ECOLOGY

Amid fields of rubble, scars, and lost gear, signs of recovery observed on seamounts on 30- to 40-year time scales

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Although the expectation of lack of resilience of seamount vulnerable marine ecosystems has become a paradigm in seamount ecology and a tenet of fisheries management, recovery has not been tested on time scales >10 years. The Northwestern Hawaiian Ridge and Emperor Seamounts have experienced the highest documented fish and invertebrate seamount fisheries takes in the world. Surveys show that, despite visible evidence of substantial historic fishing pressure, a subset of these seamounts that have been protected for >30 years showed multiple signs of recovery including corals regrowing from fragments and higher abundances of benthic megafauna than Still Trawled sites. Contrary to expectations, these results show that, with long-term protection, some recovery of seamount deep-sea coral communities may be possible on 30- to 40-year time scales. The current practice of allowing continued bottom-contact fishing at heavy trawled sites may cause damage to remnant populations, which likely play a critical role in recovery.

INTRODUCTION

High-flow hard substrate areas on seamounts are generally colonized by dense assemblages of suspension feeders, which, in many areas, are dominated by deep-sea corals (1–5). With growth rates on the order of micrometers to millimeters per year, and life spans ranging from decades to millennia, the life history characteristics of deep-sea corals connote a high vulnerability to, and protracted recovery from, disturbance (6–9). Adding to this picture of protracted recovery time is research that indicates that recruitment of coral larvae is sporadic or limiting for deep-sea species, with larvae being selective of substrate type and with slow-growing recruits (10, 11). These life history characteristics are the primary reasons seamount deep-sea coral communities are designated as vulnerable marine ecosystems (VMEs) and as ecologically and biologically significant areas (EBSAs) and have led to the prediction that recovery of seamount coral communities following anthropogenic disturbance likely takes decades to centuries, if recovery is even possible at all [reviewed in (6)]. Although the opportunities to test this hypothesis have been rare, existing studies support the lack of recovery on 5- to 10-year time scales (12–14).

Despite the lack of opportunity to test the hypothesis on longer time scales, these observations, combined with the expectation of low resilience based on life history characteristics, have resulted in wide-scale acceptance among fisheries managers and seamount ecologists of the idea of decadal to century time scales for recovery from anthropogenic disturbance (6). While this paradigm provides a logical argument for minimizing the expansion of bottom trawling efforts, the argument has also been flipped, with high-seas regional fisheries management organizations (RFMOs) and domestic fisheries management workshops using the lack of recovery potential as a justification to continue fishing an area. For example, in both Alaska and in the South Pacific RFMO, seafloor areas with little or no history of trawling have been closed to trawling, but areas that have already experienced high impacts have been left open to fishing, with the justification that areas that have already experienced high trawling damage are unlikely to recover (15–17). The expectation of no recovery has also been used in cost-benefit analyses of fisheries to select areas within the existing trawling footprint to prioritize for protection, with areas with higher fisheries impact considered to have reduced "benefit" to protection (15, 18).

An excellent opportunity to gain additional and longer-term insights into the recovery potential of seamount deep-sea coral communities occurs in the U.S. Exclusive Economic Zone (EEZ) around the Hawaiian Archipelago and in adjacent international waters of the far Northwestern Hawaiian Ridge (NHR) and lower Emperor Seamount Chain (ESC). Heavy fishing efforts in the far NHR and ESC seamounts in the 1960s to the 1980s, concentrated at depths of 300 to 600 m, resulted in the largest amount of fish and invertebrate biomass removed from any documented seamount fishery in the world [as quantified in (19)]. This included two types of fisheries: trawling, which removed up to 210,000 metric tons of fishes per year, and coral tangle net fishing, which removed as much as 200,000 metric tons of deep-sea precious corals per year (19, 20) (table S1). After the establishment of the U.S. EEZ in 1977, a subset of the affected sites were protected from further fishing (21), which has allowed those sites up to 40 years to recover, while the remaining sites experience continued but reduced bottom fisheries. To test for recovery on 30- to 40-year time scales, we conducted replicate imaging surveys at depths of 200 to 700 m on four "Recovering" and three "Still Trawled" sites with the autonomous underwater vehicle (AUV) Sentry and the Pisces IV and V submersibles in 2014 through 2017 (Fig. 1 and table S1).

RESULTS

Reflecting the documented fishing at these sites (19, 20), explorations of these seamounts showed significant adverse impacts from fisheries including vast areas of barren substrate scarred by bottom-contact gear (Fig. 2A), coral rubble (Fig. 2B), coral stumps (Fig. 2C), and lost fishing gear (Fig. 2, D to F). Of the Still Trawled seamounts, 18 to 25% of images per seamount included scarred substrate (table S1).

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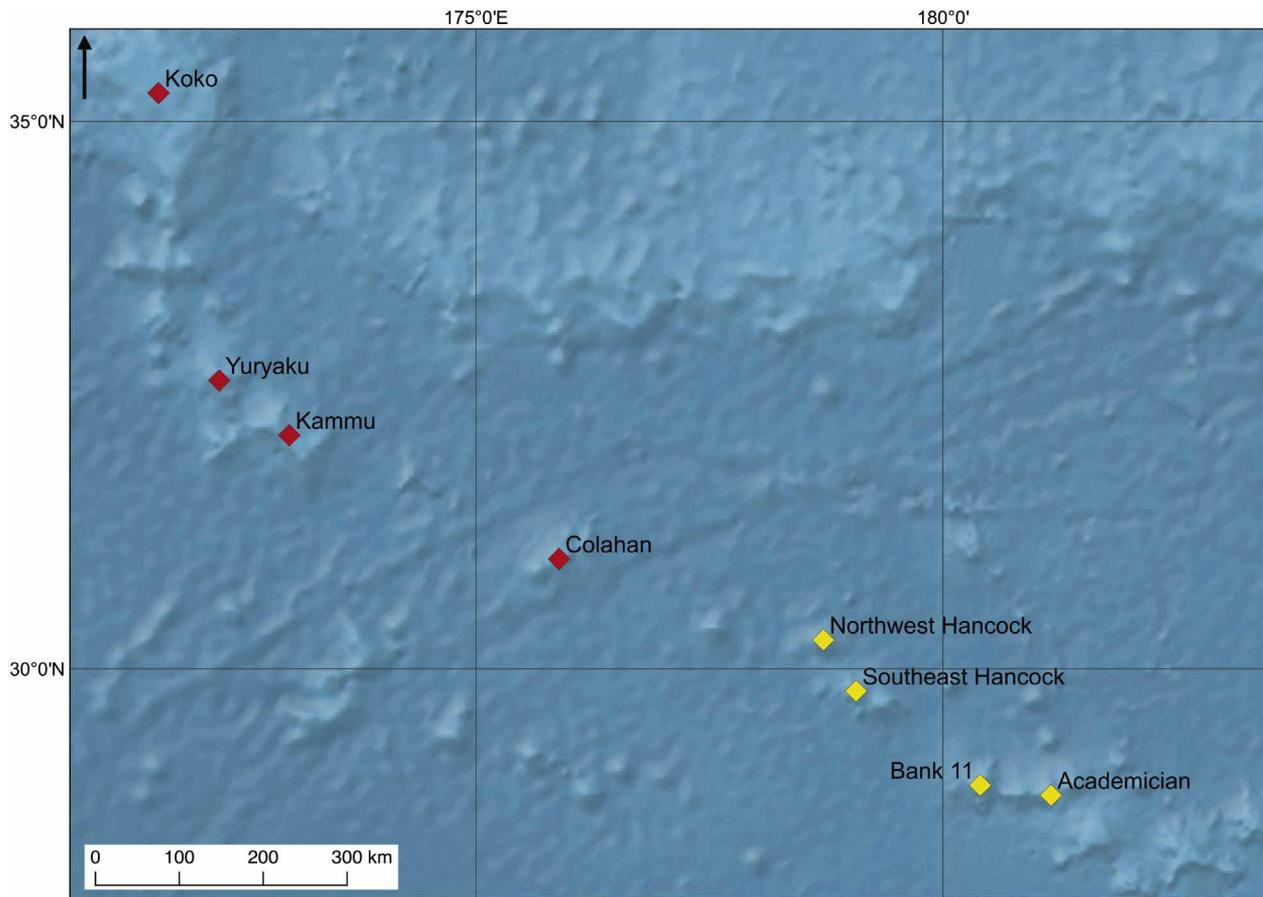*Corresponding author. Email: abacotaylor@fsu.edu

Fig. 1. Map of the study area including the northwestern end of the Hawaiian Ridge and the southern portion of the ESC. Yellow diamonds indicate the location of Recovering seamounts. Red diamonds indicate the location of Still Trawled seamounts. Map created in QGIS v. 2.18 Las Palmas (*34*) using ocean bottom layer downloaded from the Natural Earth public domain database (*35*).

However, evidence of recovery was also observed, both on the Recovering seamounts and in small pockets on the seamounts that are Still Trawled. The Recovering seamounts of Northwest (NW) and Southeast (SE) Hancock received comparable levels of historic fishing pressure to the Still Trawled seamounts in terms of total catch removed and had the highest levels of catch per unit area of any of the studied seamounts in either group (table S1) (*19*, *22*). Evidence of significant adverse impacts were still apparent on these features and included hard substrates scarred by bottom-contact gear (6 to 9% of images), coral rubble, and lost fishing gear including fishing nets, lines, and large areas of coral rubble. Despite this, there were signs of recovery on both of these seamounts. These included corals growing over areas of trawl marks (Fig. 3, A and B), the coralliid precious coral *Hemicorallium laauense*, and the reef-forming coral *Enalopsammia* regrowing from fragments in coral rubble spilling out of lost nets (Fig. 3, C and D), and healthy octocoral beds and *Solenosmilia* scleractinian reefs (Fig. 3, E and F).

Perhaps even more unexpected, given the continued trawling, were the pockets of recovering corals observed on the Still Trawled features. These include two areas of the young primnoid octocoral *Thouarella* on Kammu (Fig. 4, A and B), young *H. laauense* colonies on Yuryaku (Fig. 4C), and denser, more diverse areas that may be either recovering or remnant populations on Koko (Fig. 4, D and E).

Colahan Seamount also had areas of intact scleractinian reefs not included in previous observations (Fig. 4F) (*23*). These combined with observations of scattered live polyps among the coral rubble on Yuryaku and Kammu, and bushy scleractinian colonies at several sites, suggest that elements of the original communities remain at these sites to reseed recovery on Still Trawled seamounts.

Data from replicate quantitative AUV image transects at three depths (table S2) on three Still Trawled seamounts and four Recovering seamounts also show that, at a given depth, there was a higher number of total megafaunal individuals per image on the Recovering seamounts ($P < 0.0249$) and a higher number of corals per image ($P < 0.0100$, interaction $P < 0.0076$). There was also a higher mean number of taxa observed per image on the Recovering seamounts ($P < 0.0198$) (table S3).

DISCUSSION

There is no consensus definition of the word "recovery" in the scientific literature as to whether recovery is a "process" or a "state" and, if it were a "state," whether it only applies to a state of being "fully recovered" [e.g., (*24*–*26*)]. Previous papers on recovery on seamounts have not given their definition of the term (*6*, *12*–*14*), and dictionaries include multiple definitions for the word including
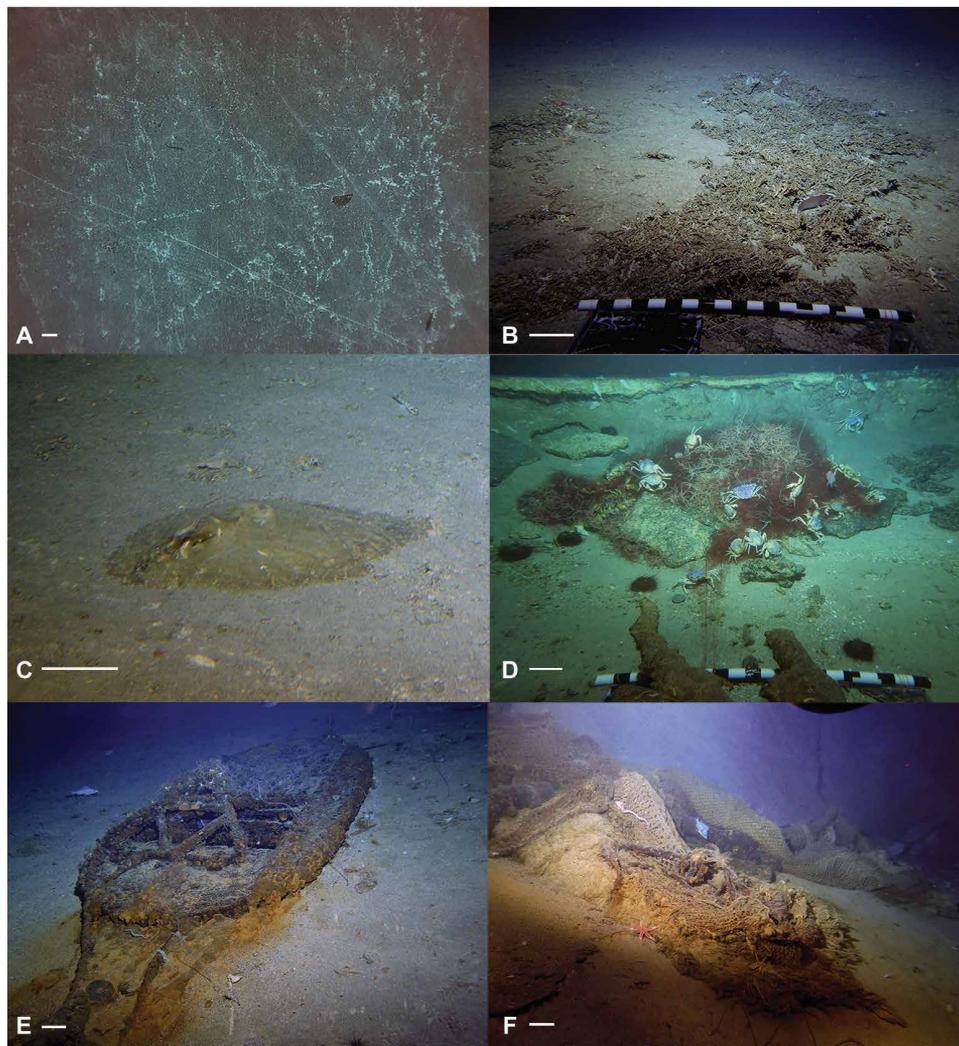
Fig. 2. Example images of adverse impacts of fisheries on seamount deep-sea coral communities. Scale bars, 10 cm. (**A**) AUV Sentry image of barren substrate with scars from bottom-contact gear on Yuryaku Seamount at 400 m. (**B**) Scleractinian reef rubble on Kammu at 600 m. (**C**) Gold coral stump on Kammu at 400 m. (**D**) Lost net with scavengers on Kammu at 400 m. (**E**) Lost trawl door on NW Hancock at 300 m. (**F**) Lost trawl net from a second location on NW Hancock at 400 m. Photo credits: (A) A. Baco-Taylor (FSU) and E. B. Roark (TAMU), NSF, AUV Sentry; (B to F) A. Baco-Taylor (FSU) and E. B. Roark (TAMU), NSF, with HURL pilots T. Kerby and M. Cremer.

both a process definition and a state definition. Westwood *et al.* (*26*) proposed that "recovery" be considered a "process" and "fully recovered" be the "state" a population or ecosystem reaches after the recovery process is complete. Here, the use of the word "recovery" aligns with this approach, with references to observations of seamounts being in the "process" of recovery, rather than in a "state" of being fully recovered.

With these definitions in mind, evidence presented here indicates that long-term protection of heavily trawled seamounts does allow for measurable recovery of seamount deep-sea coral communities on time scales of 30 to 40 years. These findings are contrary to the expectations and previous observations on seamount coral communities following disturbance (*6, 12–14*), which concluded that there were not yet signs of recovery at all on seamounts: They were "effectively denuded of large sessile fauna and no longer support habitat forming corals in any significant numbers" 9 to 10 years after the secession of trawling (*12*) or had some animals but a different

community and much lower abundances 5 to 10 years after trawling (*13, 14*). Considering these conclusions, any recovery observed in a seamount community at all, even if it is partial recovery, can be considered remarkable.

Differences between these results and previous findings may be due to the longer time scales of this study, with 30 to 40 years since the end of trawling compared to 5 to 10 years. The depth range of this study was also slightly shallower, 300 to 600 m, compared to depths ranging from ~700 to 1700 m in previous recovery studies (*12–14*). Since food supply is expected to decrease with increasing depth [e.g., (*27*)] and available data to date suggest that deep-sea coral growth rates also decrease with increasing depth [e.g., (*28*)], recovery rate may be expected to change with increasing depth. However, at least within the narrow depth range sampled here, this prediction is not supported, since the increases in the median faunal abundance seen at 600 m (higher in recovering sites by 225%) in this study were comparable to the increases at 350 m (250% higher).
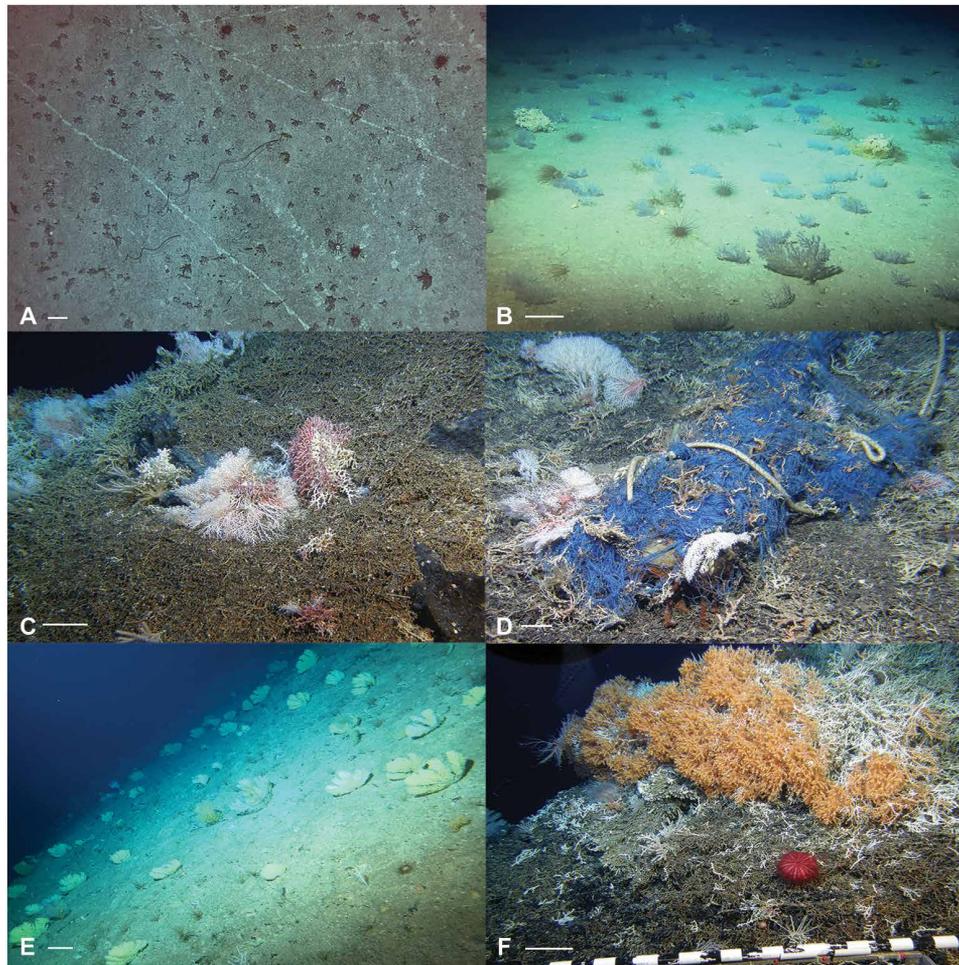
Fig. 3. Example images of recovering assemblages on the Recovering Seamounts of NW and SE Hancock. Scale bars, 10 cm. (**A**) Down-looking AUV Sentry image of soft corals growing over historic trawl scars on NW Hancock at 300 m. (**B**) Image of the same type of soft coral assemblage from the submersible on SE Hancock at 400 m (scars are not as obvious using the oblique angle of the submersible camera). (**C**) The precious red octocoral *H. laauense* and the reef-forming scleractinian *Enalopsammia* regrowing from fragments amid a field of coral rubble on SE Hancock at 600 m. (**D**) *H. laauense* regrowing from fragments pouring out of lost fishing nets on SE Hancock Seamount at 600 m. (**E**) A bed of young octocorals on SE Hancock at 600 m. (**F**) A patch of recovering scleractinian reef on SE Hancock at 650 m. Photo credits: (A) A. Baco-Taylor (FSU) and E. B. Roark (TAMU), NSF, AUV Sentry; (B to F) A. Baco-Taylor (FSU) and E. B. Roark (TAMU), NSF, with HURL pilots T. Kerby and M. Cremer.

A final source of potential difference among studies may have to do with the dominant taxa in the region. In the North Pacific, octocorals are the dominant taxon [e.g., (*4*, *29–31*)]; in Althaus *et al.* (*13*) and Williams *et al.* (*14*), the dominant coral taxa are scleractinians. However, in Waller *et al.* (*12*), the dominant coral taxa are also octocorals.

The level of taxonomic resolution possible with the AUV images prevents us from quantitatively determining whether the recovering communities are returning to the same communities that were present before fishing activities started or whether an alternative state is developing [e.g., (*24*)]. On the basis of published studies on the seamount fauna of the Northwestern Hawaiian Islands (NWHI) in the depth ranges of this work, we expect the predisturbance communities to have been dominated by octocorals and antipatharians, with a high abundance of coralliid and primnoid octocorals, as well as gold coral (*4*, *29–31*). While octocorals do dominate the Recovering sites, long-lived gold corals were nearly absent and coralliids were not among the more abundant morphotypes. Also, the soft corals that were colonizing the trawl marks near the summits of NW and SE Hancock (Fig. 3, A and B) have not been previously observed in

these depth ranges in other areas. However, primnoid octocorals were common in Recovering areas (Fig. 4) and are also among the dominant families in Hawaiian coral beds in these depths (*30*). These observations suggest that the recovering communities observed contain some, but not yet all, of the elements of the predisturbance communities. Therefore, the question of whether the recovering community is an alternative community or an early community that, with successive community change, will eventually return to an assemblage similar to the predisturbance communities composed of long-lived octocorals and antipatharians is still open.

The current scientific and management literature on recovery and resilience of seamount communities do not take into account the potential for some corals to regrow from fragments, and there is minimal consideration given to the possibility of remnant or recovering populations on heavily affected sites. There are taxa that certainly would be expected to have protracted recovery times, such as reef-forming species and long-lived [decades to millennia (*7–9*)] species such as coralliid octocorals, some antipatharians, and zoantharian gold corals. However, these results show that both remnant populations
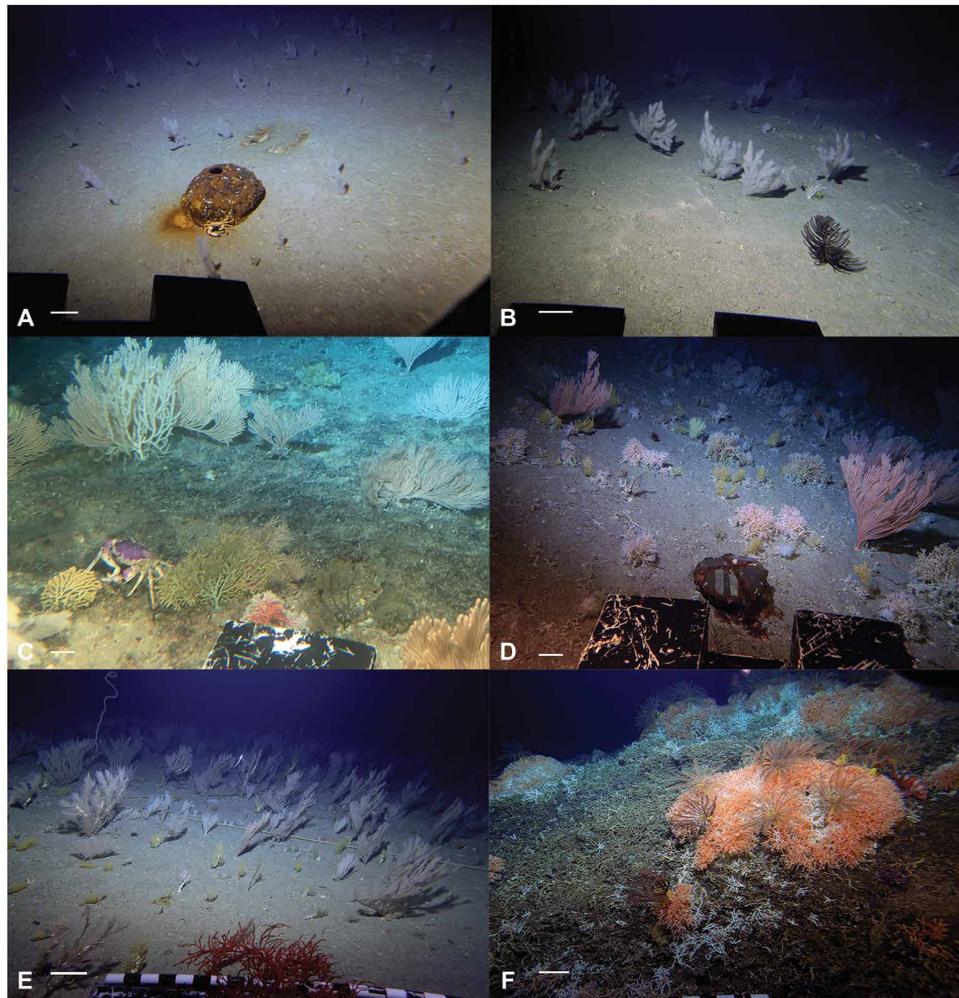
Fig. 4. Example images of recovering or remnant communities on Still Trawled seamounts. Scale bars, 10 cm. (**A**) Young colonies of the primnoid octocoral *Thouarella* on Kammu Seamount at 400 m. (**B**) Slightly older colonies of *Thouarella* with the antipatharian coral *Bathypathes* on Kammu at 500 m. (**C**) A young colony of *H. laauense* (pink colony near the center in front of the biobox) amid a bed of other octocorals on Yuryaku at 500 m. (**D**) A mixed bed of scleractinian and octocorals that appear to be recovering on Koko at 500 m. (**E**) A bed of more mature octocoral colonies with visible epifauna, amid lost fishing lines on Koko at 450 m. (**F**) An area of scleractinian reef on Colahan at 600 m. Photo credits: (A to F) A. Baco-Taylor (FSU) and E. B. Roark (TAMU), NSF, with HURL pilots T. Kerby and M. Cremer.

and regrowth from fragments may help to accelerate the recovery process and increase the probability of the community returning to the same predisturbance state, thereby increasing the resilience of seamount deep-sea coral communities.

These findings raise critical considerations for the management of seamount coral communities, both domestically and in areas beyond national jurisdiction. Domestically, the two Recovering seamounts with the highest abundance communities, Northeast and Southwest Hancock, fall into the 2016 expansion of the boundaries of the Papahānaumokuākea Marine National Monument (PMNM). The recent expansion of the PMNM has been called into review as part of the Department of the Interior's review of National Monuments established since 1996 (*32*). The presence of fragile recovering deep-sea coral communities on these seamounts should be taken into consideration in future reviews of PMNM boundaries and in any potential changes to bottom-fish fishing and trawling regulations within the PMNM.

In areas beyond national jurisdiction, management organizations should consider that the current protocol of allowing continued bottom-contact fishing at sites that have already experienced heavy trawling may cause damage to remnant VME populations. If these remnant populations are large enough to be reproductively viable, then they are likely to play a critical role in the recovery process as a source of propagules for heavily disturbed areas on seamounts, and further impacts could thereby limit the recovery process. The time scales for recovery observed on these seamounts additionally suggest that short-term "crop rotation"–type closures [e.g., (*33*)] would not allow sufficient time for affected communities to recover; instead, a long-term or even permanent closure will be needed for significant recovery to be attained on seamounts.

MATERIALS AND METHODS
Experimental design
A total of seven seamounts in the NWHI and ESC were surveyed in 2014 and 2015 using the AUV Sentry. On the basis of the trawling history, the seamounts were categorized as Recovering or Still

Trawled. Sites that were once actively trawled, but were protected with the establishment of the US EEZ in 1977 (*21*), were placed into the Recovering treatment and included Academician Berg, Bank 11, and SE and NW Hancock Seamounts. Sites that are still actively trawled, including Kammu, Yuryaku, and Koko Seamounts, were placed into the Still Trawled treatment (table S1).

AUV photo surveys with a length of ~30 to 40 km were designed to include replicate 1-km transects at depth intervals of 50 m from depths of 200 to 700 m. This survey design was then replicated on two to three sides of each seamount to reduce effects of within-seamount variability on comparisons between treatments. The depth range of 200 to 700 m was chosen to encompass the full range of depths that were part of the historic trawl and coral fisheries, which were concentrated at 300 to 600 m (*21*). The AUV flew at a height of ~5 m above the seafloor at a rate of 0.45 to 0.65 m/s, taking photos at a rate that ensured a continuous visual (photo) survey of the seafloor. Images were taken with a down-looking digital still camera, and each individual AUV image covered approximately 12 m^2 of seafloor. Observations were made from all of the >536,000 dive images, with a subset used for the quantitative analyses as described below. Additional qualitative observations and images were obtained on dives with the Pisces IV and V submersibles, which returned to the same sites in 2016 and 2017, as well as to Colahan Seamount.

Quantitative site comparisons

For quantitative comparisons, only images from depths of 350, 450, and 600 m were analyzed for each feature. Initial analyses included surveying every other image on each transect for trawl or drag marks and the proportion of soft substrate, totaling over 54,000 images analyzed. For quantitative comparisons, images along a transect that were <75% soft substrate were then used to count benthic megafauna, totaling 22,188 images analyzed. From these, all of the visible megafauna were counted in every other image to avoid duplicate counts. The primary benthic megafaunal taxa observed included cnidarians, sponges, and echinoderms. The height above the seafloor that the AUV must be flown over rough terrain and the angle of the camera make identification to the species level unreliable, so instead, we used a morphotype classification that allowed for a consistent level of resolution of the observed fauna. These categories included "wire coral," "antipatharian fan," "octocoral fan," "scleractinian fan," "scleractinian bush," "sea pen," *Eguchipsammia*," "encrusting zoanthid," "stalked crinoid," "unstalked crinoid," "brisingid," and "sponge." Urchins were also present on most features, but the abundances made counting them time prohibitive; thus, they were not included. The gold coral, *Kulamanamana haumeaae*, common in precious coral beds in the NHWI (*4, 29–31*), was notably absent from all included transects. By coincidence, extensive areas of live reef as shown in Fig. 4F also did not occur in the AUV images on the targeted depth transects in either treatment.

Statistical analyses

Data for each transect were standardized as number of observations of fauna divided by number of images included from that transect. A two-way crossed analysis of variance (ANOVA) was used to compare Recovering and Still Trawled sites at depths of 350, 450, and 600 m for two groups: Total Megafauna, including all of the morphotypes listed above, and Coral, which included all cnidarians except soft substrate–associated sea pens, fast-growing wire corals, and encrusting species that were difficult to accurately quantify

by count methods. All statistical comparisons were performed in JMP version 13.2 (SAS).

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Science Advances

Amid fields of rubble, scars, and lost gear, signs of recovery observed on seamounts on 30- to 40-year time scales

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