



Original Article

Assessing the ecological importance of red tree coral thickets in the eastern Gulf of Alaska

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Red tree corals (*Primnoa pacifica*), the largest structure-forming gorgonians in the North Pacific Ocean, form dense thickets in some areas. These thickets are a dominant benthic habitat feature in the Gulf of Alaska (GOA), yet little is known about the ecosystems they support. In 2005, we used a submersible to study the ecology of thickets inside or near five small areas of the eastern GOA later designated in 2006 as habitat areas of particular concern (HAPCs)—areas closed to all bottom contact fishing. We show that red tree corals are keystone species in habitats where they form thickets (mean density 0.52 corals m⁻²)—the densest and largest thickets documented anywhere. Measured sponge densities (2.51 sponges m⁻²) were also among the highest documented anywhere. The corals and sponges in the study areas provide essential fish habitat for some fish species, and we show with logistic regression models modified with a scaled binomial variance that bedrock, while important habitat for some fish, is even more important when paired with corals and sponges. Red tree corals were not equally distributed with regard to habitat characteristics, and we show that their presence was correlated with bedrock substrate, moderate to high seabed roughness, and slope > 10°. Most corals and sponges are vulnerable to disturbance from longlining, the principal bottom contact fishing in this region, but the larger corals and sponges are the most vulnerable. We observed evidence of infrequent recruitment events and a strong pulse of predation, apparently from fishing gear-induced trauma, that could exacerbate slow recovery of red tree corals from disturbance. Some red tree coral thickets are provided protection within designated HAPCs and some are not. Modifications to longline gear and an expanded network of HAPCs could help preserve these keystone species and the ecosystems they support.

Keywords: cold-water corals, correlation, emergent epifauna, fishing disturbance, gorgonians, Gulf of Alaska, HAPC, logistic regression, longlining, odds ratio, *Primnoa*, sponges.

Introduction

Red tree corals (*Primnoa pacifica* Kinoshita, 1907) are large, structure-forming gorgonians that form dense thickets in some regions of the North Pacific Ocean. In the eastern Gulf of Alaska (GOA), thickets are a prominent benthic habitat feature where they occur, but surveys to date indicate that they may be relatively rare. Thickets are sometimes found in areas where both mobile bottom-contact fishing gear and fixed-gear such as longlines are used. Red tree corals are caught as bycatch in fisheries and research stock assessment surveys (Krieger, 2001) for demersal species. Colonies are easily damaged or dislodged from the seabed by external forces such as that exhibited by fishing gear, and manned submersible observations

in the GOA clearly indicate that some thickets have been disturbed by past fishing activities (Krieger, 2001). The potential for interaction between current fishing activities and red tree coral habitat is high, given their nearly coincident spatial and bathymetric distribution in the GOA (Stone and Shotwell, 2007). Also, the large size of red tree corals and their highly arborescent form increase the likelihood that fishing gear will interact with them. Red tree corals have relatively slow growth rates (Andrews *et al.*, 2002; Stone *et al.*, 2005) and reproductive characteristics (Waller *et al.*, 2014) that imply slow recovery from disturbance.

Groundfish surveys in the 1990s using submersibles documented the presence of red tree coral thickets in several areas of the eastern

GOA (Krieger, 2001; Krieger and Wing, 2002). During these investigations, commercial species including rockfish (*Sebastes* spp.) and golden king crab (*Lithodes aequispinus*) were observed in close association with coral colonies. The primary function of the associations is unknown, but high-relief corals undoubtedly provide refuge for shelter-seeking species at various life stages and may serve as focal areas for foraging (Auster, 2005; Stone, 2006). In the light of these findings, NOAA proposed to the North Pacific Fisheries Management Council (NPFMC) that some of these areas in the eastern GOA be designated as habitat areas of particular concern (HAPCs) while prohibiting the use of all bottom-contact fishing gear with the purpose of protecting thickets in those areas. The NPFMC subsequently in July 2006 designated five small areas at two sites in the eastern GOA (subsets of the proposed closures) as HAPCs, totalling an area 46 km² (Figure 1).

The primary goal of the study was to assess the ecological importance of dense, red tree coral thickets, a unique and little-

studied benthic habitat feature, in and/or near five HAPCs in the GOA. The assessment included investigation of distribution, preferred habitat characteristics, fishing disturbance, predation, recruitment, and fine-scale use of coral habitat by FMP species (species managed under an NPFMC fisheries management plan). The results of this study will provide evidence whether small-scale area closures are an appropriate tool to protect red tree coral thickets and the ecosystem services they provide. Also, we provide guidance on how to more effectively preserve red tree coral habitat.

Material and methods

Study area

The study area was chosen to overlap five HAPCs and included two sites in the eastern GOA. Site 1 was located at the Fairweather Ground, a large offshore shoal on the outer edge of the continental shelf in the northeastern GOA (Figure 2). Geological interpretation

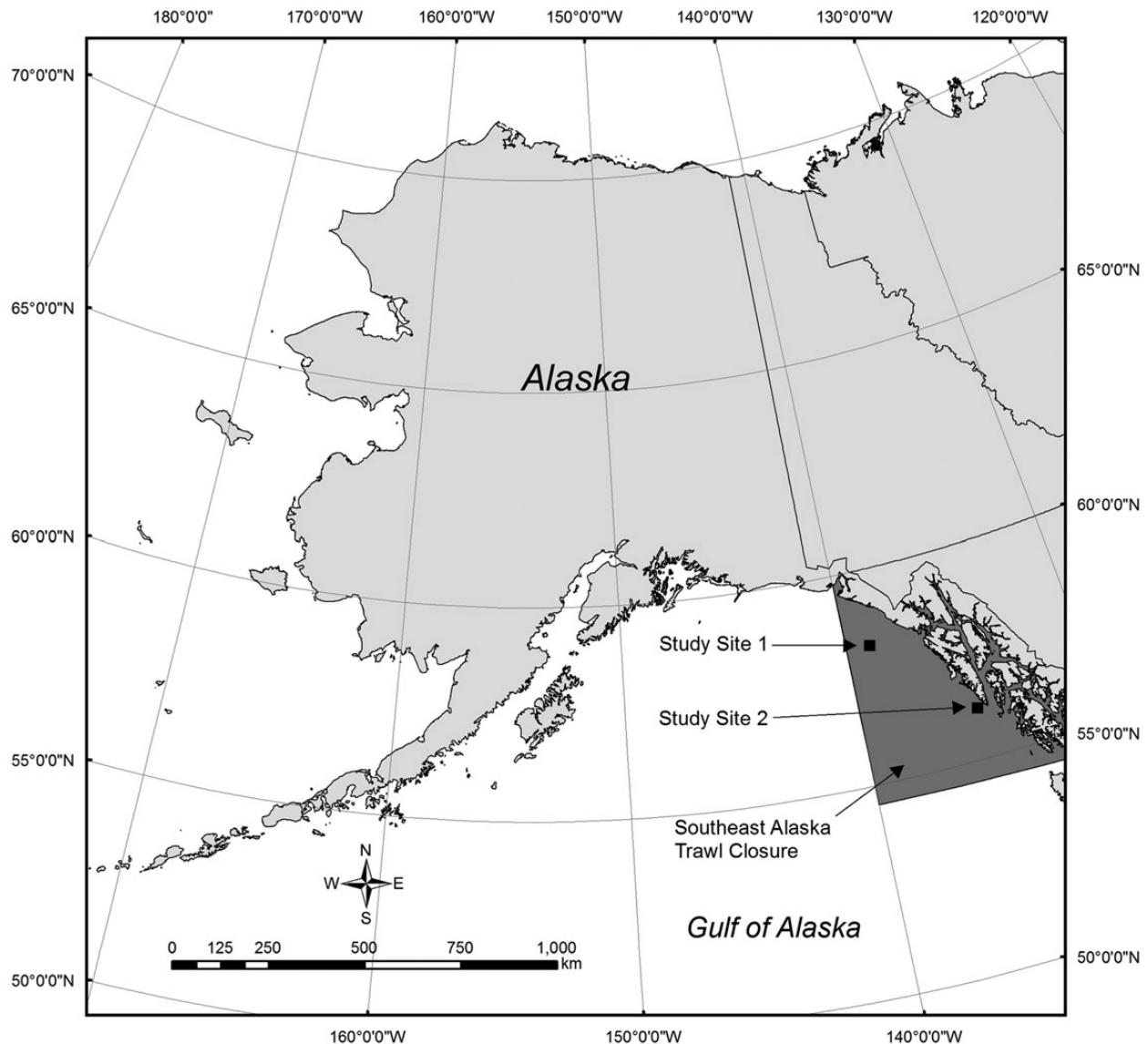


Figure 1. Locations of the two study sites in the eastern GOA within the Southeast Alaska Trawl Closure area. Site 1 is located at the Fairweather Ground and Site 2 is located on the Shutter Ridge west of Cape Ommaney.

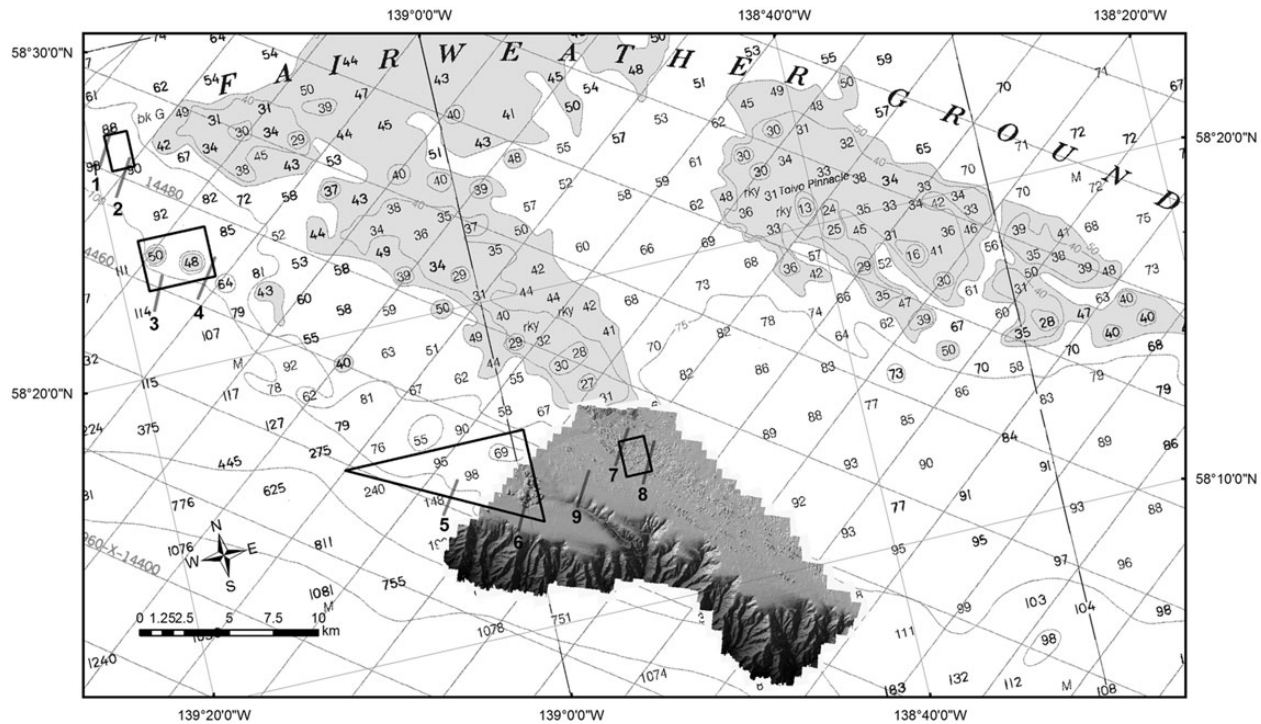


Figure 2. Study Site 1 at the Fairweather Ground showing the four small HAPCs (polygons) where video footage was collected along 9 strip transects (numbered lines) with the submersible *Delta*. Multibeam data are available for only a small portion of the study area, shown in this figure as a grey overlay. Depth soundings are from a NOAA nautical chart and are in fathoms.

of multibeam data collected by the Alaska Department of Fish and Game (ADF&G) and subsequent mapping of seabed habitats from those data indicate that the area has complex bathymetry and highly varied seabed geological features (G. Greene, pers. comm.; Figure 2). Large catches of red tree corals have been observed as bycatch during National Marine Fisheries Service (NMFS) groundfish surveys in several areas along the south and west flanks of the Fairweather Ground. Submersible surveys later confirmed the presence of thickets located in areas of bedrock, fractured bedrock, or talus and scattered large boulders at depths between 150 and 200 m. Two areas of the Fairweather Ground were proposed as HAPCs based on the best available information regarding red tree coral distribution. After consulting with NOAA resource managers and stakeholders, the NPFMC approved precautionary closure of two smaller areas within each of the proposed HAPCs (Figure 2) until more detailed coral distribution data could be collected.

Site 2 was located at the Shutter Ridge, 28 km west of Cape Ommaney, Baranof Island, on the continental shelf (Figure 1). Red tree coral thickets were first documented there during submersible studies of groundfish distribution and behaviour in the early 1990s (K. Krieger, pers. comm.) and during subsequent reconnaissance to assess the suitability of the area as a potential HAPC in 2000 (J. Lincoln Freese, pers. comm.). The area was subsequently mapped with multibeam in 2001, and seabed habitat maps were constructed (Figure 3). Detailed mapping revealed that the dominant geological feature where red tree coral thickets are located is a series of rocky pinnacles orientated north–south on a 6-km long “shutter” ridge along a subduction zone. The bedrock feature is part of the basement rock complex of a tectonostratigraphic terrane of the Pacific Plate that has docked with Alaska (G. Greene, pers. comm.).

Previous submersible observations were limited to the southern 2 km of the ridge. The HAPC proposed by NMFS included the entire

feature because scientists suspected that the entire ridge supports red tree coral thickets based on geology and bathymetry. However, the NPFMC designated as an HAPC only the area where the presence of thickets had been confirmed with *in situ* observations—approximately the southern half.

Current fisheries

The study sites are within the Southeast Alaska Trawl Closure that was established in 1998 (Figure 1). The Closure encompasses an area of 180 418 km² in the eastern GOA and Southeast Alaska where all trawling is prohibited (Witherell and Woodby, 2005). Some regions within this closure area supported important trawl fisheries for Pacific ocean perch (*Sebastes alutus*) before the closure, but fisheries data indicate that the study sites were virtually untrawled during the 10-year period before the closure (J. Olson, pers. comm.). Small, but locally important longline fisheries still occur in or near the study sites (O’Connell and Carlile, 1993) for yelloweye rockfish (*Sebastes ruberrimus*), Pacific halibut (*Hippoglossus stenolepis*), and sablefish (*Anoplopoma fimbria*).

Experimental design

The submersible *Delta* was used to collect video of the seabed along strip transects at nine stations at Site 1 (Figure 2) between 14 and 16 August 2005 and at ten stations at Site 2 (Figure 3) between 17 and 20 August 2005. Two transects were established at each of the four closure areas at Site 1 that were bisected by the boundary of the closure (Figure 2). An additional transect was established in an area between two of the closures where red tree coral thickets had previously been reported (Bizzarro, 2002). Ten transects were established at Site 2 that crisscrossed the entire length of the Shutter Ridge, and each spanned the entire width of the feature (Figure 3).

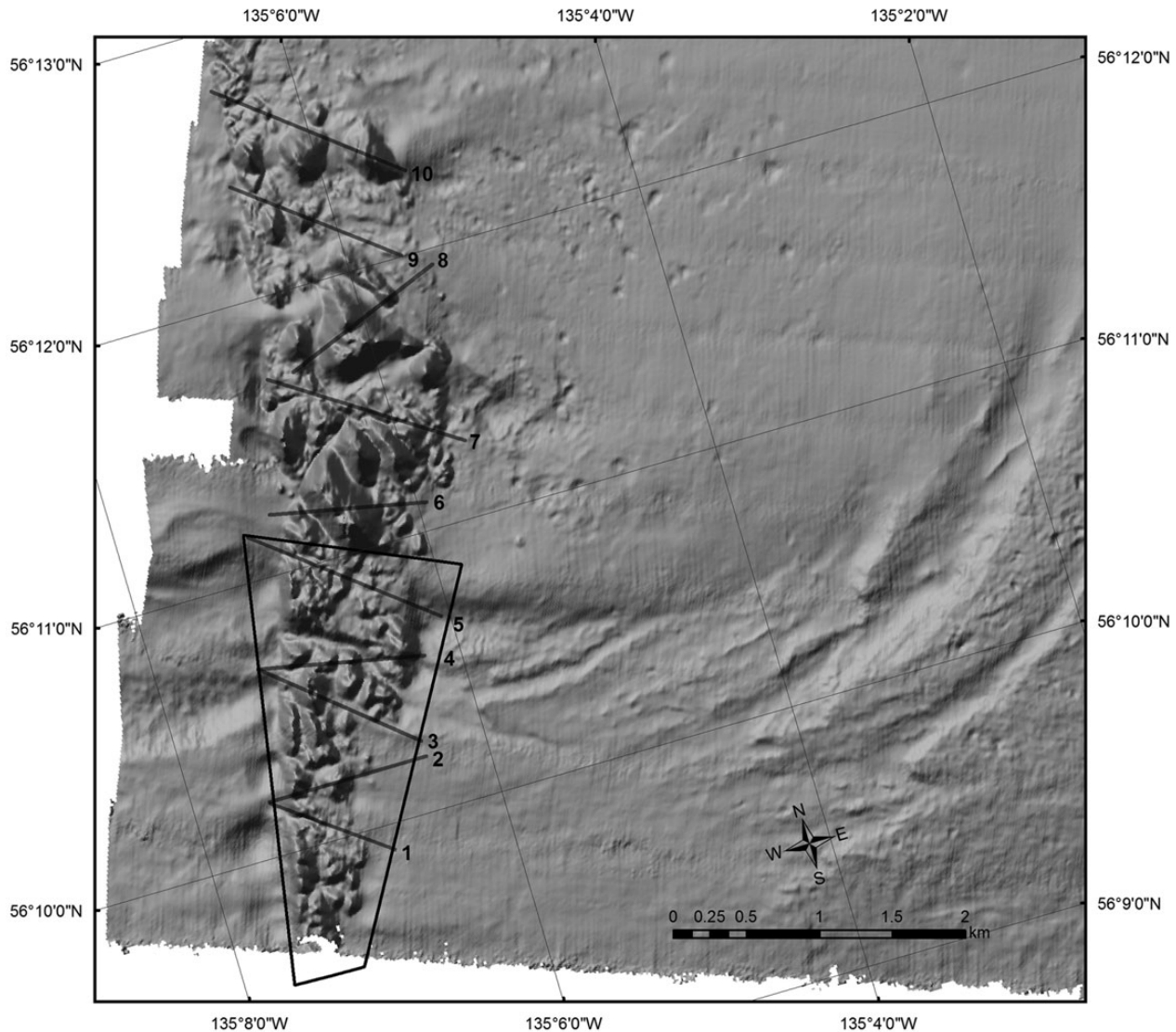


Figure 3. Study Site 2 at the Shutter Ridge west of Cape Ommaney showing the HAPC (polygon) where video footage was collected along 10 strip transects (numbered lines) with the submersible *Delta*. The background image is the multibeam data interpretation.

The submersible carried a pilot and scientist and was equipped with external halogen lights, internal and external video cameras, gyro and magnetic compasses, sonar altimeter, sub-tender vessel communications, and a Seabird Electronics SeaCat Profiler (mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the NMFS, NOAA) used to collect depth, temperature, salinity, and density profiles of the water column. The submersible was also equipped with an acoustic transponder that allowed tracking of the submersible by the tender vessel with differential global positioning and ultra-short baseline acoustic tracking. The submersible followed a predetermined bearing generally from deep to shallow water (Site 1 only) along each transect, and its course was modified when necessary via communication with the tender vessel. Submersible speed varied $\sim 0.3\text{--}0.8\text{ m s}^{-1}$, depending on seabed terrain and near-bottom currents.

The scientist viewed the image area laterally, recorded voice observations, and operated a video camera to gather footage from that perspective, including close-up footage. Voice observations included

those by both the pilot and observer regarding the presence and location of red tree corals relative to the transect. Continuous video footage of the seabed was collected with two externally mounted cameras. Data continuously displayed on the video images included real time and depth. In addition, the video cameras recorded two parallel laser marks 10 cm (primary camera) or 20 cm (secondary camera) apart projected onto the seabed to provide calibration for measurements of the width and length of the image area and size of fauna and substrate.

The primary camera was mounted laterally with the imaging plane directed $\sim 45^\circ$ to the seabed. The width of the image area varied 90–779 cm, depending on the submersible's altitude and position relative to the seabed slope; average width for all transects was 234 cm. The length of the image area (measured to the scaling lasers directed 45° to the seabed) varied 40–296 cm; average length for all transects was 84 cm. The image area was calculated as a trapezoid [$A = 1/2 \times (b_1 + b_2) \times h$; frame height (h) and outside base length (b_1) were measured directly with the 10-cm scaling lasers; inside base length (b_2) was estimated using the ratio

of b_2 to b_1 (60%) measured on the deck of the tender vessel]. When the seabed approached vertical (i.e. $>45^\circ$; $n = 1006$ frames), biota were counted in the entire frame rather than only to the scaling lasers. The area of this perspective was assumed flat-planed and calculated as a rectangle. The width of the image area averaged 225 (range = 68–496 cm) and length averaged 144 (range = 47–345 cm).

A second camera was mounted with the imaging plane directed perpendicular to the seabed with the lens at a near-constant altitude of 80 cm when the submersible was in contact with the seabed. This view was used to enumerate biota on the transect when the submersible was transiting down-slope and the primary camera was consequently projecting into the water column ($n = 36$). The image area was assumed flat-planed and calculated as a rectangle. The width of the image area varied 182–735 cm, and length of the image area varied 126–501 cm.

Video processing

Analogue video was collected with a Hi-8 colour camera and recorded on a Sony mini DV cassette recorder. In the laboratory, video was encoded to mpeg2 format at 30 frames s^{-1} bit rate, copied onto a PC hard-drive for post-processing and onto DVDs for long-term storage. Event logging software (VideoRuler 7) was used to post-process all video (Stone and Brown, 2005) and is described in detail by Stone (2014). Consecutive, non-overlapping frames were “captured” to create a mosaic of each transect. The following data were collected from each video frame: (i) depth, (ii) length, width, and area, (iii) seabed roughness, (iv) slope, (v) seabed exposure, and (vi) primary substrate or surficial substrate texture. Seabed roughness was visually estimated and recorded on a five-point scale as follows: (1) very low (e.g. smooth), (2) low (e.g. sand with a few small cobbles), (3) moderate (e.g. approximately one-third of the seabed not smooth), (4) high (e.g. approximately two-thirds of the seabed not smooth), and (5) very high (e.g. highly jagged substrate with no smooth areas). Slope was visually estimated and recorded on a four-point scale as follows: (1) no slope or $<1^\circ$, (2) low or $<10^\circ$, (3) medium or between 10° and 30° , and (4) high or $>30^\circ$. Slope was measured at the scale of the surrounding area (i.e. 100 s m^2), whereas seabed roughness was measured at the scale of the frame (i.e. less than $\sim 10 \text{ m}^2$). Seabed exposure (or aspect) was the direction (relative to true north) that the slope, if any, faced and was estimated using the compass heading measured onboard the submersible. Exposure was scored as follows: (i) no appreciable exposure (i.e. $<1^\circ$ slope), (ii) north or $315\text{--}045^\circ\text{T}$, (iii) east or $045\text{--}135^\circ\text{T}$, (iv) south or $135\text{--}225^\circ\text{T}$, and (v) west or $225\text{--}315^\circ\text{T}$. The primary substrate texture was based on the Wentworth grade classification (Holme and McIntyre, 1971) and was recorded on a hierarchical three-point scale as follows: (i) bedrock, (ii) boulder, (iii) cobble, (iv) pebble, (v) sand, (vi) silt, and (vii) shell. While we were unable to directly measure current speed and direction at our study sites, we did make qualitative observations during our dives of relative current strength and approximate direction on the seabed transects.

We defined thickets as distinct (i.e. non-overlapping and separated by more than 10 m) patches of more than one red tree coral, and a video frame was classified as thicket habitat if it contained red tree corals or habitat within a 10-m radius of corals, whether on or off the transect. We adopted this classification to maintain consistency with our earlier noted observations of fish behaviour with red tree coral habitat.

Corals and sponges were identified to the lowest possible taxon and were individually enumerated if their bases (e.g. stalk) were within the boundaries of the video frame. Red tree corals were classified into four size (i.e. height) categories as follows: (i) small (<0.5 m high), (ii) medium (0.5–1 m high), (iii) large (1–2 m high), and (iv) very large (>2 m high). Colony stumps (i.e. bases attached to substrate), skeletons attached to substrate but completely denuded of tissue, and detached skeletons were categorized separately (as “stumps”) since accurate size classes could not be determined. The sponges Aphrocallistidae included both *Heterchone calyx* and *Aphrocallistes vastus* since they are difficult to differentiate *in situ*. Similarly, Rossellidae included both *Rhabdocalyptus dawsoni* and *Staurocalyptus solidus*. The demosponge *Mycale loveni* was further classified as small (<8 cm high and wide) and large (>8 cm high and wide) since they undergo an obvious morphological transformation at that size (Stone et al., 2011). Corals and sponges were classified as damaged if they had missing or broken branches, were detached from the seabed (with and without tissue), were attached but overturned and lying in contact with the seabed, or had areas of necrosis. For red tree corals, we distinguished damage attributable to interaction with fishing gear from that caused by predation based on the presence or absence of predators and derelict fishing gear and the pattern of the observed damage. Crinoids (*Florometra serratissima*) were enumerated since they were abundant and presumably ecologically important as was the predacious sea star *Hippasteria phrygiana*. The submersible’s mechanical arm was used to collect voucher specimens for taxonomic identification.

Mobile fauna (fish and crabs) were enumerated if they were within the bounds of the strip transect and their presence there did not appear to be in response to the submersible (Buckland et al., 1993). Fish species enumerated on transects included sharpchin rockfish (*Sebastes zacentrus*), Pacific ocean perch (*S. alutus*), harlequin rockfish (*S. variegatus*), rosethorn rockfish (*S. helvomaculatus*), silvergray rockfish (*S. brevispinis*), yelloweye rockfish (*S. ruberimus*), redstripe rockfish (*S. proriger*), redbanded rockfish (*S. babcocki*), roughey rockfish (*S. aleutianus*), dusky rockfish (*S. ciliatus*), tiger rockfish (*S. nigrocinctus*), quillback rockfish (*S. maliger*), shortspine thornyhead (*Sebastolobus alascanus*), Pacific halibut (*H. stenolepis*), righteye flounders (Pleuronectidae), Pacific cod (*Gadus macrocephalus*), sablefish (*A. fimbria*), lingcod (*Ophiodon elongatus*), skates (Rajidae), and spotted ratfish (*Hydrolagus collieri*). All other fish were grouped into the category Teleostei. Crabs included the brown box crab (*Lopholithodes foraminatus*) and juvenile golden king crab (*L. aequispinus*). Pleuronectidae and rockfish were further classified as juveniles if the fish’s total length was <20 cm. Most rockfish species attain sexual maturity at a size larger than 20 cm (Love et al., 2002). Juvenile rockfish were grouped except for yelloweye, rosethorn rockfish, and shortspine thornyhead, which are easily distinguished from the others. Yelloweye juveniles were classified as such by the classic colour pattern rather than the size limit of 20 cm used for the other species (Love et al., 2002). Rockfish were further classified as young-of-year (YOY) if they were extremely small (less than ~ 6 cm) and displayed the characteristic off-bottom schooling behaviour.

Statistical analyses

Association with habitat characteristics

Simple Pearson correlation coefficients were used to measure associations between the presence of red tree coral and variables characterizing the habitat: depth, primary substrate, seabed roughness, slope, and seabed exposure. We treat the habitat types (e.g. low

slope, medium slope, etc.) as dichotomous nominal variables (1/0 variables), and compute pairwise correlations between the presence/absence of coral (1/0 variable) with each of the habitat types. Pearson’s correlation coefficient is an appropriate measure of association for dichotomous variables and is sometimes referred

Table 1. Depth range, transect length, and area and number of frames sampled for 19 transects surveyed with the submersible *Delta* at two sites (FW, Fairweather; OM, Ommaney) in the eastern GOA.

Transect	Depth range (m)	Transect length (m)	Area sampled (m ²)	Frames sampled
FW1	143–174	2409	1063	1278
FW2	163–179	2239	987	1140
FW3	177–203	1770	973	957
FW4	167–187	2457	1455	1189
FW5	153–306	2394	1383	1281
FW6	132–232	2528	2261	1014
FW7	140–168	2469	2495	776
FW8	152–165	2239	2046	783
FW9	167–255	1844	1123	977
Total	132–306	20 349	13 786	9395
OM1	217–254	893	824	329
OM2	203–253	1017	993	351
OM3	192–248	957	1065	362
OM4	184–244	1223	1669	406
OM5	181–218	1327	1217	541
OM6	81–209	1364	1851	497
OM7	144–193	1460	1426	562
OM8	69–175	1313	1194	562
OM9	158–178	1158	1045	410
OM10	109–171	1284	1286	449
Total	69–254	11 996	12 570	4469
Both sites	69–306	32 345	26 356	13 864

to as the phi coefficient (Chedzoy, 1985). We computed pairwise correlation coefficients between red tree coral presence or absence in the video frames (1/0 variable) and the presence or absence of each level of the categorical habitat characteristics. The tests were modified to account for the autocorrelation of serial observations of red tree coral presence and habitat characteristics on transects. We used a modified *t*-test for testing the significance of correlation between two spatial processes (Clifford *et al.*, 1989) as implemented by software PASSaGE (Rosenberg and Anderson, 2011). The method reduces the degrees of freedom based on an approximation of the variance of the sample correlation coefficient. Although transects were not continuous, we joined transect data in the nearest geographic fashion for testing associations.

Association with fish and crabs

To determine small-scale associations of fish and crabs with red tree coral habitat, we first simply calculated the relative frequency that all individuals of a particular species were found in a sampling frame designated as red tree coral habitat. A frame was designated as red tree coral habitat if a colony, including attached stumps, was within about a 10-m radius of the centre of that frame. We chose 10 m since we had observed several species of rockfish, particularly yelloweye rockfish, swimming intentionally into coral colonies from a distance of at least 10 m when startled by the submersible in open (e.g. relatively unstructured) habitat. This relatively simple measure of association, however, does not necessarily take into account the abundance or availability of a particular habitat type (i.e. bedrock with or without emergent epifauna). Auster (2005) proposed that examination of fish distribution in relation to all available habitats is one method to assess the “essential” role of emergent epifauna. Therefore, we used a second method, logistic regression

Table 2. Total number (*n*), frequency of occurrence (percentage of transects), mean depth, depth range, and percentage of corals damaged observed on 19 transects surveyed with the submersible *Delta* in the eastern GOA.

Taxon	<i>n</i>	Frequency (%)	Depth (m)		Damage (%)
			Mean	Range	
Site 1					
<i>Primnoa pacifica</i> : category 1	172	56	161	135–204	12.8
<i>Primnoa pacifica</i> : category 2	253	67	157	135–198	13.4
<i>Primnoa pacifica</i> : category 3	366	67	159	135–198	16.9
<i>Primnoa pacifica</i> : category 4	104	67	164	136–199	27.9
<i>Primnoa pacifica</i> : stump/skeleton	141	67	170	140–205	100.0
<i>Primnoa pacifica</i> : total	1036	67	161	135–205	27.8
<i>Calcigorgia spiculifera</i>	0	–	–	–	–
<i>Calcigorgia beringi</i>	0	–	–	–	–
<i>Paragorgia</i> sp.	0	–	–	–	–
<i>Halipterus willemoesi</i>	57	44	215	192–255	7.0
Stylasteridae	3821	89	164	132–250	5.6
Site 2					
<i>Primnoa pacifica</i> : category 1	1981	90	199	133–251	5.1
<i>Primnoa pacifica</i> : category 2	1306	90	198	127–248	9.3
<i>Primnoa pacifica</i> : category 3	507	90	194	127–238	16.0
<i>Primnoa pacifica</i> : category 4	36	70	193	151–214	55.6
<i>Primnoa pacifica</i> : stump/skeleton	246	90	189	127–239	100.0
<i>Primnoa pacifica</i> : total	4076	90	197	127–251	14.0
<i>Calcigorgia spiculifera</i>	670	50	97	69–220	0
<i>Calcigorgia beringi</i>	30	80	192	158–254	6.7
<i>Paragorgia</i> sp.	2	10	177	170–183	0
<i>Halipterus willemoesi</i>	411	90	222	155–254	3.9
Stylasteridae	39 373	100	191	69–254	7.9

(Lunneborg, 1994), to assess the “essential” role of emergent epifauna by examining whether the presence of some taxa (those for which we had enough data) is related to the presence of particular habitat types and the degree of those relationships. Individuals of a taxon were considered to be actively associated with bedrock alone or bedrock with or without emergent epifauna (i.e. red tree corals and/or large sponges) if they were found more frequently in video frames with those habitats than would be expected, given the habitat type’s overall availability (Stone, 2014). Only two taxa, juvenile rockfish and sharpchin rockfish, were abundant enough to examine with this second method. We considered only those frames within the observed depth range of each faunal group.

The logistic regression model is a special type of linear regression model where the measured response takes on two categorical values, in our case, presence or absence of the taxa in a video frame. In logistic regression, the proportion of observations with either of the two values is expressed as a function of explanatory variables. Therefore, we can determine from the model if the proportion of frames with taxa increases or decreases with the presence of various habitat types, specifically bedrock with or without emergent epifauna. If π is the proportion of frames with taxa, then the odds in favour of observing the taxa is defined as $\pi/(1 - \pi)$. Values >1 indicate a favourable relationship or increased odds; values <1 indicate an unfavourable relationship or decreased odds; and odds equal to 1 indicate no relationship. The logit transformation of the proportion of frames with taxa present, $\ln \pi/(1 - \pi)$, linearizes the relation between the transformed proportion and the explanatory variables, in our case, categorical habitat types determined for each video frame. We defined five discrete, mutually exclusive habitat types: (i) no bedrock, (ii) bedrock with no red tree coral habitat or sponges, (iii) bedrock with sponges only, (iv) bedrock with red tree coral habitat only, and (v) bedrock with both red tree coral habitat and sponges. We defined the logistic regression model relating the log-odds of observing taxa to habitat types as

$$\ln\left(\frac{\pi}{1 - \pi}\right) = \beta_0 + \sum_{i=1}^4 \beta_i X_i + \beta_5 X_5 + \sum_{j=1}^4 \beta_{j+5} X_j X_5, \quad (1)$$

where, π is the proportion of frames with taxa present; β_0 , intercept; β_i , regression parameter for the habitat type indicated by X_i , $i = 1, 2, 3, 4$; β_5 , regression parameter for the species indicated by X_5 ; β_j , regression parameter for the interactions between the fish species variable, X_5 , and the habitat variables, $X_1 - X_4$, $j = 6, 7, 8, 9$; X_i , indicator variable for habitat type of bedrock with or without emergent epifauna, $i = 1, 2, 3, 4$; and X_5 , indicator variable for the fish species.

Specifically, the dummy variables used to code the discrete habitat types and fish species are $X_1 = 1$ if bedrock is present with no red tree coral habitat or sponges (0 otherwise); $X_2 = 1$ if bedrock is present with sponges only (0 otherwise); $X_3 = 1$ if bedrock is present with red tree coral habitat only (0 otherwise); $X_4 = 1$ if bedrock is present with both red tree coral habitat and sponges (0 otherwise); and $X_5 = 1$ if juvenile rockfish are present or 0 if sharpchin rockfish are present. Our coding of the habitat types and fish species by default makes the intercept correspond to the comparative baseline category of no bedrock present and sharpchin rockfish present (i.e. $X_1 = X_2 = X_3 = X_4 = X_5 = 0$). The model was fit to data from the two study sites separately.

The fit of the regression models provided estimates of the log-odds, or odds by simple exponentiation, of observing the taxa, given the various habitat types; therefore, the relative importance of the explanatory variables could be determined. Adequacy of the

model was determined by comparing the residual deviance from the model fit to the χ^2 distribution (Lunneborg, 1994). One assumption of the logistic regression model is that observations are independent. Since the sampling units in this study are consecutive video frames on discrete transects, the observations made are unlikely independent. Dependent or clustered observations can result in what is called overdispersion, meaning that the variance of the response is greater than, in our case, the assumed binomial variance (Aitkin et al., 1994; McCullagh and Nelder, 1994). The risk of ignoring the independence assumption is that significance of explanatory variables may be over-stated. One solution for handling moderate overdispersion is to assume the variance is scaled by a constant factor, called the dispersion parameter (Aitkin et al., 1994; McCullagh and Nelder, 1994). The dispersion parameter, estimated from the residuals of the fitted model, provided for more realistic estimated standard errors of model effects.

Results

We surveyed 32 345 m of seabed and enumerated biota in 26 356 m² at the two sites (Table 1). Depths surveyed at both sites ranged from 69 to 306 m (Table 1). Sampling was not uniform with respect to depth with most effort concentrated at depths 150–200 m at both

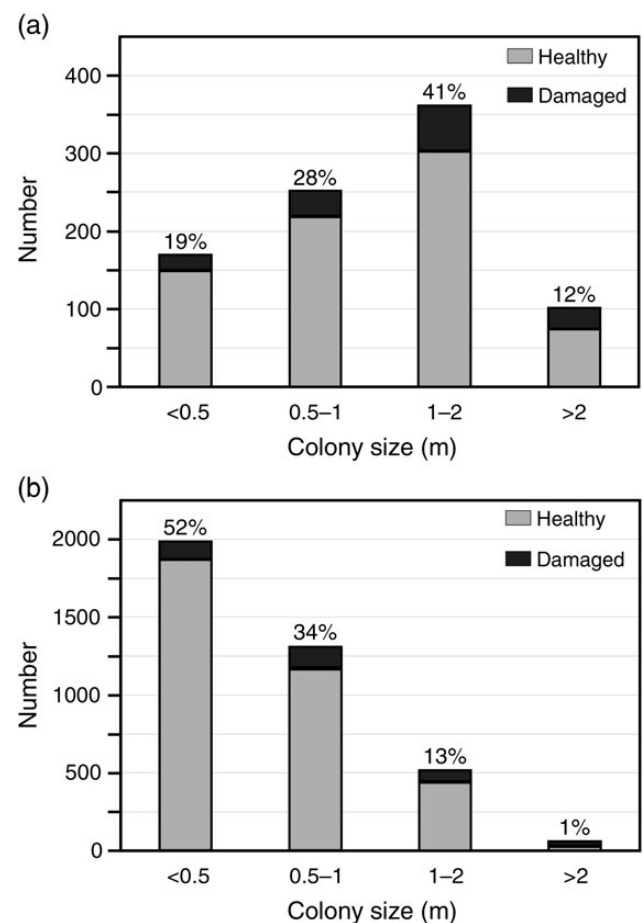


Figure 4. Number of red tree corals and percentages of four size categories at (a) Site 1 and (b) Site 2. Note that the scale of the ordinate for Site 1 is one-fifth the scale of Site 2. Damaged proportions shown for each size class exclude stumps since their sizes could not be accurately determined.

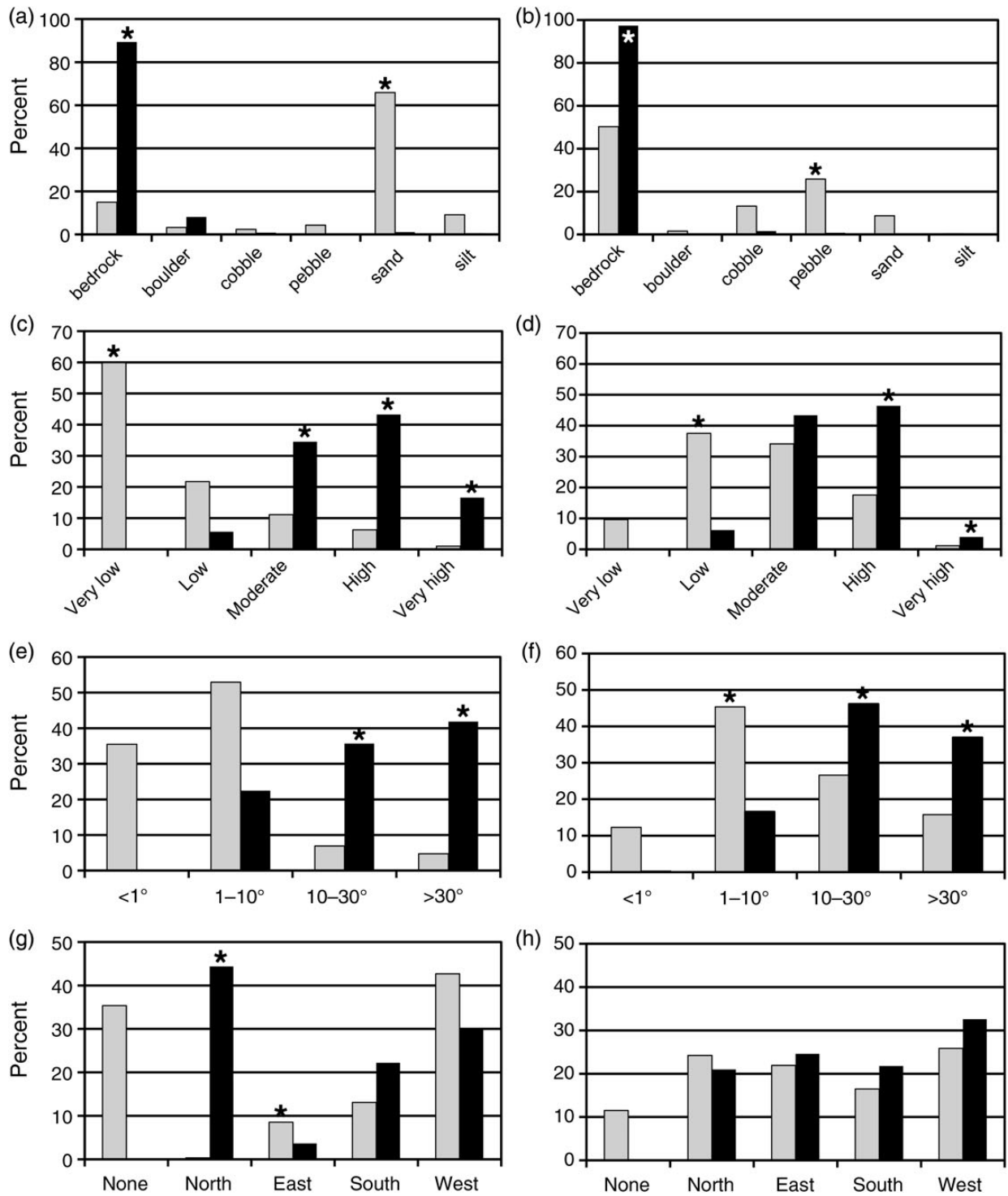


Figure 5. Distribution (%) of video frames by site classified into habitat types (light grey bars; $n = 9395$ at Site 1 and $n = 4469$ at Site 2) and distribution (%) of video frames with red tree corals present classified by habitat types (solid bars; $n = 356$ at Site 1 and $n = 500$ at Site 2) for (a) primary substrate type at Site 1, (b) primary substrate type at Site 2, (c) seabed roughness at Site 1, (d) seabed roughness at Site 2, (e) seabed slope at Site 1, (f) seabed slope at Site 2, (g) seabed exposure at Site 1, and (h) seabed exposure at Site 2. Percentages in each graph designated by light grey bars or solid bars sum to 100%. An “*” indicates a significant positive or negative correlation between red tree coral presence and habitat type (Table 3). Note that the scale of the ordinate for each attribute pair differs.

sites. Water temperatures where red tree corals were observed on transects at both sites ranged 5.43–6.47°C and salinities ranged 32.97–33.76 psu.

Red tree corals were widespread and abundant at both sites. Red tree corals were found on 67% of the transects at Site 1 and observed colonies including stumps totalled 1036 (Table 2). Red tree corals

were found on 90% of the transects at Site 2 and including stumps totalled 4076 colonies (Table 2). Red tree corals ranged in depth 127–251 m at the two sites but were more broadly distributed at Site 2 (Table 2). The depth distributions of the four size classes and stumps were similar at both sites. The population structure at Site 1 (Figure 4a) was dominated by large colonies (41%) followed by medium (28%), small (19%), and very large colonies (12%). The population structure at Site 2 was very different where small colonies were most abundant (52%), followed by medium (34%), large (13%), and very large (1%) colonies (Figure 4b).

Red tree corals were patchily distributed in thickets at both sites and were rarely observed individually. A total of 30 and 27 thickets were encountered on transects at Sites 1 and 2, respectively, and ranged in length (along the transect) 17–203 and 19–288 m at both sites, respectively. The mean density of red tree corals in thickets was 0.31 corals m⁻² (s.e. = 0.03, range = 0.05–0.71 corals m⁻²) at Site 1 and 0.75 corals m⁻² (SE = 0.14, range = 0.03–2.58 corals m⁻²) at Site 2. We found some evidence that coral density was positively related to thicket size. The maximum density of red tree corals per frame reached 11.7 and 15.3 corals m⁻² at Sites 1 and 2, respectively; corals in these frames were obviously small colonies. Overall red tree coral density (i.e. in all habitat surveyed) ranged from 0.08 corals m⁻² at Site 1 to 0.32 corals m⁻² at Site 2. The overall coral density (i.e. all corals including hydrocorals) ranged from 0.36 corals m⁻² at Site 1 to 3.55 corals m⁻² at Site 2. Overall sponge density was 2.10 sponges m⁻² at Site 1 (1.45 sponges m⁻² for demosponges and 0.65 sponges m⁻² for hexactinellid sponges) and 2.96 at Site 2 (1.63 sponges m⁻² for demosponges and 1.33 sponges m⁻² for hexactinellid sponges). Two species of hydrocorals (*Stylander parageus* and *Distichopora borealis*), the former accounting for ~95% of the hydrocorals, were also abundant at both sites. At Site 2, small numbers of *Stylander campylecus* were observed below ~100 m, and *Stylander verrillii* was abundant at depths between ~69 and 107 m.

Association with habitat characteristics

Red tree corals were not equally distributed with regard to habitat characteristics of the seabed at either site and were more common on bedrock with moderate to high roughness and habitats with slope > 10°, but were relatively uniformly distributed with respect to exposure (Figure 5; Table 3). At Sites 1 and 2, respectively, 89.3 and 97% of the video frames containing red tree corals had bedrock as the primary substrate, although only 15 and 50% of the total frames had bedrock as the primary substrate (Figure 5a and b). A few colonies observed in this study were attached to boulder or fractured bedrock, but otherwise all colonies were attached directly to bedrock. Similarly, red tree corals were found disproportionately in frames with moderate, high, and very high seabed roughness at both sites (Figure 5c and d). Eighty and 90% of the video frames containing red tree corals at Sites 1 and 2 had moderate to very high seabed roughness compared with only 10 and 52% of the total frames, respectively (Figure 5c and d). Seventy-eight and 83% of the frames with red tree corals at Sites 1 and 2 had a slope > 10°, whereas only 12 and 42% of the total frames had slope > 10° (Figure 5e and f), respectively. No colonies were found at either site in frames with no exposure (Figure 5g and h). At Site 1, a higher percentage of red tree corals was found in frames with a north exposure than would have been expected based on the availability of habitat with that exposure (Figure 5g). Otherwise, the presence of red tree corals in each exposure quadrant at both sites was in proportion to the availability of habitat with those

Table 3. Pairwise Pearson correlation coefficients between the presence of red tree corals in the video frames (1/0 variable) and the presence of each of the habitat characteristics.

Variable	Site 1		Site 2	
	Correlation	p-value	Correlation	p-value
Depth	-0.14	0.05	0.07	0.60
Primary substrate				
Bedrock	0.41 ^a	<0.001	0.33 ^a	<0.001
Boulder	0.05	0.09	-0.04	0.21
Cobble	-0.02	0.48	-0.12	0.02
Pebble	-0.04	0.44	-0.20 ^a	<0.001
Sand	-0.27 ^a	<0.001	-0.11	0.07
Silt	-0.06	0.14	-0.02	0.50
Seabed roughness				
Very low	-0.24 ^a	0.001	-0.12	0.11
Low	-0.08	0.10	-0.23 ^a	<0.001
Mid	0.15 ^a	<0.001	0.07	0.08
High	0.30 ^a	<0.001	0.27 ^a	<0.001
Very high	0.31 ^a	<0.001	0.09 ^a	<0.001
Slope				
None	-0.15	0.07	-0.13	0.09
Low	-0.12	0.06	-0.21 ^a	0.001
Med	0.23 ^a	<0.001	0.16 ^a	0.004
High	0.35 ^a	<0.001	0.21 ^a	0.001
Seabed exposure				
None	-0.15	0.07	-0.13	0.10
North	0.25 ^a	<0.001	-0.03	0.65
East	0.11 ^a	<0.001	0.02	0.71
South	0.05	0.33	0.05	0.40
West	-0.05	0.28	0.05	0.26

^aSignificant correlation.

Significance of the correlations was tested with the method of Clifford et al. (1989), using α = 0.10 and a Bonferroni correction of 1/21.

exposures (Figure 5g and h). At Site 2, 21% of the frames with red tree corals had a northerly exposure, 25% had an easterly exposure, 22% had a southerly exposure, and 32% had a westerly exposure (Figure 5h).

Damage by fishing gear and predation

Damage to red tree corals was observed at fairly high levels at both sites. A total of 288 (27.8% of the total) and 570 (14% of the total) damaged red tree corals (including stumps and skeletons) were observed on transects at Sites 1 and 2, respectively (Table 2). At both sites, the percentage of damaged colonies within size categories increased from small colonies to large colonies (Table 2). We attributed most of the observed damage to red tree corals to that caused by fishing gear (Figure 6a). Predation on red tree corals was observed only at Site 2 where we attributed 90.7% (517 colonies) of the damage directly to fishing gear disturbance and 9.3% (53 colonies) to predation. We observed or suspected predation by the spiny red sea star (*H. phrygiana*; Figure 6c) on 49 colonies and observed predation by calliostomatid snails (*Akoya platinum*; Figure 6d) and the nudibranch *Tritonia diomedea* (Figure 6e) on two colonies each. Predation by the spiny red sea star was limited to small patches and appeared to be intense in those areas. We often observed that the three predators were operating in tandem (Figure 6f). *Hippasteria phrygiana* was also observed preying on

the hexactinellid sponges *A. vastus*, *R. dawsoni*, and *S. solidus* and the demosponge *Poecillastra tenuilaminaris* at both sites.

A total of 24 derelict longlines were observed at the two study sites and on 13 of 19 transects (68%). Damaged corals and/or sponges were observed in the immediate vicinity of all derelict longlines. Anchor drag furrows were also noted in soft-sediment areas. A single-trawl door furrow was noted in non-coral habitat at Site 1, and we suspect that this was from a fisheries trawl survey conducted by the NMFS since the trawl fishery closure went into effect in 1998.

The incidence of fishing gear damage to red tree corals is highly related to size with large colonies being much more susceptible at both sites. Thirty-five per cent (49 of 140 colonies) of very large colonies, 16.4% of large colonies, 9.9% of medium colonies, and only 5.8% of small colonies were damaged. We also enumerated 387 stumps and skeletons on transects (7.6% of all red tree corals), and the vast majority appeared (based on diameter) to be large and very large colonies, so the actual percentages of damaged larger colonies were much higher than reported above. Larger

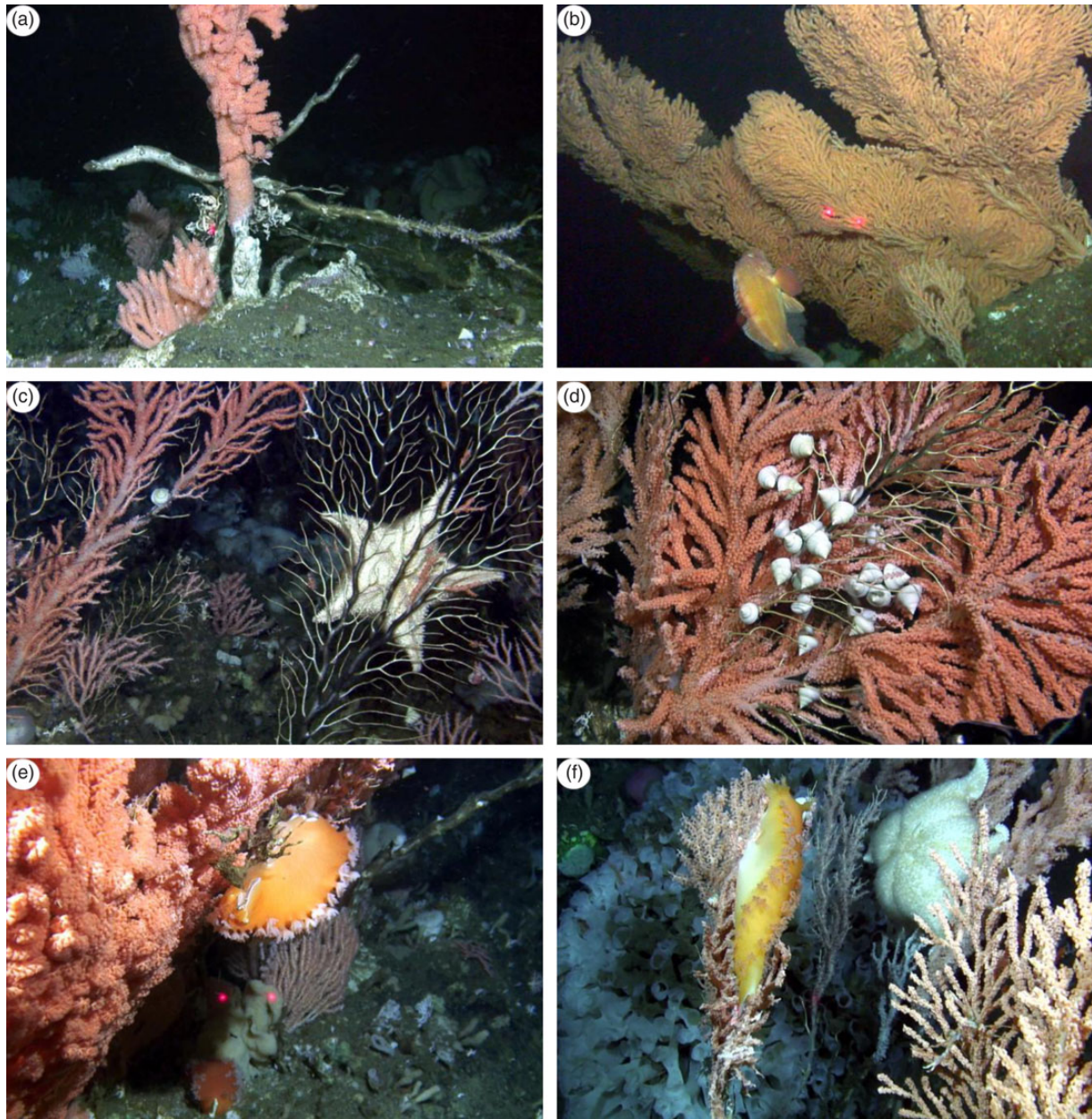


Figure 6. (a) Damage to a large red tree coral caused by longline fishing gear at a depth of 193 m. (b) A healthy, large red tree coral at a depth of 160 m shown for comparison. A large yelloweye rockfish (*Sebastes ruberrimus*) uses the coral as cover. (c) Predation on a red tree coral by the spiny red sea star (*H. phrygiana*) at a depth of 207 m. (d) Predation on a red tree coral by calliostomatid snails (*A. platinum*) at a depth of 224 m. (e) Predation on a red tree coral by the nudibranch *T. diomedea* at a depth of 208 m. (f) All three predators preying together on red tree coral colonies at a depth of 219 m. Predatory snails are present to the left and just above the nudibranch (at left). All photos are at Site 2 and the red laser marks, if present, are separated by a distance of 10 cm.

Table 4. Total number (*n*), frequency of occurrence (percentage of transects), mean depth, and depth range of demosponges, hexactinellid sponges, crinoids, and sea stars observed on 19 transects surveyed with the submersible *Delta* in the eastern GOA.

Taxon	<i>n</i>	Frequency (%)	Depth (m)		Damage (%)
			Mean	Range	
Site 1					
Demosponges	19 988	100		133–289	5.8
<i>Amphilectus digitatus</i>	62	67	168	152–218	11.3
<i>Auletta krautteri</i>	13 935	89	183	143–262	5.2
<i>Geodia</i> sp.	152	67	161	144–213	12.5
<i>Mycale loveni</i> : small	5018	100	169	143–255	5.8
<i>Mycale loveni</i> : large	253	89	163	151–289	26.1
<i>Poecillastra tenuilaminaris</i>	568	78	157	133–255	7.7
Hexactinellid sponges	8943	100		140–259	23.4
<i>Farrea occa</i>	8	44	176	150–216	25.0
Aphrocallistidae	5211	100	176	140–259	32.5
Rossellidae	3724	100	159	140–253	10.6
Crinoids					
<i>Florometra serratissima</i>	1797	100	168	149–267	–
Sea stars					
<i>Hippasteria phrygiana</i>	23	78	166	133–222	–
Site 2					
Demosponges	20 393	100		71–251	2.1
<i>Amphilectus digitatus</i>	0	–	–	–	–
<i>Auletta krautteri</i>	15 505	100	193	87–238	0.7
<i>Geodia</i> sp.	76	80	185	137–236	6.6
<i>Mycale loveni</i> : small	133	90	173	152–222	9.8
<i>Mycale loveni</i> : large	258	100	183	152–225	39.9
<i>Poecillastra tenuilaminaris</i>	4421	100	161	71–251	4.4
Hexactinellid sponges	16 755	100		70–246	11.9
<i>Farrea occa</i>	268	100	187	138–238	36.2
Aphrocallistidae	8700	100	183	70–254	17.8
Rossellidae	7787	100	174	82–246	4.5
Crinoids					
<i>Florometra serratissima</i>	19 589	100	193	136–254	–
Sea stars					
<i>Hippasteria phrygiana</i>	59	90	170	81–248	–

Percentages of sponge taxa damaged are provided.

sponge taxa also appear more susceptible to damage (Table 4). Sponges such as *M. loveni* (large) and *Farrea occa* had damage rates exceeding 25%, while smaller sponges such as *Auletta krautteri* had damage rates of only 0.7–5.2% (Table 4). Overall, 11.2 and 6.5% of the sponges observed on transects at Sites 1 and 2, respectively, were damaged (Table 4). Similar to corals, a larger proportion of sponges were damaged at Site 1 than Site 2, and a larger proportion of hexactinellid sponges were damaged than demosponges at both sites (Table 4).

Association with fish and crabs

Fish and crabs were abundant at both study sites; juvenile and YOY rockfish and sharpchin rockfish were the most abundant taxa (Tables 5 and 6). Sixty-two per cent of all fish and crabs were found in red tree coral habitat at Site 1 with more than 50% of the individuals for 9 of 29 taxa found in red tree coral habitat (Table 5). Contrastingly, only 33% of all fish and crabs were found in red tree coral habitat at Site 2 with more than 50% of the individuals for only 3 of 29 taxa found in red tree coral habitat (Table 6). However, only 20.3% of the area (11.1% of the video frames) and 30.1% of the area (21.1% of the video frames) at Sites 1 and 2, respectively, were classified as red tree coral habitat.

When we examined the distribution of the two most abundant fish taxa (juvenile rockfish and sharpchin rockfish) relative to the availability of habitat types (Table 7), we found that both taxa at both sites were much more abundant in bedrock compared with non-bedrock habitat and had even greater relative abundance if the habitat was classified as red tree coral habitat, contained sponges, or both (Figure 7; Table 7). Logistic regression models relating fish presence to bedrock with or without emergent epifauna were fit to data from the two sites separately. Two-way interactions between fish species and habitat variables were not significant ($\alpha = 0.05$) at either site based on χ^2 tests for comparison of fuller models to reduced models. Dispersion parameters were estimated as 11.4 and 0.8 at Sites 1 and 2, respectively, indicating over- and under-dispersion of the data. Assuming a scaled binomial variance, standard errors of model effects were adjusted by the estimated dispersion parameters (Table 7). The fitted models appeared adequate based on deviance statistics compared with the χ^2 distribution (Lunneborg, 1994), and the 95% confidence intervals of all estimated odds ratios did not overlap 1 (Table 7). Data from the two sites were consistent in the relative importance of the habitat types to fish presence. The odds of observing juvenile rockfish or sharpchin rockfish were decreased when no bedrock was present and all other variables were fixed (Table 7). Contrariwise, the odds

Table 5. Total number (*n*), frequency of occurrence (percentage of transects), mean depth, and depth range of commercially important fish and crabs observed on nine transects surveyed with the submersible *Delta* at Site 1.

Taxon	<i>n</i>	Frequency (%)	Depth (m)		Red tree coral habitat % association
			Mean	Range	
Rockfish: juveniles	5066	100	163	132–289	76.4
Rockfish: YOY	314	11	133	132–138	34.7
Sharpchin rockfish	392	89	163	135–241	61.0
Pacific ocean perch	143	100	178	150–250	16.1
Harlequin rockfish	139	78	180	149–251	63.3
Rosethorn rockfish	122	89	185	149–262	32.8
Rosethorn rockfish: juveniles	85	67	190	149–252	41.2
Silvergray rockfish	73	67	162	140–196	83.6
Yelloweye rockfish	71	78	130	136–196	76.1
Yelloweye rockfish: juveniles	17	56	161	136–198	82.4
Redstripe rockfish	68	44	159	143–171	16.2
Redbanded rockfish	12	44	182	153–197	92.3
Rougheye rockfish	0	–	–	–	–
Dusky rockfish	0	–	–	–	–
Tiger rockfish	0	–	–	–	–
Quillback rockfish	0	–	–	–	–
Shortspine thornyhead	53	33	227	193–305	0
Shortspine thornyhead: juveniles	205	33	223	168–304	0
Pacific halibut	49	100	173	153–195	6.1
Righteye flounders	88	100	182	154–232	3.4
Righteye flounders: juveniles	238	100	175	153–228	2.1
Pacific cod	0	–	–	–	–
Sablefish	1	11	219	219	0
Lingcod	40	78	169	135–246	62.5
Other fish	243	100	180	136–245	11.5
Skates	4	33	189	165–217	0
Spotted ratfish	0	–	–	–	–
Brown box crab	34	67	183	136–297	61.8
Golden king crab: juveniles	0	–	–	–	–
All taxa	7456	100	166	132–305	62.1

Percentage of each taxon/life history group associated with red tree coral habitat is also provided.

of observing juvenile rockfish or sharpchin rockfish were increased by factors of 5.6–43.0 and 4.1–10.4 at Sites 1 and 2, respectively, when bedrock was present with or without emergent epifauna. The relative importance of habitat types to fish presence was consistent between the two sites. The increasing order of importance for the habitat types was bedrock with no red tree coral habitat or sponges, bedrock with sponges only, bedrock with red tree coral habitat, and bedrock with both red tree coral habitat and sponges.

Discussion

Red tree corals are highly vulnerable to disturbance in GOA habitats where they form dense thickets and exhibit keystone species characteristics (King and Beazley, 2005). They are functionally important species in thicket habitats and fill unique and essential roles by maintaining biodiversity and providing three-dimensional structure that is clearly used by several fish and crab species and in a way consistent with the definition of essential fish habitat (EFH). The Magnuson–Stevens Fishery Conservation and Management Act defines EFH as “those waters and substrate necessary for spawning, breeding, feeding, or growth to maturity” [16 USC. 1802 (10)].

In this study, we made systematic detailed observations with a submersible to gauge the appropriateness of the HAPC boundaries that were established based on limited information on red tree coral distribution and abundance. Our observations at Site 1 indicated that two of the four HAPC closures contained extensive thickets

and that two likely did not. Additionally, the one non-HAPC site we investigated there did contain red tree coral thicket habitat. Examination of fisheries stock assessment catch data and video footage of the seabed collected before and after this study indicates that scattered thickets occur throughout much of the Fairweather Ground, where Site 1 is located. A more extensive analysis of all available data in conjunction with spatial modelling and subsequent *in situ* ground-truthing is necessary to fully map the thicket habitat at this site. Our observations at Site 2 provide a much more straightforward picture of red tree coral habitat there—the extent of the Ridge feature, which is particularly well defined, contains scattered thickets, including the most extensive we are aware of anywhere in the world. The current HAPC protects approximately one half of that habitat.

Relatively high levels of damage to red tree corals and sponges occurred at both sites. Most of the disturbance to the habitat can be attributed to interactions with longline gear. This region of the GOA has been closed to bottom trawling since 1996 and we found very little evidence of past trawling and most of the habitat at both sites is untrawlable (rough and complex). We also found derelict longline gear on 68% of the transects. These observations are noteworthy since the effects of longline gear on seabed habitat have been considered relatively benign compared with, for example, bottom trawl gear (Krieger, 2001; Chuenpagdee *et al.*, 2003; Lumsden *et al.*, 2007; Munoz *et al.*, 2010; Pham *et al.*, 2014). But our results

Table 6. Total number (*n*), frequency of occurrence (percentage of transects), mean depth, and depth range of commercially important fish and crabs observed on ten transects surveyed with the submersible *Delta* at Site 2.

Taxon	<i>n</i>	Frequency (%)	Depth (m)		Red tree coral habitat association (%)
			Mean	Range	
Rockfish: juveniles	3139	100	166	90–244	45.1
Rockfish: YOY	1488	40	92	69–165	0
Sharpchin rockfish	848	100	182	127–252	50.0
Pacific ocean perch	120	100	177	127–254	15.0
Harlequin rockfish	119	100	184	149–230	48.7
Rosethorn rockfish	68	100	200	138–253	35.3
Rosethorn rockfish: juveniles	30	80	183	145–237	46.7
Silvergray rockfish	140	90	185	114–243	82.9
Yelloweye rockfish	111	80	130	74–237	33.3
Yelloweye rockfish: juveniles	13	40	151	112–185	7.7
Redstripe rockfish	4	20	165	164–166	0
Redbanded rockfish	44	60	196	164–242	68.2
Rougheye rockfish	13	50	227	196–247	46.2
Dusky rockfish	3	10	137	128–143	33.3
Tiger rockfish	2	10	101	98–104	0
Quillback rockfish	10	20	91	81–107	0
Shortspine thornyhead	91	80	218	163–253	15.4
Shortspine thornyhead: juveniles	26	60	218	186–252	3.8
Pacific halibut	24	80	204	83–253	8.3
Righteye flounders	33	80	213	164–251	0
Righteye flounders: juveniles	0	–	–	–	–
Pacific cod	6	40	211	185–218	0
Sablefish	1	10	209	209	0
Lingcod	284	80	96	69–238	1.1
Other fish	21	70	200	101–254	23.8
Skates	2	20	222	217–226	0
Spotted ratfish	20	30	116	103–182	0
Brown box crabs	133	100	175	113–252	25.6
Golden king crab: juveniles	3	10	243	243	0
All taxa	6796	100	175	69–254	32.9

Percentage of each taxon/life history group associated with red tree coral habitat is also provided.

Table 7. Odds ratios and 95% confidence intervals (CI) in parentheses, estimated from logistic regression models with scaled binomial variance, of taxa being observed in the same video frame with habitat types at Sites 1 and 2.

Habitat	Site	
	1 Odds ratio	2 Odds ratio
No bedrock		
Rockfish: juveniles	0.08 (0.06–0.10)	0.09 (0.08–0.10)
Sharpchin rockfish	0.008 (0.005–0.014)	0.043 (0.038–0.049)
Bedrock		
No red tree coral habitat or sponges	5.6 (2.6–12.1)	4.1 (3.2–5.2)
Sponges only	13.9 (6.7–28.6)	5.5 (4.8–6.4)
Red tree coral habitat only	20.8 (11.2–38.8)	7.9 (5.1–12.5)
Red tree coral habitat and sponges	43.0 (21.9–84.6)	10.4 (9.0–12.0)

document that in certain highly structured habitats, this gear too can effectively remove large emergent epifauna, and damage rates observed during this study are comparable to those observed in the central Aleutian Islands that were attributed to all fishing gears combined (Stone, 2006, 2014; Heifetz et al., 2009).

We observed damage to corals caused by strain and entanglement. Both forces appear to cause mortality and sublethal trauma.

Whole or nearly whole colonies are often removed as evidenced by many observed stumps, and *Primnoa* are common bycatch in longline fisheries surveys (Krieger and Wing, 2002) and longline fisheries (R. Stone, pers. observation). Damage consisting of up to 50% removal of a colony’s branches appears sublethal but effectively removes that proportion of a colony’s reproductive potential (Waller et al., 2014). Modifications to the gear to suspend most of the longlines and hooks above the thickets should be a high research priority. Such modifications may allow fishing to continue in these habitats while minimizing coral mortality or otherwise disturbing EFH.

Predation appears to account for only a minor fraction of the total damage to corals observed in this study. One cause for concern was the presence of many spiny red sea stars in areas of fishery-gear disturbance and the apparent opportunistic predation of the sea stars on injured or detached coral colonies. A similar scavenging/predatory response has been noted by the nudibranch *T. diomedea* on damaged sea whips *Halipteris willemoesi* (Malecha and Stone, 2009) that may exacerbate the overall effects of fishing activities on the corals by limiting the potential for colonies to heal tissue damaged by the physical forces of fishing gear contact. And as noted previously for this same suite of predators of corals in the central Aleutian Islands (Stone, 2014), there is some evidence that these predators may be operating in tandem.

Red tree corals prefer habitat dominated by bedrock, moderate to high seabed roughness, and areas where the seabed has some slope

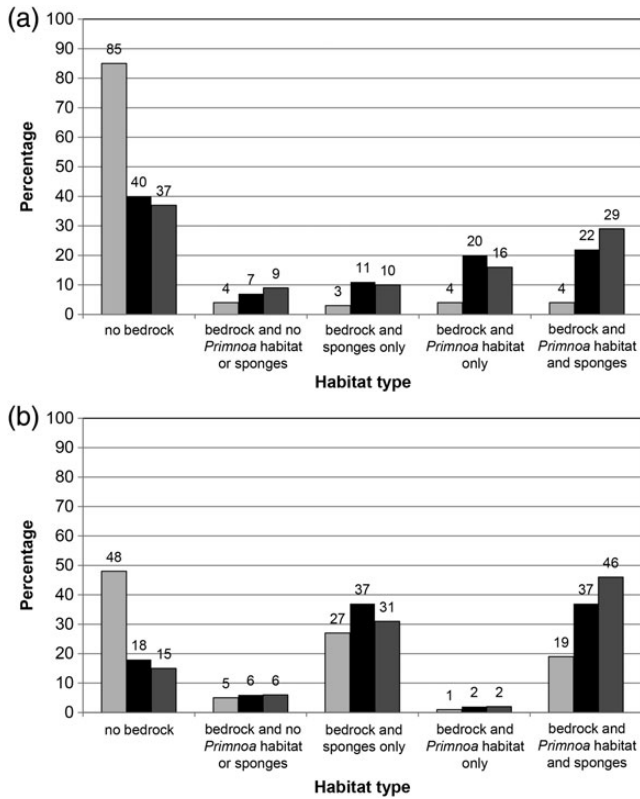


Figure 7. Percentages of video frames sampled with each of five habitat types (light grey bar), each of those habitat types with juvenile rockfish (solid bar), and each of those habitat types with sharpchin rockfish (dark grey bar) at Site 1 (a) and Site 2 (b). Numbers above the bars are the actual percentages.

(>10°). Because these habitats are typically areas with increased seabed currents, we hypothesized that red tree corals would be orientated in a non-random fashion and would be concentrated in areas with the dominant or most favourable currents. While currents in the eastern GOA are dominated by the north–northwest flow of the Alaska Current (Stabeno *et al.*, 2004), bottom currents observed during our dives at both sites were noted as present, often moderate, and predominantly from the southwest with apparent reciprocal currents from the NNE to ENE. Based on these observations, we expected red tree corals to be more abundant on slopes with SW and NE exposures, and there is some evidence that this may be the case at Site 1. But red tree corals are equally abundant in all exposure quadrants at Site 2. So while our observations and simple principles of coral biology implicate the importance of bottom currents, the relationship between red tree corals and bottom currents does not appear intuitively straightforward. The relationship of these habitat variables with the presence of red tree corals on the transects using a Bayesian logistic mixed-effects model is described in detail in a manuscript in preparation (M. Masuda, unpublished data).

Our overall density values for red tree corals are the highest ever reported and were 13–53 times higher than the density (0.006 corals m⁻²) measured on Learmonth Bank, northern British Columbia located 220 km south of Site 2 where many thickets have been documented (Du Preez and Tunnicliffe, 2011). The actual density value was not explicitly presented in Du Preez and

Tunnicliffe (2011) but similarly calculated by us from data presented therein. Overall coral densities (i.e. all corals including hydrocorals) ranged from 0.36 at Site 1–3.55 corals m⁻² at Site 2. These density values are comparable to those measured in the Aleutian Islands and in coral garden habitats there (Stone, 2006; Stone, 2014). The density values (2.10 and 2.96 sponges m⁻²) for sponges observed at the two study sites were quite high but still only about half of those measured in the central Aleutian Islands (5.25 sponges m⁻²; Stone, 2014).

A major difference between the red tree coral thicket habitats and the Aleutian Island coral garden habitats is that the former are dominated by just a few coral and sponge species. Red tree coral thickets are dominated by *P. pacifica*, four to five species each of demosponges and hexactinellids, and two species of hydrocorals. Red tree corals are the dominant emergent epifauna in the study region and provide the bulk of biogenic structural habitat at both sites. The hydrocorals rarely exceed 10 cm in height or width but are important perching habitat for crinoids (*F. serratissima*). Both hydrocorals and crinoids were abundant at both sites (Tables 3 and 4), and the abundance of each is related at an ~1:2 ratio. Together, they provide vast swathes of structural habitat elevated off the seabed where there would otherwise be little. The other gorgonians (*Calcigorgia spiculifera*, *Calcigorgia beringi*, and *Paragorgia* sp.), observed only at Site 2, provide little important structure to the seabed due to their small size, spindly growth form, and/or low abundance.

Similar to previous studies in Alaska (Krieger and Wing, 2002; Rooper and Boldt, 2005; Stone, 2006, 2014; Rooper *et al.*, 2007) and in British Columbia (Du Preez and Tunnicliffe, 2011), we found that some taxa, particularly juvenile rockfish, are strongly associated with coral and sponge habitat. Additionally, we observed gravid females for several species of rockfish and pre-mating pairs of the brown box crab (*L. foraminatus*) using red tree corals as refuge habitat. Interestingly, YOY rockfish are not associated with red tree coral habitat. They were generally found shallower than most red tree coral habitat and our observations indicate that they rely on schooling behaviour as a predator defence mechanism rather than using corals as refuge habitat. Our results indicate that bedrock habitat is clearly more important to fish than non-bedrock habitat, but it is even more important if it included sponges, red tree corals, or both. This observation indicates that bedrock with and without corals and sponges are not functionally equivalent habitats in the ecosystems we studied as has been suggested in other regions (Auster, 2005; Tissot *et al.*, 2006). We suggest that the function of the habitats to fish may depend on the density and behaviour of fish and the density and physical structure of the corals, all of which may vary greatly from region to region. In other words, deep-sea corals are not important fish habitat everywhere, especially when present at low densities.

The population structure of red tree corals was very different at the two study sites. Based on minimum size at maturity (Waller *et al.*, 2014) and known growth rates (Andrews *et al.*, 2002), Site 1 was characterized as having a large spawning biomass (~81% of the population) but few recruits (19% of the population) in the past 25 years. Contrastingly, at Site 2, there were approximately equal numbers of immature colonies (recent recruits) and mature colonies. The factors that appear to limit recruitment (Lacharité and Metaxas, 2013) at Site 1 are unknown but do not appear inadequate spawning biomass, despite the obvious effects of fishing, or the lack of adequate recruitment habitat. We did not measure the absolute size of each coral colony but rather grouped them into

relatively large size bins. However, we observed at both sites that patches of individuals generally did not consist of a full range of sizes but rather of many individuals of distinct size classes (i.e. cohorts), indicating that successful recruitment events are infrequent and approximately once a decade or more. The factors controlling successful recruitment in this species should be a high priority for study since it may be the limiting factor in recovery of the species from disturbance.

Red tree corals are keystone species in the habitats where they form thickets in the eastern GOA. They are highly vulnerable to disturbance from all bottom contact gear and provide EFH for some managed species. A few small HAPCs in the eastern GOA currently provide some protection to red tree coral thickets and one of those studied by us could be expanded to protect the entire feature supporting thickets. Ongoing research in areas of high red tree coral bycatch, habitat modelling, and site reconnaissance would provide information regarding the location of additional appropriate HAPCs. Until we know if the observed levels of damage observed in these important ecosystems are sustainable, we recommend precautionary management that would include fishing gear modifications and an expanded network of HAPCs. With these tools, resource managers could more effectively preserve red tree coral habitat and the ecosystem services that it provides in the eastern GOA.

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