Bathymetric segregation among demersal benthos and its contributions to the differences in the bycatches on bottom fisheries in the Emperor Seamounts area, Northwestern Pacific Ocean

メタデータ	言語: English
	出版者: Elsevier
	公開日: 2024-02-21
	キーワード:
	作成者: 大澤, 祐美子, 奥田, 武弘, 宮本, 麻衣
	メールアドレス:
	所属: 水産研究・教育機構, 水産研究・教育機構, 日本エヌ・ユー・エス株式会社
URL	https://fra.repo.nii.ac.jp/records/2000204

Regional Studies in Marine Science 68 (2023) 103261

Contents lists available at ScienceDirect

Regional Studies in Marine Science

journal homepage: www.elsevier.com/locate/rsma

Bathymetric segregation among demersal benthos and its contributions to the differences in the bycatches on bottom fisheries in the Emperor Seamounts area, Northwestern Pacific Ocean

Yumiko Osawa[a,*], Takehiro Okuda[a], Mai Miyamoto[b]

[a] *Highly Migratory Resources Division, Fisheries Stock Assessment Center, Fisheries Resources Institute, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Kanazawa, Yokohama, Kanagawa 236-8648, Japan*
[b] *JAPAN NUS Co., LTD., 7-5-25 Nishi-Shinjuku, Shinjuku, Tokyo 160-0023, Japan*

ARTICLE INFO

Keywords:
Vulnerable marine ecosystems
Cold-water corals
Observer data
Bycatches
Emperor Seamounts
Fishing gear

ABSTRACT

The need for the management of commercially targeted species and surrounding ecosystems has become more apparent in conjunction with the thriving commercial exploration of open seas. Despite the growing global interest in how fishing activity impacts seamount ecosystems, data regarding to the fishing impacts of gillnets on seamount ecosystems are scarce, and quantitative comparisons between trawls and gillnets are surprisingly limited. Our quantitative comparative studies using observer data collected at the southern Emperor Seamounts area revealed that the quantity and quality of bycatches of four key demersal benthos, denoted as Vulnerable marine ecosystem (VME) indicator taxa designated in the convention text of The North Pacific Fisheries Commission (three orders of dominant corals, Antipatharia, Scleractinia, and “Gorgonian” (Alcyonacea with solid axis), and Porifera), were not inherently different between the gear types, and operational tactics, such as depth or positions, might be prior factors largely affecting bycatches of benthic assemblages in the fishing activities carried out at Emperor Seamounts. Additionally, assessments of multiyear operational data revealed temporal shifts in the species composition of cold-water coral bycatches. Overall, the synthesis of bycatch occasions provided by scientific observers enabled us to reveal (1) the variations in bathymetric distributions and the contribution of local topographies toward demersal benthic organisms and (2) fishing operational features, such as operation positions and depth, which may strongly affect bycatches.

1. Introduction

Seamounts have attracted both commercial and research attention since the earliest ages of ocean exploration. As a consequence of their geographical and hydrological properties, seamounts induce unique local currents, which can enhance upwelling and support the flux of suspended food (Genin, 2004), leading this geographically ubiquitous landform to be one of the most enriched maritime ecosystems, harbouring large aggregations of benthopelagic fishes and flourishing benthic assemblages dominated by suspension feeders, such as corals and sponges (Clark, 1999; Genin et al., 1986; Wilson and Kaufmann, 1987; Pitcher et al., 2007).

Similar to shallow-water tropical coral reefs, some species of cold-water corals are known to form reefs and host distinct communities on seamounts (Rogers, 1999; Freiwald et al., 2002). Even in ahermatypic species, forests of black corals (Antipatharia), Alcyonacea, or sponges may contribute to the modification of habitat complexity and may serve as habitat, feeding grounds, or spawning/nursery grounds for surrounding organisms (Roberts, 2002; Roberts et al., 2006; Baillon et al., 2012). Thus, these benthic organisms are often categorised as ‘ecosystem engineers’ (Jones et al., 1994; Pitcher et al., 2007). In addition to their ecological importance, similar to other deep-sea species, which can inhabit seamounts or not, these benthic organisms generally have slow growth, long lifespans, and slow recovery from physical damage; therefore, cold-water corals and sponges have attracted attention as important indicator species of vulnerable marine ecosystems (VMEs) in most regional fisheries management organisations (RFMOs) (Roberts et al., 2009; Miyamoto et al., 2017).

Although several previous studies have indicated the relative distributional variations of cold-water corals and the importance of

---

* Corresponding author.
E-mail address: oosawa_yumiko93@fra.go.jp (Y. Osawa).

https://doi.org/10.1016/j.rsma.2023.103261
Received 10 May 2023; Received in revised form 18 October 2023; Accepted 23 October 2023

surrounding oceanographic/topobathymetric environments for the occurrence of these fauna (Pitcher et al., 2007), our basic knowledge of the ecology of demersal benthic biota is still scarce. Thus, the synthesis of the physical and biological patterns of seamounts is essential for future ecosystem-based management and conservation of seamounts (Pitcher et al., 2007). Ironically, because of their remoteness and oceanographic uniqueness with harsh hydrodynamic properties (Rogers, 1994), studies on demersal assemblages are often time and effort intensive.

Detailed commercial fisheries often be the informative sources to investigate the ecology of aquatic organisms. Large-scale commercial fishing, targeting benthopelagic fishes on the Emperor Seamount chain, located at 30–55°N and 168–178°E in the Northwestern Pacific Ocean (Fig. 1), began in the 1960s (Sasaki, 1986; Grigg, 1993; Kiyota et al., 2015). Today, the North Pacific armourhead and splendid alfonsino are the two main target species for the Japanese fishing fleets operating in these regions, and trawls and gillnets are the two main fishing gears utilised in the Emperor Seamounts area (Kiyota et al., 2015; SWG-NPA-SA, 2021). Physical impacts on the seamount habitat of bottom trawl, the principal contributor of the world's total catch in the high seas' fisheries, are intensively studied and well summarised in a number of papers (ex. Pitcher et al., 2007; Grieve et al., 2014; Ragnarsson et al., 2017). Gillnets are considered to cause significant impacts on VMEs at the time of hauls by entangling corals in the nets or can trap and kill marine organisms when the gear is lost (Pitcher et al., 2007; Ragnarsson et al., 2017), though the quantitative evaluation of the effects of gillnets on demersal benthos is insufficiently investigated and the data is scarce (Ragnarsson et al., 2017; Dias et al., 2020). The aim of this study was to reveal the potential effects of fishing operations and to investigate the distributional properties of demersal benthic species using data collected during fishing activities.

2. Methods

2.1. Study sites and fishing operations

This study was conducted based on data collected by onboard scientific observers who have taken the scientific observer programme to collect scientific data necessary to assess the impact of fisheries on marine species and VMEs (North Pacific Fisheries Commission, 2017). Japan started onboarding scientific observers on all fishing vessels and collecting operational data autonomously in 2009, five years prior to the establishment of The North Pacific Fisheries Commission (NPFC) and the enforcement of obligations for collecting operational data by scientific observers. Among all data provided by scientific observers onboard vessels of the Japanese commercial bottom fisheries (five of the bottom trawlers, Vessel A-E, and one of the gillnetters, Vessel F) operating in the southern Emperor Seamounts area, around the five seamounts around which both gears types were utilised by commercial fisheries (Northern Koko (36.5–37°N, 171.5°E, 840–1250 m deep); Koko (34.5–35°N, 171–172°E, 275–1070 m deep); Yuryaku (32.5°N, 172°E, 391–1225 m deep); Kammu (32°N, 172–173°E, 349–1300 m deep); and Colahan (31°N, 175–176°E, 822–1365 m deep) during the fishing seasons (January to October) from 2009 to 2020 were used in this study (Fig. 1). Detailed data regarding the catches of the commercially targeted species and details of the operations, such as the operational location where the nets were set/retrieved, depth of the gears operated using the net monitoring systems for the trawls, and echo sounders for the gillnets, were provided by scientific observers for each haul.

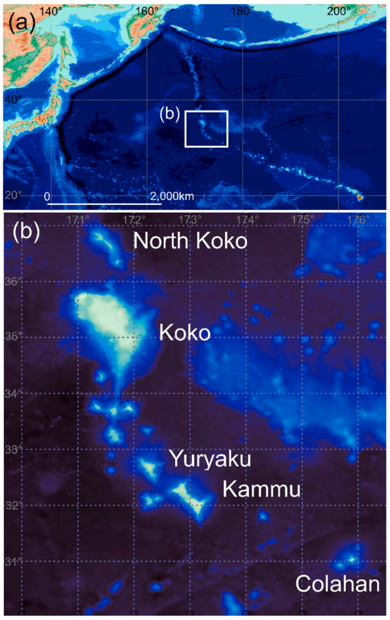

Fig. 1. (a) Map of the Northwestern Pacific Ocean representing the location of Emperor Seamounts chain. White rectangle represents the (b) seamounts of data used in this study.

In order to increase the sample size, we collated data across seasons. The depth of each operation was calculated as the average depth at the location where the net was set and retrieved. The distance of fishing operations was estimated from the longitude and latitude of the fishing gears by directly connecting the points of start/end of hauls. For gillnets, although their operational distance is logically restricted by the length of one net (c. 30 m) and the number of net panel sets per haul (56 net panel sets), their position can be affected as a result of drifting due to by waves or current flows. Thus, in this study, the operational distance of the gillnet was calculated based on its start and end positions. Data with unreliably elongated fishing operations (>6000 m and >25,000 m in gillnets and trawls, respectively) or those outside the seamount range were removed from the analyses to ensure data reliability. Operational tactics may vary not only among vessels but also from year to year to optimise the cost-benefit ratios of fishing behaviours (Janc et al., 2021). Thus, temporal effects were verified in further analysis by accessing data separately both before and after the establishment of the NPFC (in total, 9017 operations from 2009 to 2014, and 9069 operations from 2015 to 2020). R package "FactoMineR" was used to conduct Principal Component Analysis (PCA) for the investigation of fishing operational variations among vessels and between the two different fishing periods by incorporating three numeric variables (depth, longitude and latitude) and three categorical factors (gear type, seamount, and fishing period) as the key parameters for characterising fishing operations.

2.2. Target species and data analysis

In the case of fishing operations that caught any unwanted organisms (bycatches), all bycatch of cold-water corals and sponges were preserved in the freezer on board. After the catches were landed, samples were immediately sent to and preserved at the laboratory of the Highly Migratory Resources Division, Yokohama Field Station, Fisheries Resources Institute, Japan Fisheries Research and Education Agency. In most cases, all specimens were identified to the lowest possible taxon, namely species, genus, or family for cold-water corals. Owing to the limited identification knowledge on demersal Porifera, taxonomic resolution for these specimens was limited to the phylum level.

In this study, we were mainly focused on the bycatches of four taxonomic groups, including three orders of corals (Antipatharia, Scleractinia, and "Gorgonian", Alcyonacea excluding soft coral) and Porifera that are designated as "VME indicator taxa" in the convention text of NPFC. In this study, we separately categorised Alcyonacea with solid axis, terming them "Gorgonians", because of their unique morphological/ontogenetic characteristics compared to other Alcyonacea (soft corals) and following the fact that these suborders are still treated as separate VME indicator taxa by many fishery management bodies. Other Alcyonacea, another VME indicator taxon assigned in the NPFC convention text, were excluded from the detailed analyses because of the limited number of bycatch samples (n < 10).

Mean individual weight was calculated using following equation:

$$mean\ individual\ weight\ of\ sp.A = \frac{total\ catch\ weight\ of\ sp.A\ per\ hual\ (g)}{no.\ of\ individuals}$$

The length of each specimen was measured as a rule of thumb. The total weights and sizes of the individuals were compared among the vessels. Differences in the species composition of cold-water corals were compared between the early (2009–2014) and later (2015–2020) fishing periods based on the proportional occurrences of each family. If any statistically significant variations were observed in taxonomic compositions among the different fishing periods, Simpson's diversity index was calculated for further analysis. The Kolmogorov–Smirnov test, Kruskal–Wallis rank sum test, Fisher's exact test for count data, and Wilcoxon test were conducted for statistical comparisons using respective packages (e.g. '*ggplot2*' (Wickham, 2016) and '*ggpubr*' (Alboukadel, 2020)) of R ver. 4.1.1 (RStudio Team, 2020; R Core Team, 2021).

3. Results

3.1. Occurrence of benthos bycatches and fishing operational trends in Emperor Seamounts area

Among 18,920 total hauls, the proportion of hauls catching bycatches was 7.02% (1328 hauls) and 2.47% (468 hauls) in trawls and gillnets, respectively. Gorgonian was the most abundant bycatch (approximately 60% of all operations with bycatches). Antipatharia was the next-most abundant, making up 16.8% of the proportional occurrence. The proportion of Porifera and Scleractinia were 4.4% and 2.6%, respectively. Alcyonacea (excluding "Gorgonian") was the least abundant species, with 0.3% of the total bycatch.

Principal Components Analysis (PCA) indicated differences in the operational trends of each vessel (Fig. 2a). PCA showed that 95.45% of the information was presented by two axes (PC1 and PC2 accounted for 76.89% and 18.56% of the total variance, respectively). PC1 was mainly correlated with latitude (eigenvalue: 0.958), longitude (-0.834) and average depth (0.833) (Table 1). Two groups were observed with respect to gear type: vessels A-E and vessel F with trawls and gillnets, respectively. Trawlers were correlated with a higher longitude, while gillnetters were correlated with higher latitude and greater depth (Fig. 3a).

The fishing operations varied between the early and later fishing periods (Figs. 2b-c, 3b-c). The positions of each circle shifted slightly toward the positive side of PC1 from the fishing periods of 2009–2014–2015–2020 (Table 1), suggesting shifts in fishing operations toward higher latitudes and deeper depths during the latter fishing period. The degree of the shifts in operational depth was greater in the gillnetter (mean±SD: 618.85 ± 217.71 m and 826.98 ± 216.77 m in early and latter fishing seasons, respectively) than in the trawlers (mean ±SD: 387.94 ± 119.74 m and 402.13 ± 95.32 m in early and latter fishing seasons, respectively).

3.2. Depth relation of bycatches

Operational depth was strongly related to bycatch occurrence (Kruskal–Wallis rank sum test, KS $\chi^2 = 134.97$, df = 4, $p < 0.001$ for gillnets, and KS $\chi^2 = 75.97$, df = 4, $p < 0.01$ for trawls). Gillnet hauls with bycatches of Antipatharia, Gorgonian, and Scleractinia showed a significantly greater operational depth than hauls with no bycatch (Fig. 4). Although the median depth of the operation that caught Porifera was greater than that of non-bycatches, the difference was not significant. Similar tendencies were observed in trawls, except for Antipatharia and Scleractinia. The operational depth of the gillnets caught with Antipatharia was not significantly different, and those caught with Scleractinia were significantly shallower than those without bycatches.

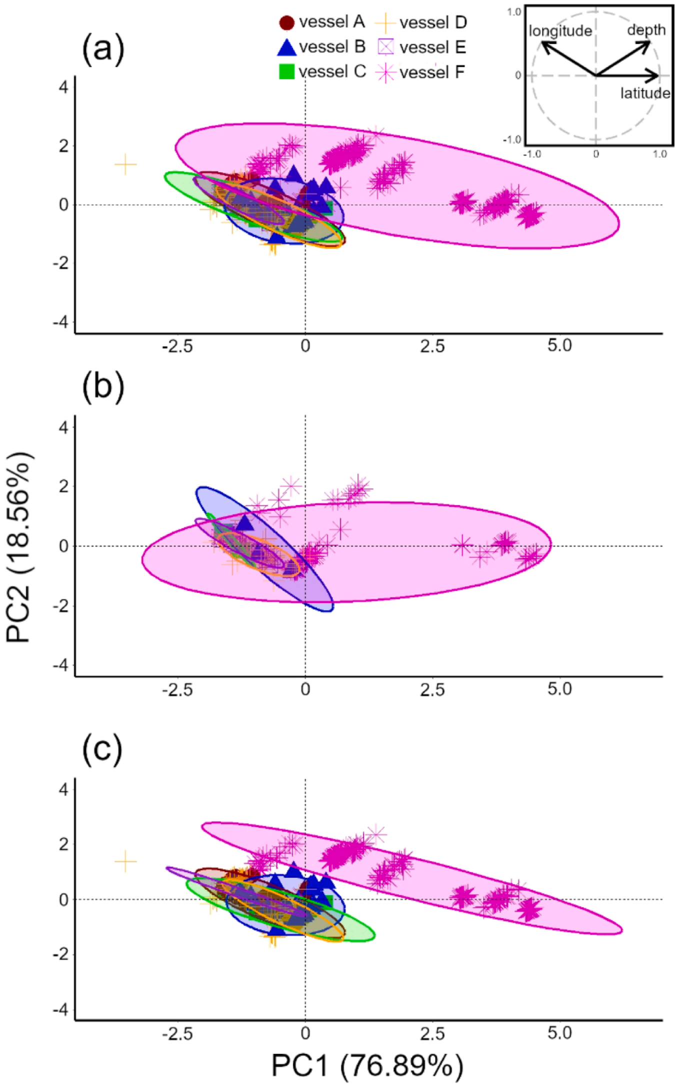

Fig. 2. PCA plots of (a) all fishing vessels with respective environmental factors with indicative arrow directions, (b) fishing vessels operated between 2009 and 2014, and (c) vessels operated between 2015 and 2020.

Overall, gillnets tended to mark higher values of total catch weights and individual sizes of bycatches than trawls, however, they highly varied among vessels (especially in Antipatharia and Gorgonian, Figs. 5, A.1). Individual height was also largely varied within trawlers. Porifera tended to exhibit occurrence/heavier catch weight in trawlers, however, this was not a statistically significant trend. In addition to the occurrence of bycatch, the total weight and individual size of bycatches also interacted with depth (Fig. 6). For instance, the weight and size of the Gorgonian and Scleractinia were positively correlated with depth. Interestingly, for Gorgonian, the variation in individual weights was greater in gillnets; nonetheless, the variation in individual heights was greater in trawls. In addition to Gorgonians and Scleractinia, Antipatharia showed a negative trend with depth. Although no clear trends were observed for Porifera, the catch appeared to be concentrated at a certain depth between 400 and 600 m.

3.3. Temporal shift of bycatch compositions

Differences in the bycatch family composition were observed between the fishing gear groups (Fig. 7). In Gorgonian, Acanthogorgiidae

Table 1
Summary of PCA analyses of all fishing operations.

Eigenvectors				
Variable		**PC1**	**PC2**	**PC3**
Longitude		-0.834	0.527	0.165
Latitude		0.958	-0.001	0.287
Average depth (m)		0.833	0.528	-0.164
Supplementary categories				
Variable		**PC1**	**PC2**	**PC3**
Gears	Gillnet	1.66	0.554	-0.087
	Trawl	-0.671	-0.224	0.035
Seamounts	Jingu	1.645	1.009	-0.067
	Koko	-0.511	-0.011	-0.044
	Nintoku	3.098	0.086	0.025
	Suiko	4.407	-0.367	0.813
	Youmei	3.828	0.02	0.139
Fishing periods	2009–2014	-0.219	-0.081	0.065
	2015–2020	0.064	0.024	-0.019
Eigenvalues				
PC		**Eigenvalues**	**% Variation**	**Cumulative % of variation**
1		2.307	76.887	76.887
2		0.557	18.559	95.446
3		0.137	4.554	100

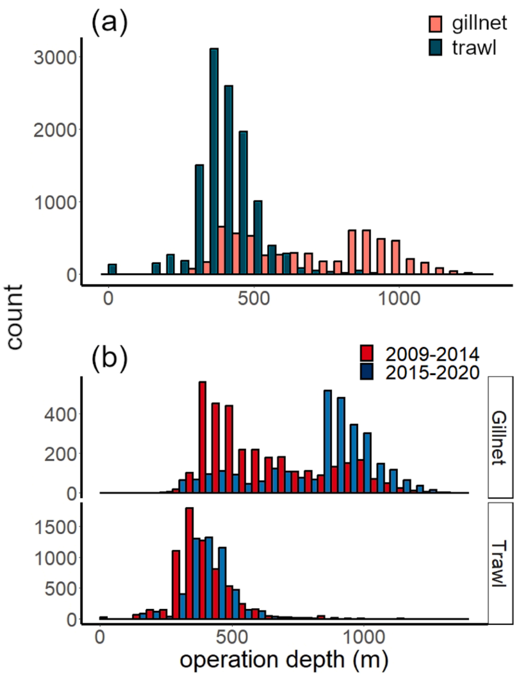

Fig. 3. Histograms of average depth of operations of (a) gillnet (orange) and trawl (dark blue) in whole fishing seasons and (b) in different fishing periods (red and dark blue represent the pre- and post-2015 fishing periods, respectively).

and Plexauridae were dominant in the trawls, whereas Anthothelidae, Chrysogorgiidae, Coralliidae, and Paragorgiidae were dominant in the gillnets. The proportions of Isididae and Primnoidae were similar between the two fishing gear types. Schizopathidae and Antipathidae are the Antipatharian families that characterise the bycatches of gillnets and trawls, respectively.

The proportional composition of the Gorgonian family was significantly different between the two fishing periods in both gear types (Fisher's exact test for count data with simulated *p*-value: $p < 0.01$ for both trawls and gillnets). Simpson's diversity index of the Gorgonian decreased in the later periods for both types of fishing gears (0.682–0.577, and 0.691–0.554, in gillnets and trawls, respectively). Primnoidae, Paragorgiidae, Isididae, Plexauridae, and Coralliidae exhibited conspicuous differences (> 0.05) in proportional occurrences: the former two families increased their proportions in gillnets, whereas Isididae in trawls and Plexauridae and Coralliidae in gillnets decreased their proportional occurrence in the 2015–2020 fishing period.

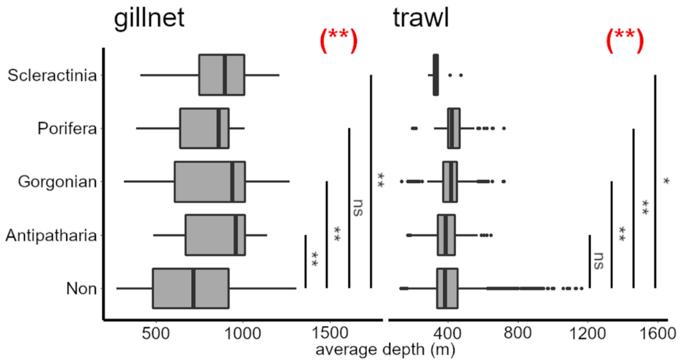

Fig. 4. Boxplots of average depth in gillnets and trawls without/with respective bycatches (Antipatharia, Gorgonian, Porifera, Scleractinia). Boxes show the 75%, median, and 25% interval and upper and lower whiskers show the greatest and least values excluding outliers. Outliers, black circle over or below the whiskers, were plotted if the values were less than 1.5 times the upper and lower quartiles. Statistical differences with Kruskal–Wallis rank sum test are represented in red symbols in parenthesis (** - $p < 0.01$; * - $p < 0.05$; ns no significant difference), and post-hoc comparisons (Holm adjusted pairwise comparisons using t-tests with pooled SD) between the values without/with bycatches are represented above boxes (** - $p < 0.01$; * - $p < 0.05$; ns no significant difference).

The proportional composition of Antipatharia was significantly different between the two fishing periods (Fisher's exact test for count data with a simulated *p*-value of $p < 0.05$). Although Antipatharian corals caught by gillnets showed proportional shifts, we did not observe any significant differences (Fisher's exact test for count data with a simulated *p*-value *p* of 0.85). The diversity index in trawls increased slightly in the later fishing seasons (0.698–0.726 in the early and later fishing periods, respectively). Among the five families of Antipatharia, Schizopathidae and Leiopathidae were the two families whose proportional occurrence notably differed between the early and later fishing years. Compositional comparisons of Scleractinian bycatches were unreliable between fishing gear and periods because the bycatch incident was limited to gillnets (and we could not observe a significant difference in the gillnets between early and later fishing periods).

4. Discussion

4.1. *Contributions of fishing tactics toward benthos bycatches*

The need for the management of commercially targeted species and surrounding ecosystems has recently become more apparent, revealing how fishing activities may impact seamount ecosystems as one of the urgent aims of worldwide investigation. However, our knowledges about fishing effects on demersal ecosystems are leaning toward trawls, and the data on gillnet physical impacts on demersal ecosystems is particularly scarce. The synthesis of instances of bycatch using fishing operational data enabled us to reveal the bathymetric distributional ranges of demersal benthic species and their susceptibility to different fishing gear operated on the Emperor Seamounts. Note that the usage of scientific observer data and its interpretations require caution as they might inherently possess some biases (e.g. unvicious asymmetric data collection due to the behavioural adaptations by fishing vessels to avoid additional bycatch, damage to gears, or to change operational tactics to

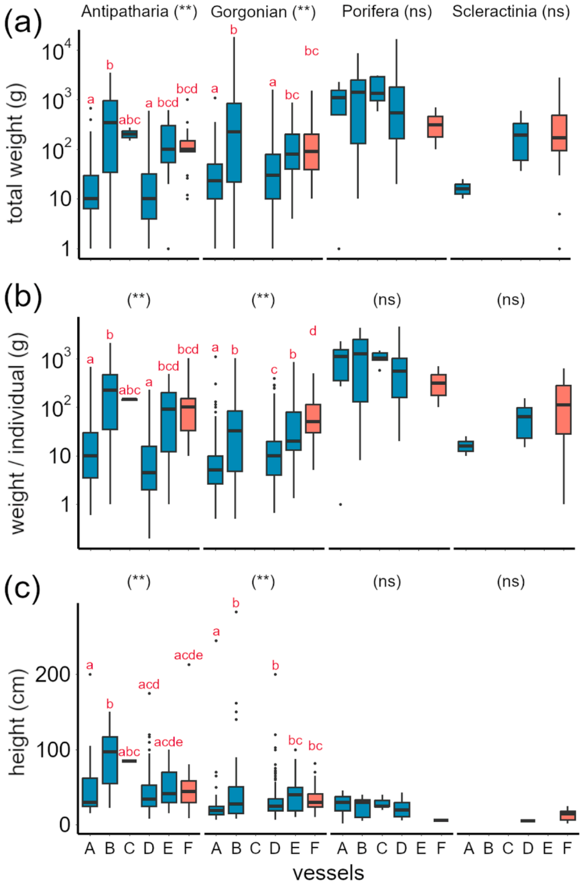

Fig. 5. Boxplots of (a) total catch weight, (b) individual weights and (c) individual height of bycatches (Antipatharia, Gorgonian, Porifera, Scleractinia) per vessel (trawls in blue and gillnet with orange). Boxes show the 75%, median and 25% interval and upper and lower whiskers show the greatest and least values excluding outliers. Outliers, black circle over or below the whiskers, were plotted if the values were less than 1.5 times the upper and lower quartiles. Symbols in parenthesis are the results of statistical analysis using Kruskal–Wallis rank sum test (** - $p < 0.01$; * - $p < 0.05$; ns - no significant difference), and the results of the post-hoc comparisons (Holm adjusted pairwise comparisons using t-tests with pooled SD) are shown above boxes in red alphabets (a–e).

focus on different target species; Akimoto personal communication). Nevertheless, it could be a valuable data resource detailing how existing fishing operations interact with the surrounding environments, especially for the cases where data are chronically scarce, and the chance of the investigations is limited, such as in seamount ecosystems in high-sea areas.

Bottom trawls and gillnets are the main fishing gears utilised by fishing vessels operating in the Emperor Seamounts area. Generally, owing to the different characteristics of fishing gears, the operations of vessels using different gear types are mostly spatially segregated within and among seamounts (Fisheries Agency of Japan, 2008a, 2008b, 2022). Trawls mainly target the flat summits of seamounts, pulling the gear by fleets to chase and obtain the fish. Gillnets, on the other hand, are suitable for operation at the slopes of seamounts or gaps between summits by laying nets across (Fisheries Agency of Japan, 2008a, 2008b, 2022). Regarding the spatial segregation of fishing vessels, our PCA analysis indicated that the operational tactics of vessels using the two fishing gears were slightly different: trawlers mainly operated in shallower areas at higher longitudes and gillnetters were set at deeper areas at relatively higher latitudes. Despite these substantial differences, our study revealed that the bycatch trends are highly variable among vessels, even within vessels using the same fishing gear. Moreover, our results suggest that operational depth is the predominant factor affecting demersal benthic bycatch trends. This may indicate that variations in fishing tactics, particularly the positions/fishing depth, are the major factors affecting the occurrence of benthic bycatches, rather than the features of the gears per se. Our results exhibited a higher variance in bycatch among vessels using trawls; nevertheless, PCA analysis could not clearly differentiate the operational tactics of vessels using trawls. These results suggest that the distribution of the demersal benthic taxa was highly patchy, and that local-scale environmental differences may have contributed to their distributions, rather than regional-scale differences.

Operations at the slopes/edges of a summit with gillnets might have contributed to the higher tendencies of bycatches (Fig. A.1) because these topographies tend to be suitable for most demersal suspension feeders, such as Gorgonian and/or Scleractinia, due to the upwelling of nutrient-rich seawater from the deep stratum, removing sediment on the seamount surface and providing suitable hard substrates, and contributing to the dispersal of offspring (Genin et al., 1986; Rogers, 1994, 1999; Matsumoto, 2005; Pitcher et al., 2007; Baco et al., 2017; Sigler et al., 2023). Depth is alternative good indicator of the distribution of demersal benthos, as the depth strongly interact with pressures, temperatures, food availability (e.g. the depth of the deep scattering layers of plankton migrating), or chemical composition like the depth of the aragonite saturation horizon (ASH) (Pitcher et al., 2007; Williams, 2011; Miyamoto et al., 2017).

Indeed, our study also indicate the contribution of water depth to coral distribution and individual sizes, but this is inconsistent with previous reports on some coral taxa. For example, the catch weight and individual size of Scleractinian corals tend to increase with increasing water depth. Interestingly, the majority of the specimens of Scleractinia in our study were captured using gillnets, indicating that the Scleractinia caught in this study originated from the slopes and edges of the summit. According to Thresher et al. (2011) and Cohen and Holcomb (2009), a larger food supply by upwelling could be one of the possibilities for Scleractinia to distribute under ASH depths by neutralising the negative effect of the increased energy requirement for the growth of stony corals under lower aragonite saturation levels. Perhaps, the reason why Scleractinian bycatch is concentrated in slopes is simply because its distribution may be concentrated on the hard substrate with lower sediment coverage. Although a higher food supply from upwelling or/and the presence of suitable hard substrate in the slopes could be a possible reason for the presence of stony corals below the ASH depth, it may not fully explain why the individual size of stony corals positively interacted with water depth. Historical anthropogenic activities may be another factor contributing to the current distribution of corals in the present day, however, limited knowledge precludes full discussion of this point.

Antipatharia, which are expected to occupy a wider bathymetric distribution capacity similar to that of the Gorgonian (Ribes et al., 2003; Etnoyer and Morgan, 2005; Pitcher et al., 2007; Baco et al., 2017; Miyamoto et al., 2017) were conspicuous as bycatches by trawls, and their catch weight and individual sizes exhibited a negative relationship with water depth. According to Yesson et al. (2017), the contribution of warm temperatures might be one of the reasons why our Antipatharian samples were more concentrated in shallower water depths. Indeliberate sampling bias (e.g. substantially limited incidental catch of flexible and relatively simple structured cold-water corals in gillnets) could be an alternative to the bycatch concentrations of Antipatharia in trawls.

Contributions of surrounding environmental factors (such as silicic acidity) and/or the sampling bias of fishing gear might be expected even in the greater bycatch tendencies of Poriferans by trawls (though its catches were not significantly different among vessels; Fig. 5; Santín et al., 2019; Chu et al., 2019). Further investigations of bathymetric geochemistry or physical conditions around the North Pacific Ocean may be essential to reveal the details of the distribution of demersal benthos.

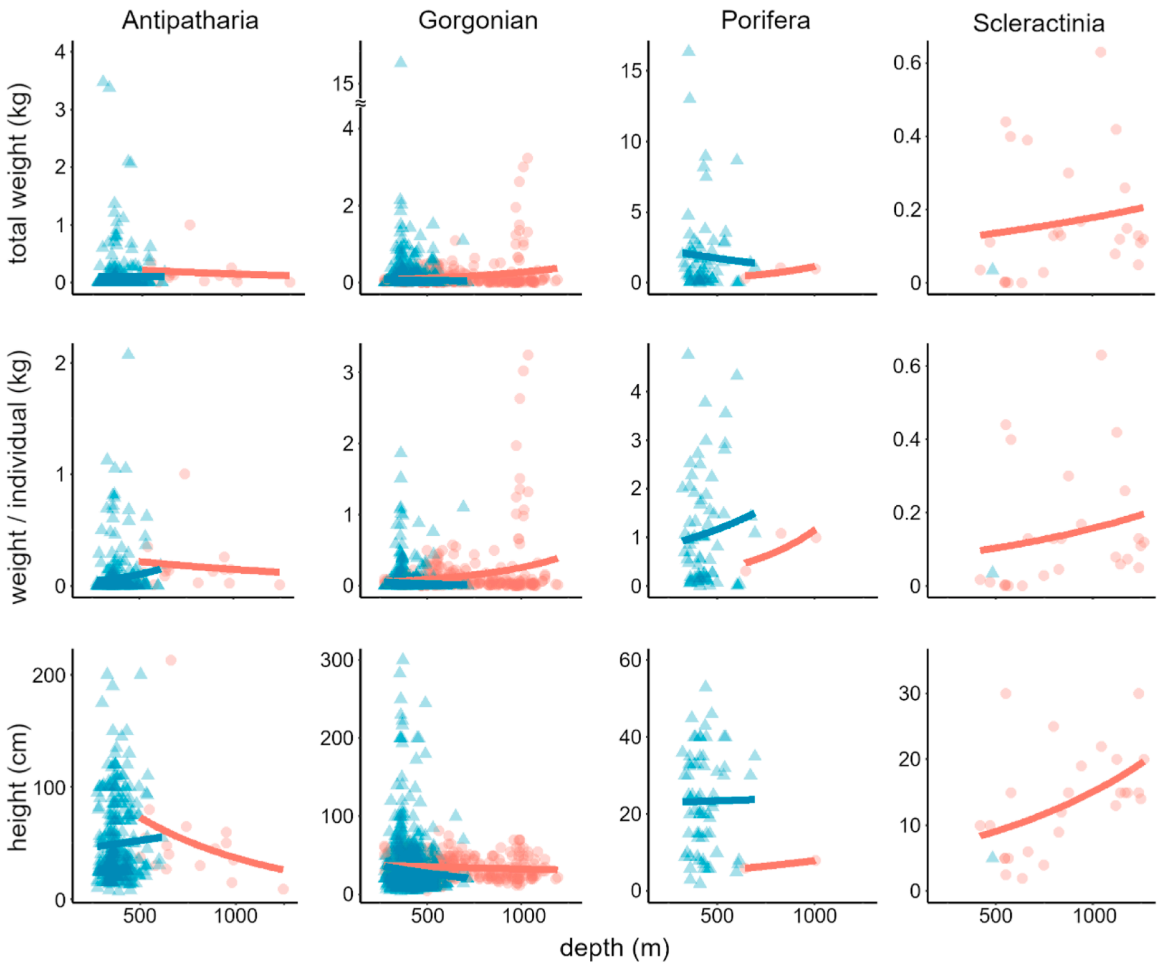

Fig. 6. Scatter plots of total weights (first row), individual weights (second row), and individual height (third row) with the collected depth of each bycatch taxa. Blue lines with triangles and orange lines with circles represent the results in trawls and gillnets, respectively.

4.2. *Morphological variations of Gorgonian*

Although the interactions between the distributions and bathymetric ranges of the Gorgonian, one of the major benthic taxa structuring Emperor Seamount ecosystems (Miyamoto et al., 2017), have often been reported in previous studies (Ribes et al., 2003; Etnoyer and Morgan, 2005; Pitcher et al., 2007; Baco et al., 2017), their morphological trends remain underreported on till date. As many terrestrial/oceanic sedentary organisms can often express wide morphological plasticity against physical environmental disturbances (such as wind disturbance for the trees or hydrodynamic forces for corals, Brüchert and Gardiner, 2006; McArthur et al., 2010; Thomas et al., 2015; Chindapol et al., 2013; Zawada et al., 2019; Sanna and Freiwald, 2021), the variations in individual weight and height in the Gorgonians observed in our study may imply morphological variations in samples collected under different hydrodynamic conditions. For instance, Gorgonians collected using gillnets are expected to originate from subhabitats facing stronger hydrodynamic forces induced by upwelling (such as the slopes of seamounts), which may contribute to the shortening or thickening of arborescent organisms (Brüchert and Gardiner, 2006; Thomas et al., 2015; Zawada et al., 2019). In contrast, tall and sparse branching patterns observed in trawl samples might be more suitable for coping with food scarcity on shallower flat platforms that experience relatively weaker water disturbances (Thiem et al., 2006; Sanna and Freiwald, 2021). Although historical anthropogenic activities could be the alternative possibility of catching short and thick individuals by gillnet due to the higher vulnerability of tall arborescent corals to the encounter fishing lines (De la Torriente Diez et al., 2022), it cannot explain the tendencies of tall-individual-bycatches by trawls. Hence, the contribution of the hydrological phenomena toward coral population toward bycatch tendencies might be more plausible explanation in our study. A detailed study of the morphological variations in Gorgonians under different hydrodynamic environments would be helpful in investigating the causal mechanisms of variations in individual height and weight in cold-water corals.

4.3. *Temporal variations of bycatches and future concerns*

Our study, using multiyear operational data, revealed that the operational features shifted between early and later fishing periods toward deeper and higher latitudes. Consequently, the species composition of coral bycatches differed significantly between the two fishing periods. As the majority of cold-water corals in Emperor Seamounts are dominant at a depth of < 800 m (Miyamoto et al., 2017), the decreased species diversity of Gorgonian bycatches in the later fishing period might be reasonable. Compared with Gorgonians, the degree of shift in the diversity index of Antipatharian bycatches was marginal (+0.028 by trawls operated from 2009 to 2014–2015–2020). As the degree of the shift observed in the operational depth of trawls was relatively smaller than that seen in gillnets (although statistically significant different; Fig. 3), the shift in trawl depth was negligible for shallow-intermediate-dominant Antipatharia to exhibit conspicuous compositional differences.

According to previous studies (Matsumoto, 2005; Miyamoto et al.,

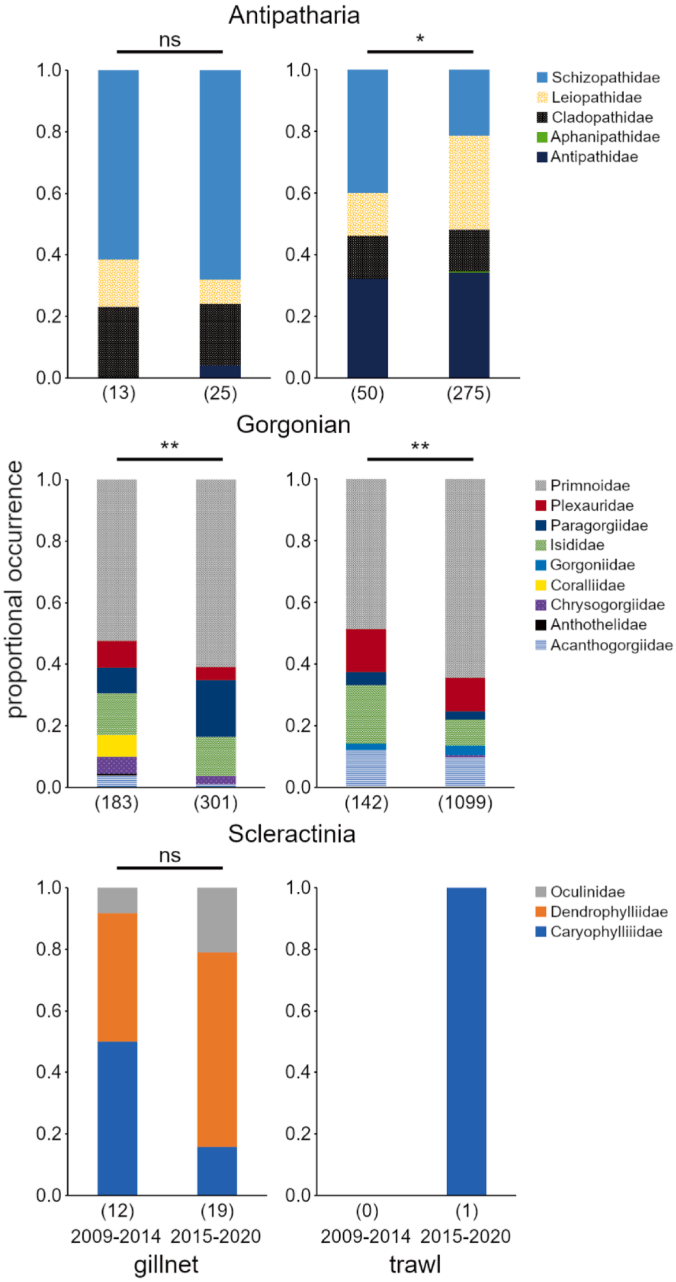

Fig. 7. Differences in the proportional occurrence of Antipatharian, Gorgonian, and Scleractinian families collected in 2009–2014 (left) and 2015–2020 (right) by gillnets and trawls. Statistical differences in proportional compositions between two fishing periods are shown above bars (** - $p < 0.01$; * - $p < 0.05$; ns - no significant difference with Fisher's exact test for count data).

2017), the temporal shift of operational depth in fishing vessels might be the major effect of temporal compositional variations in Gorgonian bycatches, such as the catches of Acanthogorgiidae, Gorgoniidae, and Plexauridae by trawls or Coralliidae by gillnets. This may indicate that their distributions were concentrated mainly around the depth of the trawls/gillnets operated in the early fishing period. Other deep-dominant species such as Paragorgiidae and Chrysogorgiidae were predominantly caught using gillnets or during later fishing periods. Overall, the proportional shifts in the Gorgonian among different fishing gears and fishing periods might be interpreted as the segregation of suitable distribution depths among families.

The reason for the remarkable proportional shifts in Antipatharian species is not yet clear, as their trends are inconsistent with bathymetric distributions. Shifts in operational positions might be one of the possible causes of the changes in species composition. For example, morphological differences between Schizopathidae and Leiopathidae may contribute to differences in feeding efficiency (Frederiksen et al., 1992; Sanna and Freiwald, 2021). If flow conditions vary along latitudes and longitudes, shifts in operational positions can cause variations in species composition. Detailed environmental studies might help investigate the differences in the species distributions of cold-water corals.

Cold-water corals are often in the limelight as symbolic species of VMEs, and the requirements for their urgent protection and management are being declared in most RFMOs (Roberts et al., 2009; Miyamoto et al., 2017). Although spatial closures are often introduced as one of the most powerful tools for ecosystem-based management in fisheries (Pitcher et al., 2007; Baco et al., 2020; Pons et al., 2022), enforcement of such management measures may require particular caution, because the limitation of fishing fields may forcibly remove fishermen and redistribute the fishing effort to areas outside of the closure areas, which can augment the risks of capturing other vulnerable species or leading to the destruction of other intact fragile marine ecosystems (Baum et al., 2003; Lewison et al., 2004; Abbott and Hayne, 2012).

It is worth noting that none of the operations of the Japanese fleets have reached the threshold values for coral (North Pacific Fisheries Commission, 2021) and sponge (North Pacific Fisheries Commission, 2023) bycatches stated in the NPFC till date. Furthermore, actual fishing grounds are limited to certain parts of each seamount, and past research has not revealed the existence of serious adverse impacts of fishing activities on VMEs and marine species along the Emperor Seamounts (Fisheries Agency of Japan, 2008a, 2008b). As our present study showed the different bycatch trends between two fishing gears, implementation of gear specific conservation measures, such as gear specific encounter threshold, might be valuable to ensure the precautionary conservation and management of VMEs in this region.

However, limitation of our knowledge regarding to demersal ecosystems impedes the evaluation of comprehensive fishing impacts (DOSI, 2022). Furthermore, consideration of other ecosystem components, such as the impacts toward pelagic organisms including the target species, is often left behind at the time of risk assessments (DOSI, 2022). Like in the cases that incorporating fishing efforts in the model of estimating bycatch spatial patterns (Sims et al., 2008), investigations of the ecological aspects of the splendid alfonsino or Pacific armourhead, two of the main commercially important species caught at the Emperor Seamounts, might be a meaningful step forward for ecosystem and resource management around the Emperor Seamounts. As several previous studies have indicated that the individual size of splendid alfonsino varies among different water depths (Seki and Tagami, 1986; Lehodey et al., 1994; Santamaría et al., 2006; Akimoto et al., 2010; Shotton, 2016), its interactions with fishing gear, operational trends, and surrounding environments might be required to provide an overview of ecosystem-fishing interactions in the Northwestern Pacific Ocean. Continuous enforcement of precautionary conservation and management considering comprehensive ecological assessment, including both targeting/non-target organisms, might be effective in achieving the coexistence of long-term conservation and sustainable use of fishery resources and the protection of marine ecosystems.

5. Conclusion

Our study contributes to the sustainability of demersal VMEs in Northwestern Pacific Ocean by comparing the bycatch trends among commercial fleets using different fishing gears, trawls and gillnets, and revealed that (1) the distributions of demersal benthic organisms (including VME indicators) and their individual sizes seem to vary among bathymetric ranges and local topographies, and (2) operational features, such as geographic positions and depth, may strongly affect the bycatches of demersal benthos rather than the features of the gears per se. Further investigations of demersal ecosystems and comprehensive risk assessments, considering both target/non-target organisms, will be worthwhile tasks for the sustainable fishery in high seas and the protection of demersal ecosystems.

CRediT authorship contribution statement

Yumiko Osawa: Conceptualization, Methodology, Data curation, Investigation, Formal analysis, Statistical analysis, Writing – original draft. **Mai Miyamoto:** Data curation, Writing – review & editing. **Takehiro Okuda:** Project administration, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

Acknowledgements

We thank all fishery observers who collected valuable data and samples as part of the Program of Scientific Observer of The North Pacific Fisheries Commission (NPFC). We also thank Dr. T. Ichi, Dr. K. Sawada in the Japan Fisheries Research and Education Agency, Mr. N. Akimoto from Japan Overseas Fishing Association, and Mr. T. Fukuda and Mrs. S. Takeda from the Fishery Agency of Japan for their valuable comments, suggestions, and support.

Appendix

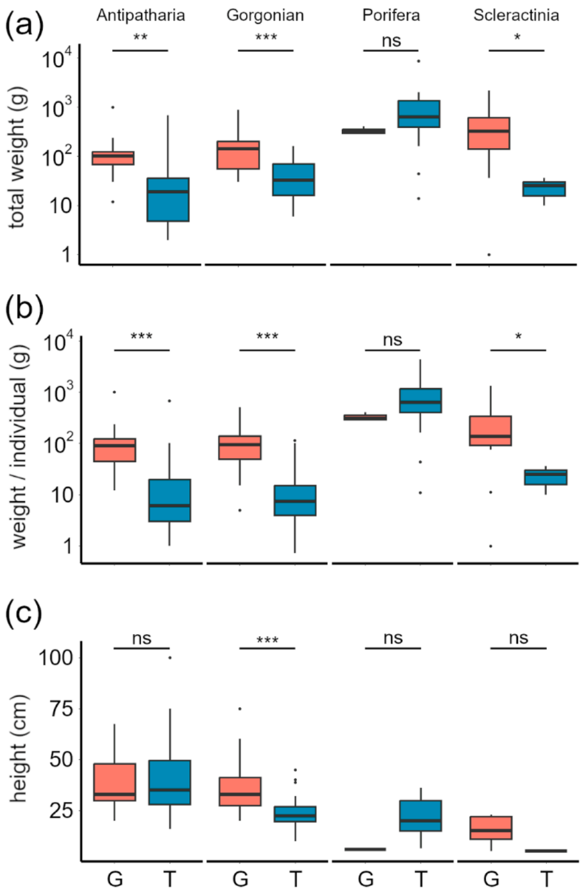

Fig. A1. Boxplots of (a) total catch weight, (b) individual weights, and (c) individual height of bycatches (Antipatharia, Gorgonian, Porifera, Scleractinia) per fishing gears (gillnet and trawls with orange and blue, respectively) within the same global grids (30″×30″ grid). Boxes show the 75%, median, and 25% interval, and upper and lower whiskers show the greatest and least values excluding outliers. Outliers, black circles over or below the whiskers, were plotted if the values were less than 1.5 times the upper and lower quartiles. ** - $p < 0.01$; *- $p < 0.05$; ns, no significant differences with Wilcox test.

References

Abbott, J.K., Hayne, A.C., 2012. What are we protecting? Fisher behavior and the unintended consequences of spatial closures as a fishery management tool. Ecol. Appl. 22, 762–777. https://doi.org/10.1890/11-1319.1.

Akimoto, S., Kotake, A., Arai, T., 2010. Movements and lifehistory patterns of the alfonsino *Beryx splendens* collected around Japan, as inferred by otolith Sr:Ca Ratios (Japanese with English absract). Bull. Kanagawa Prefect. Fish. Technol. Cent. 4, 1–8.

Alboukadel, K., 2020. ggpubr: 'ggplot2' Based Publication Ready Plots. R Package Version 0.4.0. ⟨https://CRAN.R-project.org/package=ggpubr⟩.

Baco, A.R., Morgan, N., Roark, E.B., Silva, M., Shamberger, K.E.F., Miller, K., 2017. Defying dissolution: discovery of deep-sea Scleractinian coral reefs in the North Pacific. Sci. Rep. 7 (5436), 1–11. https://doi.org/10.1038/s41598-017-05492-w.

Baco, A.R., Morgan, N.B., Roark, E.B., 2020. Observations of vulnerable marine ecosystems and significant adverse impacts on high seas seamounts of the northwestern Hawaiian Ridge and Emperor Seamount Chain. Mar. Policy 115 (103834), 1–13. https://doi.org/10.1016/j.marpol.2020.103834.

Baillon, S., Hamel, J., Wareham, V.E., Mercier, A., 2012. Deep cold-water corals as nurseries for fish larvae. Front. Ecol. Environ. 10, 351–356. https://doi.org/10.1890/120022.

Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., Doherty, P.A., 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science 299, 389–392. ⟨https://www.science.org/doi/full/10.1126/science.1079777⟩.

Brüchert, F., Gardiner, B., 2006. The effect of wind exposure on the tree aerial architecture and biomechanics of Sitka spruce (*Picea stichensis*, Pinaceae). Am. J. Bot. 93, 1512–1521. https://doi.org/10.3732/ajb.93.10.1512.

Chindapol, N., Kaandorp, J.A., Cronemberger, C., Mass, T., Genin, A., 2013. Modelling growth and form of the Scleractinian coral *Pocillopora verrucose* and the influence of hydrodynamics. PLOS Comput. Biol. 9 (e1002849), 1–15. https://doi.org/10.1371/journal.pcbi.1002849.

Chu, J.W.F., Nephin, J., Georgia, S., Knudby, A., Rooper, C., Gale, K.S.P., 2019. Modelling the environmental niche space and distributions of cold-water corals and sponges in the Canadian northeast Pacific Ocean. Deep-Sea Res. Plan I Oceanogr. Res. Pap. 151 (103063), 1–15. https://doi.org/10.1016/j.dsr.2019.06.009.

Clark, M., 1999. Fisheries for orange roughy (*Hoplostethus atlanticus*) on seamounts in New Zealand. Oceanol. Acta 22, 593–602. https://doi.org/10.1016/S0399-1784(00)88950-1.

Cohen, A.L., Holcomb, M., 2009. Why corals care about ocean acidification: uncovering the mechanism. Oceanography 22, 118–127. https://doi.org/10.5670/oceanog.2009.102.

De la Torriente Diez, A., González-Irusta, J.M., Serrano, A., Aguilar, R., Sánchez, F., Blanco, M., Punzón, A., 2022. Spatial assessment of benthic habitats vulnerability to bottom fishing in a Mediterranean seamount. Mar. Policy 135, 104850. https://doi.org/10.1016/j.marpol.2021.104850.

Dias, V., Oliveira, F., Boavida, J., Serrão, E., A., Gonçalves, J.M.S., Coelho, M.A.G., 2020. High coral bycatch in bottom-set gillnet coastal fisheries reveals rich coral habitats in Southern Portugal. Front. Mar. Sci. 7, 603438 https://doi.org/10.3389/fmars.2020.603438.

DOSI, 2022. A Review of Impact Assessments for Deep-Sea Fisheries on the High Seas against the FAO Deep-Sea Fisheries Guidelines. Deep Ocean Stewardship Initiative Report. ⟨https://www.dosi-project.org/fisheries-review-2022/⟩.

Etnoyer, P., Morgan, L.E., 2005. Habitat-forming deep-sea corals in the Northeast Pacific Ocean. In: Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin/Heidelberg, pp. 331–343.

Fisheries Agency of Japan, 2022. Splendid alfonsino *Beryx splendens* (in Japanese). Present Status Int. Fish. Resour. 77, 1–8.

Fisheries Agency of Japan, 2008a. Report on Identification of Vulnerable Marine Ecosystems in the Emperor Seamount and Northern Hawaiian Ridge in the Northwest Pacific Ocean and Assessment of Impacts Caused by Bottom Fishing Activities on Such Vulnerable Marine Ecosystems Or Marine Species as Well as Conservation and Management Measures to Prevent Significant Adverse Impacts (Bottom Gillnet).

Fisheries Agency of Japan, 2008b. Report on Identification of Vulnerable Marine Ecosystems in the Emperor Seamount and Northern Hawaiian Ridge in the Northwest Pacific Ocean and Assessment of Impacts Caused by Bottom Fishing Activities on Such Vulnerable Marine Ecosystems Or Marine Species as Well as Conservation and Management Measures to Prevent Significant Adverse Impacts (Bottom Trawl).

Frederiksen, R., Jensen, A., Westerberg, H., 1992. The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. Sarsia 77, 157–171. https://doi.org/10.1080/00364827.1992.10413502.

Freiwald, A., Hühnerbach, V., Lindberg, B., Wilson, J.B., Campbell, J., 2002. The Sula Reef Complex, Norwegian shelf. Facies 47, 179–200. https://doi.org/10.1007/BF02667712.

Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. J. Mar. Syst. 50, 3–20. https://doi.org/10.1016/j.jmarsys.2003.10.008.

Genin, A., Dayton, P.K., Lonsdale, P.F., Spiess, F.N., 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. Nature 322, 59–61. https://doi.org/10.1038/322059a0.

Grieve, C., Brady, D.C., Polet, H., 2014. Review of habitat dependent impacts of mobile and static fishing gears that interact with the sea bed. Mar. Steward. Counc. Sci. Ser. 2, 18–88.

Grigg, R.W., 1993. Precious coral fisheries of Hawaii and the U. S. Pacific Islands. Mar. Fish. Rev. 55, 50–60.

Janc, A., Guinet, C., Pinaud, D., Richard, G., Monestiez, P., Tixier, P., 2021. Fishing behaviours and fisher effect in decision-making process when facing depredation by marine predators. Fish. Manag. Ecol. 28, 528–541. https://doi.org/10.1111/fme.12503.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386. https://doi.org/10.2307/3545850.

Kiyota, M., Nishida, K., Murakami, C., Yonezaki, S., 2015. History, biology, and conservation of Pacific endemics 2. The North Pacific armorhead, *Pentaceros wheeleri* (Hardy, 1983) (Perciformes, Pentacerotidae). Pac. Sci. 70, 1–20. https://doi.org/10.2984/70.1.1.

Lehodey, P., Marchal, P., Grandperrin, R., 1994. Modelling the distribution of alfonsino, *Beryx splendens*, over the seamounts of New Caledonia. Fish. Bull. 92, 748–759.

Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of fisheries bycatch on marine megafauna. Trends Ecol. Evol. 19, 598–604. https://doi.org/10.1016/j.tree.2004.09.004.

Matsumoto, A.K., 2005. Recent observations on the distribution of deep-sea coral communities on the Shiribeshi Seamount, Sea of Japan. In: Freiwald, A., Roberts, J. M. (Eds.), Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin/Heidelberg, pp. 345–356. https://doi.org/10.1007/3-540-27673-4_17.

McArthur, C., Bradshaw, O.S., Jordan, G.J., Clissold, F.J., Pile, A.J., 2010. Wind affects morphology, function, and chemistry of eucalypt tree seedlings. Int. J. Plant Sci. 171, 73–80. https://doi.org/10.1086/647917.

Miyamoto, M., Kiyota, M., Hayashibara, T., Nonaka, M., Imahara, Y., Tachikawa, H., 2017. Megafaunal composition of cold-water corals and other deep-sea benthos in the southern Emperor Seamounts area, North Pacific Ocean. Galaxea J. Coral Reef. Stud. 19, 19–30. https://doi.org/10.3755/galaxea.19.1_19.

North Pacific Fisheries Commission, 2017. Conservation on the Conservation and Management of High Seas Fisheries Resources in the North Pacific Ocean. ⟨https://www.npfc.int/system/files/2017-01/Convention%20Text.pdf⟩.

North Pacific Fisheries Commission, 2021. Conservation and Management Measure for Bottom Fisheries and Protection of Vulnerable Marine Ecosystems in the Northwestern Pacific Ocean. NPFC-CMM 2021-05.

North Pacific Fisheries Commission, 2023. Seventh Meeting. Meeting Report. NPFC-2023-COM07-Final Report. p. XX.

Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S., 2007. Seamounts: Ecology, Fisheries & Conservation. Blackwell Publishing, p. 526.

Pons, M., Watson, J.T., Ovando, D., Andraka, S., Brodie, S., Domingo, A., Fitchett, M., Forselledo, R., Hall, M., Hazen, E.L., Jannot, J.E., Herrera, M., Jiménez, S., Kaplan, D.M., Kerwath, S., Lopez, J., McVeigh, J., Pacheco, L., Rendon, L., Richerson, K., Sant'Ana, R., Sharma, R., Smith, J.A., Somers, K., Hilborn, R., 2022. Trade-offs between bycatch and target catches in static versus dynamic fishery closures. PNAS 119 (e2114508119), 1–11. https://doi.org/10.1073/pnas.2114508119.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org/⟩.

Ragnarsson, S.Á., Burgos, J.M., Kutti, T., van den Beld, I., Egilsdóttir, H., Arnaud-Haond, S., Grehan, A., 2017. In: Rossi, S., Bramanti, L., Gori, A., Orejas, C. (Eds.), The impact of anthropogenic activity on cold-water corals. Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots, pp. 989–1023. https://doi.org/10.1007/978-3-319-17001-5_27-1.

Ribes, M., Coma, R., Rossi, S., 2003. Natural feeding of the temperate asymbiotic octocoral-gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia). Mar. Ecol. Prog. Ser. 254, 141–150. https://doi.org/10.3354/meps254141.

Roberts, C.M., 2002. Deep impact: the rising tool of fishing in the deep sea. Trends Ecol. Evol. 17, 242–245. https://doi.org/10.1016/S0169-5347(02)02492-8.

Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312, 543–547. https://doi.org/10.1126/science.1119861.

Roberts, J.M., Davies, A.J., Henry, L.A., Dodds, L.A., Duineveld, C.A., Lavaleye, M.S.S., Maier, C., van Soest, R.W.M., Bergman, M.J.N., Hühnerbach, V., Huvenne, V.A.I., Sinclair, D.J., Watmough, T., Long, D., Green, S.L., van Haren, H., 2009. Mingulay reef complex: an interdisciplinary study of cold-water coral habitat, hydrography and biodiversity. Mar. Ecol. Prog. Ser. 397, 139–151. https://doi.org/10.3354/meps08112.

Rogers, A.D., 1994. The biology of seamounts. Adv. Mar. Biol. 30, 305–350. https://doi.org/10.1016/S0065-2881(08)60065-6.

Rogers, A.D., 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. Int. Rev. Hydrobiol. 84, 315–406. https://doi.org/10.1002/iroh.199900032.

RStudio Team, 2020. RStudio: Integrated Development Environment for R. RStudio, Inc, Boston, MA, URL ⟨http://www.rstudio.com/⟩.

Sanna, G., Freiwald, A., 2021. Deciphering the composite morphological diversity of *Lophelia pertusa*, a cosmopolitan deep-water ecosystem engineer. Ecosphere 12 (e03802), 1–13. https://doi.org/10.1002/ecs2.3802.

Santamaría, M.T.G., Abellán, L.J.L., González, J.F., 2006. Growth of alfonsino *Beryx splendens* Lowe 1834 in the South-West Indian Ocean. Afr. J. Mar. Sci. 28, 33–40. https://doi.org/10.2989/18142320609504131.

Santín, A., Grinyó, J., Ambroso, S., Uriz, M.J., Dominguez-Carrió, C., Gili, J.M., 2019. Distribution patterns and demographic trends of demosponges at the Menorca Channel (northwestern Mediterranean Sea). Prog. Oceanogr. 173, 9–25. https://doi.org/10.1016/j.pocean.2019.02.002.

Sasaki, T., 1986. Development and present status of Japanese trawl fisheries in the vicinity of seamounts. In: Uchida, R.N., Hayasi, S., Boehlert, G.W. (Eds.), The Environment and Researches of Seamounts in the North Pacific. Proceedings of the Workshop on the Environment and Resources of Seamounts in the North Pacific, 43. NOAA Technical Report NMFS, pp. 21–30.

Seki, M., Tagami, D.T., 1986. Review and present status of handline and bottom longline fisheries for alfonsin. In: Uchida, R.N., Hayasi, S., Boehlert, G.W. (Eds.), The Environment and Researches of Seamounts in the North Pacific. Proceedings of the Workshop on the Environment and Resources of Seamounts in the North Pacific, 43. NOAA Technical Report NMFS, pp. 31–33.

Shotton, R., 2016. Global Review of Alfonsino (Beryx spp.), Their Fisheries, Biology and Management. FAO Fisheries and Aquaculture Circular, (C1084), I.

Sigler, M.F., Rooper, C.N., Goddard, P., Wilborn, R., Williams, K., 2023. Alaska deep-sea coral and sponge assemblages are well-defined and mostly predictable from local environmental conditions. Mar. Ecol. Prog. Ser. 712, 67–85. https://doi.org/10.3354/meps14317.

Sims, M., Cox, T., Lewison, R., 2008. Modeling spatial patterns in fisheries bycatch: improving bycatch maps to aid fisheries management. Ecol. Appl. 18, 649–661. https://doi.org/10.1890/07-0685.1.

SWG-NPA-SA, 2021. Species Summary of Splendid alfonsino (Beryx splendens) in the Emperor Seamounts. NPFC-2021-SSC BF-ME02-WP07, p. 9.

Thiem, Ø., Ravagnan, E., Fosså, J.H., Berntsen, J., 2006. Food supply mechanisms for cold-water corals along a continental shelf edge. J. Mar. Syst. 60, 207–219. https://doi.org/10.1016/j.jmarsys.2005.12.004.

Thomas, S.C., Martin, A.R., Mycroft, E.E., 2015. Tropical trees in a wind-exposed island ecosystem: height- diameter allometry and size at onset of maturity. J. Ecol. 103, 594–605. https://doi.org/10.1111/1365-2745.12378.

Thresher, R.E., Tilbrook, B., Fallon, S., Wilson, N.C., Adkins, J., 2011. Effects of chronic low carbonate saturation levels on the distribution, growth and skeletal chemistry of deep-sea corals and other seamount megabenthos. Mar. Ecol. Prog. Ser. 442, 87–99. https://doi.org/10.3354/meps09400.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Williams, A., 2011. Bottom Fishery Impact Assessment Australian Report for the South Pacific Regional. Positions, 1:3.

Wilson, R.R., Kaufmann, R.S., 1987. Seamount biota and biogeography. In: Keating, B.H., Fryer, P., Batiza, R., Boehlert, G.W. (Eds.), Seamounts, Islands and Atolls. Geophysical Monographs, 43, pp. 355–377. https://doi.org/10.1029/GM043p0355.

Yesson, C., Bedford, F., Rogers, A.D., Taylor, M.L., 2017. The global distribution of deep-water Antipatharia habitat. Deep-Sea Res. II Top. Stud. Oceanogr. 145, 79–86. https://doi.org/10.1016/j.dsr2.2015.12.004.

Zawada, K.J.A., Madin, J., Baird, A.H., Bridge, T.C.L., Dornelas, M., 2019. Morphological traits can track coral reef responses to the Anthropocene. Funct. Ecol. 33, 962–975. https://doi.org/10.1111/1365-2435.13358.