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Bottom-contact fisheries disturbance and signs of recovery of precious corals in the Northwestern Hawaiian Islands and Emperor Seamount Chain

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ABSTRACT

Deep-sea precious corals in the octocoral family Coralliidae are among the dominant benthic megafauna at depths of 300–600 m on seamounts of the Northwestern Hawaiian Islands and lower Emperor Seamount Chain. *Pleurocorallium secundum* and *Hemicorallium laauense* were once abundant enough on these seamounts to support a targeted coral fishery in the 1960s and 1970s. Significant trawl finfish fisheries were also occurring in the same time frame on the same seamounts. Because they had high enough abundance to support a targeted fishery for two decades, these two coralliid species must have been a key component of the baseline community on these seamounts. Therefore, they provide an ideal indicator species for testing effects of large-scale disturbance and potential for recovery in deep-sea coral and seamount communities. Using AUVs and submersibles, we explored seamounts outside the US EEZ that are still actively fished by trawl, seamounts within the US EEZ that were historically trawled but have been protected since the establishment of the EEZ, and seamounts that have never been trawled, to determine population distributions and colony sizes for the targeted coral species. *P. secundum* had only one individual on actively trawled seamounts and occurred in low abundance on most Recovering seamounts. *H. laauense* was present in a few areas in Recovering and Still Trawled seamounts. Colony size distributions for *H. laauense* showed a smaller median size on Recovering and Still Trawled seamounts compared to the Never Trawled sites. *P. secundum* had a slightly smaller median colony size on the Recovering Seamounts than on the Never Trawled seamounts. These results indicate a reduction in abundance for both species in disturbed areas with some unexpected potential for recovery on protected seamounts. Recovery was uneven among sites and species with SE Hancock and Koko showing the largest populations of *H. laauense* among the Recovering and Still Trawled seamounts, respectively. *P. secundum* showed much less recovery, with its largest population on Bank 11 in the Recovering seamounts. Kammu, one of the primary seamounts of the coral fishery, had only a single coralliid observed. The other primary target, Yuryaku, had a small number of coralliids in a steeply sloped area. These two Still Trawled seamounts do not appear to be able to recover under the current levels of fishing pressure.

1. Introduction

Resilience is the capacity of an ecosystem to return to its original state after disturbance (Holling, 1973). As a key topic in management, resilience, and the related concept of recovery, are rooted in ecology, providing insights into ecosystem function, connectivity, and succession. In the marine realm, most resilience studies have focused on shallow-water marine ecosystems (e.g. Estes and Duggins, 1995; Hughes et al., 2005; Obura, 2005). As the deep sea is becoming increasingly impacted by anthropogenic activities (e.g. Ramirez-Llodra et al., 2011), a better understanding of resilience and related ecological processes is becoming time-critical. Previous work in the deep sea has focused largely on disturbance in soft-sediments, primarily relating to small-scale disturbance and patch dynamics (e.g. Dayton and Hessler, 1972; Grassle et al., 1990; Glover et al., 2010). Hard-substrate habitats and large-scale disturbances have received substantially less effort (e.g. Lissner et al., 1991; Mullineaux et al., 2010; Williams et al., 2010).

Large-scale disturbances can be challenging to create experimentally, and studies generally rely on natural events such as hurricanes or tsunamis (e.g. Tilmant et al., 1994; Busing et al., 2009). In the deep-sea,

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natural disturbance is much harder to detect or to monitor. Instead, anthropogenic disturbances may be used to gain insights into natural responses and the recovery rates of a given ecosystem (e.g. Lissner et al., 1991; Thiel et al., 2005). Ironically, one of the most destructive human impacts to the deep-sea seafloor, trawling, can create a disturbance experiment that can provide insights into resilience and recovery for deep-sea hard-substrate communities. Trawling has been likened to forest clear-cutting (Watling and Norse, 1998) because trawling removes the structure-forming benthic megafauna along with the habitat they provide. Areas where trawling has occurred may be used to study recovery rates and also whether communities recover to the same state, or move to an alternate state (*sensu* Lotze et al, 2011) after large-scale disturbance (e.g. Schratzberger et al., 2002; Althaus et al., 2009; Williams et al., 2010).

The scale of trawling effort on seamounts places trawling into the large-scale disturbance category. The ability and time scales of seamount benthic communities to recover from disturbance are not well constrained. The sessile nature of the adults of the key habitat-forming species suggests larval dynamics will play the primary role in recovery. The biology of the structure forming organisms, which are generally deep-sea corals, may further exacerbate the low resilience of seamount communities. Early work on recruitment in deep-sea corals showed that recruitment of coral larvae is sporadic or limiting for deep-sea species (Grigg, 1988; Krieger, 2001). Recent work has shown the larvae of some species may be selective of substrate type (Sun et al., 2010). Deep-sea corals are also long lived, living for 100′s to 1000′s of years and are generally very slow growing, on the order of millimeters per year (Andrews et al., 2005; Roark et al., 2006, 2009; Sun et al., 2010). All these factors indicate that seamount coral communities are likely to have low resilience and long recovery times.

This low resilience of coral communities may be further compounded on seamounts by the potential isolation of seamount features. The key isolating factors for seamounts are geographic distance to seafloor of the same depth, along with specialized flow features such as Taylor columns (reviewed by Rogers, 1994) or tidally rectified flows (Mullineaux and Mills, 1997), which may retain larvae over the seamount. Some evidence supports the idea of seamount isolation, including high levels of faunal endemicity (e.g. Parin et al., 1997; Richer de Forges et al., 2000). Although every seamount may not be isolated (e.g. Samadi et al., 2006; McClain et al., 2009), building on the predictions from Lissner et al., (1991) for recovery in large scale disturbances, we would anticipate that seamounts that are isolated would have lower resilience and slow recovery rates, with recruitment primarily from either remnant populations that escaped the disturbance or from rare, long-distance colonizers. On the other hand, seamounts that are not isolated would have larvae available from outside sources, potentially leading to faster recovery rates and greater resilience.

There has been little opportunity to address these predictions or to test the paradigm that seamount coral communities have slow recovery rates, as most seamounts occur in the high seas, where fishing activity is ongoing, so there are few "protected" or "after trawling" locations to test, and records of trawling history for most locations are also limited. The primary opportunity to test these ideas has been on nearshore seamounts in recently established seamount Marine Protected Areas of Australia and New Zealand. Studies at these locations have shown little recovery after 5–15 years (Althaus et al., 2009; Williams et al., 2010; Clark et al., 2019), supporting the idea of low ecosystem resilience for seamount coral communities.

The Hawaiian Archipelago and adjacent international waters of the far Northwestern Hawaiian Islands (NWHI) and lower Emperor Seamount Chain (ESC) provide an opportunity to gain further and more long-term insights into the recovery potential of seamount communities from large-scale disturbance. Seamounts in these chains from Bank 8 to at least Koko Seamount were heavily fished at depths of 300–600 m in the 1960s-1980s for pelagic armourhead (*Pseudopentaceros wheeleri*) and for splendid alfonsino (*Beryx splendens)* (reviewed in Clark et al., 2007; NOAA Fisheries Report, 2008). In the same region, depth range, and time frame, 50–70 % of the annual global catch of precious corals, in the octocoral family Coralliidae, which have been part of a profitable jewelry fishery, came from the NWHI and ESC (reviewed in Grigg, 2002). Thus, between these two fisheries, these seamounts have had the largest amount of fish and invertebrate biomass removed of any documented seamount fishery in the world (as quantified in Clark et al., 2007).

For a subset of the fished seamounts, there is a known time for cessation of trawling. With the establishment of the US EEZ in 1977, trawl fishing became prohibited in the portion of the NWHI within the EEZ (Hancock Seamounts to Bank 8; Fig. 1) with some trawling still permitted to foreign vessels on the Hancock Seamounts until 1986 (NOAA Fisheries Report, 2008). Fishing has continued for both Armourhead and Alfonsino species at seamounts in the target area outside the EEZ (northwest of the Hancock seamounts) but at reduced effort and substantially lower catch rate (e.g. NPFC, 2022).

This history allows for a well-structured sampling design to test for seamount recovery from trawling impacts. Within the region of interest are seamounts that fall into three "treatment" types - features that have *never been trawled* (southeast of Bank 8; "Never Trawled"), seamounts that were *trawled but have now been protected* for 28–37 years (Bank 8 to the Hancock Seamounts; "Recovering") and seamounts that are *still trawled* (northwest of Hancock Seamounts and into the ESC; "Still Trawled") (Fig. 1).

Initial surveys of this region using the AUV Sentry indicated some potential for recovery on the disturbed seamounts, with observations of remnant populations, corals regrowing from fragments, and a higher abundance of corals and other benthic megafauna on recovering seamounts compared to still trawled seamounts (Baco et al., 2019). However, the coarse taxonomic resolution possible with AUV images prevented an assessment of whether the communities were recovering to the same or an alternate state.

To determine whether a community has returned to its original state after disturbance requires some knowledge of the baseline community. Because of the remote location of the trawled areas in the NWHI and ESC, and because the trawling started in the 1960s, there are no data on the pre-disturbance communities at these sites. However, it can be inferred that there was a high abundance of precious corals in the targeted areas because there was a fishery specifically for these species. The targeted species in the octocoral Family Coralliidae were the Pink Coral *Pleurocorallium secundum* and the Red Coral *Hemicorallium laauense*. In addition to the fishery records, previous work in this depth range across a broad portion of the NWHI has shown that these species are community dominants in hard substrate areas of seamounts throughout the NWHI at depths of ~ 350–700 m (e.g. Parrish and Baco, 2007; Baco, 2007). Recent habitat-suitability modeling studies also confirm high habitat suitability for scleraxonian octocorals (the suborder that includes the Coralliidae) in this region (Yesson et al., 2012). Thus, it can be inferred that coralliids will be an important element of the recovering community if it is recovering to its original state. These two species can therefore be used as indicator species of recovery and resilience of seamount communities from large-scale disturbance.

The goal of this study was to better assess recovery and resilience of deep-sea coral communities on seamounts, using *H. laauense* and *P. secundum* as indicator species, across a series of locations in the far NWHI and ESC. The overarching hypothesis tested, based on the prediction of low resilience and decadal recovery times, was that deep-sea precious coral beds in the NWHI have not recovered despite the end of trawling 30+ years ago. To address this hypothesis, comparisons of the abundance of coralliids were made among disturbed and undisturbed seamounts, using the "Never Trawled", "Recovering" and "Still Trawled" seamounts as the three treatment types. Additionally, if any recovery has occurred on the disturbed seamounts, then it would be expected that the new recruits to the disturbed seamounts would be of smaller size classes. Therefore, comparisons were also made of colony sizes among the

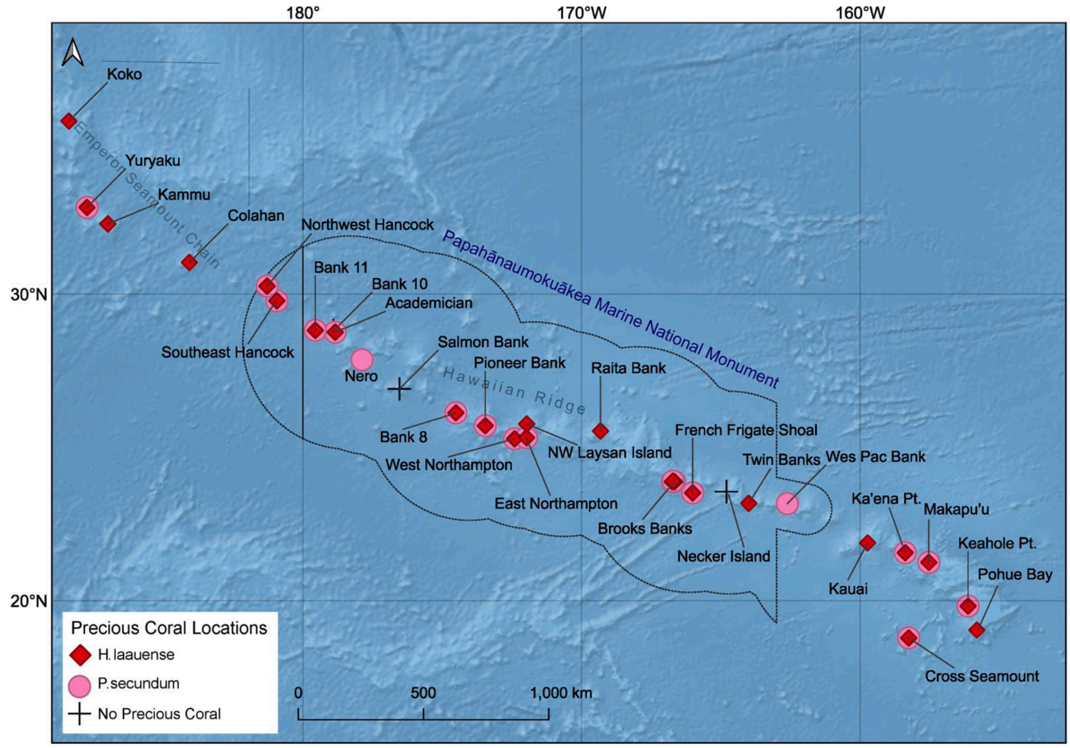

Fig. 1. Map of sampled sites for this study, coded by coralliid species. Positions for each site can be found in Table 1.

disturbed and undisturbed sites. If seamount coralliid populations were not impacted or were resilient to trawling impacts, we would anticipate that at least at the “Recovering” sites, coralliid abundance and colony sizes would be comparable to or approaching those at “Never Trawled” sites. If the sites were impacted, coralliids would have reduced abundances compared to the “Never Trawled” sites, and any new colonists would be of smaller sizes.

2. Methods

2.1. Study sites

Data and samples were combined across multiple projects and sampling efforts from 1998 to 2017 from 28 seamounts along the Hawaiian Ridge and Emperor Seamount Chains (Fig. 1, Table 1). For the purposes of analyses of the impacts of trawling disturbance and protection, the sites were analyzed as three treatment types, Never Trawled, Recovering, and Still Trawled. Sites southeast of Bank 8 were in the “Never Trawled” treatment. Makapu‘u and Keahole Points have been harvested for precious corals using submersibles but target depths of the harvest were <400 m (NOAA Fisheries Report, 2008). Sampling for the current study occurred primarily at depths $\geq$ 400 m, therefore these sites are still included in the “Never Trawled” treatment. Sites from Bank 8 to the edge of the US EEZ at NW Hancock were trawled and/or were dragged with tangle nets (NOAA Fisheries Report, 2008), but have been protected since the establishment of the US EEZ in 1977 and were included in the “Recovering” treatment. Finally, sites northwest of NW Hancock are outside the US EEZ and are still actively trawled (NPFC (North Pacific Fisheries Commission), 2022) and so were placed in the “Still Trawled” Treatment. The list of sites with their treatment designation are included in Table 1 and Fig. 1. The trawling history for the disturbed sites is provided in Table 2. Raw data for all figures is provided in Supplemental Tables 1–5.

2.2. AUV abundance data

Abundance data for the two coralliid species were available from two sources. The first is AUV imagery data for 10 seamounts, obtained in 2014 and 2015 with the AUV Sentry (https://ndsf.whoi.edu/sentry/), (Table 1, Fig. 1). AUV surveys included quantitative replicate 1 km length transects at 50 m depth intervals from 200 to 700 m. However, at many sites coralliids were more common on transit areas between transects, for example when moving upslope, so the complete set of dive images, both inside and outside of transects, was used for the analyses of coralliid abundance.

Survey dives targeted areas of seafloor that were expected to be hard substrate based on multibeam or backscatter data. Sentry flies at speeds of 0.5–0.7 m/s with an altitude between 4 and 8 m (average of 5 m). A down-looking Allied Vision Technologies Prosilica GE4000C camera mounted on the AUV was used to take photos every 3–4 s with a resolution of 96 dpi (4,008 $\times$ 2,672 pixels) and a field of view of approximately 12 m^2. Dives ranged in length from $\sim$ 16–73 km over a period of up to 36 h per dive.

Coralliids can readily be distinguished from other corals in the AUV images because of their darker red or pink centers and lighter white or yellow outer edges, however the two species could not be distinguished from each other at the resolution of an AUV image. Data were collected from video analyses as counts of coralliids in each image and also as number of images with coralliids per dive. Some AUV images could not be used for analyses because of altitude of the vehicle or lighting issues. To allow for uneven survey lengths and number of usable images, count data were standardized as the number per 1000 usable images.

The standardized abundances were compared among treatments with ‘Treatment’ as a Fixed factor. Unfortunately, the surveyed areas in the “Never Trawled” treatment ended up having a high sediment cover (47–94 % soft substrate). Because coralliids prefer hard substrate (Parrish, 2002), these sites did not represent suitable habitat for coralliids and so this treatment was excluded from the AUV abundance analyses. Individual Sentry dives were treated as replicates within treatments because there was not a balanced number of dives per seamount (range

Table 1
List of all sites with location and sampling data. Sites with dates of 2014 and 2015 were surveyed with the AUV Sentry, all other dates correspond to Pisces IV and V surveys and sampling. Descriptions of the Treatments are included in Section 2.1 Study Sites. NT: Never Trawled.

Seamount Name	Year(s) Sampled	Lat °N	Long °W/E	Treatment
Cross Seamount	2000, 2002, 2004	18.733	158.259 W	NT
Pohue Bay	2000	19.001	155.814 W	NT
Keahole Point	2000, 2004	19.815	156.129 W	NT
Makapu'u	1998, 2004	21.293	157.536 W	NT
Ka'ena Point	2000	21.617	158.383 W	NT
Kaua'i	2000	21.944	159.736 W	NT
Wes Pac Bank	1998, 2000	23.253	162.613 W	NT
Twin Banks	2003	23.264	163.998 W	NT
French Frigate Shoals	1998, 2000, 2015	23.609	166.010 W	NT
Necker Island	2015	23.65	164.800 W	NT
Brooks Bank SE	1998, 2017	23.976	166.663 W	NT
Brooks Bank SW	1998, 2017	23.977	166.739 W	NT
Brooks Bank NW	1998	23.997	166.716 W	NT
West Northampton	2017	25.383	172.404 W	NT
East Northampton	2017	25.419	171.976 W	NT
Raita Bank	2003	25.639	169.318 W	NT
Pioneer Bank	2003, 2014, 2015, 2016, 2017	25.81	173.454 W	NT
NW Laysan Island	2003	25.867	171.966 W	NT
Bank 8	2003	26.226	174.509 W	Recovering
Salmon Bank	2003	26.997	176.536 W	Recovering
Nero	2003	27.927	177.878 W	Recovering
Academician	2015, 2017	28.804	178.841 W	Recovering
Bank 10	2003	28.845	178.904 W	Recovering
Bank 11	2003, 2014, 2015, 2016	28.864	179.556 W	Recovering
Southeast Hancock	2015, 2016, 2017	29.79	179.065 E	Recovering
Northwest Hancock	2015, 2017	30.249	178.715 E	Recovering
Colahan	2017	30.983	175.926 E	Still Trawled
Kammu	2015, 2016, 2017	32.167	173.000 E	Still Trawled
Yuryaku Smt	2014, 2015, 2016	32.668	172.250 E	Still Trawled
Koko Smt	2015, 2017	35.25	171.599 E	Still Trawled

1–4) to allow for a nested design of seamount within treatment. The Still Trawled treatment also had several orders of magnitude lower variance than the other treatment and so a non-parametric one-way Wilcoxon test was used in JMP v 16.0 (SAS 2020).

2.3. Pisces abundance data

The second source of abundance data came from Pisces IV and V submersible survey transects in 2016 and 2017 at 11 seamounts. Because of heavy sediment in the Never Trawled Treatment sites in 2014 and 2015, Necker Island and French Frigate Shoals were not revisited in 2016 and 2017 and were replaced in the Never Trawled Treatment with East and West Northampton seamounts. Additionally, the Pisces could operate in steeper areas than the AUV, which was limited to a slope < 40 %.

The Pisces have a mini Zeus HDTV camera that is positioned on the light bar above the basket with a viewing area of approximately 14 m^2 and takes continuous video. Three replicate transects of 500 m length were carried out on each seamount at depths of 400, 500, and 600 m on the southeast slope of each seamount. Coralliid abundances were counted within each transect, but the two coralliid species could not be distinguished consistently in the transects, so counts again include both species. The hypothesis of equal variance among treatments was rejected for the Pisces abundance data at all depths. Therefore, a non-parametric one-way Kruskal-Wallis test with Wilcoxon pairwise comparisons was used to compare abundance among treatments in JMP v 16.0 (SAS 2020).

Table 2
Trawling history for the disturbed sites in this study listed from northwest to southeast. Heavy lines separate treatment types, with top group "Still Trawled" and the bottom group "Recovering". Yuryaku and Kammu are two of the three features of the Milwaukee Banks. Southeast Hancock is also referred to as Equator Seamount or as Townsend Cromwell Seamount. Bank 11 in some sources is referred to as Zapadnaya or as Helsley Seamount. *NOAA Report (2008), ong = ongoing. **Data from Clark et al. (2007) and Clark and Tittensor (2010) were provided as estimates split into 1-degree latitude and longitude grid cell boxes and given as metric tons (mt). Values for each feature were taken as the grid cell they fell into. SA = Surface area given as area within 300–600 m depth range.

Seamount Name	*Last Year Trawled	**Total Catch (mt)	SA (km^2)	Catch per km^2
Koko Smt	Ong	92,500	3874	24
Yuryaku Smt	Ong	98,000	72.7	1348
Kammu	Ong	28,000	610.3	46
Colahan	Ong	92,500	15.8	5872
NW Hancock	1986	98,300	5.6	17,558
SE Hancock	1986	92,500	10.9	8525
Bank 11	1977	11,500	42.3	272
Academician	1977	11,500	30.9	152
Bank 10	1977	11,500	75.6	152
Nero Smt	1977	7000	51.5	135.9
Salmon Bank	1977	6000	75.9	79
Bank 8	1977	6000	26.9	222.9

2.4. Collections and depth distribution

As neither source of quantitative data allowed for distinguishing between the two coralliid species, qualitative data were compiled for the depth distribution and abundances of each species from coralliid collection data from 1998 to 2017 for all sites (Suppl. Table 3). Precious coral samples were collected with the submersibles Pisces IV and Pisces V during cruises onboard the *RV Ka'imikai-O-Kanaloa* at sites ranging in depth from 300 to 700 m. Data are only included from dives that were focused on precious coral studies. Dives targeted known sites from precious coral fishery management (Makapu u, Keahole, Wes Pac) or explored for new coral beds based on bathymetry and likelihood of hard substrate and began with surveys to locate corals. Once precious corals were observed, sampling began and followed a random pattern across the coral bed. The basket sampling capacity per dive was 30 individuals of each species and targeted *Hemicorallium laauense*, *Pluerocorallium secundum* and *Kulumanamana haumeeae*. Seafloor distance covered per dive ranged from < 1 km to > 10 km in an 8hr dive depending on the amount of exploration needed and the size and density of the coral bed. The two coralliid species could more easily be distinguished from each other when the vehicle stopped and zoomed in on the colonies as was done prior to collections. Because a small piece of the corals was also collected for genetic studies (e.g. Baco and Shank, 2005; Baco et al., 2006; Morgan et al., submitted) the identifications could also be confirmed based on closer observations of the specimens onboard ship. Depth distributions and means based on the identification of collected specimens were computed in JMP v 16.0 (SAS 2020). Data were also used to generate a qualitative collecting curve, graphed using the number of individuals of each species collected versus the adjusted number of dives at each site. The adjusted number of dives was calculated by removing aborted dives and lander-focused dives from the total count of dives on a seamount, with dives where other scientists collected samples opportunistically on the same seamount on shared cruises counted as 0.5 of a dive (Table S3).

Data for *Kulumanamana haumeeae* were not included in this study because, unlike coralliids which were a part of a fishery, there are currently no data available to determine if the range of *K. haumeeae* extended into the still trawled area prior to fishing.

2.5. Colony size data

Data on colony sizes were also taken at the time of sample collections. The pilot estimated the height and width of the colony *in situ* using a graded ruler on the edge of the basket or bioboxes as a size reference. Colonies had to be measured *in situ* because generally only small subsamples were collected for genetic studies.

Colony size data were compared among treatments for each of colony height and colony width for each species using a non-parametric one-way Kruskal-Wallis test with Wilcoxon pairwise comparisons in JMP v 16.0 (SAS). For *P. secundum*, only one individual was observed and subsampled from seamounts in the Still Trawled treatment, so statistical tests of sizes for this species only compared the Never Trawled and Recovering Treatments.

3. Results

3.1. Depth distribution

Across all sampling efforts, 357 *P. secundum* were collected from a depth range of 326–603 m with a mean depth of 424.8 m ± 2.6 m (SE) (Fig. 2a). A total of 395 *H. laauense* were collected from 385 to 702 m depth with a mean depth of 512 m ± 3.6 m (SE) (Fig. 2b).

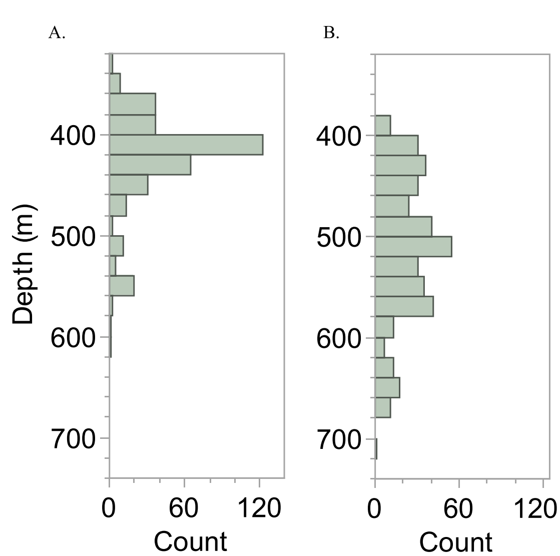

Fig. 2. Depth distributions of collections for 1998–2017 for (a) *P. secundum* and (b) *H. laauense*. For each panel 'count' is the number of individual colonies collected.

3.2. Abundance

From the AUV Sentry surveys, the number of images with coralliids per 1000 usable images was 0–6.8 with a mean of 1.2 and a median of 0.2. Dive S353 on SE Hancock, a Recovering Seamount, was a significant outlier with 6.8 images including coralliids and 50.3 coralliids counted per 1000 usable images. Images with coralliids were much less abundant in the Still Trawled treatment and the difference was statistically significant (p = 0.0011, Fig. 3a, Table S6).

With counts calculated as number of coralliids per 1000 usable images, the range of abundance was 0–50.3, with a mean of 5.7 individuals per 1000 usable images and a median of 0.3. Coralliid counts were much lower in the Still Trawled treatment and the difference was statistically significant (p = 0.0011, Fig. 3b, Table S6). Similar results were obtained using dive length for standardization instead of number of usable images (not shown).

From the quantitative Pisces surveys in 2016 and 2017, at 400 m, the range of abundances per transect was 0–450 coralliid individuals per 500 m length transect with a mean of 35.66 and a median of 1. All transects on Pioneer had outlier abundances with a range of 193–450 individuals (Fig. 4 a,b). Without these outliers, the mean number of individuals per transect was 4.5. In the Still Trawled sites, the only observed coralliids were one individual on each of 2 transects on Koko. There was a statistically significant difference among treatments (p = 0.013, Table S6), with the Still Trawled having the fewest observed individuals of the three treatments. When all Pioneer transects were removed, the significance of the tests was reduced (p = 0.042).

At 500 m, the range of abundances per transect was 0–126 individuals per transect with a mean of 16.03 and a median of 1. All the seamounts in the Recovering and Still Trawled Treatments had only 0–2 individuals per transect, except Koko which had 10–80 coralliids per transect. There was a statistically significant difference among treatments (p = 0.004, Table S6) with Recovering having the lowest median number of individuals (Fig. 4 c).

At 600 m, the range of abundances per transect was 0–155 coralliids with a mean of 14.3 and a median of 2.5. Two transects on SE Hancock had outlier abundances, transect 3 on P5-875 had 155 individuals and transect 2 on P5-910 had 138 individuals (Fig. 4 d). There was a statistically significant difference among treatments (p = 0.002, Table S6), with the median for Recovering larger than for the other two treatments. Removing the outlier points on SE Hancock changed the significance of the Kruskal-Wallis tests to p = 0.007.

Unfortunately, neither the AUV nor Pisces surveys could consistently distinguish between the two coralliid species. The species could only be distinguished when the submersible stopped to collect samples and then the identifications were verified when the collected colony fragments were processed at the surface. Using identities of collected samples provides qualitative insights into which species were most likely represented in the AUV and Pisces images. Collection data were compiled from 1998 to 2017 across 28 sites in the NWHI and ESC (Suppl. Table 3). In 20 Pisces dives in the Still Trawled treatment across 4 seamounts, only 1 individual of *P. secundum* was observed, on Yuryaku Seamount. Among the Recovering Seamounts, 9 individuals were collected across 22 dives on 6 seamounts, but one Recovering seamount, Bank 11, had 115 individuals in 10 dives on that seamount and another, Bank 8 had 19 individuals in 2 dives. In comparison, among the 16 Never Trawled seamounts, the collections of *P secundum* ranged from 0 to 28 individuals per dive with a mean of 4.5. *H. laauense* were collected at all but 4 of the explored seamounts, three Recovering and one Never Trawled, with abundances of 1–104 individuals (Suppl. Table 3). For *H. laauense*, each treatment had an equal number of seamounts above and below the qualitative collecting curve (Fig. 5 a). In contrast for *P. secundum*, all four Still Trawled seamounts fell below the collecting curve, along with 5 of the 7 Recovering seamounts, while all but 3 of the Never Trawled seamounts fell above the curve (Fig. 5 b).

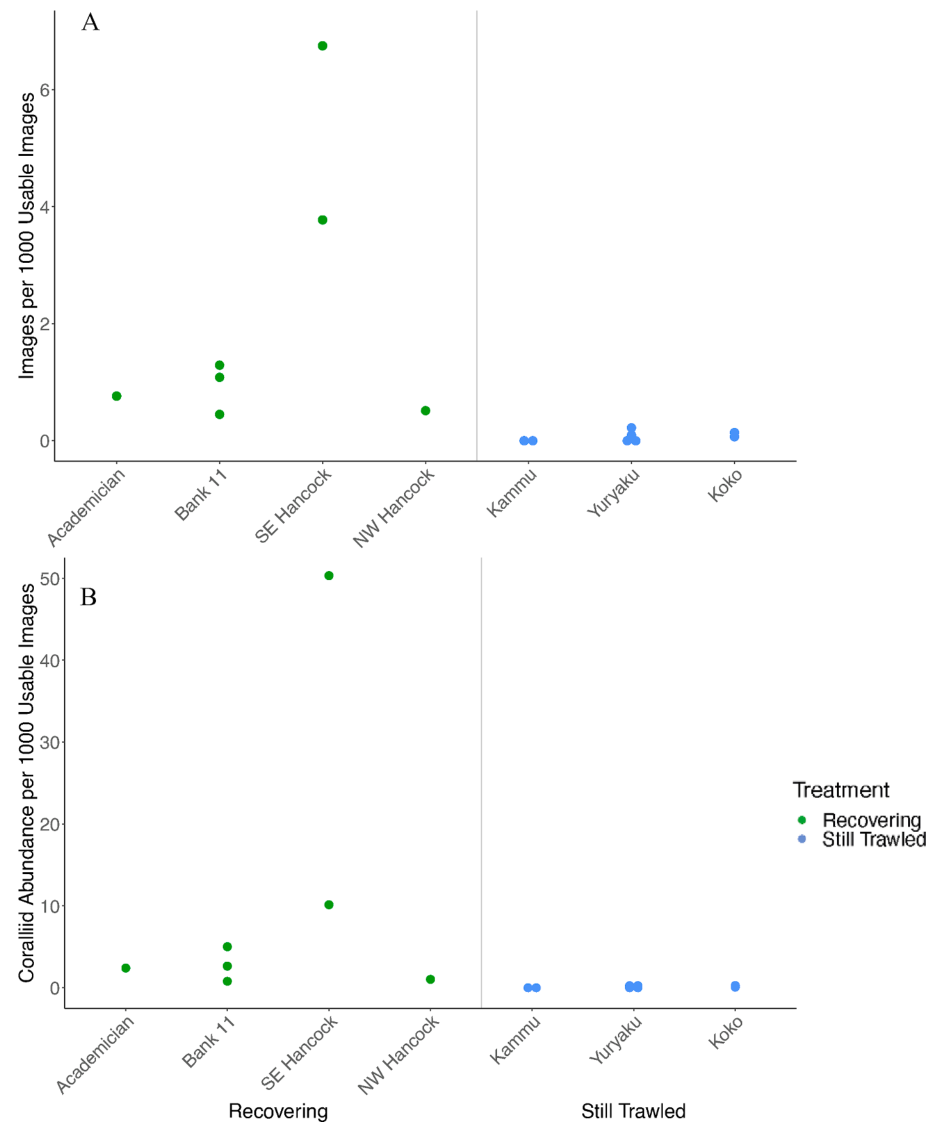

Fig. 3. Abundance of both coralliid species based on AUV Sentry surveys. Each point represents a single AUV dive. (A) Data are standardized as number of images with coralliids present per 1000 usable images. (B) With the data standardized as number of coralliids observed per 1000 usable images.

3.3. Colony sizes

For *H. laauense* colony height ranged from 2 to 127 cm (Fig. 6a). Depth was tested as a potential confounding factor and was found to be non-significant for both height and width for *H. laauense* ($p = 0.1659$ and $p = 0.2706$, respectively). Using all sites, the overall Kruskal-Wallis test was highly significant for comparisons of colony height among treatments ($p < 0.0001$) with all pairwise tests also significant at $p < 0.0001$ (Table S6). The median size was largest for the Never Trawled sites (25 cm) and smallest for the Still Trawled sites (10 cm). Using a random subset of four Never Trawled sites to generate a more balanced design for a nested ANOVA gave the same overall p value (not shown).

For *H. laauense* colony width ranged from 2 to 254 cm (Fig. 6b). Using all sites, the overall Kruskal-Wallis test for comparison of widths among treatments was highly significant ($p < 0.0001$) with all pairwise tests also significant (Never vs either other treatment $p < 0.0001$, Still vs Recovering $p = 0.0005$, Table S6). The median width was largest for the Never Trawled sites (34 cm) and smallest for the Still Trawled sites (15 cm).

For *P. secundum* colony height ranged from 3 to 60 cm (Fig. 7a). *P. secundum* showed a statistically significant ($p < 0.0001$) increase in both height and width with depth (Height = –32.60 + 0.11*Depth), (Width = -20.38 + 0.10*Depth), but this trend explained little of the variance for either ($R^2 = 0.28$ for height and $R^2 = 0.14$ for width). The mean depth for the Recovering treatment (458.2 m) was deeper than the mean depth for the Never Trawled Treatment (413.3 m) ($p < 0.0001$). Despite this potential confounding depth influence however, the mean and median sizes of the colonies in the Recovering treatment were smaller in height and width than in the Never Trawled treatment ($p < 0.0001$ for both height and width, Table S6). The median height was larger for the Never Trawled sites (12 cm) than for the Recovering sites (6.5 cm). For *P. secundum,* colony width ranged from 2 to 76 cm (Fig. 7b), with the median width for the Never Trawled sites (20 cm) larger than the Recovering sites (15 cm).

4. Discussion

4.1. Abundance data as evidence of disturbance

As the key ecosystem engineers on seamounts, corals can be considered the “drivers” in the sense of Walker (1992) and the associated invertebrate communities as the “passengers.” It has been suggested that removing the drivers has a bigger effect than removing passengers, resulting in longer time for recovery, and a greater

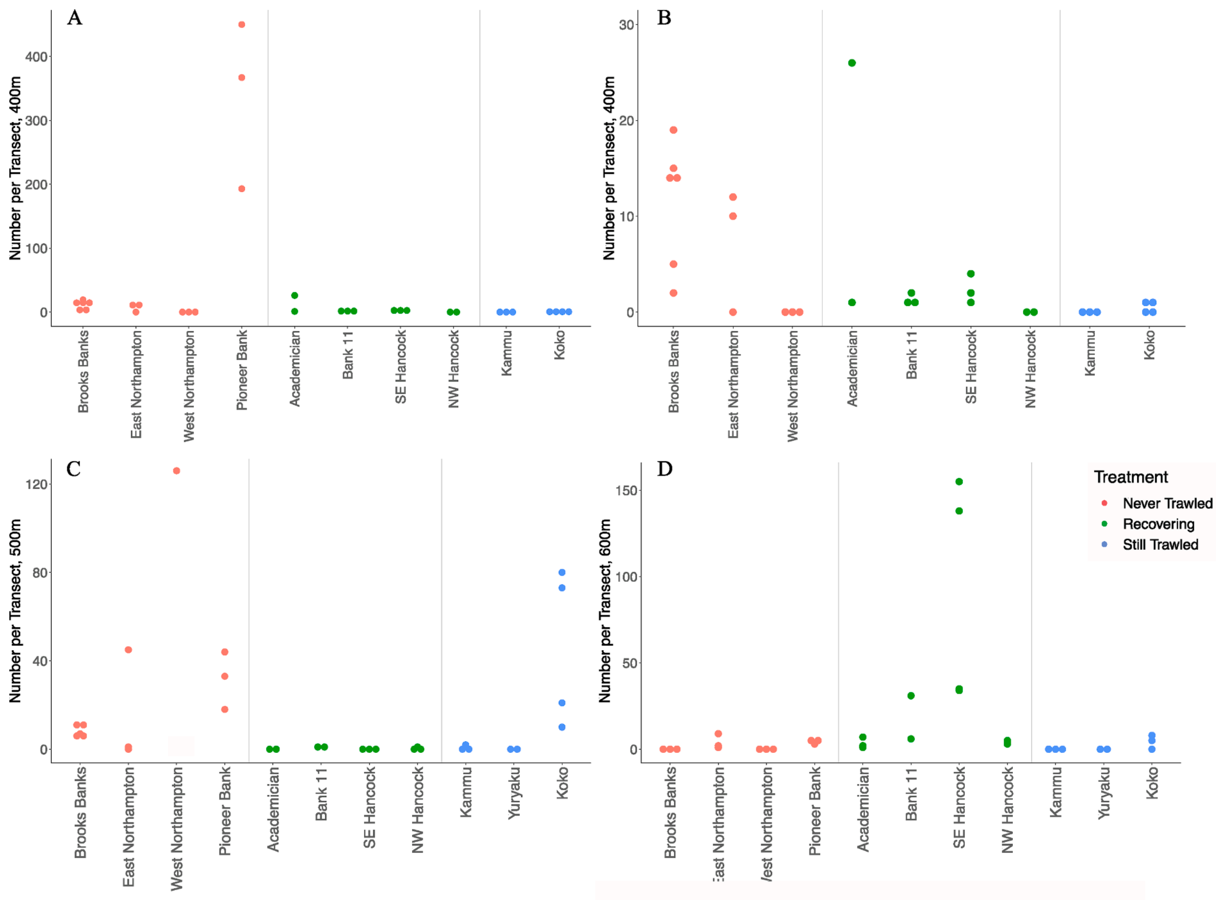

Fig. 4. Abundance of Coralliids from quantitative Pisces transects in 2016 and 2017. (a) 400 m, (b) 400 m without the outlier Pioneer points, (c) 500 m, (d) 600 m depth. Each point represents a transect of 500 m length. Sites are organized along the x-axis from southeast to northwest.

likelihood to move to an alternate state (Walker, 1992; Gunderson, 2000). To fully assess the impacts of disturbance to seamount deep-sea coral communities and the state of recovery then, we must first establish the degree of impact and potential and time scales of recovery for the drivers, which in the NWHI and ESC, include coralliid octocorals. In this study, reductions in coralliid abundance were observed on seamounts that experienced trawling disturbance, with lower abundances on most of the Recovering and Still Trawled seamounts. These results are consistent with a number of studies that have shown reductions in abundance and biomass of deep-sea corals and other megabenthos in trawl disturbed areas compared to undisturbed areas (Heifetz et al., 2009; Du Preez and Tunnicliffe, 2011; Buhl-Mortensen et al., 2016; Clark et al., 2016; Colaço et al., 2022).

It is important to note however that the distribution of coralliids was very patchy in all treatments and a few individual disturbed sites had high abundance. In the AUV surveys and the Pisces transects at 600 m, SE Hancock had outlier abundances compared to all other sites. In the Pisces transects at 500 m, Koko was the only seamount in the Still Trawled and Recovering treatments to have any significant abundances of coralliids, with values comparable to or greater than many of the Never Trawled sites. These outliers somewhat confounded the abundance analyses. There are two possible explanations for the sites with outlier abundances. The first is that these sites harbor remnant populations that were missed by previous trawling efforts. The second possibility is that these outlier observations represent new recruitment and recovering populations of coralliids.

4.2. Outlier abundance data as evidence of remnant populations or new recruitment

Potential remnant populations of deep-sea corals as a group were previously noted for these sites, particularly in steeper areas (Baco et al., 2019, 2020). If the high coralliid abundances at these few disturbed sites are also interpreted as remnant populations, then it can be inferred that there has been no recovery of coralliids on the Recovering and Still Trawled seamounts. A lack of recovery of these sites would be consistent with the stated hypothesis and with previous studies on seamounts off New England, New Zealand and Australia, which showed no recovery of seamount coral communities over 5–15 year time scales (Waller et al., 2007; Althaus et al., 2009; Williams et al., 2010; Clark et al., 2019).

Alternatively, if the high coralliid abundances at the few sites instead are interpreted as new recruitment, then it can be inferred that there is some potential for recovery of coralliids to disturbed sites. However, this potential varied among species, with *H. laauense* being present on more seamounts and in higher numbers than *P secundum*, and *P. secundum* essentially only occurring on protected sites. The abundances also varied widely among disturbed seamounts. The disparity in abundance among sites may be tied to either the historic coralliid fishery or potentially to the more recent fisheries footprint on the Still Trawled seamounts.

The coralliid fishery in the 1960s and 70s covered many seamounts, but was focused on the three seamounts that made up the “Milwaukee Banks” (reviewed in Grigg, 2002). Some of the highest takes from the fish fishery also occurred on the Milwaukee Banks (Clark et al., 2007). Kammu and Yuryaku are two of these banks (Milwaukee Banks Seamounts identified in Mundy, 2005) and fall into the Still Trawled treatment. The fact that the coral fishery was focused on these features

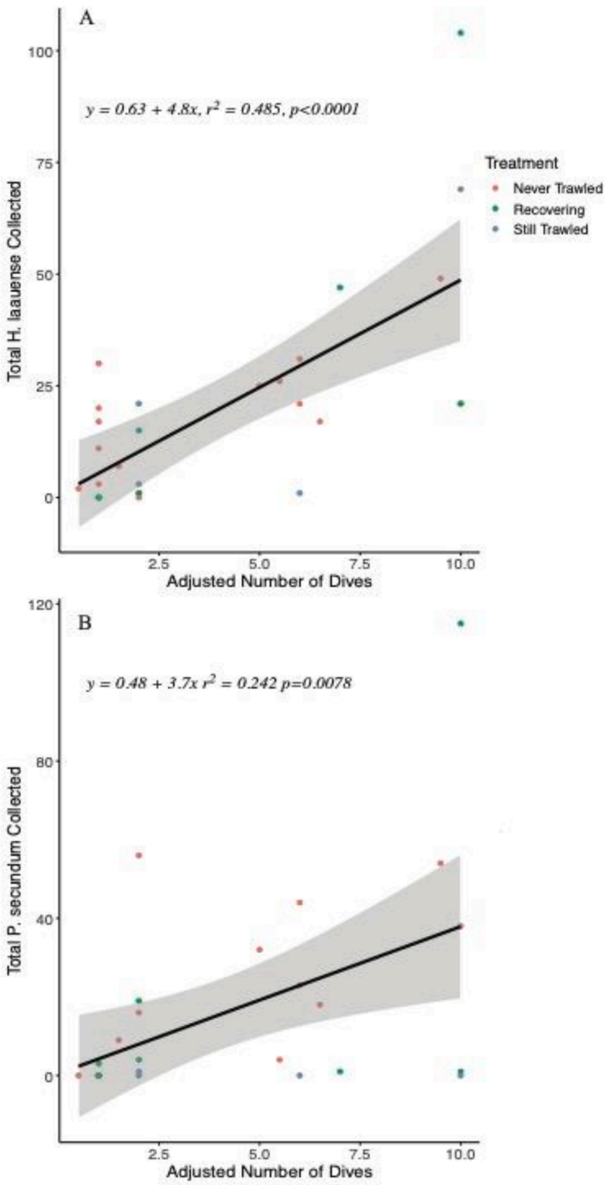

Fig. 5. Number of coralliids collected per adjusted number of dives for (a) *H. laauense* and (b) *P. secundum.*

implies that they had the highest abundances of coralliids of any of the seamounts in the region. In contrast, at the time of the current study, these two seamounts had particularly low abundances compared to Koko and most other seamounts. Kammu had only 2 coralliid individuals observed in 6 sub dives and two 30-hr AUV dives (>100 hr total bottom time, and well over 100 km of linear distance surveyed). Yuryaku had 5 coralliids observed in 3 AUV dives and 0 observed on transects in 2 Pisces video surveys dives, with 1 *P. secundum* and 21 *H. laauense* collected outside transect areas. It may be that the fishing pressure for the Milwaukee Banks seamounts was so high that it removed all the local populations that could potentially reseed these seamounts, and longer distance recruitment events have not yet occurred (or have not produced coralliids of a size that was visible through a submersible camera).

Recovery timelines of sessile organisms in hard substrate habitats are a function of scale of the disturbance, the distance to the nearest patch, and the dispersal capabilities of the larvae. For large scale disturbances, populations are expected to take longer to recolonize and to depend more on long-range sources and therefore on long-distance dispersal events than in small scale disturbance patches (e.g. Lissner et al., 1991). Reliance on long-distance dispersal events for recovery is expected to reduce resilience of populations as these events are often rare even in shallow water (e.g. Ayre and Hughes, 2004; Graham et al., 2006; Lotze et al., 2011). However, the presence of remnant populations has been shown to accelerate the recovery process in seagrasses (Johnson et al., 2021), in terrestrial ecosystems (reviewed in Turner, 2010), and in isolated populations of shallow-water corals (e.g. Gilmour et al., 2013) and this in turn reduces the dependence on long-distance dispersal events to initiate the recovery process. Koko is a very large seamount and had a much lower historic catch per unit area than either Kammu or Yuryaku (Table 2). If Koko has larger remnant populations than Kammu and Yuryaku, local recruitment may be facilitating the recolonization process in disturbed areas at this site.

Another potential explanation may be extrapolated from examining the modern fishing footprint for the fish fisheries on the high-seas seamounts. Morgan and Baco (2021) used publicly available satellite AIS data from 2012 to 2018 to determine the fishing footprint of the bottom contact fisheries at these sites. Out of all the features of the NWHI and ESC, Kammu and Yuryaku experienced the highest degree of modern fishing effort. In contrast, the area surveyed on Koko for the current study had almost no overlap with the modern fishing footprint. However, trawl scars and lost gear have been noted in the surveyed areas on Koko (Baco et al., 2019, 2020) suggesting these areas were likely a part of the historical fishing efforts. If the surveyed areas on Koko have had a significant temporal lapse in fishing effort, it may have allowed for some time for recovery of coralliids, which is supported by the data in this study. Models suggest that the combination of high frequency disturbance over large spatial scale may result in a loss of ecosystem resilience and a regime shift to an alternate state (Zelnik et al., 2018). The high level of continued fishing effort on Yuryaku and Kammu may be preventing recovery and may explain the low abundances of the target species observed on these features.

4.3. *Colony size data as evidence of remnant populations or new recruitment*

The colony size data provide additional insights into the possible alternative explanations of the outlier sites with higher abundances. *H. laauense* showed larger colony sizes in the Never Trawled treatment compared to the Recovering and Still Trawled sites. Similarly, *P. secundum* had a slightly larger median size in the Never Trawled seamounts compared to the Recovering sites. Findings of smaller size individuals of benthic megafauna in trawled disturbed areas are common (e.g. Krieger, 2001; Du Preez and Tunnicliffe, 2011; Buhl-Mortensen et al., 2016; Pierdomenico et al., 2018; Yoklavich et al., 2018; Baker et al., 2019; Bo et al., 2021; Colaço et al., 2022) and have been attributed to two potential processes; new recruitment, and a size refuge for smaller individuals that allows them to escape trawl impacts.

Smaller colony sizes could imply that the colonies in the Recovering and Still Trawled seamounts are of younger size classes than in the Never Trawled sites on average. Younger size classes would imply new recruitment has occurred since trawling disturbance. Potential recolonization after disturbance has been documented for octocorals in the Gulf of Alaska and on Learmonth Bank, where although time scales since disturbance could not be determined, disturbed areas had a higher proportion of small colonies compared to undisturbed areas (Krieger, 2001; Du Preez and Tunnicliffe, 2011).

An alternative explanation of colony size is that smaller size colonies may be less prone to trawling damage than larger colonies. Studies of octocorals on the US West Coast found smaller sizes for bamboo coral colonies in disturbed areas and that there was more damage to colonies in the 20–80 cm size range than there was to smaller colonies (Yoklavich et al., 2018). Similarly, in a western Mediterranean canyon, comparison of high and low intensity trawling sites suggested that *Isidella elongata* specimens>20 cm in height were more vulnerable to trawling impacts (Pierdomenico et al., 2018). On two seamounts in the Ligurian Sea,

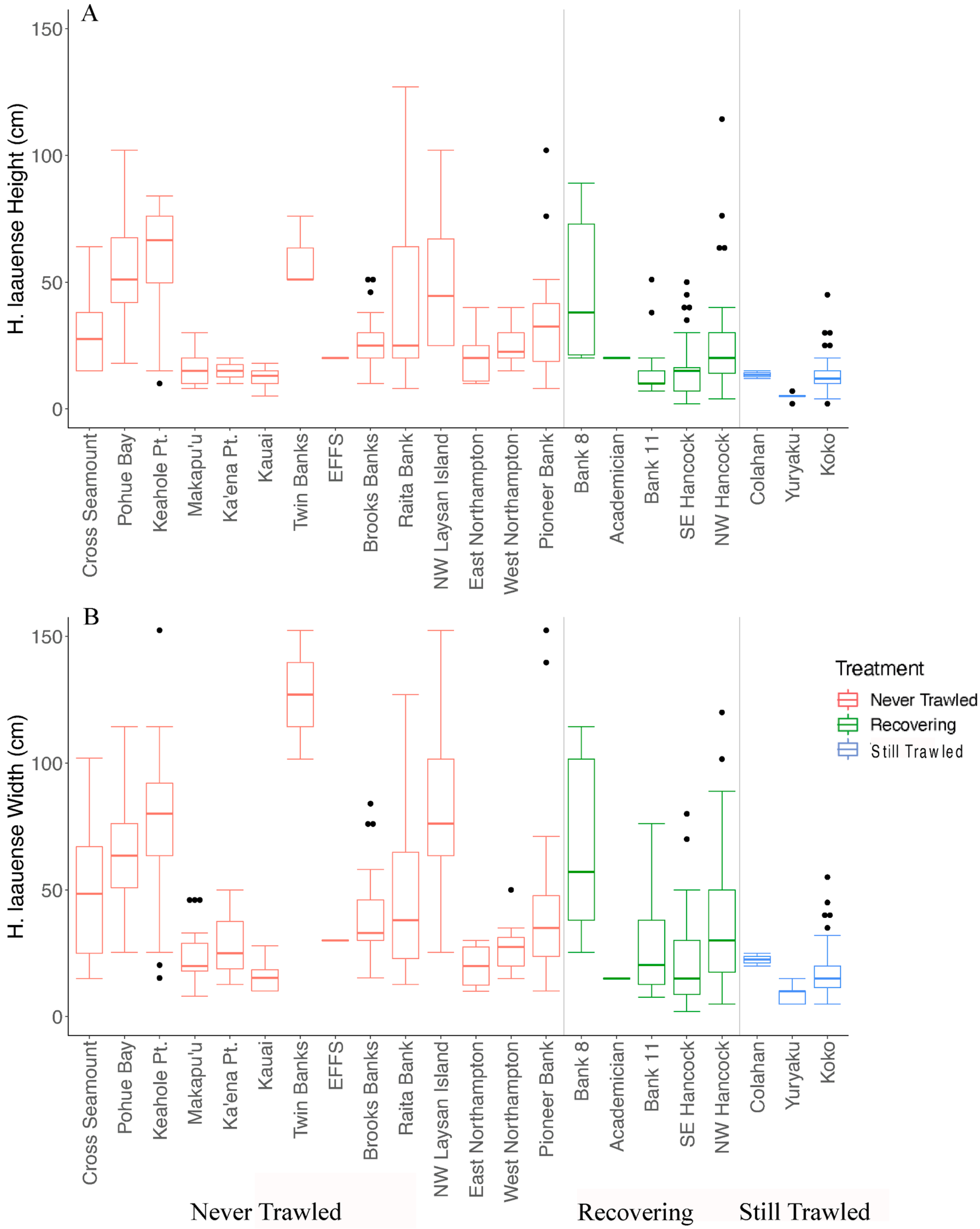

Fig. 6. Range of observed colony sizes for *H. laauense* across all sampling sites from 1998 to 2017. Individual dots represent outlier values. (a) Height in cm, (b) Width in cm.

40–75 % of *Callogorgia verticillata* colonies between 10 and 60 cm in height showed loss of branches and long line entanglement (Bo et al., 2021). *Keratoisis grayi* on the Grand Banks within trawled sites were smaller in size and more likely to be broken or damaged (Baker et al., 2019).

4.4. Growth rates as evidence of new recruitment

To resolve the question of remnant versus new recruitment, insights may be gained from published growth rates for *P. secundum*. Roark et al., (2006) found that an individual colony of *P. secundum* that was 28 cm tall was 71 ± 9 yrs old. Assuming linear growth gives a rate of ~ 0.39 cm in height per year. With this estimate any individuals that are less than ~ 16 cm in height are likely to represent new recruitment since the cessation of trawling (~40 yrs prior) at the recovering sites. The size range of *P. secundum* in the Recovering treatment was 3–60 cm with a mean of 13.4 ± 1.3 cm (SE) and a median of 6.5 cm. Thus, we can conservatively estimate that at least 50 % of the individuals can be attributed to new recruitment since protection of the area. The 75 % quartile size was 25 cm, so we can estimate that about 25 % of the

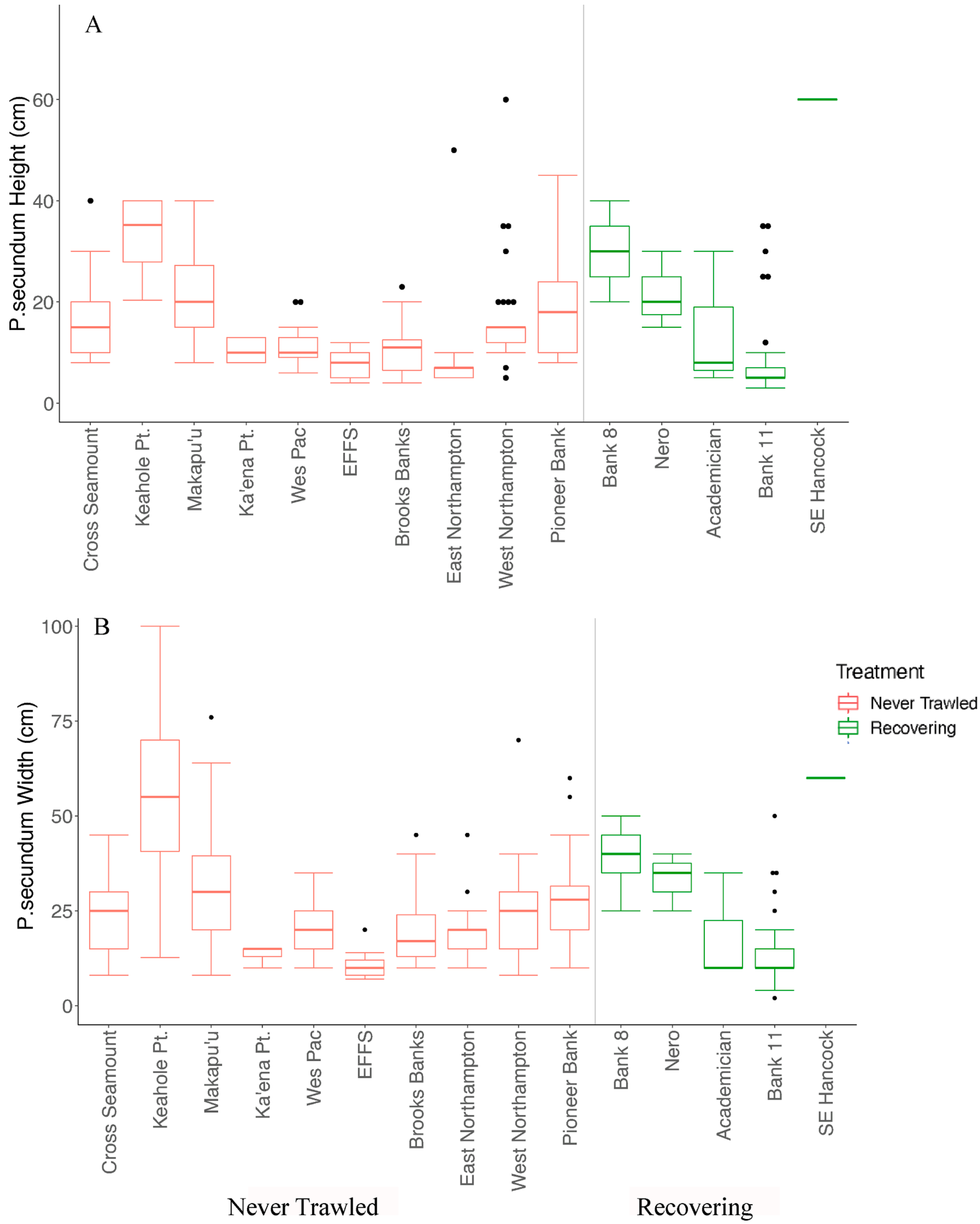

Fig. 7. Range of observed colony sizes for *P. secundum* across all sampling sites from 1998 to 2017 (a) Height in cm, (b) Width in cm.

individuals in this treatment were from remnant populations. At Bank 11, the disturbed site with the largest population of *P. secundum*, 90 % of the individuals were ≤ 10 cm in height and likely represent new recruitment. New recruitment implies greater resilience than expected for these corals, albeit over long timeframes. Unfortunately, there are no published growth rates for *H. laauense* to carry out the same analyses. *H. laauense* generally has a different range of colony sizes and is in a different genus that *P. secundum*, therefore using the same growth rates would not provide accurate estimates.

5. Conclusions and management implications

Combining the results of the abundance data and the size data, it can be inferred that coralliids have been adversely impacted by fisheries efforts, but some recovery is occurring at a few sites, especially SE Hancock and Koko seamounts for *H. laauense*, and Bank 11 for *P. secundum*. Recruitment may be stronger at these sites due to the presence of larger remnant populations that enhance local recruitment (e.g. Turner, 2010; Gilmour et al., 2013; Johnson et al., 2021). Assuming there has been new recruitment, *H. laauense* appears to be the more resilient of the two species, as evidenced by its higher abundance in the

Still Trawled treatment compared to *P. secundum*. This species may have higher recruitment rates or faster growth rates. Alternatively, *P. secundum* may not have adequate remnant populations or source populations in the Still Trawled treatment sites to allow for recruitment on those sites.

As key structure formers with vulnerable life history characteristics, coralliids, like other deep-sea corals in high seas areas, are considered Vulnerable Marine Ecosystem (VME) indicator taxa and within this region VMEs are managed by the North Pacific Fisheries Management Council (NPFC). In US waters, coralliids of the Hawaiian Ridge seamounts are managed as a fisheries species by the West Pacific Fisheries Management Council. Within both of these management frameworks, it is important to document the locations of coralliid populations to establish protection for these sites. Remnant and recovering populations likely provide an important source of propagules for further recovery of disturbed sites (e.g. Turner, 2010; Gilmour et al., 2013; Johnson et al., 2021). Therefore, these populations of coralliids should be a high priority for protection.

The UN FAO and NPFC also have regulations to determine if VMEs are or have experienced Significant Adverse Impacts (SAIs). For these seamounts, particularly Kammu and Yuryaku, to go from having the highest abundances of coralliids in the region during the fishing period to having only a few rare individuals, is a substantial reduction in a VME species and therefore should be considered an SAI to these VMEs (Baco et al., 2020).

This study further supports the idea that seamount deep-sea coral communities have some potential for recovery from trawling impacts, given protection and enough time for recovery, even in heavily fished areas (Baco et al., 2019). At these sites remnant populations and a cessation of trawling will be critical for the recovery process.

CRediT authorship contribution statement

Amy R. Baco: Conceptualization, Funding acquisition, Data Acquisition, Analysis, Investigation, Visualization, Methodology, Writing – original draft, Writing – review & editing. **Nicole B. Morgan:** Data Acquisition, Writing – review & editing. **E. Brendan Roark:** Writing – review & editing, Funding acquisition. **Virginia Biede:** Data Acquisition, Data Visualization, Analysis, 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

All data are included in the supplemental material

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Permits

This work was conducted under permit numbers: SCP 1999-31 and SCP2001-14, within the Papahānaumokuākea Marine National Monument permits: PMNM-2011-037, PMNM-2014-028, PMNM-2016-02, and PMNM-2019-016. Corals collected in the Northwestern Hawaiian Islands in 2003 were collected when it was the NWHI Coral Reef Ecosystem Reserve, prior to the establishment of the PMNM, under permit numbers NWHICRER-2003-003 and NWHICRER-2003-004.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.110010.

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