Coral Translocation as a Method to Restore Impacted Deep-Sea Coral Communities

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Corals and sponges in rocky deep-sea environments are foundation species postulated to enhance local diversity by increasing biogenic habitat heterogeneity and enriching local carbon cycling. These key groups are highly vulnerable to disturbances (e.g., trawling, mining, and pollution) and are threatened by expansive changes in ocean conditions linked to climate change (acidification, warming, and deoxygenation). Once damaged by trawling or other disturbances, recolonization and regrowth may require centuries or longer, highlighting the need for stewardship of these deep-sea coral and sponge communities (DSCSCs). To this end, the sustainability of DSCSCs may be enhanced not only by protecting existing communities, but also repopulating disturbed areas using active restoration methods. Here, we report one of the first studies to explore methods to restore deep-sea coral populations by translocating coral fragments of multiple coral species. Branches of deep-sea corals were collected by ROV from 800 to 1300 m depth off central California and propagated into multiple fragments once at the surface. These fragments were then attached to "coral pots" using two different methods and placed in the same habitat to assess their survivorship (n = 113 total fragments, n = 7 taxa, n = 7 deployment groups). Mean survivorship for all translocated coral fragments observed within the first 365 days was ∼52%, with the highest mortality occurring in the first 3 months. In addition to an initial temporal sensitivity, survival of coral fragments varied by attachment method and among species. All coral fragments attached to coral pots using zip ties died, while those attached by cement resulted in differential survivorship over time. The latter method resulted in 80–100% fragment survivorship after 1 year for *Corallium* sp., *Lillipathes* sp., and *Swiftia kofoidi,* 12–50% for the bamboo corals *Keratoisis* sp. and *Isidella tentaculum*, and 0–50% for the bubblegum corals *Paragorgia arborea* and *Sibogagorgia cauliflora*. These initial results indicate differences in sensitivities to transplanting methods among coral species, but also suggest that repopulation efforts may accelerate the recovery of disturbed DSCSCs.

Keywords: deep-sea coral restoration, *Corallium* sp., *Lillipathes* sp., *Swiftia kofoidi*, *Keratoisis* sp., *Isidella tentaculum*, *Paragorgia arborea*, *Sibogagorgia cauliflora*
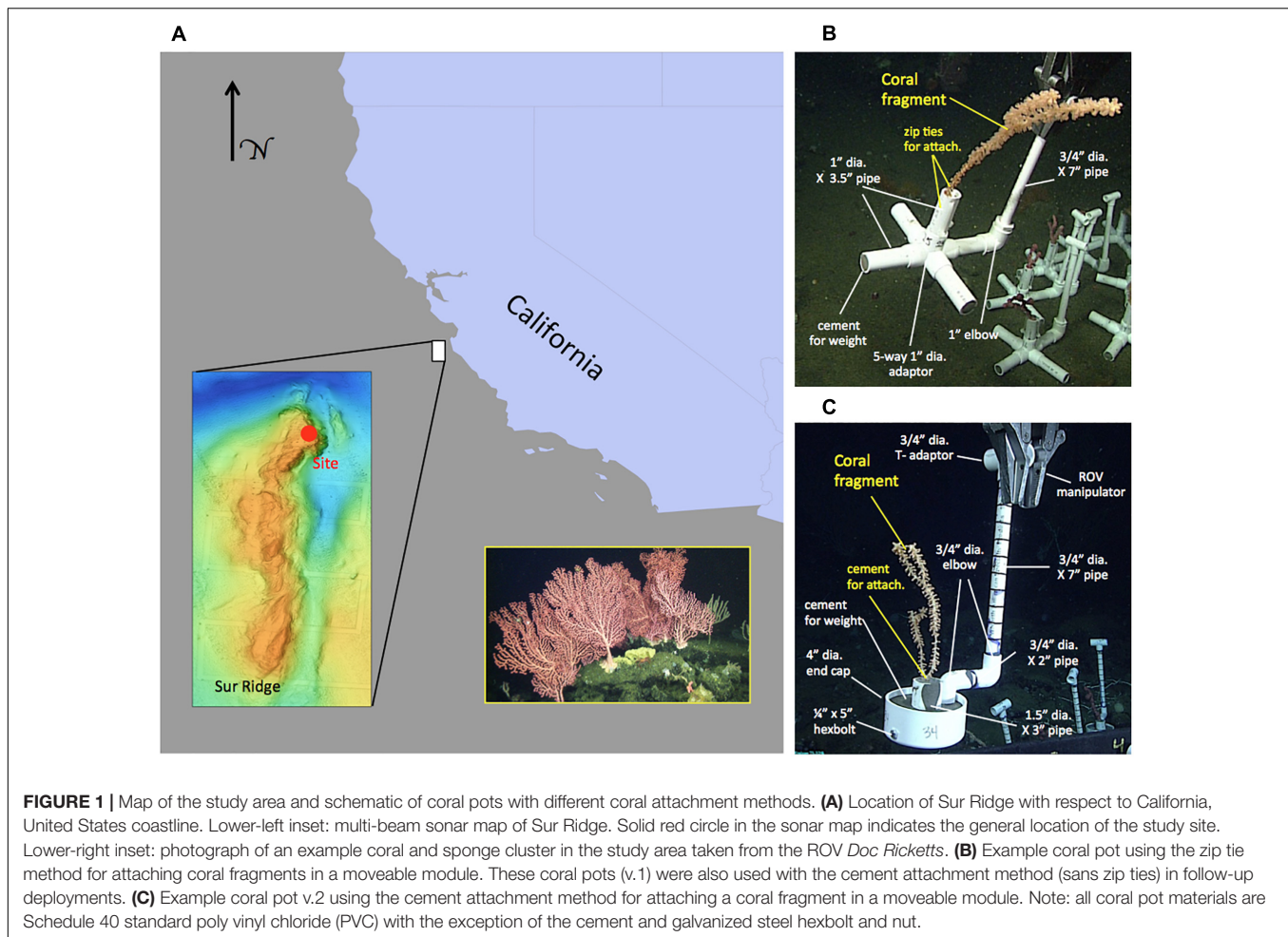
INTRODUCTION

Human impacts in the deep-sea are increasing from direct extractive activities (e.g., fishing, mineral extraction), pollution (e.g., oil spills, trash), and expansive changes in ocean conditions linked to anthropogenic climate change (ocean acidification, warming, and deoxygenation). While the integrated impacts of human activities in the deep-sea remain largely unknown, there is clear evidence that bottom trawling for fishes and invertebrates alone is leaving a global footprint from the nearshore to >1000 m depth (Amoroso et al., 2018). Catastrophes such as the 2010 BP Deepwater Horizon oil spill in the Gulf of Mexico also demonstrated that an oil spill from a single platform can have far ranging effects spanning from ecological impacts in the deep-sea to economic depression for the adjacent coastal communities—with the full potential impacts still unknown (McCrea-Strub et al., 2011; White et al., 2011; Sumaila et al., 2012). Although the Magnuson-Stevens Fishery Conservation and Management Act (2006) establishes a legal mandate to minimize negative impacts to these and other ecosystems within the United States Exclusive Economic Zone, the slow rates of recovery for some damaged deep-sea assemblages suggest that active restoration efforts may be beneficial.

Recovery and resilience of impacted deep-sea ecosystems may be enhanced by efforts to propagate species that form key biogenic structures. Species that form biogenic structures are hypothesized to facilitate positive species interactions, further promoting both biodiversity and ecosystem function (Bruno and Bertness, 2000; Bruno et al., 2003). In deep-sea ridge and seamount systems, suspension feeders such as corals and sponges typically dominate the benthos and provide critical biogenic habitat for a variety of associated deep-sea fishes and invertebrates (Rogers, 1999; Koslow et al., 2000; Roark et al., 2005; Stone, 2006; Love et al., 2007; Baillon et al., 2012; Bourque and Demopoulos, 2018). Furthermore, suspension feeding by these organisms may enhance carbon sequestration (Murray et al., 1994; Cathalot et al., 2015; Kahn et al., 2015). Thus, efforts to translocate healthy or rehabilitated corals and sponges may accelerate the recovery of local diversity and ecosystem function in deep-sea coral and sponge communities (DSCSCs) that have been disturbed or destroyed by human activity.

Understanding how to actively enhance or facilitate the recovery of disturbed DSCSCs is a new frontier for restoration science. Van Dover et al. (2014) evaluated hypothetical scenarios of ecological restoration of the deep sea but lacked empirical data from active restoration studies, bringing to light a major gap in applied scientific knowledge. Although experimental restoration of the deep-sea corals *Lophelia pertusa* (∼ 500 m in depth) and *Oculina varicosa* (∼60–120 m) has been somewhat successful in the Gulf of Mexico (Koenig et al., 2005; Brooke et al., 2006; Brooke and Young, 2009), studies examining the sensitivity of multiple coral taxa to differential handling and processing remain a gap in knowledge for all deep-sea efforts. However, insights gained from these initial efforts, in combination with information from coral reef restoration studies from shallow habitats (<30 m), may serve as a more comprehensive guide to expanding mitigation strategies for the deep sea.

While studies of both asexual and sexual propagation of shallow water corals are prevalent, we focused on translocating coral fragments from multiple coral taxa as a first step to understanding the feasibility and facilitation of DSCSC recovery in the Eastern Pacific for several reasons. Enhancing coral reef recovery via translocation or transplanting coral fragments are presently proposed to be more advantageous than using sexual propagation methods due to the cost-effectiveness and requirements for technical knowledge (Jaap, 2000; Bowden-Kerby, 2001; Epstein et al., 2001; Spieler et al., 2001; Rinkevich, 2008; Edwards et al., 2010; Villanueva et al., 2012; Barton et al., 2015). That is, propagation of corals by harnessing gametes or larvae requires biological, culturing, and processing knowledge that may be more complicated than fragmenting corals and attaching fragments to a surface. For example, harnessing the sexual propagation of *Acropora* corals in shallow water systems required knowledge of when these corals were likely to broadcast gametes, culturing the gametes through fertilization and larval development, creating larval settlement surfaces, determining the optimal time for larval batch exposure to settlement cues, determining the optimal time for newly settled larvae outplanting, how to outplant or attach the new recruits to a natural reef, and many other steps in the process that required additional resources (Boch and Morse, 2012). Horoszowski-Fridman et al. (2011) investigated the reproductive output of transplanted coral fragments versus natural coral colonies and concluded that the reproductive role of coral transplants needs further attention. Various attachment strategies for scleractinia coral fragments have been reviewed and discussed (Barton et al., 2015) and insights from *in situ* experimental studies with shallow water gorgonians (20–25 m) are also available (Lasker, 1990; Linares et al., 2008a,b). Overall, the survivorship of both fragmented and sexually propagated corals has been shown to be most sensitive during the first post-transplant year and more successful for fragment transplants than sexually propagated corals (Epstein et al., 2001; Boch and Morse, 2012). In over three decades of shallow water coral restoration research, survivorship of asexually propagated corals has typically ranged 30–40% after the first year *in situ*.

In 2013, deep-sea coral and sponge communities (DSCSCs) were discovered at Sur Ridge (36°N; 122°W, **Figure 1A**) by collaborators from the Monterey Bay National Marine Sanctuary (MBNMS, National Oceanographic Atmospheric Administration) and the Monterey Bay Aquarium Research Institute (MBARI). Recognizing the need to establish active deep-sea coral restoration strategies in addition to protecting these highly diverse habitats, the collaborators began coral translocation studies to examine the feasibility of active deep-sea mitigation as an additional option along with protection. Here, we report insights gained from ∼3 years of deep-sea coral translocation studies and discuss some of the steps needed to potentially overcome current limitations. As there are no previous publications that report details of active deep-sea coral restoration approaches in the Eastern Pacific, we conducted our translocation experiments to determine the factors that may enhance survivorship by specifically examining coral processing protocols, the sensitivity of various deep-sea coral species to

FIGURE 1 | Map of the study area and schematic of coral pots with different coral attachment methods. **(A)** Location of Sur Ridge with respect to California, United States coastline. Lower-left inset: multi-beam sonar map of Sur Ridge. Solid red circle in the sonar map indicates the general location of the study site. Lower-right inset: photograph of an example coral and sponge cluster in the study area taken from the ROV *Doc Ricketts*. **(B)** Example coral pot using the zip tie method for attaching coral fragments in a moveable module. These coral pots (v.1) were also used with the cement attachment method (sans zip ties) in follow-up deployments. **(C)** Example coral pot v.2 using the cement attachment method for attaching a coral fragment in a moveable module. Note: all coral pot materials are Schedule 40 standard poly vinyl chloride (PVC) with the exception of the cement and galvanized steel hexbolt and nut.

translocation stress, and temporal sensitivity in survivorship as an initial foundation for further investigation.

METHODS

Study Site, Environmental Exposure, and General Coral Processing

Coral translocation studies were conducted in DSCSCs at Sur Ridge, a prominent rocky ridge ∼60 km west of Point Sur, CA (**Figure 1A**). Coral taxa of interest were identified by the onboard taxonomic experts and using the *Sur Ridge Field Guide* created by the MBNMS and MBARI collaboration[1]. Seven coral taxa (*Corallium* sp., *Lillipathes* sp., *Swiftia kofoidi*, *Keratoisis* sp., *Isidella tentaculum*, *Paragorgia arborea,* and *Sibogagorgia cauliflora;* **Table 1**) common at Sur Ridge were included in the translocation studies.

Collection and translocation studies of coral fragments were conducted using the remotely operated vehicle (ROV)

Doc Ricketts, operated from the R/V *Western Flyer*—a 36-meter long, small water-plane area twin hull vessel capable of deploying, operating, and recovering tethered remotely operated vehicles for oceanographic research. The *Doc Ricketts* has high-definition cameras, a suite of environmental sensors, robotic arms with manipulators, and storage containers ("bioboxes") for samples. A high-resolution navigation system integrated with the R/V *Western Flyer* enabled repeated visits to specific locations on Sur Ridge for these studies. The data from a SBE 19 CTDO instrument (Sea-Bird Scientific, Bellevue, WA) mounted on the ROV *Doc Ricketts* during all of the ROV dives are reported to show the approximate ambient temperature, dissolved oxygen, and salinity levels experienced by the corals during the descent and ascent of ROV operations, during the collection of the donor coral branches and translocation of processed coral fragments. A sample temperature series logged within a biobox is also reported to provide a proxy of temperature experienced by the coral fragments within the biobox relative to the ambient temperature measurements.

Branches of selected coral species were collected from one or more colonies *in situ* that appeared to be visually "healthy" and stored in bioboxes for transport to the surface. After the ROV was

TABLE 1 | Metadata for deep-sea coral translocation study.

Collection Date	Deployment Date	Taxa	Fragments[#]	Approx. length (cm)	Group	Attachment version
7/25/14	7/25/14	*Keratoisis* sp.	10	10–20	A	1
7/28/14	7/28/14	*Isidella tentaculum*	7	10–20	B	1
7/28/14	7/28/14	*Paragorgia arborea*	8	10–15	B	1
6/3/16	6/3/16	*Isidella tentaculum*	10	10–20	C	2
6/3/16	6/3/16	*Paragorgia arborea*	5	10–15	C	2
6/3/16	6/3/16	*Sibogagorgia cauliflora*	5	10–20	C	2
6/4/16	6/4/16	*Keratoisis* sp.	9	10–20	D	2
8/27/16	8/28/16	*Isidella tentaculum*	4	10–20	E_a	2
8/27/16	8/28/16	*Paragorgia arborea*	4	10–15	E_a	2
8/27/16	8/28/16	*Sibogagorgia cauliflora*	2	10–20	E_a	2
8/28/16	8/28/16	*Isidella tentaculum*	4	10–20	E_b	2
8/28/16	8/28/16	*Paragorgia arborea*	4	10–15	E_b	2
8/28/16	8/28/16	*Swiftia kofoidi*	2	10–15	E_b	2
8/7/17	8/8/17	*Keratoisis* sp.	4	10–20	F	2
8/7/17	8/8/17	*Lillipathes* sp.	6	10–15	F	2
8/7/17	8/8/17	*Paragorgia arborea*	10	10–15	F	2
8/8/17	8/8/17	*Corallium* sp.	5	10–15	G	2
8/8/17	8/8/17	*Lillipathes* sp.	4	10–15	G	2
8/8/17	8/8/17	*Paragorgia arborea*	5	10–15	G	2
8/8/17	8/8/17	*Swiftia kofoidi*	5	10–15	G	2

From left to right column: donor coral collection dates, coral pot deployment date, type of coral taxa (n = 7 unique taxa total), the number of fragments or coral pots deployed (n = 113 total coral pots), the size range in length of coral fragment used (centimeters), group denotes the deployment designation, and version of attachment used to fix coral fragments in coral pots (1 = zip tie; 2 = cement). Shaded rows indicate corals held overnight in shipboard aquaria.

recovered shipboard, branches of coral colonies (*Corallium* sp., *Lillipathes* sp., *Swiftia kofoidi*, *Keratoisis* sp., *Isidella tentaculum*, *Paragorgia arborea,* and *Sibogagorgia cauliflora*) were cut into smaller fragments using stainless steel scissors and attached to transportable modules ("coral pots") that facilitated ROV operations with the bioboxes. Each coral fragment was placed approximately 1 inch (∼2 cm) in depth at the bases of the fragments. Each coral pot holding a single coral fragment was labeled with a unique number and deployment group letter (**Figures 1B,C**). Once processed, coral pots were returned by ROV to the site of collection within Sur Ridge DSCSCs to avoid confounding the potential effects of translocation with other factors (**Figure 1A**). Overall, *n* = 8 translocated coral groups were deployed with a mix of coral taxa. Collection, translocation, and re-visitation of translocated deep-sea corals were executed by careful coordination among the ship's crew, ROV pilots, and scientists.

Coral Fragment Attachment

Survival of coral fragments may be affected by how coral fragments are attached to a transportable substrate or module. To evaluate the effects of attachment methods on translocated coral survivorship, coral pots were fabricated using polyvinyl chloride (PVC) plumbing parts with two different attachment methods (∼US$20 per pot). For attachment version 1 (coral pot v.1), fragments from multiple species were attached to a PVC base using four zip ties which "loosely" fixed the fragments to the upright 1″ PVC in the center of the coral pot (**Figure 1B**). PVC cross-legs at the pot base were filled with Sakrete® fast setting cement patcher (Charlotte, NC, United States) to

function as the weight—the total pot without coral weighed approximately 1 kg. For attachment version 2 (coral pot v.2), coral fragments from multiple species were "hard" fixed to the upright 1.5″ PVC in the center of coral pot using the fast setting cement patcher (**Figure 1C**). The 4″ diameter PVC end cap at the base was filled with cement to anchor and enclose the pot in an upright orientation. The volume of cement required to affix fragments to the center PVC varied with the size and taxon of fragments. Version 2 pots weighed approximately 1.2 kg in dry weight without coral fragments.

Transport Stress

Survival of translocated corals may also be particularly affected by the duration of exposure to potentially stressful environmental changes during transport. To evaluate the sensitivity of corals to transport stress, we examined the survival of corals collected and returned to their DSCSC on the same day with a similar group held overnight in shipboard aquaria then relocated after ca. 1 day. For this experiment, only attachment of fragments by cement (coral pot v.2) was used. For the same-day treatment, multiple species were collected and processed while the corals were held in the ROV biobox to avoid stress (**Supplementary Figure 1A**). Using a team of six people with designated responsibilities, processing and attachment of each coral fragment required an average of 7 min per fragment (*n* = 20 coral fragments of various taxa). Once all fragments were fixed in coral pots, the ROV was deployed to relocate the corals at their collection location on Sur Ridge. This same-day approach required ca. 2 h at the surface and 1 h to return the coral pots to depth. For the overnight treatment,

corals were maintained in shipboard aquaria overnight using 50-gallon acrylic aquaria ($n = 3$) in a darkened, temperature-controlled room. Chilled seawater (5–6°C) was set to flow at 1 Lmin^{-1} and the lights were turned off except during periods when corals were processed (**Supplementary Figure 1B**). Donor coral branches were constantly immersed in large Tupperware containers during movement from the ROV biobox to shipboard aquaria—ensuring the corals would not be exposed to air. Once in aquaria, the collected corals were fragmented and attached to coral pots (v.2). On the day after collection and processing (approximately 12–18 h post collection), the coral pots were transferred to the ROV biobox in large Tupperware containers for translocation to the study sites. The biobox was prepared to receive the coral pots by filling the partitions with the same shipboard chilled seawater used for the aquaria and with ice packs to maintain seawater temperature similar to their collection location.

Coral Survivorship and Analysis

Coral translocation sites were revisited one or more times per year for two plus years to determine the survival of translocated coral fragments. Corals were determined to be alive if the observed fragments were present in the coral pot at the time of the census and exhibited normal polyp and tissue color. After approximately 3 years of repeated visits to the study sites, overall survivorship patterns are reported by attachment method and by transport stress treatment. Survivorship over time was statistically analyzed using the generalized linear model (GLM) and segmented model with the deployment group and duration of transport stress as a combined fixed factor due to the low number of replicates. Segmented model analysis was used to test for any temporal sensitivity in survivorship by group deployment and transport stress—i.e., non-linear survival vs. time (Muggeo, 2003, 2008). Model fits were compared using the corrected Akaike Information Criterion (AICc). Reduction of the AICc by more than 10 by the segmented model was assumed to be a conservative indicator of a break-point in survival. Statistics were performed using the software R and the packages "lme4," "segmented," and "AICcmodavg." We also report the survivorship patterns of each coral taxon as points for further discussion.

RESULTS

Environmental Variability and Exposure

Temperature, salinity, and dissolved oxygen data logged from 0 to 1400 m depth during the coral translocation studies are shown in **Supplementary Figures 2A–D** ($n = 14$ dives). During these ROV dives, the corals were generally exposed to depths of 940.13 ± 344 m (mean ± SD), temperatures of 4.4 ± 2.18°C, salinity of 34.39 ± 0.22 PSU, and dissolved oxygen levels of 0.73 ± 0.91 ml/l (**Table 2**). Temperature sensors on the ROV and within the ROV biobox indicate that corals in the biobox experienced approximately 3°C warming during the ascent and descent of the ROV. Temperatures in the biobox rose from 5.2 to 8.5°C during ROV decent over the first 30 min

(**Supplementary Figure 3**). Subsequently, temperatures within the biobox dropped to ambient (4.5°C) over the following 45 min. For corals held overnight in shipboard aquaria, seawater temperature (digital handheld thermometer; $n = 12$ samples) was stable (5.73 ± 0.42°C) and approximately 1.3°C warmer than the bottom temperatures at Sur Ridge.
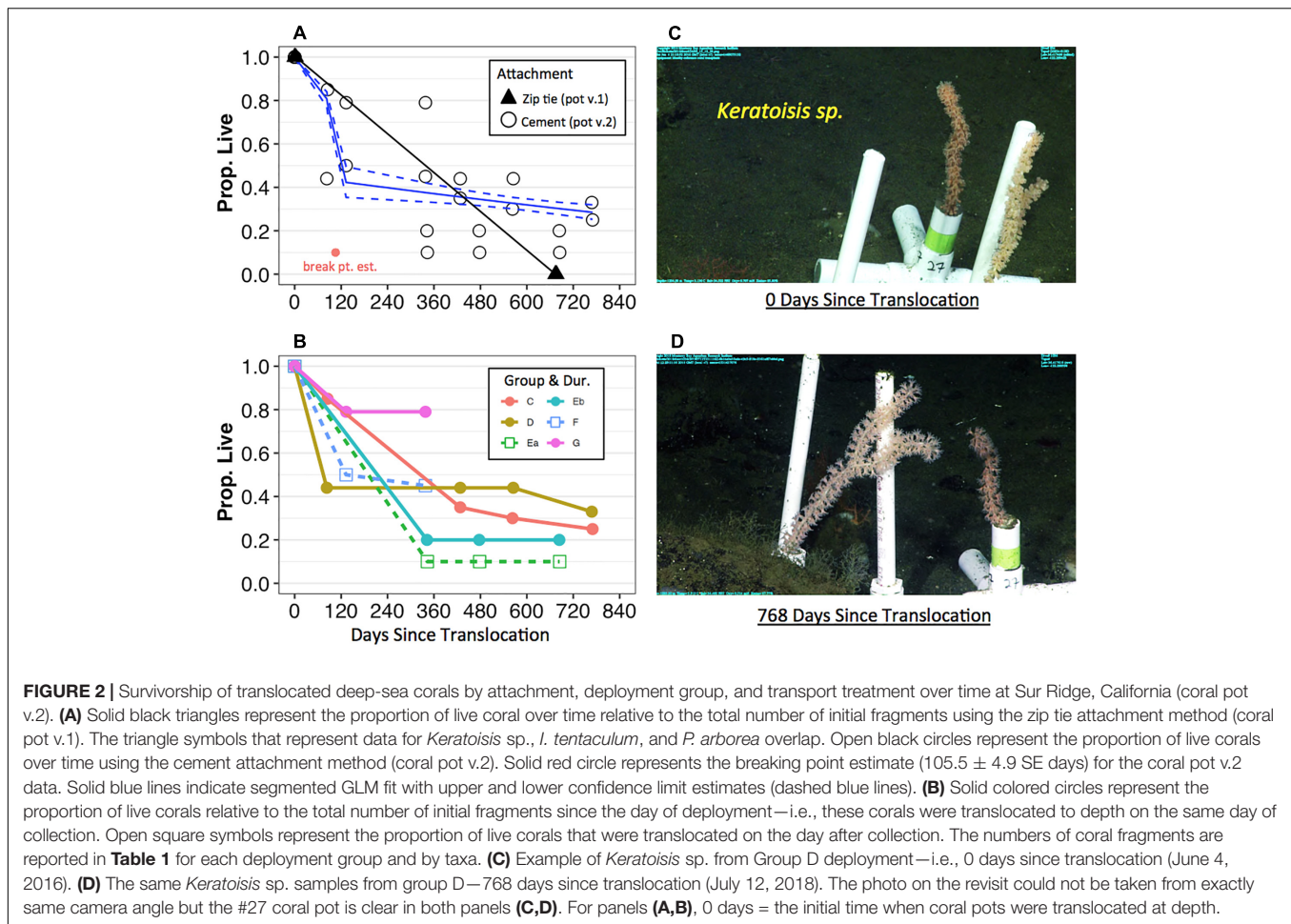
Coral Survivorship by Attachment and Temporal Sensitivity

Survival of coral fragments seemed to be dependent on the type of fragment attachment method—i.e., coral pot version—and non-linear over time. All *Keratoisis* sp., *I. tentaculum,* and *P. arborea* corals loosely attached by zip ties to a transportable module (coral pot v.1) did not survive (**Figure 2A**, black triangles). In contrast, coral fragments attached using cement (coral pot v.2) survived far better than those attached by zip-ties, but exhibited variable survival over time. Furthermore, some coral fragments survived 768 days displaying upright, colorful, and healthy polyps at the time of the census (see **Figures 2C,D**; *Keratoisis* sp. examples). Survivorship for all translocated coral fragments in coral pot v.2 observed within the first 365 days was ~52.6%. At the end of the second year—i.e., between 563 and 685 days post-translocation—the overall mean survivorship was reduced to ~23.9%. Survivorship of all the corals in coral pot v.2 was also significantly non-linear over time (**Figure 2A** and **Table 3**, $p < 0.001$). Segmented GLM analysis revealed that mortality rates were significantly higher in the first 105 ± 4.97 days (mean ± SE; **Table 3**, breaking point estimate; $p < 0.05$). After this initial period of approximately 3 months, the results indicate that overall survivorship rates became more stable with the slope of the second segment reaching near zero (**Figure 2A** and **Table 3**).

Results of the cement attachment method (coral pot v.2) may have been partially due to a species-specific response. The precious coral *Corallium* sp. and the black coral *S. kofoidi* had the highest survivorship of all translocated coral taxa when translocated using coral pot v.2. **Figure 3A** shows an example of a *Corallium* sp. fragment with extended polyps indicating good "health" 133 days after translocation. All (100%) of the translocated *Corallium* sp. ($n = 5$) survived ca. one year and *S. kofoidi* exhibited high survival with 80–100% of the translocated corals surviving approximately 1–2 years (**Figures 3B,C**). Attachment of bamboo corals (*Keratoisis* sp. and *I. tentaculum*) using coral pot v.2 resulted in ~30% and 0–50% survivorship respectively in the first year (**Figures 3E,F**). Attachment of bubble gum corals (*P. arborea* and *S. cauliflora*) resulted in the lowest survivorship over time for all corals deployed using coral pot v.2 (**Figures 3G,H**). 0–40% of *P. arborea* (**Figure 3G**, group C, E_b, and G) survived to the end of the first year. *S. cauliflora* coral fragments resulted in approximately 40% survivorship after the first year but ultimately declined to 0% over the subsequent year (**Figure 3H**, group C).

Transport Stress and Survivorship

Results from the GLM segmented model analysis indicate that proportional survivorship was not significantly dependent on coral deployment group or whether the corals had overnight

FIGURE 2 | Survivorship of translocated deep-sea corals by attachment, deployment group, and transport treatment over time at Sur Ridge, California (coral pot v.2). **(A)** Solid black triangles represent the proportion of live coral over time relative to the total number of initial fragments using the zip tie attachment method (coral pot v.1). The triangle symbols that represent data for *Keratoisis* sp., *I. tentaculum*, and *P. arborea* overlap. Open black circles represent the proportion of live corals over time using the cement attachment method (coral pot v.2). Solid red circle represents the breaking point estimate (105.5 ± 4.9 SE days) for the coral pot v.2 data. Solid blue lines indicate segmented GLM fit with upper and lower confidence limit estimates (dashed blue lines). **(B)** Solid colored circles represent the proportion of live corals relative to the total number of initial fragments since the day of deployment—i.e., these corals were translocated to depth on the same day of collection. Open square symbols represent the proportion of live corals that were translocated on the day after collection. The numbers of coral fragments are reported in **Table 1** for each deployment group and by taxa. **(C)** Example of *Keratoisis* sp. from Group D deployment—i.e., 0 days since translocation (June 4, 2016). **(D)** The same *Keratoisis* sp. samples from group D—768 days since translocation (July 12, 2018). The photo on the revisit could not be taken from exactly same camera angle but the #27 coral pot is clear in both panels **(C,D)**. For panels **(A,B)**, 0 days = the initial time when coral pots were translocated at depth.

TABLE 2 | General temperature, salinity, and dissolved oxygen conditions during ROV Doc Ricketts dives.

	n	Mean	SD	SE
Depth (m)	283062	940.13	344.45	0.65
Temperature (°C)	282985	4.48	2.18	0.00
Salinity	282917	34.39	0.22	0.00
D.O. (ml/l)	280793	0.73	0.91	0.00
Aquaria Temperature (°C)	12	5.73	0.42	0.12

*D.O., dissolved oxygen; n, number of samples logged by SBE 19 CTDO; SD, standard deviation; SE, standard error. Full dive profiles are illustrated in **Supplementary Figure 2**.*

treatment in shipboard aquaria (**Figure 2B** and **Table 3**). More specifically, while the survivorship rates of group D (same day translocation) did not significantly differ compared to the reference group C (same day translocation), the survivorship rates of groups E, F, and G did significantly differ regardless of transport duration treatment.

The responses to transport stress treatment may also have been partially due to a species-specific response. For the coral species tested for transport stress, survivorship due to treatment were mixed with the exception of *Lillipathes* sp. which resulted in 100%

survivorship regardless of treatment (**Figure 3D**). For *Keratoisis* sp. and *S. cauliflora*, percent survivorship was generally lower for the coral fragments in the overnight treatment (**Figures 3E,G,H**; data denoted by open blue squares). Furthermore, survivorship of *S. cauliflora* declined more rapidly to 0% for the coral fragments in the overnight treatment (**Figure 3H**, group E_a) but this rapid decline may have been due to the limited samples ($n = 2$) with this deployment. However, survivorship of *I. tentaculum* and *P. arborea* due to transport stress treatment seemed to be mixed. For the former, 0–50% of the *I. tentaculum* [**Figure 3F**; group C ($n = 10$) and E_b ($n = 4$)] deployed survived ca. 2 years with the same day treatment but 25% survived the same amount of time when exposed to overnight treatment [**Figure 3F**; groups E_a ($n = 4$)]. For the latter coral species, corals deployed the same day treatment resulted in 0–40% survival ($n = 5$) whereas corals exposed to overnight treatment dropped to 0–20% at the end of the first year.

DISCUSSION

Restoration of deep-sea communities is a new frontier for ocean science and resource management as human activities have increasingly broad and profound effects in the deep sea. The

TABLE 3 | Segmented generalized linear model (GLM) results and breaking point estimate for coral group survivorship over time.

Segmented GLM model	y = DST + Translocation Type + U + psi + e			
	Estimate	SE	z-value	p-value
(Intercept)	7.76	1.24	6.26	***
DST	−0.08	0.01	−5.19	***
Group D (same day)	−0.14	0.14	−0.99	0.32
Group E_a (overnight)	−1.53	0.20	−7.55	***
Group E_b (same day)	−0.73	0.16	−4.57	***
Group F (overnight)	0.31	0.14	2.21	*
Group G (same day)	1.73	0.15	11.53	***
U	0.08	0.01	5.12	NA
Null deviance	2791.76 on 23 degrees of freedom			
Residual deviance	735.48 on 17 degrees of freedom			
AIC:	1482.4			
Segmented Model BP estimate	105.56 ± 4.97 SE			
	Estimate ± SE	t-value	LCI (95%)	UCI (95%)
Segment 1 slope	−0.08 ± 0.01	−5.19	−0.11	−0.04
Segment 2 slope	−0.001 ± 0.0003	−3.14	−0.002	−0.0003

Breaking point estimate and slopes of any segments are estimated using the segmented model (Muggeo, 2008). y = proportion of initial corals alive relative to the initial number of corals deployed for each group. Data from Group C corals (same day translocation) were used as the arbitrary reference. Type of transport stress treatment— i.e., same day translocation as the day of collection or kept overnight in shipboard aquaria—are indicated in parentheses. DST, days since translocation; e, error term; U, difference in slopes of the two segments; psi, breaking point estimate at each step with standard error; BP, breaking point; SE, ± standard error; NA, not applicable. LCI, lower confidence interval; UPI, upper confidence interval; *p < 0.05 significance; **p < 0.01 significance; ***p < 0.001 significance.
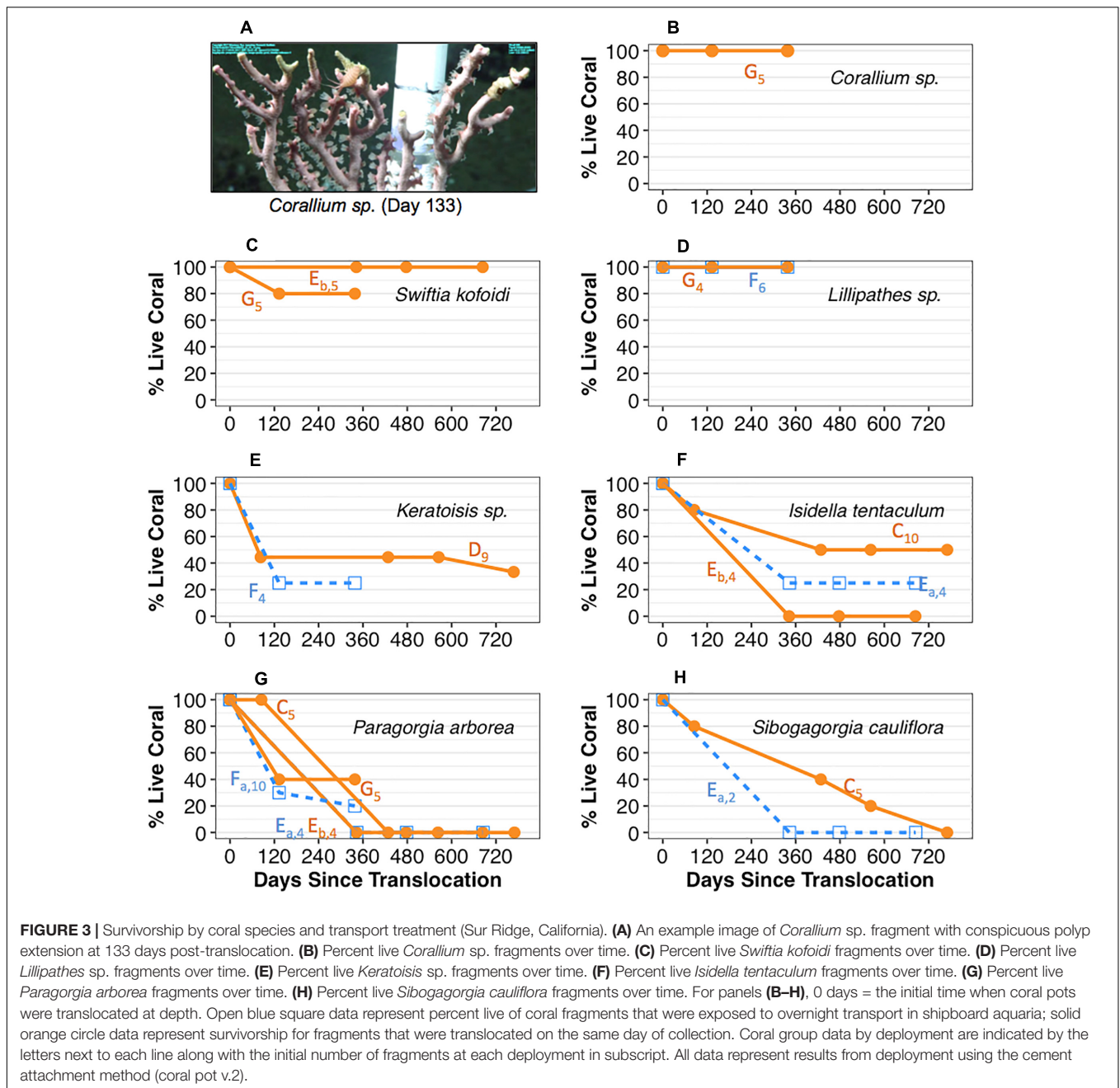
effects of trawling on deep-sea coral and sponge communities were perhaps the first deep-sea ecosystem impacts to be highlighted (Koslow et al., 2000; Van Dover, 2014; Van Dover et al., 2014; Amoroso et al., 2018). We now face continuing fishing impacts, as well as host of new local to global threats ranging from deep-sea mining to climate-linked changes in ocean conditions. The 2010 BP Deepwater Horizon oil spill and its enormous scope refocused our attention on anthropogenic impacts in the deep sea. Constraining further impacts using networks of Marine Protected Areas, a successful approach in shallow marine environments (McCook et al., 2010), shows promise, but has only been applied sparingly in the deep sea (Edgar et al., 2014). Beyond protection, active restoration of damaged deep-sea assemblages may provide meaningful mitigation, but has received little to no attention—this study is one of the first to explore methods to promote the recovery of impacted deep-sea coral populations by examining the performance of multiple coral taxa.

The high initial mortality of translocated corals observed in our investigation is similar to the general patterns observed in previous restoration studies of shallow water corals (Lasker, 1990; Epstein et al., 2001; Linares et al., 2008a,b; Edwards et al., 2010; Boch and Morse, 2012). High mortality rates shortly after translocation indicate that methods minimizing translocation stress should be one of the key factors to consider in future studies in both shallow and deep-sea environments. The variation in mortality among coral taxa observed also indicates that longer-term evaluations are needed and that successful translocation of multiple coral species will require different solutions depending on taxa. Furthermore, as the effects of habitat heterogeneity on deep-sea coral restoration success remain unknown, a more

rigorous investigation of how the conditions at the source colony location and how the conditions at the translocation sites may influence the survivorship of translocated corals need further attention.

We recognize that we have not fully explored the full range of factors that may affect the survivorship of translocated coral fragments. Our results indicate that the attachment of coral fragments to a substrate may be critical for coral survival and different methods employed for mitigation efforts (e.g., zip tie, cement, or other unexplored options) may influence restoration success. Previous studies in shallow coral ecosystems indicate that the size of fragments (Linares et al., 2008b), variation in currents (Jokiel, 1978; Boch and Morse, 2012), protection from predation (Baria et al., 2010; Shaver et al., 2018), and having a nursery phase before transplanting (Shafir et al., 2006), can also have a major influence on the survival of translocated corals. Reproductive condition of translocated corals may also affect their survival and potentially the period required for corals to produce and release viable gametes. In our study, we observed that some polyps of *Keratoisis* sp., *I. tentaculum,* and *Lillipathes* sp. contained eggs at the time of initial translocation. Although eggs were visible within several translocated fragments of each of these species looked to be decreasing over time, additional studies are required to determine the survivorship and reproductive contribution as a function of initial reproductive condition.

Differences in survival rates among species were somewhat surprising. Bubblegum corals, which have broad, flexible proteinaceous branches, appeared robust during handling for translocation, but had very high rates of mortality compared to other taxa. Many factors may have contributed to high

FIGURE 3 | Survivorship by coral species and transport treatment (Sur Ridge, California). **(A)** An example image of *Corallium* sp. fragment with conspicuous polyp extension at 133 days post-translocation. **(B)** Percent live *Corallium* sp. fragments over time. **(C)** Percent live *Swiftia kofoidi* fragments over time. **(D)** Percent live *Lillipathes* sp. fragments over time. **(E)** Percent live *Keratoisis* sp. fragments over time. **(F)** Percent live *Isidella tentaculum* fragments over time. **(G)** Percent live *Paragorgia arborea* fragments over time. **(H)** Percent live *Sibogagorgia cauliflora* fragments over time. For panels **(B–H)**, 0 days = the initial time when coral pots were translocated at depth. Open blue square data represent percent live of coral fragments that were exposed to overnight transport in shipboard aquaria; solid orange circle data represent survivorship for fragments that were translocated on the same day of collection. Coral group data by deployment are indicated by the letters next to each line along with the initial number of fragments at each deployment in subscript. All data represent results from deployment using the cement attachment method (coral pot v.2).

mortality rates, including the potentially toxic effects of cement or predation. While we did not have a persistent observation system to record any predatory behavior on the translocated corals, we did observe tissue sloughing from some bubble gum coral fragments (<4 months after translocation) followed by the fragments breaking off consistently at the base. Structural sensitivity of red gorgonian fragments at the base of fragments artificially attached to a natural substrate was discussed in a previous study; therefore high sensitivity at the point of attachment may be a general pattern for softer-bodied gorgonians (Linares et al., 2008a). In contrast, bamboo corals appeared to be highly fragile, but exhibited high survival up to ca.

2 year post-translocation. Thus, future studies should explore different attachment compounds and employ persistently present observation systems with a suite of sensors to help resolve questions related to factors such as attachment sensitivity and other factors such as flow and predation.

The cost of enhancing the restoration and recovery of deep-sea coral and sponge communities after anthropogenic disturbances will remain uncertain until all components of ecosystem services and the scale of active mitigation strategies can be explored. Spurgeon and Lindahl (2000) estimated that coral reef restoration costs could vary from US$13 K to US$100 M per hectare based on four case studies in shallow water coral reef systems. Additional

estimates made on 10 case studies indicate that shallow water efforts have a median cost of ∼ US$500 K per hectare. In contrast, Van Dover et al. (2014) estimated that deep-sea restoration efforts will likely cost two to three orders of magnitude more than shallow water efforts based solely on direct costs. In our study, the use of the R/V *Western Flyer* and the ROV *Doc Ricketts* cost approximately US$30 k per day with the study site within 4 h from port. However, the cost of establishing viable translocation methods here should also include the costs of mapping the deep-sea coral and sponge communities and re-visiting mitigated areas so that outcomes of the translocation efforts can be assessed in a rigorous manner over time. Additional evaluations will also be needed to examine larger and cost-effective aquarium systems that minimize stress while transporting deep-sea corals over long distances and time periods, which may be necessary to mitigate large scale anthropogenic disturbances such as the BP Gulf of Mexico oil spill. Despite the need for further development, the relatively high survivorship of deep-sea coral fragments in pots constructed of low-cost (US$20) materials is a promising indication that developing active mitigation strategies for the DSCSCs could have merit. However, we also acknowledge that the use of PVC and cement materials is not an ideal module as a permanent transportable solution and additional bio-friendly materials will need to be explored.

The long-term survival of translocated corals, as well as their effect on DSCSC recovery over decades to centuries is yet to be determined. Considering the slow growth rates and high longevity of deep-sea corals (Andrews et al., 2002, 2005; Roark et al., 2005), it is natural to question if coral translocation will likely accelerate the recovery of damaged DSCSCs. Additionally, understanding the impacts of sourcing coral fragments from "healthy" versus "unhealthy" or "dying" donor colonies will be a critical step prior to implementation. For example, transplanting corals by fragmenting a limited number of source colonies versus fragmenting a limited number of corals that are prolific in one area to mitigate a disturbed area are likely to have different impacts on the source population but these questions have not been studied in the deep sea. Despite the gaps in knowledge, we will need to ask what role active mitigation will play in response to past, current, and future changes in the ocean due to increased human activity. Will establishing cost-effective restoration approaches that enhance gamete contact and approaches that generate corals that are more resilient to climate-related changes in ocean conditions better prepare deep-sea ecosystems for the future? Perhaps efforts to propagate other key associated taxa such as sponges that may enhance energy flow and carbon sequestration could help mitigate climate change driven changes in the deep sea (Murray et al., 1994; Cathalot et al., 2015; Kahn et al., 2015). Overall, the most effective strategies for mitigating damage in DSCSCs are uncertain but exploring the potential value of restoration options such as coral translocation and other approaches will help shape our efforts to protect and sustain these valuable and fragile deep-sea resources.

AUTHOR CONTRIBUTIONS

CB, ADV, and JB designed the study. CB did the statistical analysis. CB, JB, ADV, EB, CK, JL, and CL conducted the translocation experiments. All authors listed made a substantial contribution to the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

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