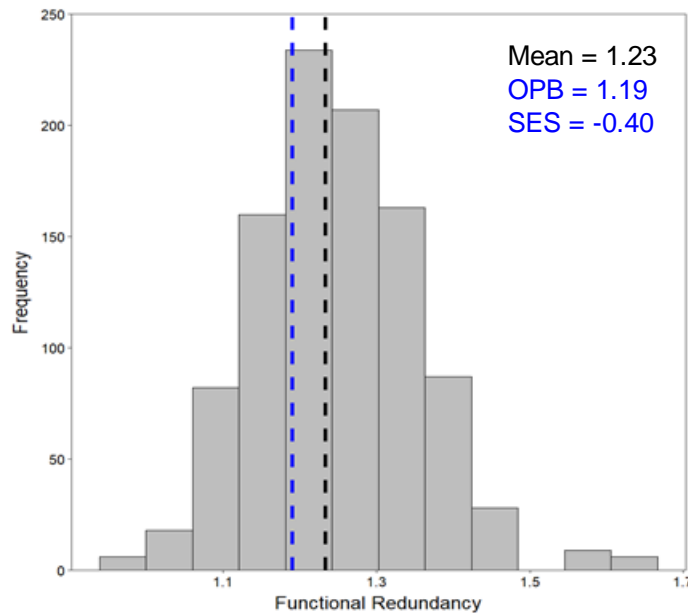


Figure 6. The null distribution of functional redundancy (FRed) generated by randomization testing of the global Cetacea species pool. Each of the 1000 observations in the null distribution represents the FRed of a random selection of 25 Cetacea spp. from the global species pool. The black dashed line is the mean of the null distribution (mean $FRed_{null} = 1.23$) while the blue dashed line represents the observed FRed of the OPB Cetacea community ($FRed_{OPB} = 1.19$). The SES of the OPB Cetacea community was statistically similar to a random assemblage of the global species pool ($SES_{OPB} = -0.40$).

Functional Redundancy (FRed)

The observed functional redundancy of the OPB was 1.19 species per functional entity, which was lower than the functional redundancy of the whole global species pool ($FRed_{Global} = 1.57$). When compared against randomly selected subsets of 25 Cetacea spp. from the global species pool, the $FRed_{OPB}$ was only slightly smaller than the null distributions mean ($FRed_{null} = 1.23$, $sd_{null} = 0.11$; Figure 6). The SES of the OPB cetacean community was between -1.96 and 1.96, indicating that the FRed of the OPB is typical of a random selection of 25 species from the global species pool ($SES = -0.40$).

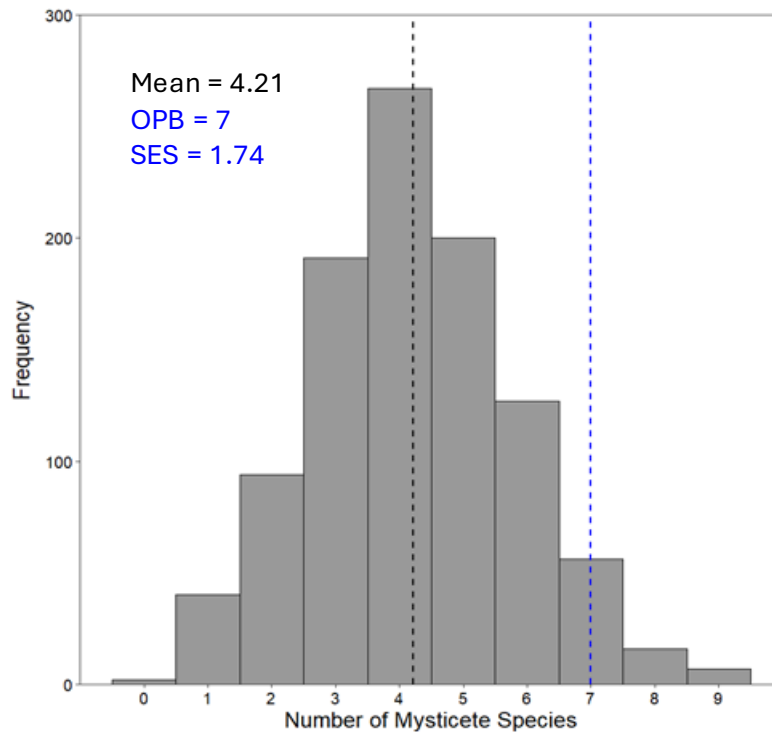


Figure 7. Histogram depicting the distribution of a randomization test assessing whether the number of Mysticete species in the OPB was a non-random subset of the global species pool. The black line indicates the mean of the null distribution (4.21), while the blue line represents the observed number of Mysticete species in the OPB (7).

Species Richness of Mysticeti

Based on the results of the randomization test, the mean number of Mysticeti spp. per simulated community was almost three fewer than in the OPB ($\text{mean}_{\text{null}}=4.12$, $\text{sd}_{\text{null}}=1.60$, $\text{OPB}=7$, $\text{SES}_{\text{OPB}}=1.74$; Figure 7). This observation, although not significantly different from the mean of the null distribution of the global species pool (i.e., $-1.96 < \text{SES}_{\text{OPB}} < 1.96$), was greater than the counts observed in over 90% of the simulated communities.

Unique Species

An increased proportion of the species in the OPB community were unique: 60.0% species located in the Offshore Pacific Bioregion are unique species (15 of 25 species), which is a greater proportion than is observed in the global species pool (43 of 88 species, 48.9%; Figure 8). A high proportion of the Odontoceti species in the OPB are unique species (13 of 18 species, 72.2%), while only 2 of the 7 Mysticeti species are unique (28.6%). Based on the uniqueness scores imputed by the “funrar” function (package “funrar”: Grenié *et al.*, 2017), the three most functionally distinct species found in the OPB were *Eschrichtius robustus* ($U_i = 0.19$), *Orcinus orca* ($U_i = 0.14$) and *Physeter macrocephalus* ($U_i = 0.12$). The randomization test comparing the OPB community and global species pool indicates that the number of unique species in the OPB was greater than the mean of the null distribution, but the SES was within +/- 1.96 ($\text{mean}_{\text{null}} = 12.24$, $\text{sd}_{\text{null}} = 2.22$, $\text{SES}_{\text{unique species}} = 1.24$).

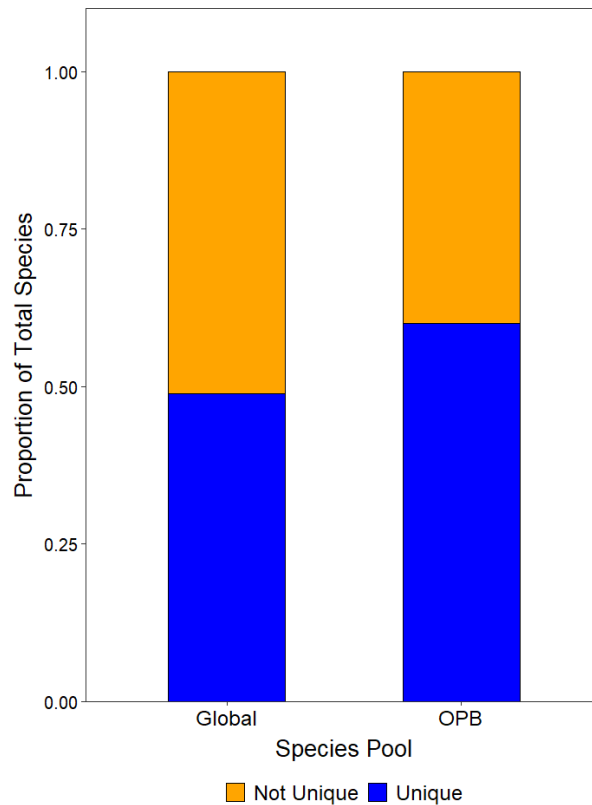


Figure 8. Stacked bar plots depicting the difference in the proportion of unique species between the global Cetacea species pool and the OPB.

Individual Trait Analyses

The OPB region had greater maximum body sizes than would be predicted based on the null distribution created from random selections of the global Cetacea species pool. For each of the three continuous traits (maximum body length, maximum body mass, and maximum mass/maximum length ratio), the mean of the OPB community ($\text{Length}_{\text{OPB}}=9.50\text{m}$, $\text{Mass}_{\text{OPB}} = 24.20 \times 10^3 \text{ kg}$, $\text{Mass}/\text{Length}_{\text{OPB}} = 1.23 \times 10^3 \text{ kg/m}$) was greater than the mean of the null distributions generated by the randomization procedure ($\text{Length}_{\text{null}} = 6.27 \text{ m}$, $\text{Mass}_{\text{null}} = 11.70 \times 10^3 \text{ kg}$, $\text{Mass}/\text{Length}_{\text{null}} = 0.73 \times 10^3 \text{ kg/m}$), with all SESs being greater than 1.96 ($\text{SES}_{\text{length}}=3.23$, $\text{SES}_{\text{mass}}=2.48$, $\text{SES}_{\text{ratio}}=2.24$). The maximum length, maximum mass, and mass

to length ratio of the OPB cetacean community is greater than would be predicted by chance alone (Figure 9).

Across all four categorical traits, no statistically significant difference was observed in the distributions of traits between the OPB and the global species pool (Dentition: $p=0.49$, Maximum Diving Depth: $p=0.16$, Average Group Size: $p=0.70$, Prey Choice: $p=0.12$; Figure 10). For prey choice, there is an increased proportion of zooplankton feeding species, and a reduced proportion which primarily consume fish in the OPB community. This result matches the expectations of a community with increased proportional abundances of baleen whale species. Dentition within the OPB showed a greater prevalence of short baleen, and a reduced contribution of species which only possessed ornamental tusks and rely on suction feeding (Non-Functional Calcareous Teeth). Epipelagic restricted species occur at a lower frequency in the OPB region than in the global species pool, with an increased proportion extending dives into the mesopelagic. Gregariousness appears to be weakly elevated overall in the OPB compared to the global species pool.

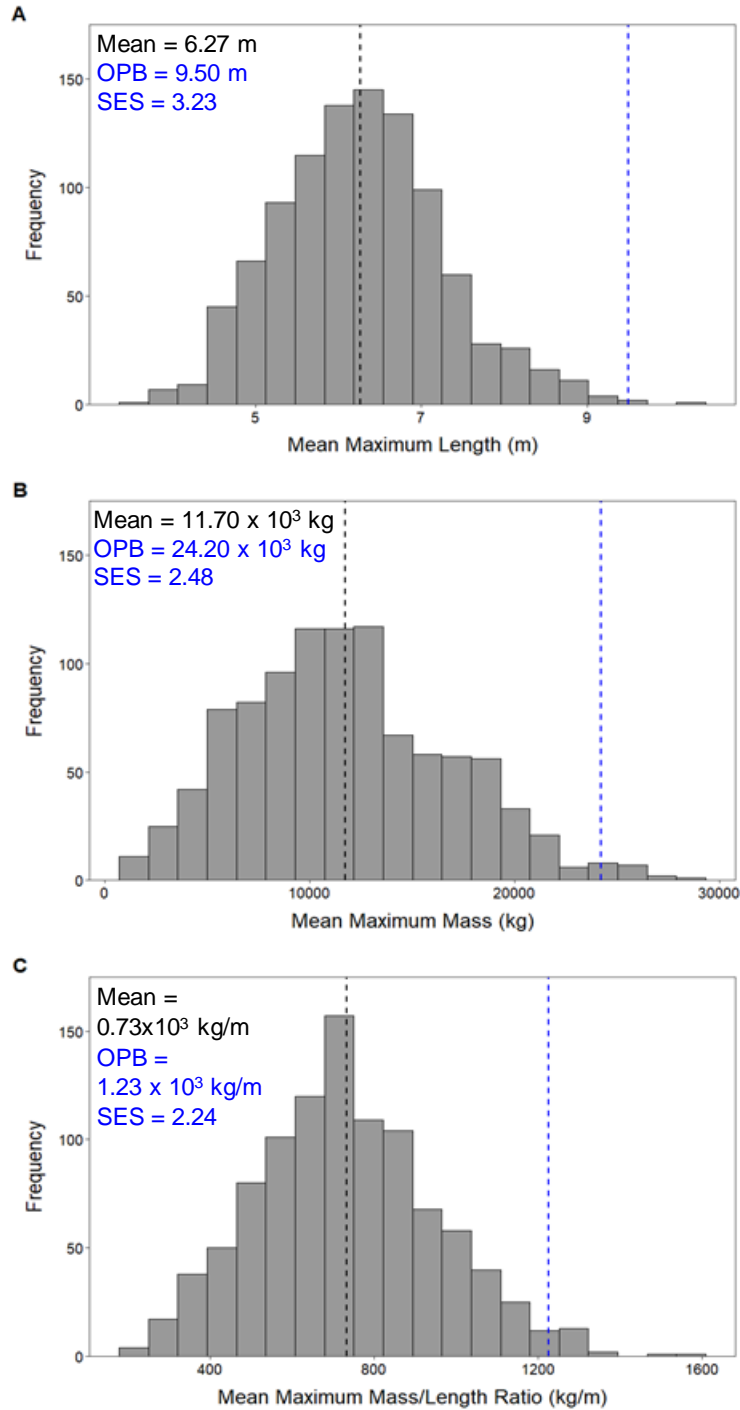


Figure 9. Histograms depicting null distributions of the three continuous traits (maximum length = A, maximum mass = B, maximum mass to length ratio = C) generated by randomization tests of the global Cetacea species pool. Each of the 1000 observations in the null distribution represents the mean of a random selection of 25 Cetacea spp. from the global species pool. The black lines indicate the means of the null distributions ($Length_{null} = 6.27$ m, $Mass_{null} = 11.7 \times 10^3$ kg, 0.734×10^3 kg/m), while the blue line indicates the mean values of the OPB community for each trait ($Length_{OPB} = 9.50$ m, $Mass_{OPB} = 24.2 \times 10^3$ kg, $Mass/Length_{OPB} = 1.23 \times 10^3$ kg/m). In OPB, all three traits show a non-random SES for elevated body sizes.

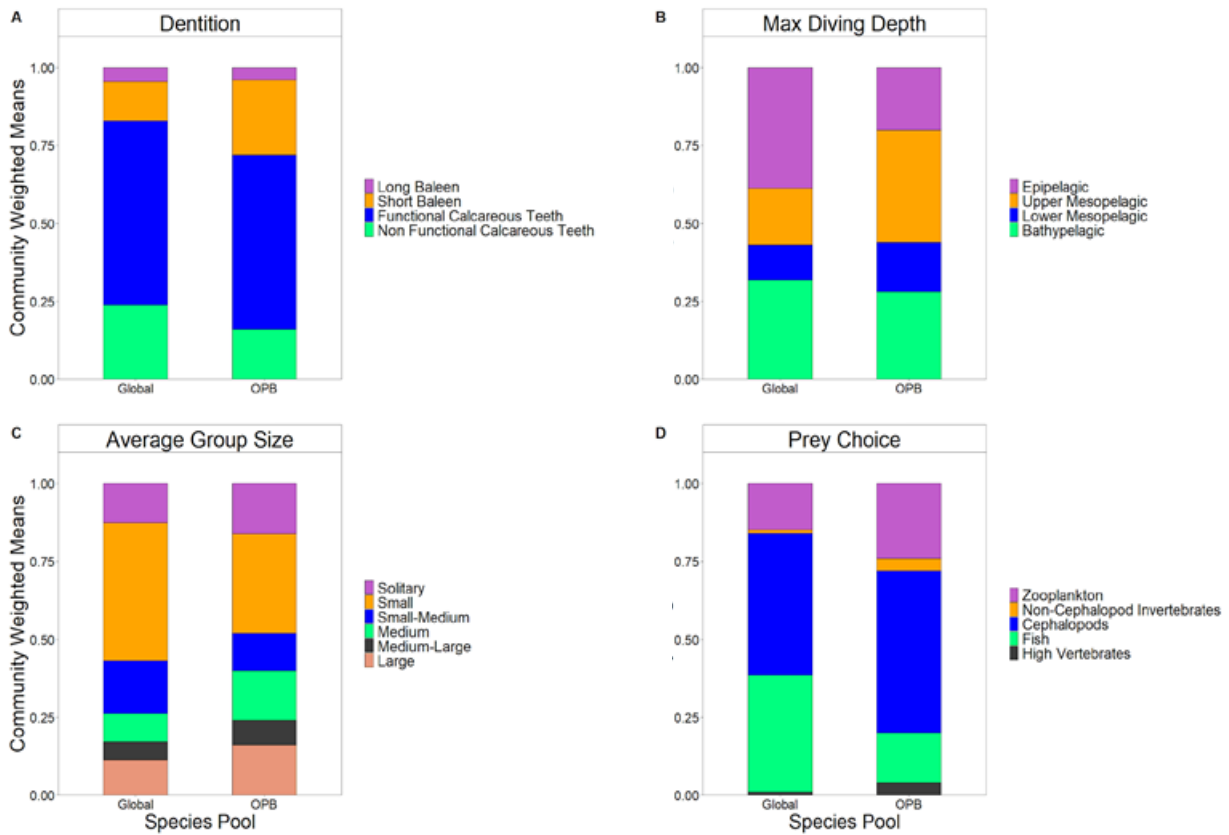


Figure 10. Community weighted means (CWMs) of the global marine cetacean species pool and the OPB for each of the categorical traits assessed in functional diversity analyses. The distribution of dentition (A), maximum diving depth (B), average group size (C), and prey choice (D) in the OPB community were all confirmed to be statistically similar to the global marine Cetacea species pool via Fisher’s Exact probability test.

Discussion

A large amount of the global Cetacea functional diversity was represented by species present in the Offshore Pacific Bioregion (OPB), which encompassed almost 70% of the global functional space ($FRI_{OPB} = 69.1\%$). Thus, limiting human activities that harm marine mammals in this region has the potential to protect a wide array of cetacean functional roles. Indeed, the NE Pacific has previously been identified as a marine mammal functional diversity hotspot despite moderate species richness (Albouy *et al.*, 2017; Pimiento *et al.*, 2020). The functional diversity of marine mammals reported in the Canadian Pacific, as measured by the functional richness,

ranked in the highest 2.5% of all marine environments globally (Albouy *et al.*, 2017). The results presented in this study appear to be consistent with this observation. However, the reported FRic from past research was much lower than in my present assessment (FRic was between 0.35-0.40, compared to 0.691 in the present study). This discrepancy is likely in part due to the prior study including all extant marine mammal clades in the functional trait space, alongside the scoring of a terrestriality trait which will strongly separate Cetacea from Pinnipedia in the functional space (Albouy *et al.*, 2017). Additionally, Albouy *et al.* (2017) assessed a greater number of traits compared to my present study (14 compared to 7), and the magnitude of FRic is known to be significantly influenced by the number of traits used in the analysis (Albouy *et al.*, 2017; Zhang *et al.*, 2021).

Protecting regions with high functional diversity is critical to maintain the health and stability of ecosystems (Yachi and Loreau, 1999; Polley *et al.*, 2013). Here, I find that the OPB hosts high cetacean functional diversity; a taxa that is known to deliver a range of ecological functions (Estes *et al.*, 1998; Savoca *et al.*, 2020; Towner *et al.*, 2022; Johnson & Nelson, 1984; reviewed in Kiszka *et al.*, 2022; Roman and McCarthy, 2014; Lundsten *et al.*, 2010; Pershing *et al.*, 2010), often across broad geographic ranges (IUCN, 2024). A unique opportunity to effectively preserve a highly diverse range of cetacean ecosystem services exists within the OPB, in part due to the large area of the region which is already protected by MPAs (DFO, 2024). Protective measures targeting Cetacea spp. need to be implemented across wide tracks of ocean due to the high amount of nomadic and migratory species in the taxa. Such efforts would create umbrella protections for other pelagic, near surface species inhabiting the same region (Hoyt, 2011).

Though I did observe many of the functional roles of the global species pool in the OPB, the region did not emerge as a functional diversity hotspot for Cetacea. The functional dispersion of the region instead mirrors the mean FDis of the null distribution, producing a weakly positive SES (0.58). This finding is inconsistent with my prediction that the highly productive region would promote a significantly elevated functional diversity (Rudjakov *et al.*, 1995; Robinson *et al.*, 2010; Pata *et al.* 2022; reviewed in Ban *et al.*, 2016), especially as the traits scored relate to species roles in food web and nutrient transport processes directly associated with ecosystem productivity (Tavares *et al.*, 2019). This result may be related to the low proportional species richness of the oceanic dolphins and porpoises with small body size to length ratios in the OPB. The functional dispersion would be significantly drawn down by the exclusion of functional groups which were on the periphery of the functional space as the average distance of points from the center of gravity would be reduced compared to those which included all periphery groups (Laliberté & Legendre, 2010). Thus, the reduced prevalence of oceanic dolphin and porpoise species in the OPB may explain the moderate observed FDis. I am presently unaware of another study which has compared the functional dispersion of a particular region against simulated populations of the global Cetacea species pool. It is difficult to draw firm conclusions as I presently have only assessed one region via this method, but it is possible that the simulation of random Cetacea communities is generating assemblages that realistically could not exist due to environmental constraints, but have a high functional dispersion. Future analyses using this methodology to assess the functional dispersion of known functional hotspots for Cetacea (e.g. California Coast, Argentinian coast, Southern Ocean; Albouy *et al.*, 2017) may be useful to determine if an artifact of the methodology is responsible for the low SES of FDis in the OPB.

Here, I identified that a large proportion of species in the OPB are filling unique functional roles. The functional redundancy of the region was lower than the mean of the null distribution ($FRed_{OPB} = 1.19$, $FRed_{null} = 1.23$), while the number of unique species was greater than the mean of the null distribution (15 species compared to 12.24 species). This seems intuitive given the high observed functional richness distributed over a relatively small number of species (< 30 species). Functional redundancy is associated with increased ecosystem stability under the insurance hypothesis, as increased redundancy buffers against the loss of functional entities due to chance extinctions or disturbances (Yachi & Loreau, 1999; Diaz & Cabido, 2001; McClean *et al.*, 2019; Biggs *et al.*, 2020). Thus, within the OPB the risk of losing a functionally entity from chance extinction or disturbance is slightly increased compared to in the global species pool itself (Yachi & Loreau, 1999; Diaz & Cabido, 2001; McClean *et al.*, 2019; Biggs *et al.*, 2020). The finding that FRed was lower, and the proportion of unique species was greater in the OPB is consistent with prior observation that the NE Pacific marine mammal community had a higher functional vulnerability than most of the world's ocean regions, or in other words that the redundancy in traits between species was low (Auber *et al.*, 2022). My findings thus provide strong support for the unique role of each species in this region and the importance of implementing offshore protection.

In particular, the three species which demonstrated the highest Uniqueness (U_i) metric within the OPB were *Eschrichitus robustus*, *Orcinus orca*, and *Physeter macrocephalus*. The Uniqueness of *Eschrichitus robustus* and *Orcinus orca*, is related to each species representing a unique feeding guild on their own, with *Eschrichitus robustus* consuming high amounts of benthic and hyper benthic invertebrates (Johnson & Nelson, 1984; Dunham & Duffus, 2002; Albouy *et al.*, 2017)

while *Orcinus orca* is the only Cetacea species which shows a prey preference for higher vertebrate species (de Bruyn *et al.*, 2013; Albouy *et al.*, 2017). *Physeter macrocephalus* are the only Odontoceti whale which reaches the largest size class ($\geq 15\text{m}$), which is why they are considered one of the great whales (Lavery *et al.*, 2010; Roman *et al.*, 2014). These species highlight that within the OPB, a great range of unique feeding modes are present. However, the loss of even one species in the region could be associated with the loss of unique feeding guilds in the cases of *Eschrichtius robustus* and *Orcinus orca*. Species with highly unique trait combinations in this region may require more thorough observation and monitoring, as losses to these species may result in the loss of a unique set of traits and hence functions.

The OPB is most strongly differentiated from the global species pool in that member species are significantly larger than would be predicted from a random assemblage of the global species pool. This trend towards increased body sizes is, in part, a product of the high species richness of Mysticeti species in the OPB compared to the global species pool. The representation of these large bodied species in the OPBs species richness was greater than in over 90% of the simulated communities. As hypothesized, this result is consistent with the evolutionary history of Cetacea in a highly productive cold water region like the OPB (Mackas *et al.*, 2007; Payne *et al.*, 2012). Cetaceans achieved the massive body sizes observed today as a product of the thermodynamic constraints of the oceanic environment (Gearty *et al.*, 2018). Larger, more robust body sizes better retain heat acting as a selective pressure towards increased body sizes in cold water environments due to the reduction of the surface area to volume ratio of their bodies (Gearty *et al.*, 2018; Glarou *et al.*, 2025). The increased body sizes of the largest Mysticeti spp. was also made possible by shifts towards highly productive food sources, and increased body sizes in turn

made hunting clusters of small zooplankton and fish more efficient (Gearty *et al.*, 2018; Goldbogen *et al.*, 2019). Odontoceti on the other hand showed selection towards smaller body sizes which were more efficient for the pursuit of larger individual prey items (Goldbogen *et al.*, 2019). This separation in feeding strategy between Mysticeti and Odontoceti is well reflected in the global functional space, with the Mysticeti forming a distinct cluster of functional entities from the Odontoceti across the two most descriptive PCoA axes (Figure 4).

As an increased proportion of the OPB species pool comprises the largest body sized cetaceans (the great whales, including Mysticeti spp. and *Physeter macrocephalus*; Roman *et al.*, 2014), threats to these species will likely have a more pronounced impact on the functional diversity of the region. The populations of many of the largest whale species are still in recovery globally, with estimates of current population sizes being as low as 10% of pre-commercial whaling levels (Pershing *et al.*, 2010; Alter *et al.*, 2007; Clements *et al.*, 2017; Whitehead & Shin, 2022). Further it has been noted that the body size of the great whales have been reduced by commercial whaling, with many species seeing reductions in 95% percentile body length greater than three meters (Clements *et al.*, 2017). The energetic efficiency of feeding, fasting capacity, and diving ability of the great whales are enhanced at greater body sizes, making decreased body sizes maladaptive for these species (reviewed in Goldbogen, 2018; Goldbogen *et al.*, 2019). The combined impacts of reduced population sizes and body lengths of the great whales will inevitably reduce the capacity of these species to move large quantities of photosynthetically limiting nutrients in the marine environment (Savoca *et al.*, 2020; Lavery *et al.*, 2010), and reduces the amount of biomass which can be sustained in the environment (Pershing *et al.*, 2010). Given the relative importance of large whale species to the region, the impact on

ecosystem functioning from whaling may be more extreme within this region than in areas where small Cetacea spp. are more functionally important (Pershing *et al.*, 2010; Alter *et al.*, 2007; Whitehead & Shin, 2022).

At present, this study scores traits at the species level, with a singular trait score representing all sub species and populations around the globe of a given species. The rationale behind this decision was that although there is comprehensive information at the species level for the majority of Cetacea species traits, trying to parse out subspecies or population level differences in many traits can be difficult. However, it is critical to note that some subspecies/populations of Cetacea can demonstrate significant differences in traits. For example, the diets of *Orcinus orca* can vary from population to population, differentially preferring bony fish, elasmobranchs, seabird, and mammal prey (de Bruyn *et al.*, 2013). Within the NE Pacific alone, three ecotypes of *Orcinus orca* are known, each preferring different prey types (de Bruyn *et al.*, 2013). Future projects could incorporate subspecies level differences to more accurately characterize the functional space of Cetacea. Furthermore, only the presence or absence of species was used while calculating the functional dispersion, meaning that all species present are considered to equally influence the functional space (weights = 1; Laliberté & Legendre, 2010). Though it does provide an initial baseline for the functional diversity of the region, ignoring species abundances does not accurately reflect how population size effects will influence the distribution of functional roles, as often species will contribute unevenly to ecosystem roles, stability and resilience based on population size or dominance (Kunze *et al.*, 2024; reviewed in Diaz & Cabido, 2001). In future renditions, attempting to scale the measure of functional dispersion in the OPB by assigning weights to each cetacean species based on their abundance in the region

would expand our understanding of functional diversity in this region. Such analyses would allow us to better observe areas of the functional space which are more strongly represented by abundant species. Abundance weighted analyses could lend itself to exploring differences in the functional diversity of cetaceans over time, by scaling functional diversity over historical population estimates, or alternatively to project how future population trajectories could influence the global or OPB functional spaces. The proposed analysis could be used to determine how whaling and human driven mortality of Cetacea has influenced the shape of the functional pool over time, and to model how existing pressures on these species may shape ecosystem functioning.

In summary, the Offshore Pacific Bioregion hosts 28% (25/88) of the global marine Cetacea species pool and effective conservation measures would protect almost 70% of the global Cetacea functional diversity. The variety of functional roles in which cetaceans provide to their ecosystems could be adequately protected by focussing conservation efforts on this region, accompanied by the potential wide sweeping benefits of umbrella protection from Cetacea. Additionally, the low functional redundancy and high number of unique species in the region suggests that the loss of species in this region is more likely to result in losses of functional roles and their associated ecosystem services than would be predicted from the global species pool. The prior establishment of large MPAs in the OPB like the ThT could be expanded into a broader conservation framework, imposing stronger protective measures in surface waters to more effectively protect Cetacea species in this region, aiding global efforts to protect some of the largest-bodied and most charismatic animals in the history of life on Earth.

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Appendix

Appendix 1. The global marine Cetacea species list utilized in this study. The species list was obtained from the IUCN redlist of species (IUCN, 2024). Species with recorded observations in the OPB region are indicated. Scientific Names are consistent with the World Cetacea Database (Fordyce and Perrin, 2025).

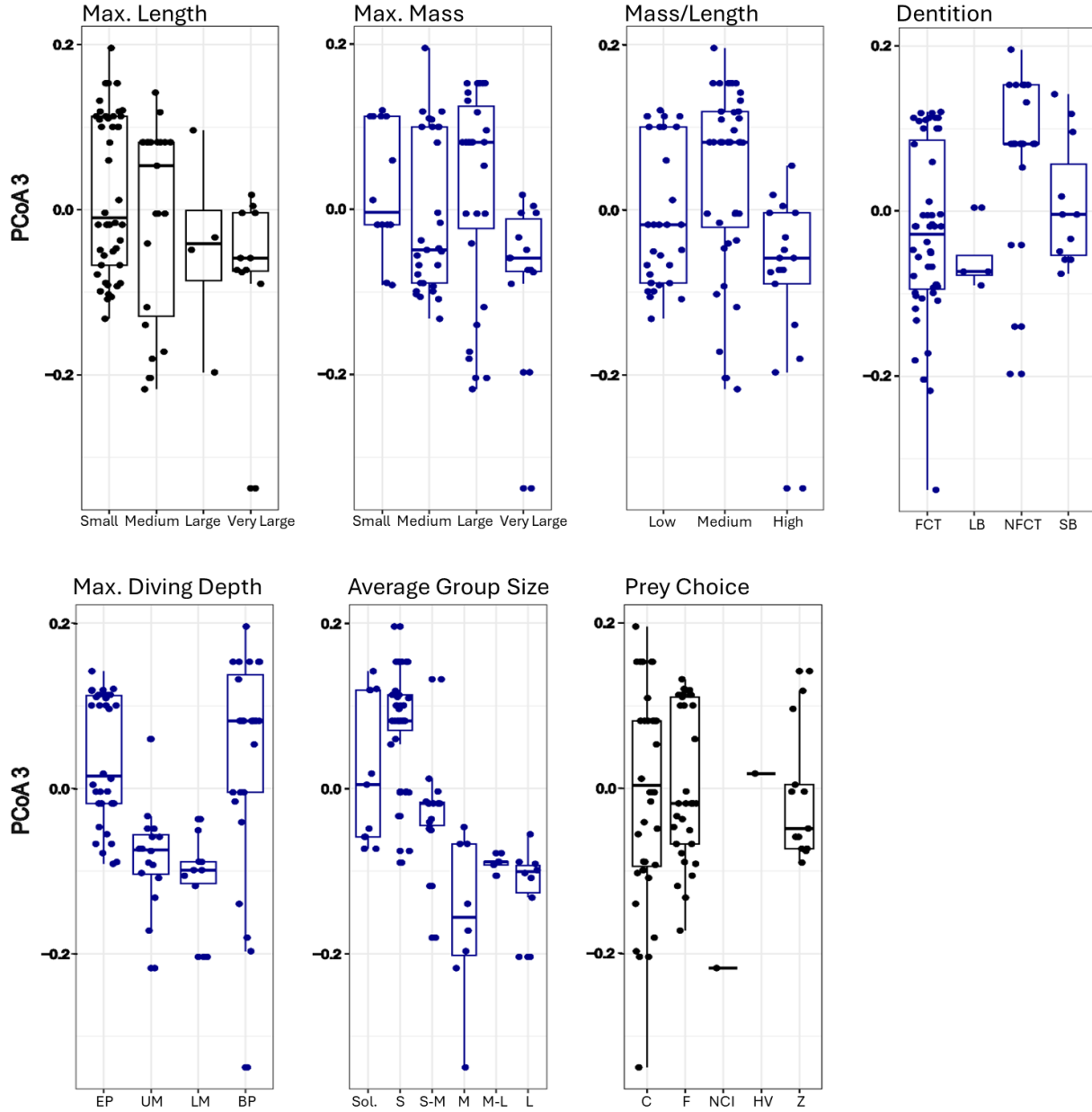
Family	Scientific Name	Common Name	OPB
BALAENIDAE	<i>Balaena mysticetus</i>	Bowhead Whale	No
BALAENOPTERIDAE	<i>Balaenoptera acutorostrata</i>	Common Minke Whale	Yes
BALAENOPTERIDAE	<i>Balaenoptera bonaerensis</i>	Antarctic Minke Whale	No
BALAENOPTERIDAE	<i>Balaenoptera borealis</i>	Sei Whale	Yes
BALAENOPTERIDAE	<i>Balaenoptera edeni</i>	Bryde's Whale	No
BALAENOPTERIDAE	<i>Balaenoptera musculus</i>	Blue Whale	Yes
BALAENOPTERIDAE	<i>Balaenoptera omurai</i>	Omura's Whale	No
BALAENOPTERIDAE	<i>Balaenoptera physalus</i>	Fin Whale	Yes
BALAENOPTERIDAE	<i>Balaenoptera ricei</i>	Rice's Whale	No
ZIPHIIDAE	<i>Berardius arnuxii</i>	Arnoux's Beaked Whale	No
ZIPHIIDAE	<i>Berardius bairdii</i>	Baird's Beaked Whale	Yes
ZIPHIIDAE	<i>Berardius minimus</i>	Sato's Beaked Whale	No
NEOBALAENIDAE	<i>Caperea marginata</i>	Pygmy Right Whale	No
DELPHINIDAE	<i>Cephalorhynchus commersonii</i>	Commerson's Dolphin	No
DELPHINIDAE	<i>Cephalorhynchus eutropia</i>	Chilean Dolphin	No
DELPHINIDAE	<i>Cephalorhynchus heavisidii</i>	Heaviside's Dolphin	No
DELPHINIDAE	<i>Cephalorhynchus hectori</i>	Hector's Dolphin	No
MONODONTIDAE	<i>Delphinapterus leucas</i>	Beluga	No
DELPHINIDAE	<i>Delphinus delphis</i>	Common Dolphin	Yes
ESCHRICHTIIDAE	<i>Eschrichtius robustus</i>	Gray Whale	Yes
BALAENIDAE	<i>Eubalaena australis</i>	Southern Right Whale	No
BALAENIDAE	<i>Eubalaena glacialis</i>	North Atlantic Right Whale	No
BALAENIDAE	<i>Eubalaena japonica</i>	North Pacific Right Whale	Yes
DELPHINIDAE	<i>Feresa attenuata</i>	Pygmy Killer Whale	No
DELPHINIDAE	<i>Globicephala macrorhynchus</i>	Short-finned Pilot Whale	Yes
DELPHINIDAE	<i>Globicephala melas</i>	Long-finned Pilot Whale	No
DELPHINIDAE	<i>Grampus griseus</i>	Risso's Dolphin	Yes
ZIPHIIDAE	<i>Hyperoodon ampullatus</i>	Northern Bottlenose Whale	No
ZIPHIIDAE	<i>Hyperoodon planifrons</i>	Southern Bottlenose Whale	No
ZIPHIIDAE	<i>Indopacetus pacificus</i>	Tropical Bottlenose Whale	No
KOGIIDAE	<i>Kogia breviceps</i>	Pygmy Sperm Whale	Yes
KOGIIDAE	<i>Kogia sima</i>	Dwarf Sperm Whale	Yes
DELPHINIDAE	<i>Lagenodelphis hosei</i>	Fraser's Dolphin	No
DELPHINIDAE	<i>Lagenorhynchus albirostris</i>	White-Beaked Dolphin	No
DELPHINIDAE	<i>Lagenorhynchus cruciger</i>	Hourglass Dolphin	No
DELPHINIDAE	<i>Lagenorhynchus obscurus</i>	Dusky Dolphin	No
DELPHINIDAE	<i>Leucopleurus acutus</i>	Atlantic White-Sided Dolphin	No

Family	Scientific Name	Common Name	OPB
DELPHINIDAE	<i>Lissodelphis borealis</i>	Northern Right Whale Dolphin	Yes
DELPHINIDAE	<i>Lissodelphis peronii</i>	Southern Right Whale Dolphin	No
BALAENOPTERIDAE	<i>Megaptera novaeangliae</i>	Humpback Whale	Yes
ZIPHIIDAE	<i>Mesoplodon bidens</i>	Sowerby's Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon bowdoini</i>	Andrews' Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon carlhubbsi</i>	Hubbs' Beaked Whale	Yes
ZIPHIIDAE	<i>Mesoplodon densirostris</i>	Blainville's Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon eueu</i>	Ramari's Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon europaeus</i>	Gervais's Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon ginkgodens</i>	Ginkgo-toothed Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon grayi</i>	Gray's Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon hectori</i>	Hector's Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon hotaula</i>	Deraniyagala's Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon layardii</i>	Strap-toothed Whale	No
ZIPHIIDAE	<i>Mesoplodon mirus</i>	True's beaked whale	No
ZIPHIIDAE	<i>Mesoplodon perrini</i>	Perrin's Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon peruvianus</i>	Pygmy Beaked Whale	No
ZIPHIIDAE	<i>Mesoplodon stejnegeri</i>	Stejneger's Beaked Whale	Yes
ZIPHIIDAE	<i>Mesoplodon traversii</i>	Spade-toothed Whale	No
MONODONTIDAE	<i>Monodon monoceros</i>	Narwhal	No
PHOCOENIDAE	<i>Neophocaena asiaeorientalis</i>	Narrow-ridged Finless Porpoise	No
PHOCOENIDAE	<i>Neophocaena phocaenoides</i>	Indo-Pacific Finless Porpoise	No
DELPHINIDAE	<i>Orcaella brevirostris</i>	Irrawaddy Dolphin	No
DELPHINIDAE	<i>Orcaella heinsohni</i>	Australian Snubfin Dolphin	No
DELPHINIDAE	<i>Orcinus orca</i>	Killer Whale	Yes
DELPHINIDAE	<i>Peponocephala electra</i>	Melon-headed Whale	No
PHOCOENIDAE	<i>Phocoena dioptrica</i>	Spectacled Porpoise	No
PHOCOENIDAE	<i>Phocoena phocoena</i>	Harbour Porpoise	Yes
PHOCOENIDAE	<i>Phocoena sinus</i>	Vaquita	No
PHOCOENIDAE	<i>Phocoena spinipinnis</i>	Burmeister's Porpoise	No
PHOCOENIDAE	<i>Phocoenoides dalli</i>	Dall's Porpoise	Yes
PHYSETERIDAE	<i>Physeter macrocephalus</i>	Sperm Whale	Yes
PONTOPORIIDAE	<i>Pontoporia blainvillei</i>	La Plata Dolphin	No
DELPHINIDAE	<i>Pseudorca crassidens</i>	False Killer Whale	Yes
DELPHINIDAE	<i>Sagmatias australis</i>	Peale's dolphin	No
DELPHINIDAE	<i>Sagmatias obliquidens</i>	Pacific White-sided Dolphin	Yes
DELPHINIDAE	<i>Sotalia guianensis</i>	Guiana Dolphin	No
DELPHINIDAE	<i>Sousa chinensis</i>	Indo-Pacific Humpbacked Dolphin	No
DELPHINIDAE	<i>Sousa plumbea</i>	Indian Ocean Humpback Dolphin	No
DELPHINIDAE	<i>Sousa sahalensis</i>	Australian Humpback Dolphin	No
DELPHINIDAE	<i>Sousa teuszii</i>	Atlantic Humpback Dolphin	No
DELPHINIDAE	<i>Stenella attenuata</i>	Pantropical Spotted Dolphin	No
DELPHINIDAE	<i>Stenella clymene</i>	Clymene Dolphin	No

Family	Scientific Name	Common Name	OPB
DELPHINIDAE	<i>Stenella coeruleoalba</i>	Spotted Dolphin	Yes
DELPHINIDAE	<i>Stenella frontalis</i>	Atlantic Spotted Dolphin	No
DELPHINIDAE	<i>Stenella longirostris</i>	Spinner Dolphin	No
DELPHINIDAE	<i>Steno bredanensis</i>	Rough-toothed Dolphin	No
ZIPHIIDAE	<i>Tasmacetus shepherdi</i>	Shepherd's Beaked Whale	No
DELPHINIDAE	<i>Tursiops aduncus</i>	Indo-Pacific Bottlenose Dolphin	No
DELPHINIDAE	<i>Tursiops truncatus</i>	Common Bottlenose Dolphin	Yes
ZIPHIIDAE	<i>Ziphius cavirostris</i>	Cuvier's Beaked Whale	Yes

Appendix 2. A table depicting the results of Kruskal-Wallis tests used to determine which traits had a significant influence on location of a species along the first three principal coordinate axes. This was accomplished using the “trait.faxes.cor” function in the “mFD” package in R.

Trait	PCoA Axis	H Statistic	p-value
Maximum Length (m)	PCoA 1	0.696	<0.0001
	PCoA 2	0.300	<0.0001
	PCoA 3	0.031	0.1335
Maximum Mass (kg)	PCoA 1	0.848	<0.0001
	PCoA 2	0.383	<0.0001
	PCoA 3	0.071	0.0303
Maximum Mass/Length Ratio (kg/m)	PCoA 1	0.810	<0.0001
	PCoA 2	0.214	<0.0001
	PCoA 3	0.133	0.0013
Dentition	PCoA 1	0.692	<0.0001
	PCoA 2	0.669	<0.0001
	PCoA 3	0.152	0.0013
Maximum Diving Depth	PCoA 1	0.359	<0.0001
	PCoA 2	0.681	<0.0001
	PCoA 3	0.365	<0.0001
Average Group Size	PCoA 1	0.243	0.0001
	PCoA 2	0.252	0.0001
	PCoA 3	0.589	<0.0001
Prey Choice	PCoA 1	0.640	<0.0001
	PCoA 2	0.820	<0.0001
	PCoA 3	-0.010	0.5243



Appendix 3. Boxplots depicting how each of the seven traits are distributed across PCoA 3. Traits highlighted in blue had a significant impact on the placement of species on PCoA 3, while traits highlighted in black showed no significant impact on species placement (see Appendix 2). Abbreviation are as follows: FCT=functional calcareous teeth; LB=long baleen; NFCT=non functional calcareous teeth; SB=short baleen; EP=epipelagic; UM=upper mesopelagic; LM=lower mesopelagic; BP=bathypelagic; Sol.=solitary; S=small; S-M=small-medium; M=medium; M-L=medium-large; L=large; C=cephalopods; F=fish; NCI=non-cephalopod invertebrates; HV=high vertebrates; Z=zooplankton.