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Seamount recovery: analysis of 20 years of time-series seafloor image data from the Graveyard Knolls, Chatham Rise, New Zealand

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EXECUTIVE SUMMARY

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Benthic faunal communities on deep-water seamount features are commonly characterised by extensive growth of branching stony corals. These corals are vulnerable to impacts from bottom trawl gear and substantial reductions in the biogenic habitat formed by corals have been recorded on fished seamount features in New Zealand. The overall resilience of benthic communities associated with such coral habitats, and the time required for recolonisation and regrowth, are unknown; however, improving our understanding of these processes is important for evaluating appropriate options for management of fishing impacts.

On Chatham Rise, there are areas where numerous small seamount features are clustered in close geographic proximity to each other, are of broadly similar size, depth range, and elevation, and have varying levels of historical fishing effort. Importantly, a number of features on Chatham Rise were also closed to bottom trawling in 2001. These characteristics provide a natural 'compare and contrast' setting to evaluate the effects of bottom fishing, particularly in the Graveyard Knolls complex on the north-western flank of the Rise, where neighbouring features have a range of pre- and post-closure fishing histories ranging from heavily fished to unfished. The Graveyard Knolls thus provide an opportunity for monitoring the rates and mechanisms of recovery of benthic fauna, and population connectivity among seamounts.

Benthic invertebrate communities on the Graveyard Knolls have now been monitored over a period of 20 years, using non-destructive seafloor photography, with surveys in 2001, 2006, 2009, 2015, and 2020. The Graveyard survey series is one of only a few globally that have regularly monitored deep-sea habitats over comparable periods. This report extends the Graveyard time series by incorporating data from the fifth survey conducted in August 2020 (RV *Tangaroa* voyage TAN2009). The methods used follow those developed for analyses at previous survey points, with univariate and multivariate comparisons of community structure among seamounts and among time steps, and descriptions of benthic fauna observed in the imagery.

The addition of data from the fifth, T5, survey of the Graveyard seamounts indicates little change in the overall pattern of similarities among the benthic invertebrate communities on five of the six features surveyed. On 'Morgue', however, which was heavily fished until its closure in 2001, there are indications that whole-seamount benthic community structure might be changing and that branching stony corals are either regrowing or recolonising. Thus, the first detectable signs of potential benthic community recovery are appearing approximately 15 to 20 years after the cessation of trawling. However, while the appearance of early-growth stony corals is an unequivocal sign of the first stages of community recovery, some of the other changes in overall community structure do not match with what might be expected in a process of recovery to a pre-disturbance state characterised by branching stony corals and other sessile taxa.

These results contribute to an emerging body of evidence that recolonisation and regrowth of deep-sea corals on previously heavily trawled deep-sea features can, indeed, take place but that the process of recovery is slow, with the first detectable signs of coral recruitment and regrowth occurring approximately two decades after the cessation of trawling. While such observations of the early stages of recovery of coral-dominated seamount communities are encouraging, full recovery to their pre-disturbance status is by no means certain and would still be likely to take centuries, rather than decades.

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1. INTRODUCTION

Seamounts, knolls, and hills (here referred to collectively as seamount features) are prominent features of underwater topography in the New Zealand region and are often sites of high biodiversity and productivity (Rowden et al. 2010). They are the focus of important commercial fisheries for deep-water species, with about 80% of known seamount features at suitable depths for deep-water fisheries having been exploited (Clark & O'Driscoll 2003).

Benthic faunal communities on deep-water seamount features are commonly characterised by extensive growth of cold-water corals (Clark et al. 2010b, Tracey et al. 2011). These are vulnerable to impacts from bottom trawl gear, and substantial reductions in the biogenic habitat formed by corals have been recorded on fished seamount features (Clark et al. 2016). However, the overall resilience of such benthic communities, and the time required for recolonisation and regrowth of impacted taxa is uncertain; yet such information is important for evaluating appropriate options for management of fishing impacts (Goode et al. 2020).

On Chatham Rise there are groups of small seamount features in close geographic proximity, of a broadly similar size, depth range, and elevation, and with varying levels of historical fishing effort. Two such groups are the Graveyard Knolls on the northwest Chatham Rise, and the Andes Knolls on the eastern margin of the Chatham Rise (Figure 1). A number of these features were closed to bottom trawling in 2001 (Brodie & Clark 2003) and the Graveyard seamount features (Figure 2), in particular, provide an opportunity to study post-trawling recovery of benthic communities because they encompass features with a range of past and present fishing histories. Since the closures in 2001, a long-term monitoring programme has been maintained to determine the mechanisms and rates of recovery of benthic fauna on seamounts in the Graveyard complex, with particular interest in 'Morgue' seamount, which was fished heavily until 2001 and has since been closed.

A core hypothesis underlying the monitoring programme is that benthic communities on 'Morgue' will become more similar to those on neighbouring seamounts that have never been trawled as community recovery progresses through regrowth and recolonisation. Analyses of data from the first four surveys in the time series (2001 to 2015), however, have shown little evidence of such change. There has been no change in the overall patterns of community similarity among features and no signs of settlement or recruitment of the main coral species (Clark et al. 2019).

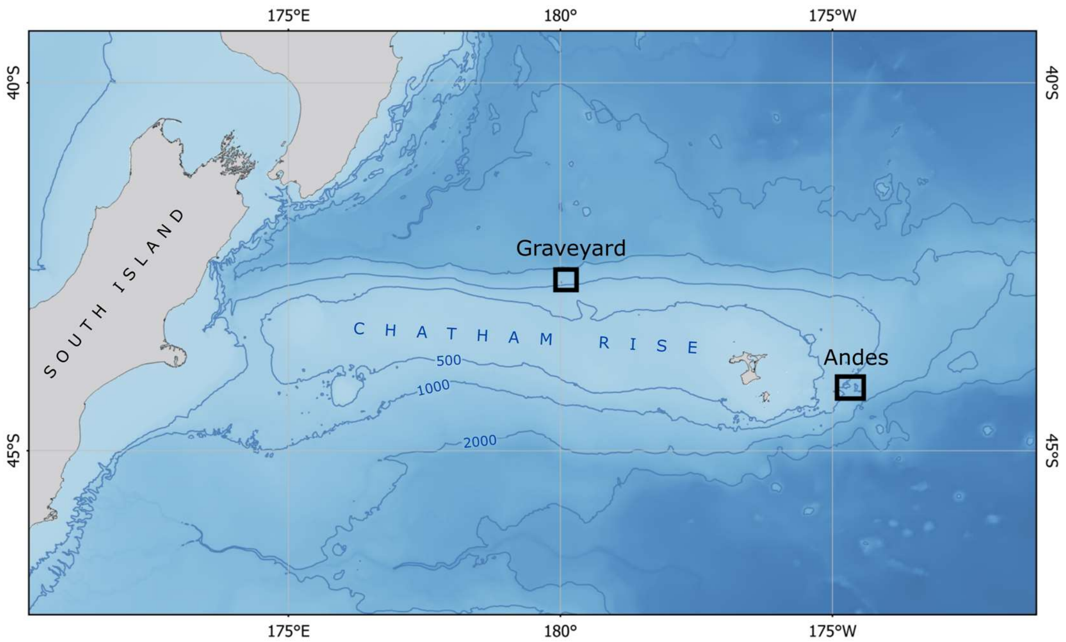

Figure 1: Chatham Rise, to the east of the South Island, New Zealand, showing the location of the Graveyard and Andes Knolls. Depths in metres.

In 2020 a fifth survey in the Graveyard monitoring series was completed (TAN2009, Clark et al. 2021) under the current Fisheries New Zealand project (ZBD202007), extending the period covered to approximately 20 years. Research on seamounts off Hawaii (Baco et al. 2019) suggests that measurable changes in benthic communities occurred in the order of 20–30 years after cessation of trawling, making this fifth survey of the Graveyard series of particular interest. This report combines data from the latest survey with those from the previous four time steps to update the analyses of Clark et al. (2019) to evaluate the current status of the benthic communities on the seamounts.

1.1 Objectives

Overall objective

The overall project objective of ZBD2020-07 was "To understand the nature and time-scale of changes and recovery dynamics of benthic invertebrate communities on seamounts following closure of certain areas to bottom trawling".

Specific objectives

1. To repeat the quantitative photographic survey of benthic invertebrate communities on features of the Graveyard Knolls complex.
2. To assess changes in benthic communities since the first survey in 2001.

2. METHODS

Because the analyses used in this project are identical to those that were applied to the 2001–2015 survey data, much of the core text here has been adapted from Clark et al. (2019).

2.1 Survey area

The Graveyard Knolls consist of about twenty small seamount features ranging in depths from 750 m to 1250 m at their peaks, and from 1050 m to 1600 m at their bases (Figure 2, Table 1). These features lie in close proximity to one another, spanning an area of approximately 140 km^2. Several features in the complex have been the focus of a bottom trawl fishery for orange roughy (*Hoplostethus atlanticus*) since the mid-1990s (Clark 1999). Fishing has been confined mainly to four of the seamounts: Graveyard, Morgue, Scroll, and Zombie; three others: Pyre, Gothic, and Ghoul have had no recorded commercial fishing activity. In 2001, Morgue, Gothic, and Pyre were closed to fishing and dredging (Brodie & Clark 2003). Morgue is of particular interest in relation to understanding the recovery dynamics of benthic habitats following trawl disturbance because it was fished intensively prior to its closure in 2001 and has been protected since that date (Table 1).

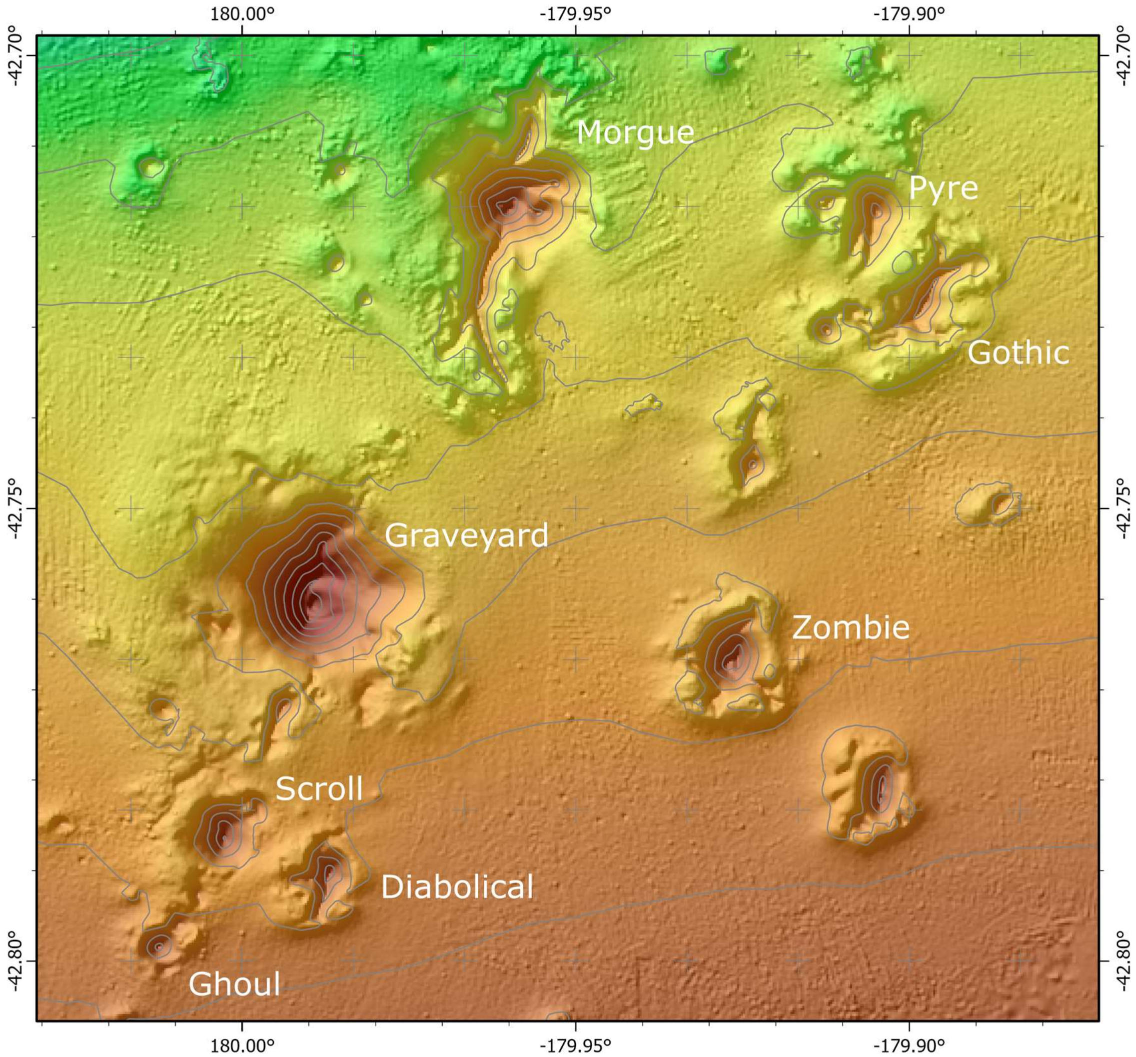

Figure 2: The Graveyard Knolls complex, Northwest Chatham Rise (see Figure 1). The eight named seamounts have been surveyed using seafloor towed camera systems, with a core set of six (Morgue, Graveyard, Diabolical, Ghoul, Zombie, and Gothic) monitored in a time-series study to assess benthic community status in relation to trawl fishing.

Table 1: Physical and fishery characteristics of the surveyed seamount features. Summit depth is depth below sea surface; elevation is height of summit above basal contour; area is area within basal contour. Fishing status shows broad categorisation of trawling intensity before and after the first photographic survey (T1) (refer Clark et al. 2019).

Seamount	Summit depth (m)	Elevation (m)	Area (km^2)	Fishing status Pre-2001; post-2001
Graveyard	748	350	3.1	high; high
Morgue	890	310	2.3	high; closed
Zombie	891	190	0.7	intermediate; low
Diabolical	894	160	0.3	intermediate; low
Gothic	987	170	1.0	very low; very low
Ghoul	935	100	0.1	zero; zero

2.2 Surveys

The Graveyard time series now spans 19 years, with seafloor photographic surveys using towed camera systems having been completed in 2001 (T1), 2006 (T2), 2009 (T3), 2015 (T4), and 2020 (T5). All surveys employed the same methods and all took place in the period from March and August. Four seamounts have been surveyed at all survey points (time steps) and, from T2 onwards, a core set of six seamount features has been surveyed using consistent equipment and methods (Table 2). On all surveys, seabed photographic transects were started at the seamount summit and run down the flanks to the base. At least eight transects were attempted on each seamount, aligned along the cardinal and intercardinal points of the compass (i.e., N, NE, E, SE, S, SW, W, NW) and following the tracks from earlier surveys as closely as possible.

Table 2: Time-series photographic surveys of seamounts in the Graveyard complex, showing seamount name (8 features), the year, time-step code (T1, T2, ...), and voyage identifier (TAN###), and which seamounts were surveyed at each time step (Y = surveyed).

					Survey
Seamount	2001 (T1) (TAN0104)	2006 (T2) (TAN0604)	2009 (T3) (TAN0905)	2015 (T4) (TAN1503)	2020 (T5) (TAN2009)
Graveyard	Y	Y	Y	Y	Y
Morgue	Y	Y	Y	Y	Y
Diabolical	Y	Y	Y	Y	Y
Gothic	Y	Y	Y	Y	Y
Zombie		Y	Y	Y	Y
Ghoul		Y	Y	Y	Y
Pyre		Y			
Scroll		Y			

Camera systems

In 2001, the towed camera frame used carried a black and white video and a colour still-image camera that captured images of 1.5 megapixel resolution triggered manually at about 1 minute intervals, with seabed image location determined by matching depths recorded by a sensor on the camera frame with the vessel track (from Global Positioning System) and seabed topography. From 2006 onwards, surveys used NIWA's Deep Towed Imaging System, DTIS (Figure 3) (Hill 2009, Bowden & Jones 2016).

DTIS is a battery-powered towed camera system that records high definition (HD 1080) colour digital video with simultaneous high definition still images at 15 second intervals. Still-image camera resolution was 5 megapixel (Nikon Coolpix E5000) in 2006 but was upgraded to 10 megapixel (Canon EOS 400D) for surveys in 2009 and 2015, and to 24 megapixel (Nikon D3200) in 2020. Full resolution video and still images were recorded in-camera at the seabed and downloaded on return to the surface. A low-resolution video image with overlaid depth and altitude data was transmitted to the surface in real time enabling control of camera altitude and initial evaluation of seabed substratum types and benthic communities. The seabed position of DTIS was monitored by an acoustic ultra-short baseline (USBL) transponder system (Kongsberg HPR up to T3, upgraded to HiPAP for T4 and T5) and plotted in real time against multibeam echosounder bathymetric maps using OFOP (Ocean Floor Observation Protocol) software.

The target speed on all surveys was 0.5 to 1.0 knots, at a height of 2–3 m above the seafloor but the accuracy and consistency of deployment parameters increased after the T3 survey, when RV *Tangaroa* was fitted with Dynamic Positioning (DP). During all deployments, spatially referenced observations on the occurrence of benthic fauna (at relatively coarse taxonomic resolution) and substratum types were recorded in real time by observers using the OFOP system. These initial observations were logged directly to an onboard database. After each transect, all still images and video files were downloaded and transferred to the ship's server for storage. Ashore, all image files and associated data (navigation files, at-sea observation logs, and conductivity, temperature, and depth data files) were archived to secure server storage and appropriate databases at NIWA.

Direct sampling

Physical samples were taken during early surveys (in particular T1 and T2) to identify specific faunal types to confirm DTIS photographs. A small epibenthic sled (the NIWA 'Seamount Sled' (Clark & Stewart 2016) with an opening of 1 m width) was used, towed at 1 knot for about 5 minutes.

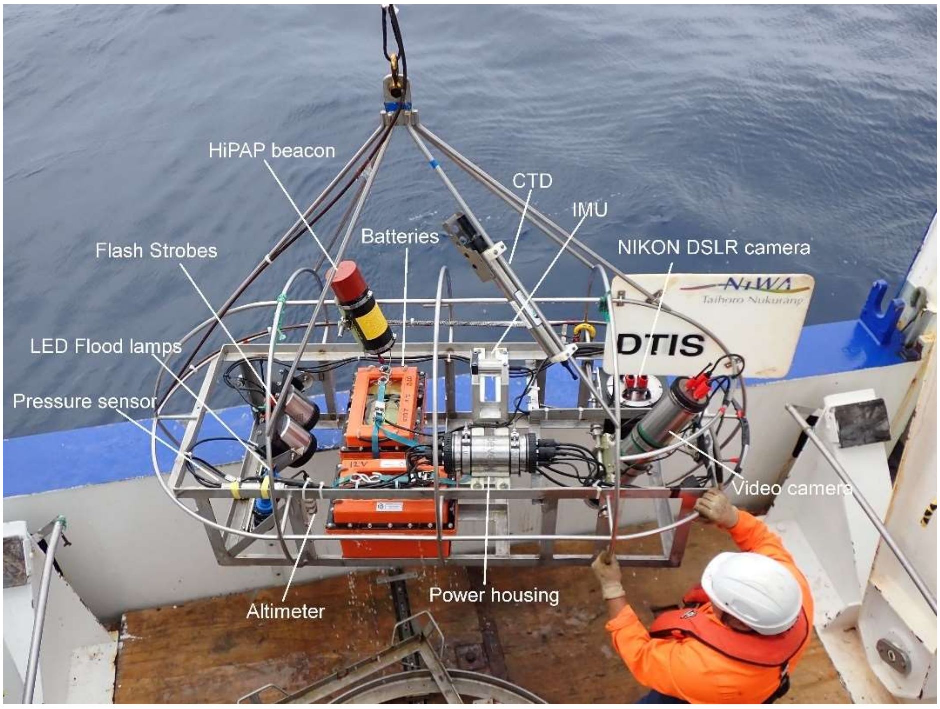

Figure 3: NIWA's Deep Towed Imaging System (DTIS) towed camera, as configured from 2015 to the present.

2.3 Image data

In total, 30 795 seabed images have been collected at the Graveyard Knolls across the five surveys. For each survey, an initial subset of the available images was selected based on two criteria: being within the basal polygon of a seamount (Table 3) and being of acceptable image quality. Following Clark et al. (2019), analyses were restricted to images with seabed area in the range of 1.5 to 8 m^2 to minimise the influence of differences in image resolution between time steps.

Image transects were first truncated at the basal polygon of each seamount feature, as defined in the NIWA SEAMOUNT database (Rowden et al. 2008, Clark et al. 2022), in a Geographic Information System (GIS, ArcGIS Pro 2.8.3). Images from the southwest spur of 'Morgue' Seamount (see Figure 4) were also excluded because this part of the seamount is too steep for trawlers to operate on (Clark et al. 2010a) and thus has a very different disturbance history from the rest of the seamount. All images within these spatial bounds were then assessed for acceptable exposure, focus, and visibility of the seabed (see Clark et al. (2010a) for details). This process yielded a subset of 12 725 images of sufficient quality for quantitative analysis across all surveys, including 2497 from the most recent survey, TAN2009. With the resources available, it was not practicable to analyse all these images. So, for all surveys except T1, in which there were relatively few images, every fourth acceptable image along each transect was selected. This compromise ensured that the full length of each transect was represented in analyses and is expected to capture a large proportion (more than approximately 60%) of the biological diversity information visible in the imagery (Bowden et al. 2020).

Table 3: Seabed images: 'Images assessed' shows total numbers of images within basal polygons and 'Images used' shows the number of images in the subsets selected for analysis, each of which meets the criteria of having acceptable image quality and imaged seabed area in the range 1.5 m² to 8.0 m².

Seamount	Voyage	Time step	Number of transects	Images assessed	Images used	Average area of used images (m^2)	SD image area
Diabolical	TAN0104	T1	7	57	18	4.1	1.74
	TAN0604	T2	8	427	80	4.9	1.65
	TAN0905	T3	8	214	97	4.3	1.88
	TAN1503	T4	8	381	152	3.3	1.32
	TAN2009	T5	8	363	180	4.7	1.83
Ghoul	TAN0104	T1					
	TAN0604	T2	9	394	37	5.3	1.38
	TAN0905	T3	4	155	35	4.7	1.82
	TAN1503	T4	8	289	95	2.6	0.85
	TAN2009	T5	4	217	128	4.5	1.84
Gothic	TAN0104	T1	8	72	13	3.6	1.67
	TAN0604	T2	8	466	78	4.7	1.68
	TAN0905	T3	10	342	193	4.3	1.65
	TAN1503	T4	9	641	254	2.8	1.16
	TAN2009	T5	8	455	202	4.8	1.73
Graveyard	TAN0104	T1	4	93	32	4.3	1.93
	TAN0604	T2	8	997	206	5.0	1.74
	TAN0905	T3	9	505	256	4.1	1.75
	TAN1503	T4	8	708	348	2.7	1.05
	TAN2009	T5	8	537	331	4.8	1.88
Morgue	TAN0104	T1	8	60	35	3.9	1.82
	TAN0604	T2	16	1 482	389	4.9	1.82
	TAN0905	T3	10	1 081	443	3.9	1.67
	TAN1503	T4	8	612	274	2.8	1.11
	TAN2009	T5	12	528	352	4.5	1.73
Zombie	TAN0104	T1					
	TAN0604	T2	8	578	193	5.2	1.72
	TAN0905	T3	8	305	136	4.1	1.71
	TAN1503	T4	8	369	164	2.6	0.99
	TAN2009	T5	8	397	196	4.7	1.84

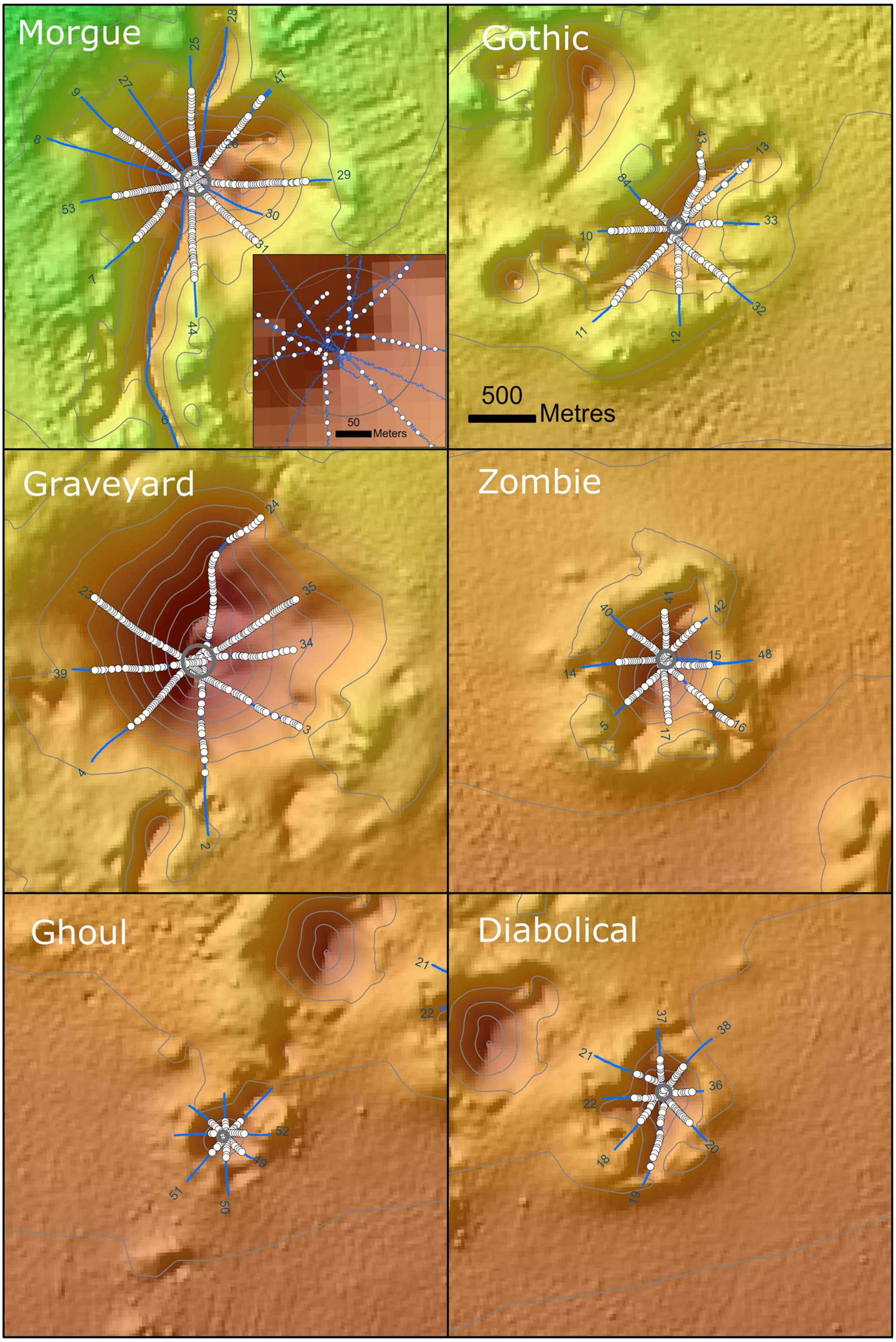

Figure 4: The six seamount features in the Graveyard Knolls complex monitored for benthic community status, showing DTIS transect lines (blue lines) and analysed image locations (white discs) from the latest survey in 2020 (TAN2009, 'T5'). Scale bar in top right panel applies to all main panels; grey circles indicate the 'summit' areas defined for each seamount, and inset for 'Morgue' shows detail of summit area as an example of the level of overlap in transect lines at the summit.

The seabed area (in square metres) framed by each image was measured using ImageJ software by reference to a pair of fixed parallel laser points, 20 cm apart, projected onto the seabed from the camera vehicle. No lasers were fitted to the camera used in 2001 (T1), so image areas for this survey were estimated from camera altitude and imaging system parameters (Bowden & Jones 2016). Substrate type, as one of eight categorical descriptors (bedrock, boulders, cobbles, gravel, sand, muddy sediment, 'coral rubble' (broken coral fragments and remains covering the seabed), and 'intact coral matrix' (upright intact branching stony coral matrix structure) was recorded (in ImageJ) as percentage cover of seabed imaged area. All visible benthic invertebrate fauna were identified to the finest taxonomic level possible from the imagery and recorded as counts of individuals. All image analyses in all years were undertaken by the same analyst (author RS). Colonial reef-forming stony corals were recorded as both a substrate type (intact coral matrix) and as counts of individual 'live heads', which are distinguishable through their distinct colouration (Williams et al. 2010). Taxonomic determinations were made by reference to both the camera imagery and physical specimens that were collected during the surveys using an epibenthic sled and photographed live under controlled conditions at sea. Specialist taxonomists were consulted wherever necessary to confirm identifications. Counts of individual fauna were standardised, for each image, to numbers of individuals per 5 m^2 of seabed. Where there were uncertainties in taxonomic identifications across the five surveys, they were pooled to coarser taxonomic level. For example, branching stony corals and sponges were often identified to species or class but ultimately were amalgamated into Stony corals and Porifera, respectively.

Individual images were categorised by seamount name, the time step at which they were collected (T1, T2, T3, T4, or T5), and their spatial location on the feature; either 'summit', if within a circle of radius 0.3 x seamount elevation centred on the seamount summit, or 'basal' for all other images. The 'summit' sector is particularly useful for comparisons among seamounts because the summit is comparable in its topographic form across all seamounts and because trawl fishers aim to land their gear on or near the summit and run downwards over the flanks. Thus, the summit sector is likely to be the most highly impacted area on all seamounts, and, because we ran camera transects in the same way, it also has the greatest spatial overlap of coverage between time steps. Thus, the summit sector is an area in which hypothesised effects of trawling are most likely to be detected.

Thus, our final dataset for analysis consisted of images with seabed areas between 1.5 m^2 and 8 m^2 and categorised by three factors: Seamount (Diabolical, Ghoul, Gothic, Graveyard, Morgue, Zombie); Time step (T1, T2, T3, T4, T5); and Sector (Basal, Summit) (Table 2). We ran all subsequent analyses twice; first on the full dataset ('Whole seamount', i.e., all image data from within the seamount basal polygons) and, second, on a subset of data from Summit sector images only.

2.4 Fishing intensity

Commercial fisheries bottom trawl data for all years up to, and including, 2020 were sourced from the Ministry for Primary Industries *trawl* data base. Trawls were assigned to individual seamount features on the basis of start position, depth, direction, and duration, and the intensity of bottom trawling on each seamount feature was then calculated as the Fishing Effects Index (O'Driscoll & Clark 2005), which summarises information on the density of trawling on a feature, taking into account the proportion of its total seabed area affected by trawling and the number of tows in a given direction. FEI was calculated for each seamount in each of the five inter-survey periods separately, i.e., 1994 to 2001 (up to T1), 2001 to 2006 (T1 to T2), 2006 to 2009 (T2 to T3), 2009 to 2015 (T3 to T4), and 2015 to 2020 (T4 to T5) (Table 4). This includes several bottom trawls on 'Morgue' which, although closed to commercial fishing, was sampled for separate stock assessment research. On the basis of earlier analyses (Clark et al. 2010a), trawling impacts were also summarised by four FEI categories: High ($FEI > 10$); Intermediate ($FEI\ 0.05 \leq FEI \geq 10$); Low/un-trawled ($FEI < 0.05$); and Closed to fishing (FEI reduced towards 0).

Table 4: **Summary of bottom trawl fishing effort and catch levels on the six core seamounts in the Graveyard surveys from 2001 (T1) to 2020 (T5), showing, for each period: number of trawls (effort), orange roughy catch (tonnes), and Fishing effects Index (FEI, rounded up to nearest integer).**

		Period				
Seamount	metric	up to T1	T1 to T2	T2 to T3	T3 to T4	T4 to T5
Graveyard	effort	1 459	575	426	227	267
	catch	7 200	3 120	2 400	960	297
	FEI	479	180	95	91	68
Morgue	effort	791	2	0	6	3
	catch	3 550	6	0	45	49
	FEI	252	0	0	1	0
Zombie	effort	35	30	12	0	1
	catch	170	35	12	0	0
	FEI	11	22	3	0	0
Diabolical	effort	3	8	5	0	2
	catch	1	4	3	0	0.3
	FEI	0	1	1	0	0.42
Gothic	effort	4	0	0	0	0
	catch	1	0	0	0	0
	FEI	0	0	0	0	0
Ghoul	effort	0	0	0	0	0
	catch	0	0	0	0	0
	FEI	0	0	0	0	0

2.5 Data analysis

Analyses under this project extend the univariate and multivariate analyses described by Clark et al. (2019) for the T1 to T4 analyses, to include data from the fifth time step, T5 (TAN2009 survey). All analyses were run using the same routines and code in R (R Core Team 2021) and PRIMER 7 (Clarke et al. 2014), which were structured to quantify differences in community structure among seamounts within a given time step, and to illustrate how these differences changed from one time step to the next. Differences within time steps are the focus here because increases in the optical resolution and consistency of deployment altitude of the camera system over time are difficult to quantify and are likely to underlie a progressive increase in faunal abundances through the time series. Quantification of differences in community composition among seamounts within time steps, by contrast, ensures that all data used in the formal analyses are directly comparable and enables changes over time to be assessed subsequently as changes in the relative similarity among seamounts from one time step to the next (Clark et al. 2019). The analyses are in three stages: comparison of the occurrence of intact stony coral matrix among seamounts in relation to trawl history, comparisons of univariate metrics of community structure, and multivariate comparisons of community structure.

Coral matrix in relation to trawling

The occurrence of intact coral matrix in individual images was recorded as percentage of imaged area, calculated in ImageJ. Average (±1 se) intact coral cover per image across all images for each seamount at each time step was then plotted against cumulative FEI values, with separate graphs for basal and summit image sets.

Univariate community metrics

In previous analyses (BEN2014-02 Final Research Report to Fisheries New Zealand), an extensive range of univariate community structure metrics was generated, including multiple metrics of diversity, evenness, and richness. While there were subtle differences among different metrics in these analyses, the broad patterns were the same in all, so, again following the logic of Clark et al. (2019), patterns are represented here by only two metrics: abundance (N) calculated as the total number of individuals standardised to an area of 5 m^2 of seafloor, and taxon richness as the expected number of taxa in a random sample of 50 individuals (ES50, based on actual counts of individuals rather than the standardised values). Values of these metrics were compared among seamounts within time steps using boxplots and one-way analysis of variance (ANOVA) with Tukey HSD multiple means comparisons at 95 % confidence level (R function *TukeyHSD*). There were too few samples (images) at T1 to support formal statistical comparisons.

Multivariate community comparisons

Comparisons of multivariate community structure were developed to track relative changes in community structure of the six seamounts over time. Analyses were based on Bray-Curtis similarities among individual images, calculated from square-root transformed standardised abundance data. Data transformations ranging from none to presence-absence were explored and because multivariate patterns were similar in all cases, square-root was selected to allow taxon densities to influence results while down-weighting the influence of those with very high densities. To enable visualisation of similarities in two-dimensional ordinations, the matrix of Bray-Curtis similarities was first used to calculate multivariate centroids for sets of images within each of two combinations of factors: (1) Seamount basal polygon × Time step and (2) Seamount summit sector × Time step. Non-metric multidimensional scaling (nMDS) ordinations were then produced for each of these sets of centroids, based on similarities among centroids, to visualise similarities among communities on each seamount within and between time steps, and with fishing intensity superimposed as bubble plots to illustrate relationships between community similarity and fishing history. In these plots, FEI was represented as $\log_{10}$(FEI), rather than raw values, in part to enable graphical representation but also because previous analyses have shown that significant reductions in intact coral matrix occur at very low FEI levels and thus are appropriately represented on a log scale (Clark et al. 2010a, Clark et al. 2019). Where changes of interest were indicated by the MDS, the taxa contributing to differences between seamount features, or between time steps for a single seamount, were examined using the Similarity Percentages routine (SIMPER, Clarke 1993) in PRIMER 7.

Fine-scale observations of branching stony coral taxa

The whole-community analyses described above were based on counts of taxon occurrences within images. During the image analysis phase of the work, however, observations were also recorded about occurrences of branching stony coral colonies. Colonies with fewer than 10 visible polyps were identified separately from larger intact colonies because smaller colonies were thought to potentially represent recent recruitment events, whereas larger colonies could represent remnant patches of stony coral reef that were unimpacted by bottom trawling. These observations were focused on Morgue, because this feature is of central interest in terms of recovery from trawl disturbance and more transects have been conducted on it over the time series of surveys than on the other features, with the aim to increase the likelihood of detecting small-scale changes in community distribution and branching stony corals.

Small branching stony coral colonies were first confirmed in images from the 2020 (T5) survey but exploiting the synergies of a parallel doctoral study (co-author SG), which is focused primarily on Morgue, it was possible to put considerable additional effort into quantifying their presence. Thus, rather than only every fourth image along a transect being analysed, as has been the practice throughout the time series to date, every available image from Morgue was examined in detail, for all transects from T1 and T2 and 4 of 8 transects from T3, T4, and T5; 20 additional images were selected for annotation from the remaining transects of T3, T4, and T5.

3. RESULTS

3.1 Image analysis data

The subset of images selected for use in analyses provided good representation of summit and flank areas of each seamount in each time step, albeit with more limited coverage at T1. In total, 171 taxa were recorded in the images, at identification levels ranging from species-level through coarser taxonomic levels to Phylum, and operational taxonomic descriptors (e.g., solitary scleractinian corals). These taxa were then refined by removal of non-benthic taxa followed by aggregation of some of the more detailed identifications to enable comparison with data from earlier surveys, in which finer taxonomic assignments were either not possible because of image resolution or were inconsistent because of variations in image quality within surveys. This yielded a final dataset for analyses consisting of quantitative counts of 38 taxa (Table 5).

Table 5: Benthic invertebrate taxa quantified in seafloor imagery from voyage TAN2009 and used in comparisons with previous surveys of the Graveyard Knolls. **(Continued on next page)**

Phylum	Class	Sub class	Order	Family	Taxon
Annelida	Polychaeta				Polychaetes
Arthropoda	Malacostraca	Eumalacostraca	Decapoda (Anomura)	Galatheidae	Galatheoidea
				Paguridae	Pagurids
			Decapoda (Caridea)		Prawns
			Isopoda		Isopods
	Maxillopoda	Thecastraca			Barnacles
	Pycnogonida		Pantopoda		Pycnogonids
Bryozoa					Bryozoans
Chordata	Ascidiacea				Ascidians
Cnidaria	Anthozoa	Hexacorallia	Actiniaria		Anemone
				Caryophylliidae	Scleractinia live colony
				Caryophylliidae	Scleractinia solitary
				Isididae	Isididae
				Primnoidae	Narella
			Antipatharia		Antipatharia
			Zoantharia		Zooanthidae
				Epizoanthidae	Epizoanthidae
		Octocorallia	Alcyonacea		Alcyonacea
				Alcyoniidae	*Anthomastus*
				Primnoidae	*Tokoprymno*
				Primnoidae	Primnoidae
					Gorgonian
			Pennatulacea		Pennatulacea
	Hydrozoa	Hydroidolina			Hydroid
			Anthoathecata	Stylasteridae	Stylasteridae

Table 5: *continued.*

Phylum	Class	Sub class	Order	Family	Taxon
Echinodermata	Articulata	Bourgueticrinida			Crinoid (stalked)
		Comatulida			Crinoid (comatulid)
	Asteroidea		Brisingida	Brisingidae	Brisingid asteroids
					Asteroids
	Echinoidea				Echinoids
	Holothuroidea				Holothurians
	Ophiuroidea				Ophiuroids
Echiura					Echiurans
Foraminifera	Monothalamea			Xenophyophoroidea	Xenophyophores
Mollusca	Gastropoda				Gastropods
	Polyplacophora				Polyplacophora
	Scaphopoda				Scaphopods
Porifera					Porifera

3.2 Intact branching coral matrix in relation to bottom trawling

The occurrence of intact branching stony coral matrix declined markedly with increases in cumulative FEI across all time steps and there was no discernible change with the addition of T5 data (Figure 5Figure 1). This pattern was maintained for both whole-seamount and summit datasets, with no increase in observed intact branching coral matrix cover on Morgue at T5. The un-trawled (low FEI) seamounts Ghoul and Gothic had consistently higher cover of intact branching stony coral matrix than the highly trawled Graveyard (high FEI throughout) and Morgue (high FEI before closure) seamounts, with Diabolical and Zombie seamounts (intermediate FEI) between these two extremes. These relationships were more pronounced when only the seamount summits were compared, with cover of intact branching coral matrix on the summit of Gothic averaging nearly 100%.

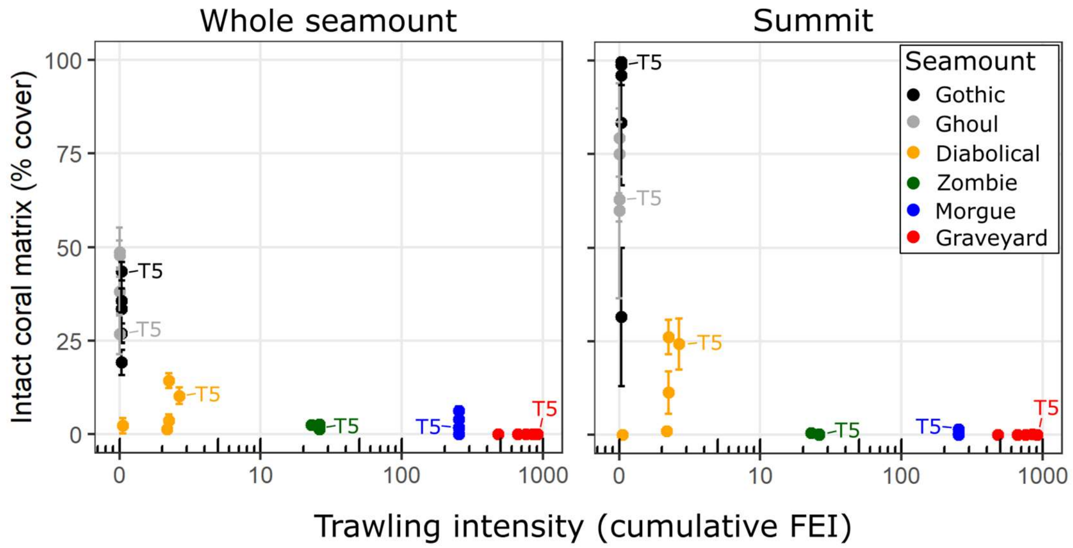

Figure 5: Seafloor cover of intact branching stony coral matrix (average percent cover in individual still images; error bars ±1 se) on six seamount features in the Graveyard Knolls complex in relation to cumulative trawl pressure (Fishing Effects Index, FEI) at five survey times: 2001 (T1); 2006 (T2); 2009 (T3); 2015 (T4); and 2020 (T5). Data plots are colour-coded by seamount feature (see legend), with plots for each seamount at each survey time step (4 for Zombie, 5 for each of the other features). For clarity, only the T5 plots are labelled. Left panel; data for all images within seamount basal polygons, right panel; summit images only.

3.3 Univariate community structure patterns

In whole-seamount analyses, patterns of abundance (N) and taxon richness (ES50) among seamount features at T5 were similar to those observed at the preceding time step (T4) but less distinct in statistical comparisons in terms of the number of significant differences (Figure 6). From T1 to T4, both N and ES50 were significantly higher on the two seamounts with the lowest trawling intensities (Ghoul and Gothic) than on trawled or previously trawled seamounts. At T5, the highest values of N and E50 were still recorded on Ghoul and Gothic and the lowest values on Graveyard. However, while Graveyard again had the lowest taxon richness, its abundance was not significantly different to that on Diabolical, both having lower abundances than the other four seamount features. On Morgue, values for both abundance and taxon richness were significantly higher than those on Graveyard, as was the case at T4, and were not statistically distinct from those on the un-trawled features Gothic and Ghoul.

For summit areas at T5, patterns among seamounts were also similar to those at T4. Abundance was significantly lower on Graveyard than on any other seamount and was highest across the least-trawled features Ghoul, Gothic, Diabolical, and Zombie, with values for Morgue intermediate between these groupings. Taxon richness was significantly higher on the least-trawled seamounts (Gothic, Ghoul, and Diabolical) than on the most-trawled (Zombie, Morgue, and Graveyard).

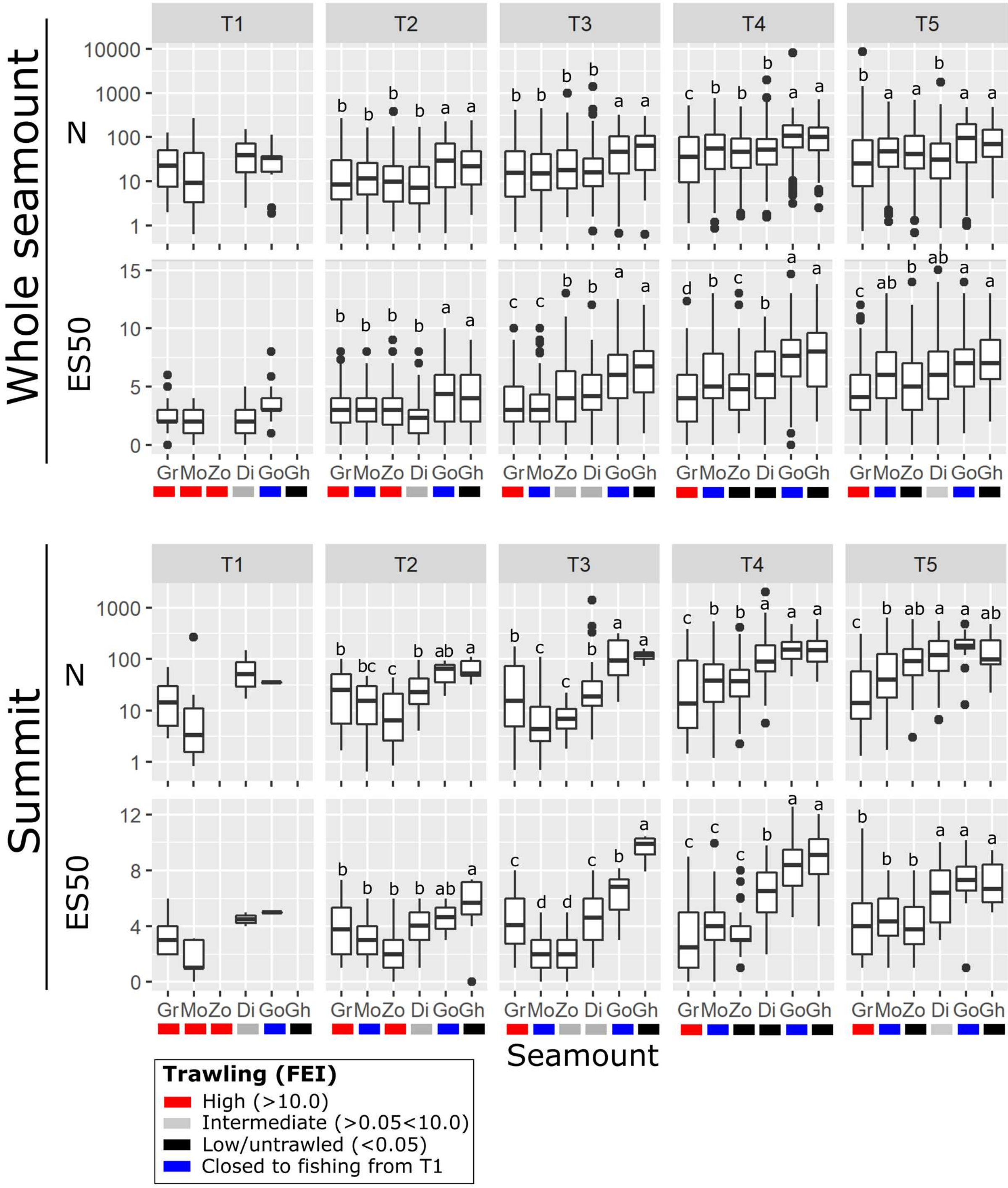

Figure 6: Univariate metrics of community structure; abundance (N) and taxon richness (ES50) calculated for all images within seamount basal polygons (Whole Seamount) and images within summit polygons only (Summit) at each of five survey times (time steps T1 to T5). Seamount features are: Graveyard (Gr), Morgue (Mo), Zombie (Zo), Diabolical (Di), Gothic (Go), and Ghoul (Gh). Box-and-whisker plots show median (central band) and 25th and 75th percentiles (top and bottom of boxes), whiskers extend to largest and smallest values no more than 1.5 times the interquartile range, and dots show outliers. Letters above each plot indicated statistically similar groupings from one-way analysis of variance (ANOVA) with Tukey HSD multiple comparison of means within each time step; metrics are not significantly different (*P* >0.05) among seamounts that share the same letter. Figure updated from Clark et al. (2019).

3.4 Multivariate community structure analyses

The nMDS ordinations based on centroids of benthic community structure for each seamount feature at each time step show broadly similar patterns for both whole-seamount and summit analyses (Figure 7). At each time step, the two low/un-trawled seamounts, Gothic and Ghoul, occupy one side of the ordination space, with the persistently trawled (high FEI) feature, Graveyard, at the opposite side and the two seamounts with intermittent trawling (intermediate or high FEI from T1 to T3, then low at T4) Zombie and Diabolical, lying between these extremes. It is also conspicuous in these ordinations that the benthic community structure of Graveyard is less variable through the T1 to T5 trajectory for both whole-seamount and summit ordinations than is the case for the other seamounts.

Morgue, on which previously high trawling intensity ceased at T1, lies close to Graveyard at all time steps in the summit-sector analysis and follows a similar trajectory from T4 to T5, indicating no detectable recovery of the benthic community in this sector of the seamount. In the whole-seamount MDS, however, the trajectory for Morgue lies closer to that of the intermediate-trawling features Zombie and Diabolical after T2 but at T5 deflects towards the right of the ordination space, indicating increased similarity with communities on the un-trawled seamount features, Gothic and Ghoul, and decreased similarity with Graveyard, on which trawling has continued throughout the time series.

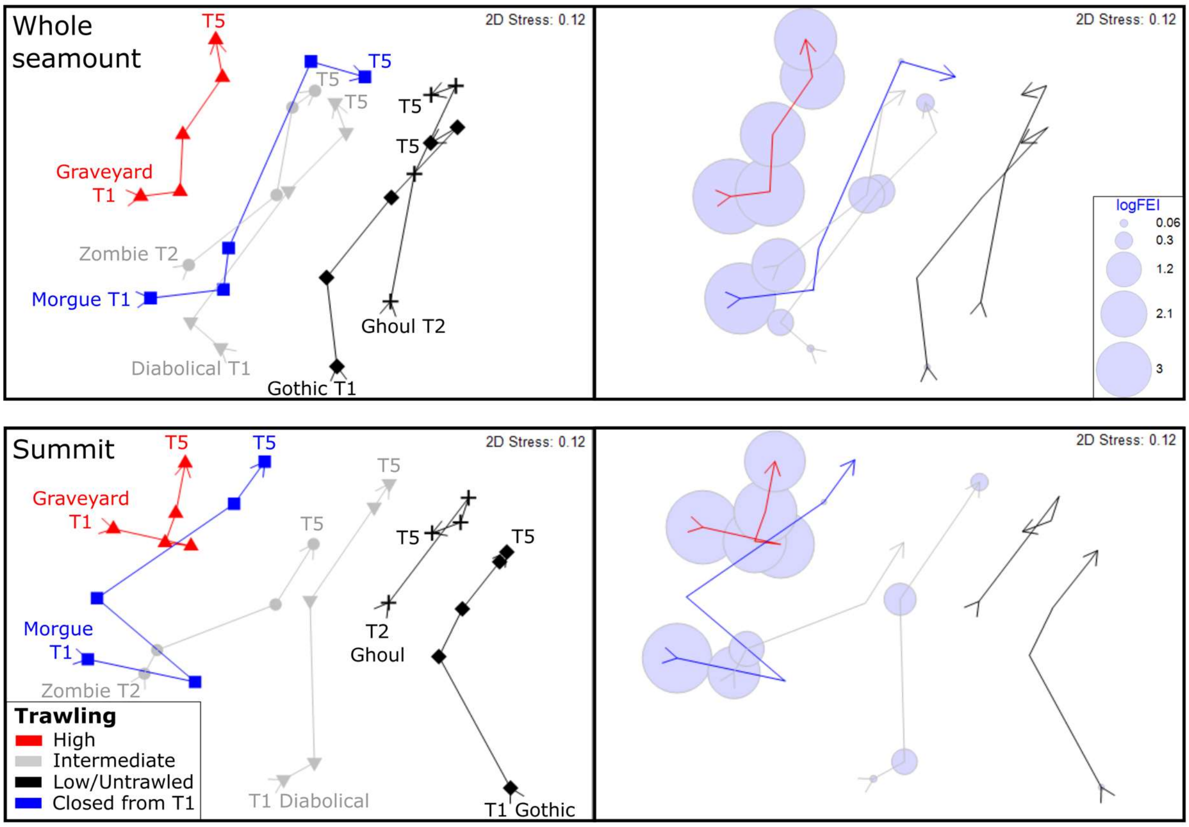

Figure 7: Ordinations (nMDS) illustrating benthic community change across time steps T1 to T5 and in relation to bottom trawl history: top panels, centroids of all images within each seamount basal polygon ('whole seamount'); bottom panels, ordination using centroids of images within only the summit sectors. Right and left windows show the same ordination: left shows seamount identities, time steps, and categorical indication of overall bottom trawl history (colour legend); right shows trawl intensity at each time step as log_{10} values of the Fishing Effects Index (logFEI) superimposed as bubble plots. Ordinations represent Bray-Curtis similarities calculated from square-root transformed abundance data derived from seafloor still photographs. Figure updated from Clark et al. (2019).

A SIMPER analysis to identify the taxa contributing to this whole-seamount shift in the Morgue trajectory at T5 (Table 6) showed changes in the densities of several taxa, with the most influential of these being increases in the abundances of comatulid crinoids (contributing 11.8% of the total dissimilarity of 64.55% between T4 and T5 for Morgue), pagurid crabs (7.8%), galatheids (7.0%), ophiuroids (6.2%), prawns (5.4%), and polychaetes (5.2%) and decreases in the abundances of stylasterid hydrocorals (11.6%), ascidians (8.1%), sponges (7.8%), and anemones (6.2%). Pairwise SIMPER comparisons among seamounts at T5 indicated that changes in taxon densities on Morgue at T5 were also important in defining the position of Morgue in relation to Gothic, Ghoul, and Graveyard in the ordination (Table 7). For example, comatulid crinoids were abundant on both Gothic and Ghoul (average densities at T5; 27 and 7.6 individuals per 5 m^2, respectively) and the average density of these taxa on Morgue nearly doubled from T4 to T5 (from 2.8 to 4.7 individuals per 5 m^2), while, by contrast, they occurred at very low densities on the trawled seamount, Graveyard (T5; 0.1 individuals per 5 m^2). Similarly, densities of anemones were low on Gothic and Ghoul at all time steps (average at T5; 0.1 individual per 5 m^2) and the average density of this taxon on Morgue decreased from T4 to T5 by nearly half (from 0.13 to 0.07 individuals per 5 m^2).

Table 6: SIMPER analysis detailing taxa contributing to changes in benthic community structure on Morgue seamount from 2015 (T4) to 2020 (T5). Total dissimilarity between time steps was 64.55 %. Abundances are shown as the average number of individuals per image (standardised to individuals 5 m^{-2}), back-transformed from square-root transformed data used for the analysis. Av.Diss; average dissimilarity across all images, Diss/SD; average dissimilarity divided by the standard deviation of similarity (a measure of consistency of influence), Contrib%; contribution to overall community dissimilarity.

	Average abundance (indivs. 5 m^{-2})				
Taxon	Morgue T4	Morgue T5	Av.Diss	Diss/SD	Contrib.%
Crinoids (comatulid)	2.77	4.67	7.62	1.12	11.8
Stylasteridae	2.01	1.63	7.52	1.02	11.64
Ascidians	1.41	0.00	5.2	0.92	8.06
Pagurids	0.81	1.26	5.06	0.93	7.84
Porifera	1.52	1.22	5.04	1.03	7.81
Galatheoidea	0.05	0.43	4.55	1.01	7.05
Anemone	0.13	0.07	4.02	0.9	6.23
Ophiuroids	0.04	0.21	3.98	0.98	6.17
Prawns	0.04	0.05	3.46	0.86	5.36
Polychaetes	0.02	0.07	3.34	0.8	5.17

Table 7: SIMPER analysis detailing taxa contributing to dissimilarity in benthic community structure between Morgue (trawling ceased in 2001), Gothic and Ghoul (un-trawled), and Graveyard (still trawled) at the 2020 time step (T5). Details as for Table 6. (Continued on next page)

	Average abundance (indivs. 5 m^{-2})				
Taxon	Morgue T5	Gothic T5	Av.Diss	Diss/SD	Contrib.%
Crinoids (comatulid)	4.67	27.02	7.61	1.16	12.35
Stylasteridae	1.63	3.52	6.45	1.06	10.47
Porifera	1.22	3.95	4.53	1.04	7.35
Pagurids	1.26	0.13	4.43	0.94	7.19
Galatheoidea	0.43	0.28	4.06	1.04	6.59
Ophiuroids	0.21	0.72	4.05	1.1	6.57
Stony corals	0.00	0.60	3.62	0.88	5.87
Anemone	0.07	0.11	3.38	0.93	5.49
Prawns	0.05	0.15	3.14	0.92	5.1
Hydroid	0.03	0.07	3.06	0.85	4.97
Polychaetes	0.07	0.00	2.64	0.75	4.29

Table 7: continued.

Taxon	Average abundance (indivs. 5 m^{-2}) Morgue T5	Ghoul T5	Av.Diss	Diss/SD	Contrib%
Stylasteridae	1.63	10.04	7.05	1.25	11.07
Crinoids (comatulid)	4.67	7.59	6.39	1.15	10.03
Pagurids	1.26	0.50	4.17	1.06	6.55
Porifera	1.22	3.84	4.1	1	6.44
Stony corals	0.00	0.50	3.86	0.92	6.06
Galatheoidea	0.43	0.19	3.72	1.09	5.84
Ophiuroids	0.21	0.05	3.31	1.05	5.2
Hydroid	0.03	0.15	3.2	0.95	5.03
Anemone	0.07	0.01	2.75	0.84	4.32
Prawns	0.05	0.01	2.58	0.9	4.06
Anthomastus	0.00	0.13	2.51	0.87	3.95
Polychaetes	0.07	0.00	2.47	0.75	3.89
Isididae	0.00	0.11	2.41	0.79	3.79

Taxon	Average abundance (indivs. 5 m^{-2}) Morgue T5	Graveyard T5	Av.Diss	Diss/SD	Contrib%
Crinoids (comatulid)	4.67	0.01	9.09	1.13	12.74
Stylasteridae	1.63	2.77	8.76	1.07	12.29
Porifera	1.22	1.46	6	1.01	8.4
Pagurids	1.26	0.81	5.74	0.88	8.04
Hydroid	0.03	0.28	5.09	0.87	7.14
Galatheoidea	0.43	0.00	4.96	1.01	6.95
Ophiuroids	0.21	0.00	4.09	0.9	5.73
Foraminifera	0.01	0.02	3.52	0.7	4.93
Anemone	0.07	0.00	3.31	0.75	4.65
Prawns	0.05	0.00	3.17	0.8	4.44

3.5 Fine-scale observations of branching stony coral taxa

Areas of live, intact branching stony coral colonies were identified in images from all the surveys on Morgue, which are likely to represent remnant reef patches unimpacted by trawling (Figure 8). The species identified were *Enallopsammia rostrata* (observed in 1 image), *Solenosmilia variabilis* (observed in 89 images), and *Madrepora oculata* (observed in 69 images). These areas of live intact coral are significant because they could provide sources of larvae to help seed current and future recovery of branching stony corals on Morgue, as well as the surrounding seamounts. Overall, the total area of intact stony coral reef was observed to increase over time (Figure 9); however, this could be due to the increase in sampling effort with time (slower towing speed) rather than representing a real increase in reef area, as these species are known to have extremely slow growth rates. The reef patches were found to occur on the north and east sides of Morgue near two small pinnacles and on a steep ridge on the south side of the seamount. The steep, rugged terrain of the pinnacles and south ridge would likely be difficult to trawl and therefore may have acted as refuge areas for these stony coral species.

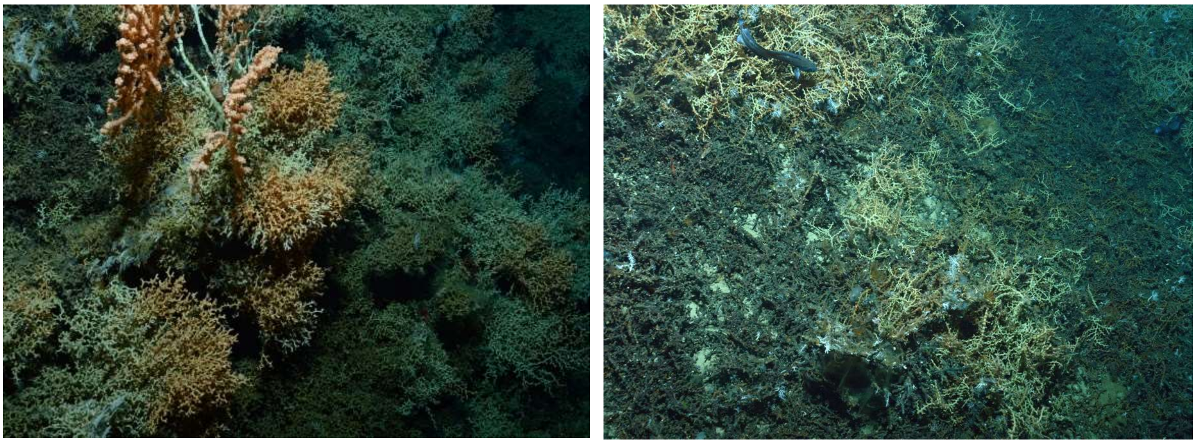

Figure 8: Remnant patches of live *Solenosmilia variabilis* (left) and *Madrepora oculata* (right) coral on the eastern flank of Morgue near a small secondary cone.

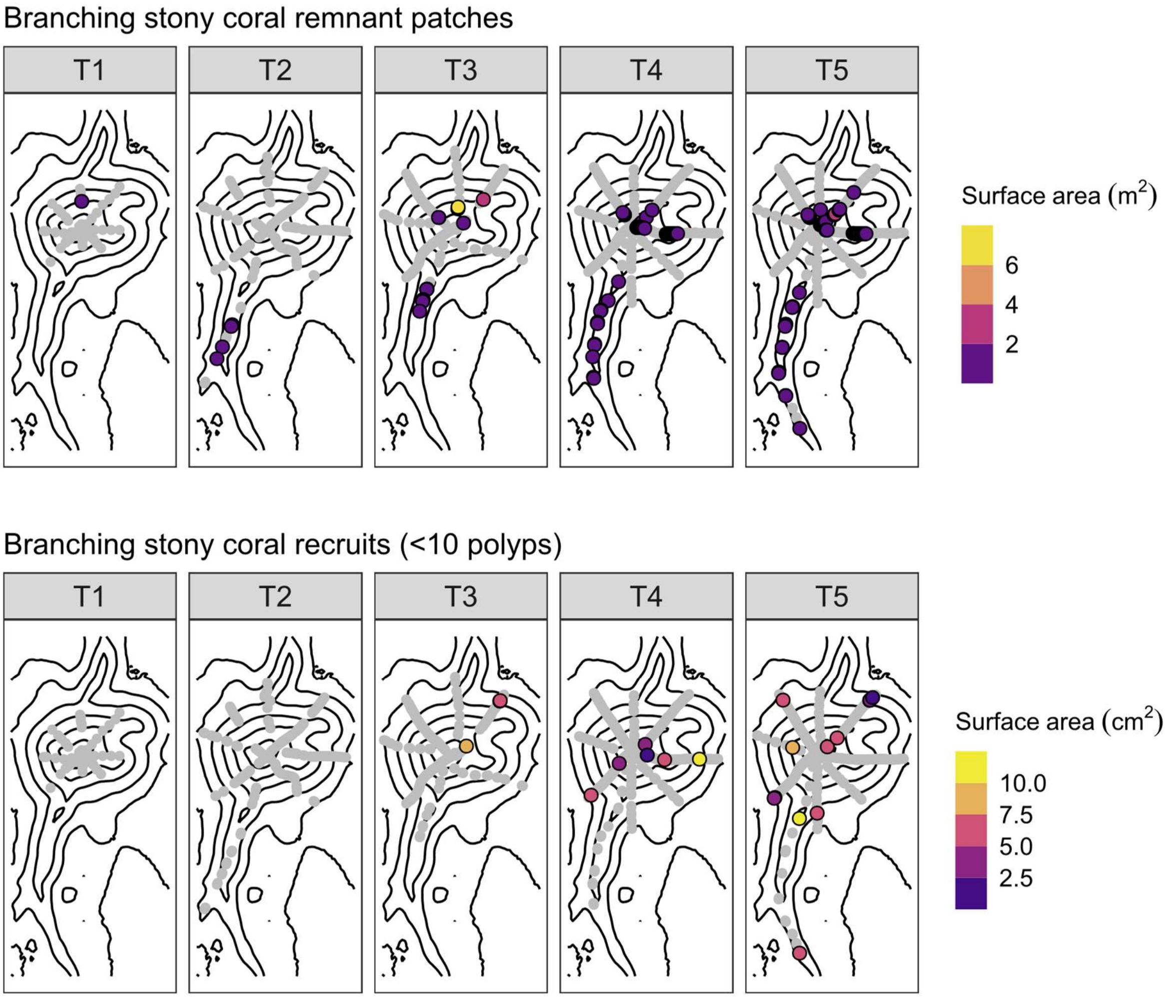

Figure 9: Visible surface area of branching stony coral remnant patches (top) and recruits (bottom) recorded in seafloor images from the 20-year time series of surveys on Morgue seamount. Grey points denote images that were analysed where stony corals were not detected; coloured points denote images where stony corals were detected. Recruits were classified as stony corals with fewer than 10 visible polyps. 'Surface area' is horizontal planar area, not 3-dimensional). Note the different units used to display surface area: m^2 and cm^2.

Small branching stony coral colonies, which are likely to represent either regrowth from trawl-damaged fragments or new recruitment (Figure 10), were recorded in images from Morgue at T3 (2009), T4 (2015), and T5 (2020). At T3, these small colonies were detected in 3 images, at T4 in 6 images, and at T5 in 13 images (lower panel of Figure 9). The lack of observed branching stony coral recruits at T1 and T2 could be partially due to the lower image quality in these surveys as well as lower sampling effort. However, the increase in the number of observed recruits from T4 to T5 may reflect recent recruitment events because these data are more comparable in terms of sampling effort and image quality. The colonies ranged overall in length from approximately 2.5 to 3.8 mm, which suggests they are between 2 and 7 years of age, based on published linear growth rate estimates that range from 0.53 to 3.07 mm per year (Fallon et al. 2014, Gammon et al. 2018). The visible surface area of the colonies ranged from 1.1 to 10.8 cm^2 overall, further indicating the colonies could vary in their ages. Indeed, several recruits observed in the northeast transect near the base of Morgue are smaller in size compared with those observed closer to the summit at T4 and T5, suggesting these individuals may have settled more recently than those observed near the summit. Together, these findings indicate that several recruitment events may have occurred on Morgue since bottom trawling was prohibited in 2001.

Stylasterid hydrocorals have previously been reported as likely early colonisers following trawl disturbance on the Graveyard Knolls (Clark & Rowden 2009). Small individuals were common in patches on fished seamounts, including Graveyard and Morgue. These were commonly on bare rocky outcrops, but also in areas of extensive coral rubble (Figure 10) and were also seen on mooring weights originally deployed in 2010 and 2012 and re-photographed in 2020 (T5, Figure 11).

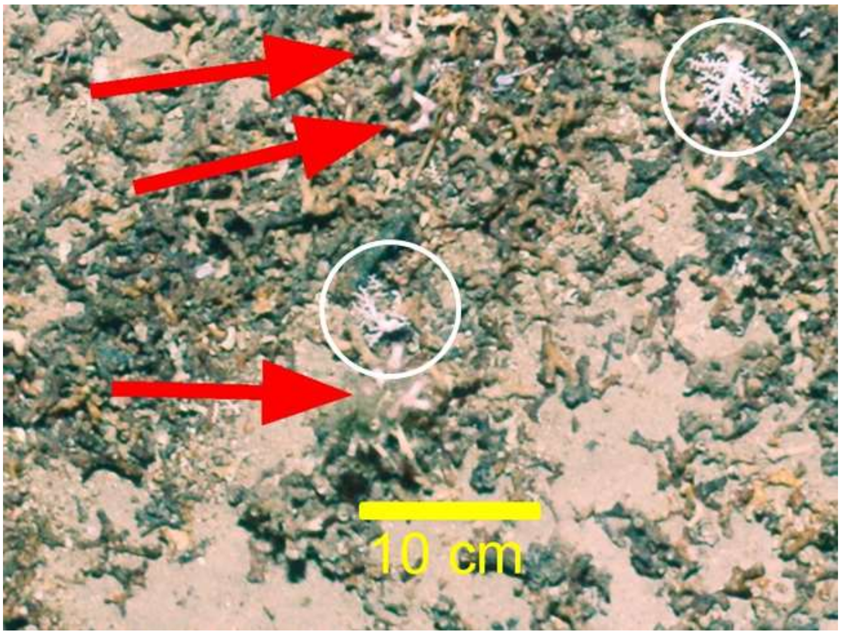

Figure 10: Small live *Solenosmilia variabilis* colonies (red arrows) and stylasterid hydrocorals (inside white circles) amongst coral rubble on Morgue at T5.

Figure 11: Morgue seamount feature. Live stylasterid hydrocorals on coral rubble with orange roughy (left panel) and small stylasterid recruits on and around a scientific mooring anchor 10 years after its deployment.

4. DISCUSSION

The addition of data from the fifth, T5, survey of the Graveyard Knolls has shown little change in the overall pattern of similarities among the benthic invertebrate communities on five of the six features surveyed since the last monitoring survey in 2015. On Morgue, however, which was heavily fished until its closure in 2001, there are indications that overall benthic community structure might be changing and that branching stony corals are either regrowing or recolonising. In multivariate analyses of whole-seamount community similarity using all image data, there was a shift of the Morgue similarity data centroid towards those of the un-trawled features, Gothic and Ghoul. This shift was not apparent for communities on the summit of Morgue, indicating that the change in community structure is primarily on the flanks of the seamount. Although the habitat-forming branching stony corals that dominate benthic communities on un-trawled features in the Graveyard Knolls complex apparently did not influence this shift (see below), fine-scale examination of seafloor images has detected very small stony coral colonies that appear to be either early-stage recruits of *Solenosmilia variabilis* or regrowth from fragments of colonies damaged by past trawling. Because *S. variabilis* is the dominant habitat-forming coral on the Graveyard Knolls, these observations are of considerable interest in relation to assessing the potential for deep-sea stony coral communities to recover from chronic bottom trawling, and the time scales over which recovery might take place.

The observations of early-stage stony coral growth here are unequivocal in their relevance to recovery of pre-disturbance communities but interpretation of the observed change in the relative composition of communities on Morgue at T5 in the multivariate analysis is less straightforward. Although the increase in similarity between communities on Morgue and those on the un-trawled features Gothic and Ghoul appears to be an indication of recovery, the taxa contributing most to these changes do not include the sessile habitat-forming taxa characteristic of communities on the un-trawled features. Rather, the overall change on Morgue was driven by changes in the abundances of several taxa, with an apparently counter-intuitive trend for increases in mobile taxa, including pagurid crabs, galatheid squat lobsters, ophiuroids, and others, some of which are characteristic of disturbed environments (Clark & Rowden 2009), and decreases in some sessile taxa, including stylasterid hydrocorals, sponges, and ascidians, that might be expected to be associated with undisturbed or recovering communities (Goode et al. 2020).

Whole-community multivariate analyses of this type tend to be influenced by more abundant and more prevalent taxa but the overall pattern of similarities changed little across a range of data transformations (analyses not shown: MDS ordinations repeated using fourth-root, logarithmic, and presence-absence data transformations, which progressively decrease the influence of abundance on the resulting similarities), suggesting that this result is a credible representation of the underlying data and that it signifies a real shift in community composition on Morgue. The SIMPER comparisons among seamounts at T5 also show, however, that the community changes on Morgue represent a shift away from the still-trawled feature Graveyard as well as an increase in similarity with the un-trawled features. For instance, comatulid crinoids, which were the single most influential taxon in the change on Morgue from T4 to T5, were at much lower abundance on Graveyard than on Gothic and Ghoul at T5. The univariate analyses of overall community abundance and taxon richness are less nuanced metrics of community status but also provide some support for a change on Morgue from T4 to T5, with the whole-seamount (basal) analyses showing, for the first time in the time series, no significant difference between Morgue and the two un-trawled seamounts at T5 for either abundance or richness.

While these results suggest that some recent change in whole-seamount community structure has occurred on Morgue, and that this might be indicative of early-stage recovery (because overall dissimilarities between Morgue and the un-trawled seamounts Gothic and Ghoul have decreased, Figure 7), the fact that the individual taxa contributing most to the change do not align fully with our expectations (Goode et al. 2020) prompts questions about alternative explanations. The first possibility we explored was that there had been changes in the way that some of the small, abundant taxa had been assigned to taxonomic groupings; notably small stylasterid hydrocorals and a form of white branching bryozoan, which can be problematic to distinguish between with confidence. To address this possibility, we constructed parallel versions of the analysis data in which these taxa were grouped together (e.g., all observations of small white branching taxa were grouped as 'Stylasteridae', or all as 'Bryozoa') and re-ran the analyses. In all cases, the multivariate pattern remained essentially the same, with Morgue at T5 shifting away from Graveyard and towards Gothic and Ghoul. Another possibility is that the community change observed on Morgue represents an artefact of the sampling caused by minor variations in camera transect paths at T5 imaging areas of the seabed on Morgue that, by chance, were more similar to areas sampled on other seamounts (excepting Graveyard) on this particular occasion, than those imaged at T4. This possibility cannot be discounted entirely but it seems unlikely that it could generate the patterns seen, given the consistency of among-seamount patterns across the first four surveys of the time series, the number of transects run on Morgue, and the mix of taxa contributing to the change.

Regardless of these counter-intuitive taxon changes underlying the shift in community structure on Morgue in the multivariate analyses, the observations of very small branching stony coral colonies are significant in relation to the potential for benthic community recovery, particularly when combined with the knowledge that 'refuge' areas of un-trawled stony coral reefs persist on Morgue (Clark et al. 2016). Such remnant patches of live stony coral habitat have been noted on the un-trawled ridge that extends SSW of the main seamount (Clark et al. 2016) but also in sectors that have in the past been trawled and are included in the basal polygon dataset used here. In these sectors, live corals remain in refugia protected from direct trawl impacts by rock outcrops, crevices, or overhangs. A key question yet to be answered, however, is whether the very small, early-stage stony coral colonies and polyps we report here represent regrowth from colony fragments that have survived after trawl impacts or are new recruitment from larval settlement. This distinction is important because confirmation of the presence of new recruits, as opposed to regrowth from fragments, would be an indication of more widespread recolonisation events, potentially seeded by reproduction of corals on neighbouring seamounts, and would have implications for approaches to spatial management of seamount biodiversity.

In summary, these results indicate that the first detectable signs of potential benthic community recovery on Morgue are appearing approximately 20 years after the cessation of trawling. While the perceived shift in multivariate community structure on Morgue appears to be driven by changes among populations of some taxa that we would not necessarily associate with recovery of the pre-disturbance coral-dominated community, the observation of very young branching stony coral colonies is an unequivocal sign of the early stages of recovery for this key taxon, at least. If early recovery is taking place, it is highly interesting in the context of earlier findings that no recovery was evident on the Graveyard and other southern hemisphere seamounts up to 15 years after the cessation of disturbance (Althaus et al. 2009, Williams et al. 2010, Clark et al. 2019). Our results also exhibit some concordance with those of a recent study of seamounts off Hawaii (Baco et al. 2019), in which signs of recovery, including corals regrowing from trawl-damaged fragments, were observed on seamounts that had been protected for more than 30 years. Our results thus contribute to an emerging body of evidence that recolonisation and regrowth of deep-sea corals on previously heavily trawled seamounts can, indeed, take place but that the process of recovery is slow, with the first detectable signs of coral recruitment and regrowth occurring approximately two decades after the cessation of trawling. While these observations of the early stages of recovery of coral-dominated seamount communities are encouraging, full recovery (*sensu* Baco et al. 2019) to their pre-disturbance status, based on existing estimates of growth rates, would still be likely to take centuries, rather than decades (Fallon et al. 2014).

5. ACKNOWLEDGEMENTS

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