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Deep-sea emergence of red tree corals (*Primnoa pacifica*) in Southeast Alaska glacial fjords

Robert P. Stone
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December 2018

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Cover image
The NOAA Ship *John N. Cobb* cruises about a quarter mile from the face of Lamplugh Glacier in 1992. Lamplugh is one of a only a handful of tidewater glaciers remaining in Glacier Bay today. (Photo courtesy of Commanding Officer John Bortniak, NOAA Corps.)

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CONTENTS

Abstract—Red tree corals (*Primnoa pacifica*) were found thriving in shallow-water areas of 2 large glacial fjord systems in Southeast Alaska during scuba surveys. Corals were found at depths as shallow as 9 m in Muir Inlet, Glacier Bay, in 2004 and 2005 and as shallow as 6 m in Tracy and Endicott arms, Holkham Bay, in 2006. These observations represent a depth range extension for the species—red tree corals typically occur at depths greater than 130 m in the Gulf of Alaska and elsewhere where they form extensive thickets. The red tree coral is an important pioneer species in the primary succession of recently deglaciated habitats. The emergence of red tree corals in shallow-water areas of these glacial fjords likely occurs because year-round oceanographic conditions (low temperature, higher than normal surface salinity, and low ambient light levels) are similar to those found in their more typical depth range. Glacier Bay was formed beginning in 1794 by rapid glacial retreat, and a deglaciation record has been meticulously documented during the past 130 years. This record provides a chronosequence that we used to study the succession of red tree corals into the bay and it presented an opportunity to evaluate the accuracy of a method previously used to age the corals. In situ access to shallow-water populations provided an invaluable opportunity to examine reproductive and recruitment processes and genetic connectivity of the most important coral species in the North Pacific Ocean. The information from these examinations provides important insights into the ability of this species to recover from disturbance and to colonize protected areas established to mitigate the effects of human activities.

Deep-sea emergence of red tree corals (*Primnoa pacifica*) in Southeast Alaska glacial fjords

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Introduction

Corals in the genus *Primnoa* are large, structure-forming gorgonians distributed in the northern boreal Pacific and Atlantic oceans and subantarctic Pacific Ocean (Cairns and Bayer, 2005). In Alaska, red tree corals (*Primnoa pacifica*) have a broad distribution and are dominant biotic elements of benthic habitats in the Gulf of Alaska (GOA) where they form extensive thickets (i.e., large aggregations) in some areas and at depths between 150 and 250 m (Stone et al., 2014). Colonies tend to be located on high- to moderate-relief bedrock (Stone et al., 2014; Masuda and Stone, 2015) and provide structural habitat for many commercially important species, particularly rockfish (*Sebastes* spp.), including gravid females and juveniles (Krieger and Wing, 2002; Stone et al., 2014).

Red tree corals are highly susceptible to disturbance from fishing activities because of their large size and arborescent morphology (Krieger, 2001; Stone et al., 2014). They are also common bycatch in Alaska fisheries for demersal species and research stock assessment surveys (Krieger, 2001; Heifetz, 2002). Furthermore, estimated growth rates are slow (Krieger, 2001; Andrews et al., 2002), and consequently disturbed thickets are likely slow to recover or may be chronically affected. Observations made from a submersible in the GOA indicate that some thickets have been disturbed by past fishing activities (Stone et al., 2014). In June 2006, the North Pacific Fishery Management Council designated as habitat areas of particular concern 5 small areas (total area of 46 km^2) known to support thickets in the eastern GOA (Federal Register, 2017). This regulation prohibits the use of all bottom-contact fishing gear in these habitat areas of particular concern in an effort to protect sensitive habitats.

In 2003, biologists discovered red tree corals in shallow water (<25 m depth) during videographic habitat surveys in Glacier Bay National Park and Preserve, Southeast Alaska (Fig. 1). These observations supported anecdotal reports by fishermen of deep-sea emergence of red tree corals in other glacial fjords in Southeast Alaska; reports that were subsequently confirmed in the fjords of Holkham Bay (Fig. 1). We define deep-sea emergence as a phenomenon whereby organisms that typically dwell in the deep sea are able to exist in shallow-water areas because of unusual oceanographic conditions there.

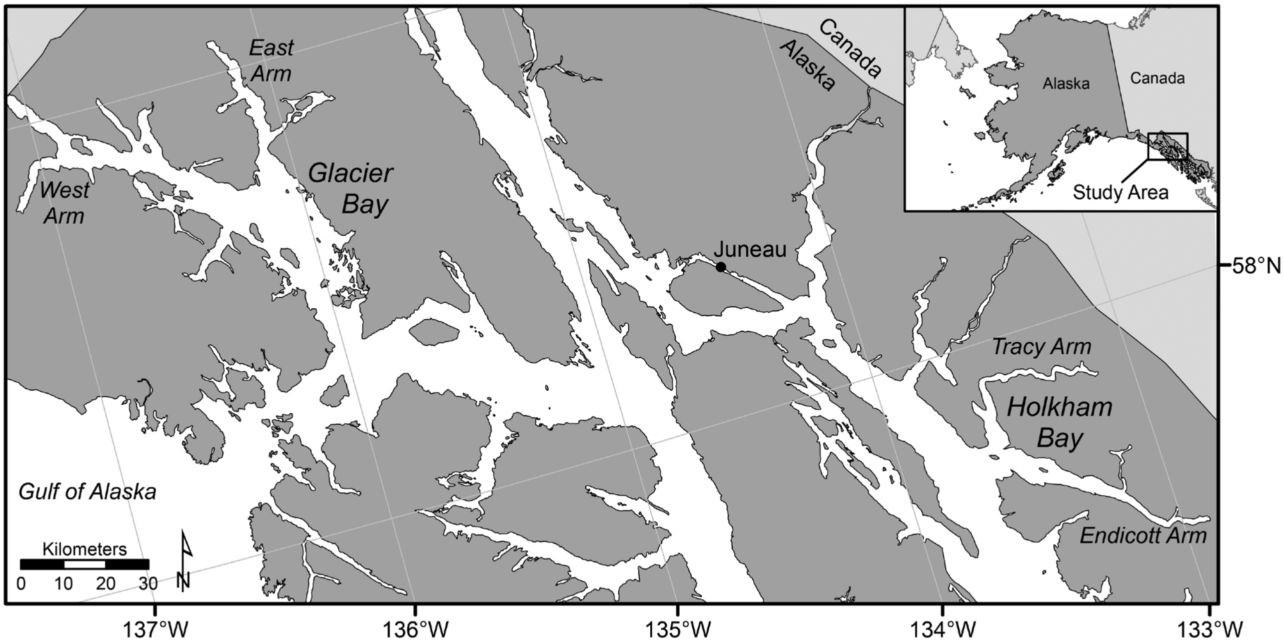

Figure 1

Map of Southeast Alaska showing the location of the 4 study areas in the East and West arms of Glacier Bay and Tracy and Endicott arms of Holkham Bay.

The purpose of this study was to document deep-sea emergence of red tree corals by determining the areal extent and depth distribution of the corals in several glacial fjord systems in Southeast Alaska. We examine the role of physical oceanographic processes in coral distribution and the potential use of an accurate deglaciation record to corroborate estimated growth rates for the species.

Glacier Bay is a system of deep glacially derived fjords with 2 main fjords—Muir Inlet (hereafter referred to as the East Arm) and the West Arm (Fig. 2). Glacier Bay was completely glaciated when discovered by Captain George Vancouver in 1794. Glaciers have continuously retreated since that time (Matthews and Quinlan, 1975), but glacial retreat in the 2 arms, beginning in 1860, has not occurred at the same rate (Fig. 2). Glacial retreat in the West Arm initially occurred much more rapidly—the entire fjord was deglaciated by 1890 except the 2 uppermost inlets (Powell, 1990). Glaciers in the East Arm have retreated at a more constant rate and the main glacier, Muir Glacier, grounded (i.e., rested completely on land with no direct calving into the sea) at the head of the fjord in 1993 (Hunter and Powell, 1995). The only remaining tidewater glacier in the East Arm is the McBride Glacier; however, both the Muir and Riggs glaciers, although now grounded, provide substantial volumes of glacial meltwater into the upper reaches of the fjord. There are 3 major tidewater glaciers in the West Arm (Johns Hopkins, Lamplugh, and Margerie), and several grounded glaciers in the upper reaches of the fjord provide substantial volumes of glacial meltwater. Glacial retreat in both fjords has exposed extensive areas of new habitat devoid of sedentary marine life (Carney et al., 1999).

The entrance to the East Arm is guarded by a broad sill (or moraine) at a depth of 55 m and several deeper intermediate sills. The entrance to the West Arm has a much more complex bathymetry with no obvious sill. The physical oceanography of Glacier Bay has been described by Matthews and Quinlan (1975) and Etherington et al. (2007) and by Reisdorph and Mathis (2014) with special regard to pH chemistry. The upper reaches of both arms have steep vertical walls, above and below sea level, consisting of well-worn schist and areas of plutonics (Greene[1]).

Holkham Bay is also a system of deep, glacially derived fjords. The bay has 2 main fjords—Tracy and Endicott arms, both with tidewater glaciers at their heads (Fig. 3). The U.S. Congress designated the area as Tracy Arm-Fords Terror Wilderness in 1980, and it is managed by the U.S. Forest Service. Much less is known regarding the chronology of glacial retreat and the physical and oceanographic settings of the fjords in this area. The 2 main fjords were largely deglaciated as long ago as the

[1] Greene, G. 2016. Personal commun. Univ. Calif., 1850 Research Park Dr., Ste. 300, Davis, CA 95618–6134.

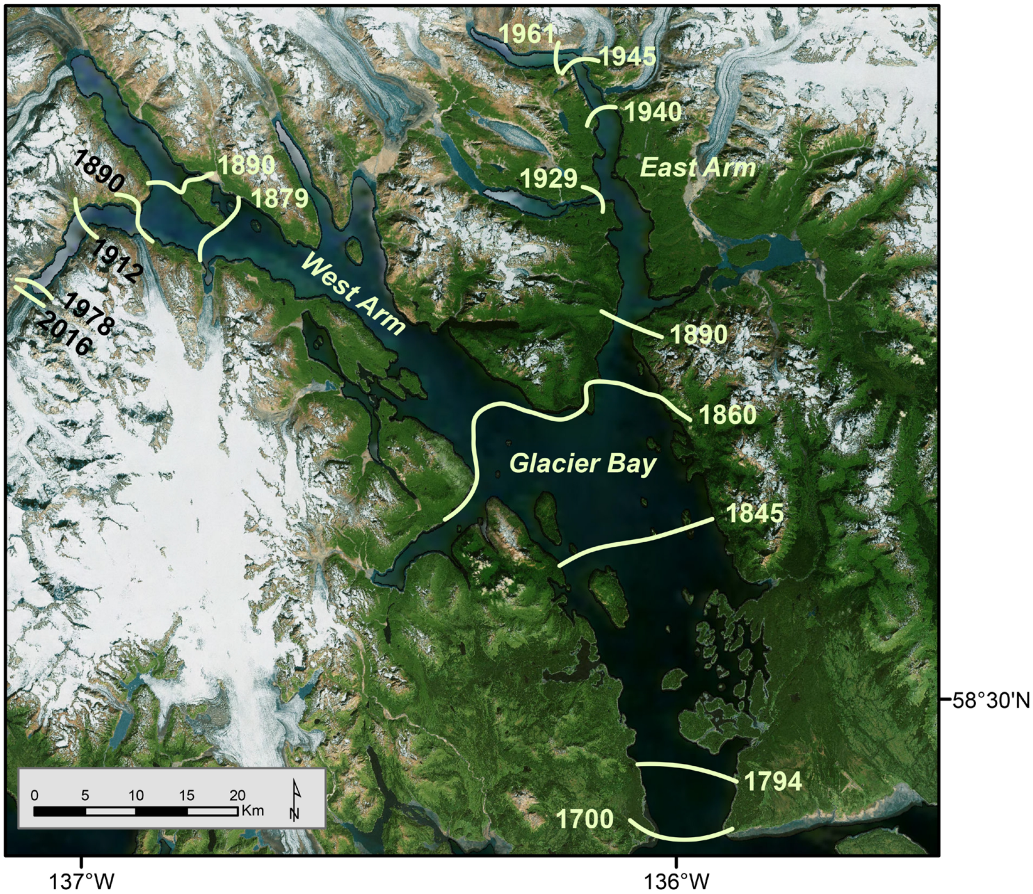

Figure 2

Map of Glacier Bay, Southeast Alaska, showing the historic extents of glaciation. Yellow lines indicate the year and location of glacial extent.

late 1800s (Fig. 3), but the tidewater glaciers in both Tracy Arm (Sawyer and South Sawyer glaciers) and Endicott Arm (Dawes Glacier) have undergone a more rapid retreat during the past few decades (Molnia, 2008). Since 1948 the Sawyer, South Sawyer, and Dawes glaciers have all retreated more than 3 km (an average rate of 50 m/year) (McNabb, 2013), and the Sawyer Glacier reportedly grounded in July 2017. Both arms of Holkham Bay are guarded by very narrow, shallow sills (<40 m depth) formed by terminal moraines at their entrances. Many areas of both arms have steep vertical walls, both above and below sea level, consisting principally of well-worn graywacke and granodiorite (Greene[1]).

Materials and methods

Field operations—investigations by scuba divers

During 2 research cruises (24–27 April 2004 and 17–22 April 2005), scuba divers conducted reconnaissance surveys at 14 locations in each arm of Glacier Bay (Fig. 4). In 2004, dives were restricted to the East Arm, but in 2005 dives were made in both the East and West arms. During 2 research cruises (22–27 March 2006 and 1–3 May 2008) scuba divers conducted reconnaissance surveys at 20 locations in Tracy Arm (Fig. 5A) and at 2 locations in Endicott Arm (Fig. 5B). Dive sites were selected on the basis of 3 criteria: 1) the presence of hard, exposed bedrock along the shoreline, 2) the presence of relatively steep bathymetry, and 3) the location allowing a somewhat systematic design along the axes of the fjords. The first 2 criteria were based on the known habitat requirements of red tree corals (Stone et al., 2014; Masuda and Stone, 2015). The third criterion was considered necessary to establish a timeline gradient among dive sites and to maximize the areal coverage of reconnaissance surveys.

At each dive site (Appendix Table 1), divers swam generally between the 20 and 30 m isobaths, and if red tree corals were observed, the divers swam vertically

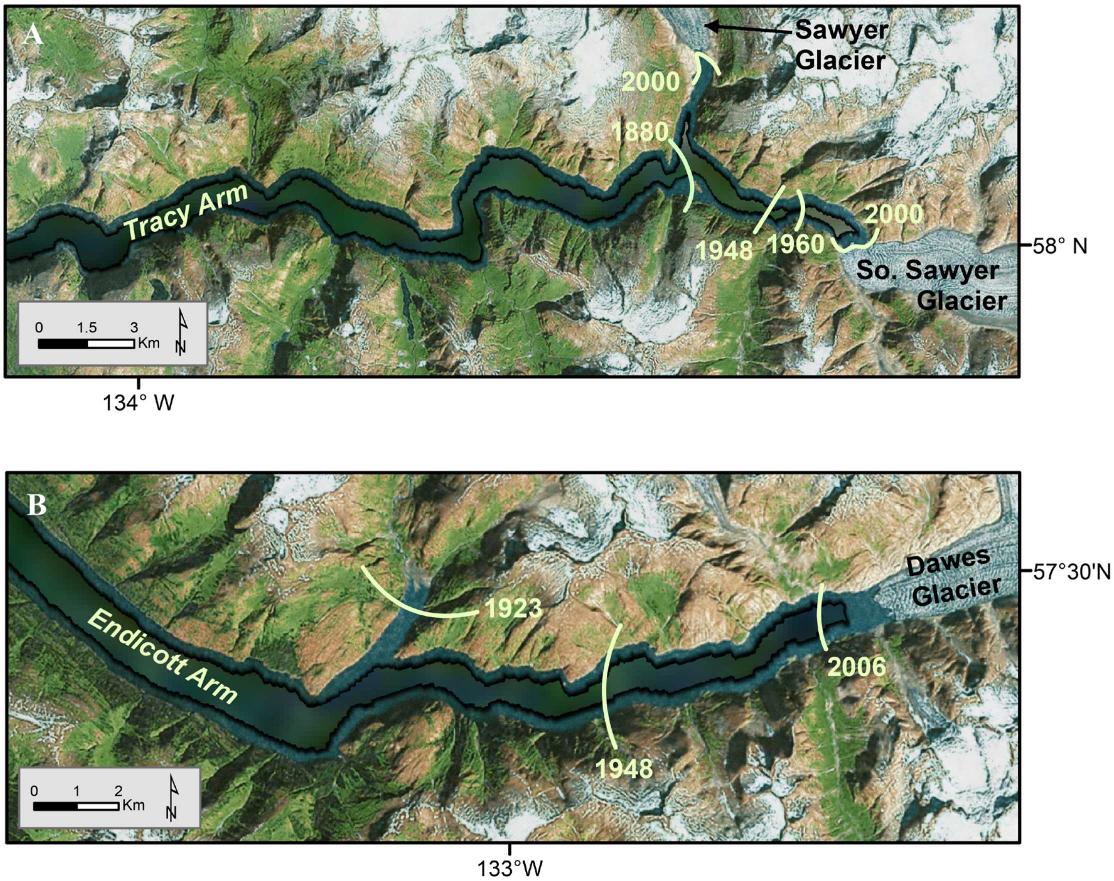

Figure 3

Map of (**A**) Tracy Arm and (**B**) Endicott Arm in Holkham Bay, Southeast Alaska, showing the historic extents of glaciation. Yellow lines indicate the year and location of glacial extent.

between a depth of approximately 30 m and the surface to establish the depth distribution of corals. A differential global positioning system was used to mark the beginning and end of each dive transect. At sites where red tree corals were found, additional dives were made often to measure the length of the largest colonies, collect samples for taxonomic verification, and collect video footage of the corals and habitat. Divers noted the habitat at each site, including type of substrate and associated flora and fauna.

Field operations—investigations by remotely operated vehicle

Video observations were recorded in Holkham Bay (Fig. 5, A and B) with a Phantom XTL remotely operated vehicle (ROV; Deep Ocean Engineering, San Jose, CA) at 7 sites in Tracy Arm and a single site in Endicott Arm during the May 2008 research cruise and at 3 locations in each arm during a June 2014 research cruise (for identification of sites where the ROV was used, see Appendix Table 1). The ROV was deployed from a small skiff at each site, and then it slowly traversed up the vertical wall. The ROV was operated through a 168 m neutrally buoyant umbilical attached to a control console. Nonlinear joystick controls on the console allowed maneuvering the ROV both vertically and horizontally (maximum cruise speed of 1.3 m/s). Depth and heading were displayed on a real-time viewing monitor and aided in navigation. A differential global positioning system was used to mark the beginning and end of each dive transect. The ROV was equipped with two 150 W lights; 3 thrusters; a low-light, high-resolution video camera (12:1 zoom); and a stainless steel crash frame. The camera was mounted with the imaging plane directed at a 45° angle and recorded a pair of parallel laser marks (10 cm apart) projected onto the seafloor or fjord wall to provide a reference for area of view and size of fauna.

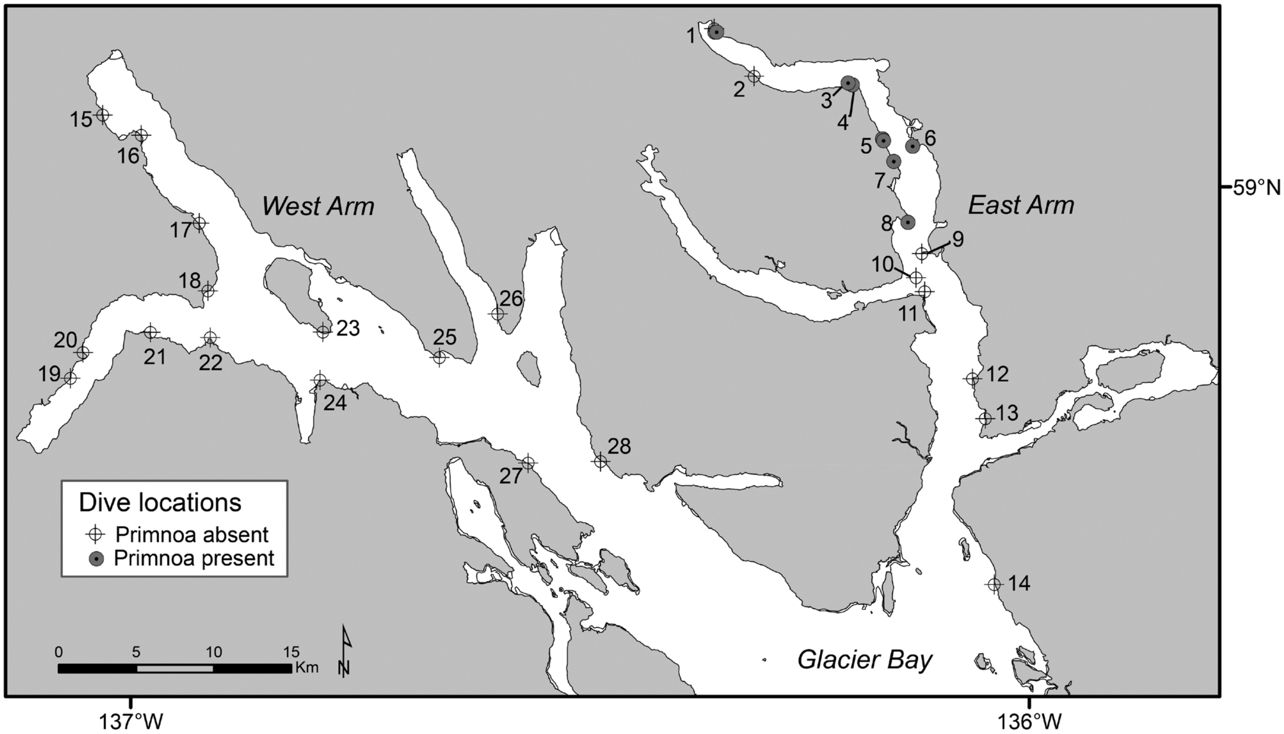

Figure 4

Map of sites in Glacier Bay, Southeast Alaska, where red tree corals (*Primnoa pacifica*) were present or absent. Surveys were conducted by scuba divers in 2004 and 2005. Numbers assigned to sites are indicated.

Field operations—physical oceanography

Conductivity, temperature, and depth (CTD) instruments (Sea-Bird Scientific, Bellevue, WA) were used to collect oceanographic profiles of the water column during each survey period (Appendix Table 2). During the surveys in 2004 and 2005, oceanographic data were recorded at stations established in the East Arm, West Arm, and central Glacier Bay and in Icy Strait near Point Couverden (Fig. 6). Oceanographic data also were recorded at several locations in Tracy and Endicott arms in Holkham Bay (Fig. 7) during the surveys conducted in March 2006, May 2008, and June 2014, and during a survey completed in 26–28 March 2007 to collect samples for genetic analysis. An instrument was lowered to various depths at an average rate of 1.5 m/s, and it measured depth, temperature, and salinity every 0.5 s. All depth measurements presented in this paper are adjusted to mean lower low water.

During several surveys, the instrument array included additional sensors to measure dissolved oxygen, photosynthetically active radiation (PAR), turbidity, and pH. Dissolved oxygen was measured in milliliters per liter (Appendix Tables 3 and 4) and converted to percent saturation by using the solubility of oxygen in seawater as a function of temperature, barometric pressure, and salinity (USGS[2]). Photosynthetically active radiation designates the spectral range or wave band of solar radiation (400–700 nm) that photosynthetic organisms, such as coralline algae, are able to use in the process of photosynthesis, and it was used to calculate the euphotic depth (i.e., the depth where light intensity falls to 1% of that at the surface). Turbidity was measured in nephelometric turbidity units and is essentially the cloudiness of seawater or the degree to which light is scattered by particles (principally sediment and phytoplankton) suspended in seawater.

Several additional oceanographic instruments were deployed at specific sites during the study period. A Minilog 12-TR miniature microprocessor-controlled temperature logger (VEMCO, Bedford, Canada) was deployed on a live red tree coral colony at a depth of 18 m at Site 5 in the East Arm of Glacier Bay. Deployed between 22 April 2005 and 14 June 2006, the logger recorded data every 6 h and had an accuracy of ±0.1°C. Four daily temperature

[2] USGS (U.S. Geological Survey). 2011. Change to solubility equations for oxygen in water. Off. Water Qual. Tech. Memo. 2011.03, 11 p. [Available from https://water.usgs.gov/admin/memo/QW/qw11.03.pdf.]

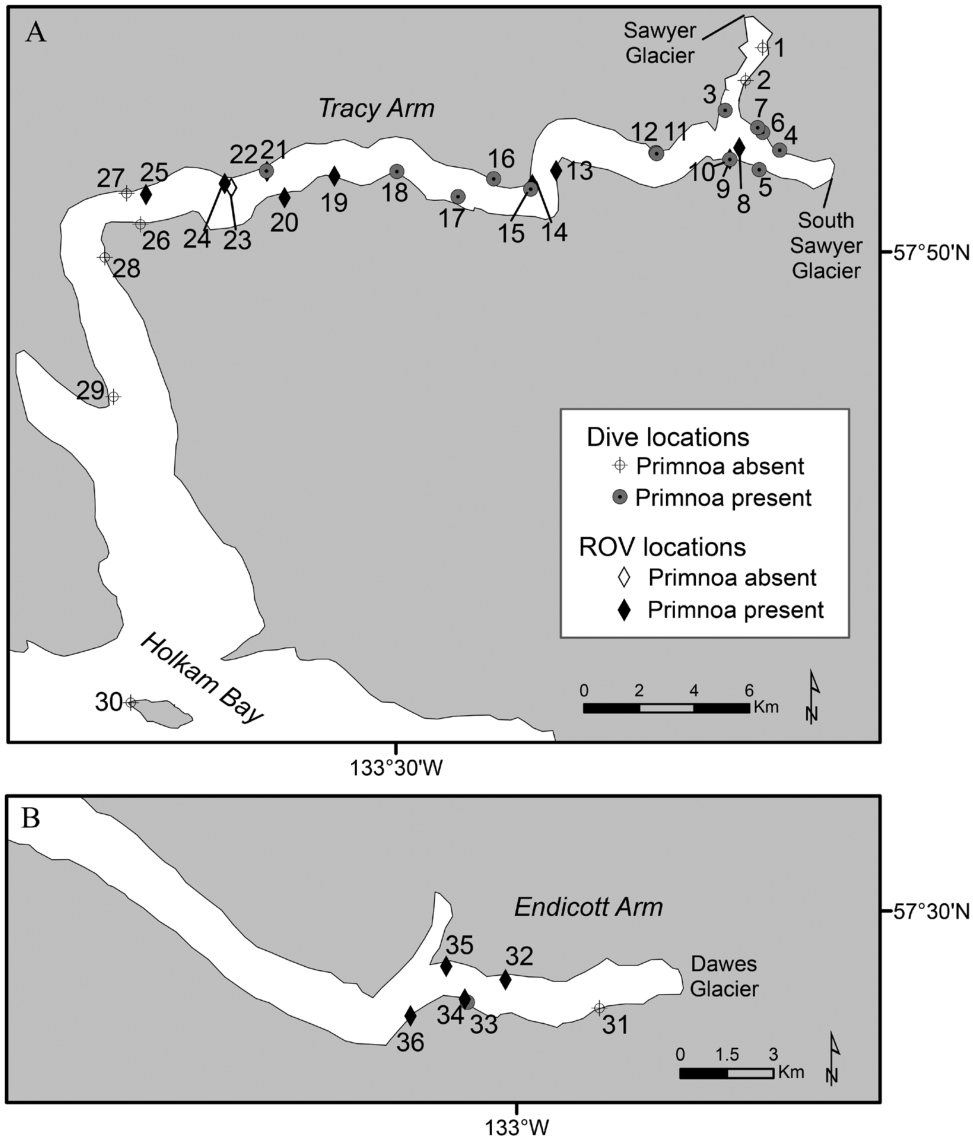

Figure 5

Map of (**A**) Tracy Arm and (**B**) Endicott Arm in Holkham Bay, Southeast Alaska, showing the location of sites where red tree corals (*Primnoa pacifica*) were present or absent during surveys conducted by scuba divers or with a remotely operated vehicle (ROV) in 2006, 2008, and 2014. Numbers assigned to sites are indicated.

measurements were recorded every 6 h and averaged to derive a mean daily temperature. We also deployed a DST CTD compact microprocessor-controlled temperature, depth, and salinity recorder (Star-Oddi, Gardabaer, Iceland) on a live red tree coral colony at a depth of 15 m at Site 15 in Tracy Arm, Holkham Bay. The logger was deployed between 9 September 2010 and 4 January 2012, recorded data every 6 h, and had an accuracy of ±0.1°C. Four daily temperature measurements recorded every 6 h were averaged and presented as mean daily temperature.

An Argonaut-MD Doppler current meter (Sontek, San Diego, CA) equipped with an internal compass was moored at a depth of 11 m in a red tree coral thicket at Site 15 in Tracy Arm. The meter was deployed between 10 March 2011 and 3 January 2012 and programmed to record average current velocity and direction every 10 min. Three acoustic transducers generated short pulses of sound at known frequencies that propagated through the water and were reflected back to the meter, where the frequency change, or Doppler shift, was measured. The meter is capable of recording current velocity (±0.5 cm/s) and heading (±2°) of a 1 m cell of water 0.5 m

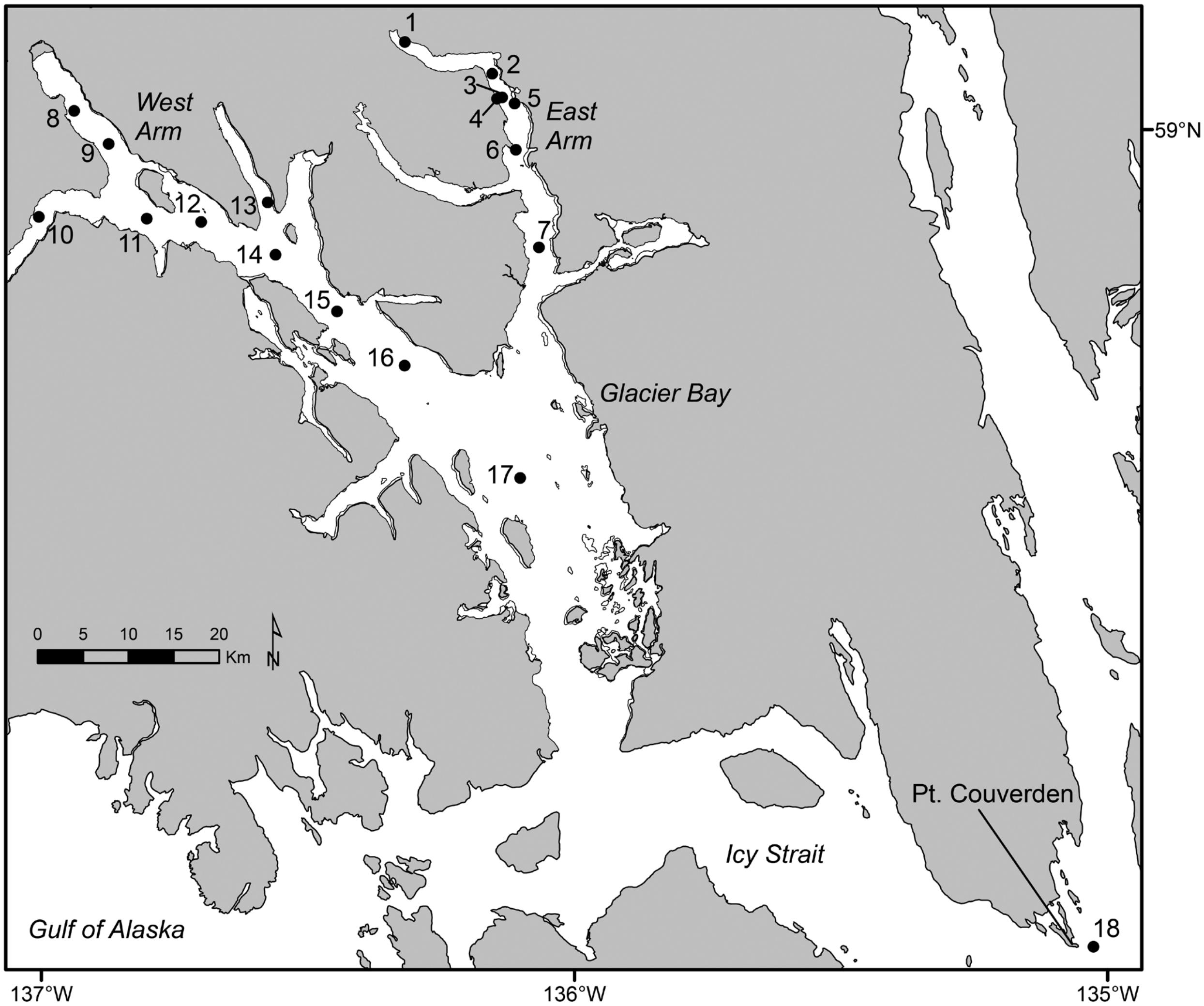

Figure 6

Map of Glacier Bay, Southeast Alaska, showing the location of stations where oceanographic data were collected in 2004 and 2005. Numbers assigned to stations are indicated.

below the meter once per second. However, to preserve memory space for data, the current meter was programmed to record average velocity and direction (based on 180 observations) every 15 min. Magnetic current headings were converted relative to true north.

Results

Distribution of red tree corals—Glacier Bay

Approximately 2220 and 3133 m of seafloor (i.e., fjord wall) was traversed and visually examined by divers during the Glacier Bay surveys in 2004 and 2005, respectively. The width of the transect and the exact area observed was difficult to determine because underwater visibility was highly variable between sites and ranged approximately from 1 to 6 m. Red tree corals were found at 7 dive sites in the upper reaches of the East Arm (Fig. 4), within 22.6 km of the head of the fjord (Table 1). Colonies generally were found in small patches and were most dense (up to approximately 0.3 colonies/m^2) at Sites 5 and 7 (Fig. 4). All colonies were attached to stable bedrock. Detailed taxonomic examination of specimens collected at several locations revealed that the corals were all *Primnoa pacifica*. The largest colony (153 cm maximum length or height) observed in the East Arm was at Site 7 located 17.7 km from the head of the fjord. No red tree corals were observed in the lower East Arm (Sites 9–14) or at any of the 14 sites in the West Arm.

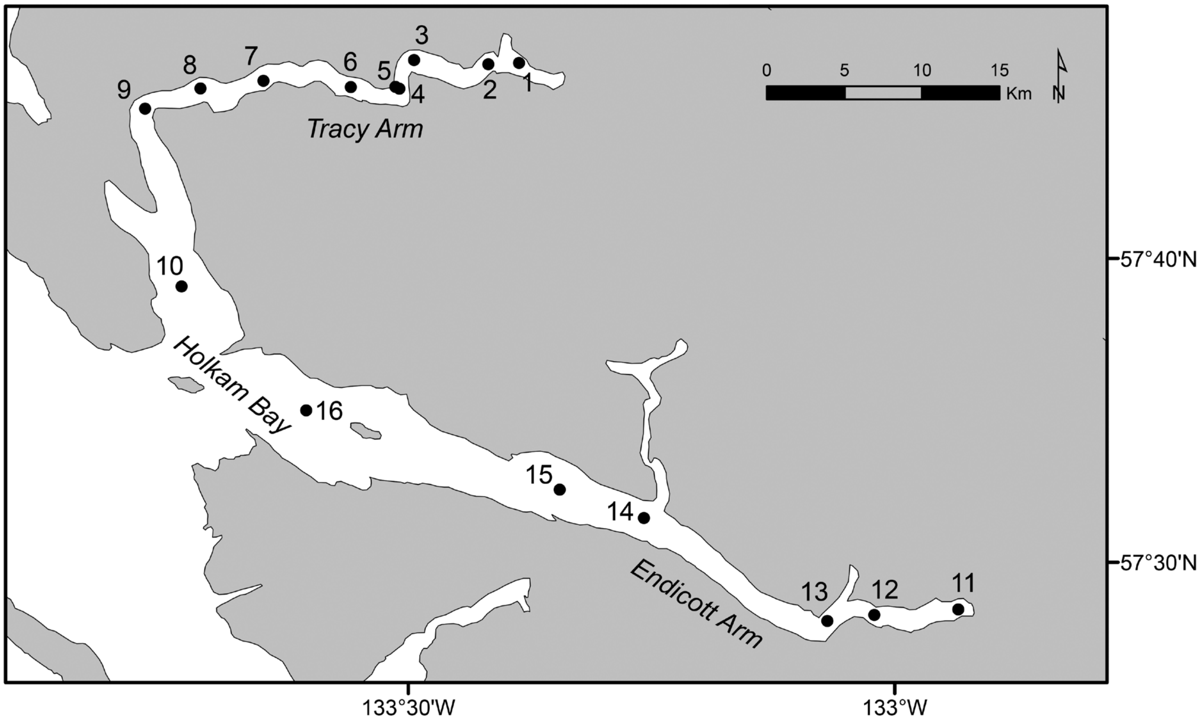

Figure 7

Map of Tracy Arm and Endicott Arm in Holkham Bay, Southeast Alaska, showing the location of stations where oceanographic data were collected in 2006, 2007, 2008, and 2014. Numbers assigned to stations are indicated.

Distribution of red tree corals—Holkham Bay

During the Holkham Bay surveys in 2006 and 2008, divers examined approximately 2804 and 530 m of seafloor (i.e., fjord wall), respectively. An additional 1931 m of seafloor was surveyed with the ROV in 2008 and 2014. Red tree corals were found at 15 of the 23 dive sites and 12 of the 13 ROV sites in Holkham Bay (Fig. 5). Detailed examination of specimens collected at several locations revealed that the corals were principally *Primnoa pacifica* with several colonies of *Primnoa pacifica* var. *willeyi* present at a few sites in Tracy Arm. All corals were attached to stable bedrock. Red tree corals were present in shallow-water areas only in the upper reaches of Tracy and Endicott arms, within approximately 3.3 km of the glacial termini in Tracy Arm and within 3.7 km of the Dawes Glacier in Endicott Arm (Table 1). Red tree corals were not observed in shallow water at sites in lower Tracy Arm greater than 24.4 km from the glacial termini. At 2 sites in upper Tracy Arm (Sites 4 and 6) red tree corals were actually found beneath the seasonal ice mélange and fast ice, which is present approximately from December through March in typical years. However, corals were not found in shallow water at the 2 sites closest to Sawyer Glacier (Sites 1 and 2, Fig. 5), and both of those sites had a thick surface layer of glacial sediment and evidence of significant iceberg scour.

Colonies were generally found in small patches and were most dense (approximately 0.5 colonies/m^2) at Sites 14 and 15 (Fig. 5A) in Tracy Arm and at Sites 33 and 34 (approximately 0.2 colonies/m^2) in Endicott Arm (Fig. 5B). The largest colony (280 cm length) observed in Tracy Arm was at Site 15, and the largest colony observed in Endicott Arm (150 cm length) was observed at Sites 32 and 34 (Table 1).

Depth of red tree corals and *Lithothamnion*—Glacier Bay

Red tree corals were observed at depths between 9 and 35 m (the maximum depth sampled during any scuba dive). Coralline algae (*Lithothamnion* sp.) were generally scarce at depths in the East Arm where red tree corals were present. The depth distributions of coralline algae and red tee corals were typically disjunct with little overlap, and coralline algae showed a clear pattern of increasing maximum depth with distance from the head of the fjord (Table 1). In the West Arm, coralline algae were more common and extended to considerably greater depths compared with sites in the East Arm at similar distances

Table 1

Maximum length and minimum depth of red tree corals (*Primnoa pacifica*) and maximum depth of encrusting corralline algae (*Lithothamnion* sp.) at sites surveyed in 3 study areas in Southeast Alaska: East Arm (Muir Inlet) of Glacier Bay in 2004 and 2005 and Tracy and Endicott arms of Holkam Bay in 2006 and 2008. The distance of each site from the head of the fjord is given. Refer to Figures 4 and 5 for locations of sites surveyed by scuba divers or with a remotely operated vehicle.

Site	Distance from head of fjord (km)	Maximum length of red tree corals (cm)	Minimum depth of red tree corals (m)	Maximum depth of *Lithothamnion* sp. (m)
East Arm, Glacier Bay				
1	1.32	55	14.0	0
2	5.24	–	–	5.0
3	11.40	40	21.6	8.0
4	11.63	20	16.2	8.0
5	15.98	144	9.1	6.0
6	17.66	89	10.7	6.0
7	17.67	153	17.4	6.0
8	22.58	21	21.6	6.0
9	24.41	–	–	12.0
10	26.00	–	–	15.0
11	27.21	–	–	15.0
12	33.13	–	–	22.0
13	35.71	–	–	22.0
14	47.62	–	–	25.0
Tracy Arm, Holkham Bay				
1	1.07	–	–	0
2	2.06	–	–	0
3	3.28	100	17.7	0
4	4.90	130	9.1	11.9
5	5.33	92	14.6	11.9
6	5.82	160	14.6	11.9
7	6.06	120	11.9	11.9
8	6.23	175	52.4	12.5
9	6.43	236	13.4	12.8
10	6.40	130	13.7	12.8
11	9.38	105	11.9	16.2
12	9.36	120	12.2	16.2
13	13.43	192	23.8	14.0
14	14.33	275	7.9	13.1
15	14.51	280	10.7	18.3
16	15.96	170	21.6	19.2
17	17.71	110	22.6	20.1
18	19.68	110	25.3	22.9
19	21.94	30	70.1	22.9
20	24.03	133	47.9	21.3
21	24.40	200	24.7	24.7
22	24.39	211	35.7	22.3
23	25.75	–	–	22.3
24	26.02	140	78.6	23.2
25	28.84	–	–	22.9
26	29.31	–	–	25.6
27	29.82	–	–	26.2
28	32.14	–	–	25.9
29	37.17	–	–	27.0+
30	48.45	–	–	27.0+
Endicott Arm, Holkham Bay				
31	3.70	–	–	6.1
32	6.80	150	30.2	14.9
33	7.80	148	9.1	13.4
34	7.90	150	11.0	11.9
35	8.60	30	55.8	12.8
36	10.00	120	16.5	14.3

from the head of the fjord. For example, coralline algae were found to depths of 12 m at Site 19 (4.6 km from the head of the fjord) compared with a depth of only 5 m at Site 2 (5.2 km from the head of the fjord), to depths of 14 m at Site 17 (12.3 km from the head of the fjord) compared with a depth of only 8 m at Site 4 (11.6 km from the head of the fjord), and to depths of 19.8 m at Site 23 (22.6 km from the head of the fjord) compared with a depth of only 6 m at Site 8 (22.6 km from the head of the fjord). Coralline algae were observed to a maximum depth of 25 m in both the East (Site 14) and West (Site 25) arms, the sites farthest from the heads of the fjords.

Depth of red tree corals and *Lithothamnion*—Holkham Bay

Red tree corals were observed at depths as shallow as 5.8 and 12.2 m in Tracy and Endicott arms, respectively, and generally were found deeper with increasing distance from the head of the fjord (Table 1). Observations made with an ROV revealed that red tree corals were distributed to depths well beyond those surveyed by scuba divers. Colonies were observed in Tracy Arm at depths to 59 m (Site 8), 30 m (Site 9), 64 m (Site 13), 84 m (Site 14), 70 m (Site 19), 74 m (Site 20), 80 m (Site 22), and 79 m (Site 24). Corals were not present in surveys at depths to 84 m at Site 23 in Lower Tracy Arm. The habitat at this site, deeper than the depth of coralline algae cover (22 m), was not optimal coral habitat, as it was heavily silt-laden with few bedrock exposures and of low relief. Red tree corals were present to a depth of 96 m in Endicott Arm. Coralline algae were generally scarce at sites in both arms where red tree corals were present, typically at depths just shallower than those of corals or at the same depth, and had a clear pattern of increasing depth with distance from the head of the fjord (Table 1). Coralline algae were observed at a depth of 27 m in Tracy Arm and at 14.3 m in Endicott Arm, the sites farthest from the heads of the fiords.

Species composition and associations—Glacier Bay

Similar benthic communities were found in both the East and West arms of Glacier Bay, but the along-fjord gradient of community composition was different for the 2 fjords. Red tree corals were found only in the upper portion (22.6 km from the head of the fjord) of the East Arm where benthic communities were apparently much less diverse. Bedrock in the upper reaches of the East Arm was typically covered with a veneer of silt but, where it was exposed, provided suitable substrate for small patches of coralline algae (Fig. 8A), the calcareous tube worm (*Serpula vermicularis*), and the thatched barnacle (*Semibalanus cariosus*). Other taxa present in these low-diversity habitats included the blue mussel (*Mytilus edulis*), the brachiopod *Laqueus californicus*, the barnacle *Chirona evermanni*, the great puncturella (*Cranopsis major*), the chevron-tentacle anemone (*Cribrinopsis fernaldi*), and the shiny orange sea squirt (*Cnemidocarpa finmarkiensis*). Species associated with red tree corals in the East Arm included the shortscale eualid (*Eualus suckleyi*) and the spiny lebbeid (*Lebbeus groenlandicus*).

An encrusting stoloniferan coral, *Sarcodictyon incrustans*, was found at many of the sites where red tree corals were present, at depths as shallow as 15 m, and often formed mats measuring over 0.5 m^2 (Fig. 8B). The stoloniferans were clearly associated with red tree corals and were often in close proximity to their bases. Other sedentary invertebrates found in close proximity to red tree corals were several hexactinellid sponges, including *Aphrocallistes vastus* (Fig. 8C), *Heterchone calyx* (Fig. 8D), a species of *Staurocalyptus*, and the demosponge *Haliclona urceolus*. *Haliclona urceolus* is common in areas of the North Atlantic and Arctic oceans, but this record is only the second one from the North Pacific Ocean (Lehnert and Stone, 2016; incorrectly listed as *H. rosea*). We observed *A. vastus* and *H. calyx* at depths of 20 and 21 m respectively, with the latter observation representing a new minimum depth record for the species (Stone et al., 2011).

Species richness markedly increased at dive sites greater than 22.6 km from the head of the fjord. The gigantic anemone (*Metridium farcimen*); anemones of the genus *Urticina*; the sea peach (*Halocynthia aurantium*); the spiny sea squirt (*Halocynthia igaboja*); the common basket star (*Gorgonocephalus eucnemis*); sea stars, including *Lethasterias nanimensis*, *Crossaster papossus*, *Stephanasterias albula*, *Solaster paxillatus*, and *Solaster endeca*; sea cucumbers, including *Cucumaria frondosa japonica* and *Synallactes challengeri*; the green falsejingle (*Pododesmus macrochisma*); the Oregon triton (*Fusitriton oregonensis*); and the spiny lithode crab (*Acantholithodes hispidus*) were observed only in those shallow-water areas farther out from the head of the fjord where red tree corals were not present. Juvenile light dusky rockfish (*Sebastes variabilis*) were observed only at Site 14 near the mouth of the East Arm using the interstices of large fractured bedrock as refuge (Fig. 8E).

The same general species composition and pattern of distribution was observed in the West Arm except for the notable absence of both red tree corals and the encrusting stoloniferan *S. incrustans*. Hexactinellid sponges, including *A. vastus* and *H. calyx*, were again observed at depths as shallow as 20 and 21 m, respectively. An increase in species richness occurred at Site 24, which is located 23.2 km from the head of the fjord.

Species composition and associations—Holkham Bay

Species associated with red tree corals in Tracy Arm included the brachiopod *Laqueus californicus* and the barnacle *Chirona evermanni*, and individuals of both species were often completely overgrown with coenenchyme if previously attached to bare sections of axial skeleton. Other associates included the shortscale eualid, the spiny lebbeid, and the scaled crab (*Placetron wosnessenskii*). Other species found in the same habitat as red tree corals included the hexactinellid sponges *A. vastus*, *H. calyx*, 2 undescribed species of *Acanthascus*, and 1 undescribed species of *Staurocalyptus* (Reiswig[3]). The stoloniferan coral *S. incrustans* that was common in the East Arm of Glacier Bay was not observed anywhere in Holkham Bay. Other fauna observed during scuba surveys were similar to those observed in Glacier Bay: the calcareous tube worm, the chevron-tentacle anemone, and the shiny orange sea squirt in the same depth range as red tree corals; and the calcareous tube worm, the sea peach, the blue mussel, the thatched barnacle, the great puncturella, and the green sea urchin *Strongylocentrotus droebachiensis* at shallower depths. We observed *A. vastus* and *H. calyx* at depths of 19 and 21 m, respectively, with the former observation representing a new minimum depth record for the species.

Species richness in Tracy Arm appeared to increase markedly at Site 25 located 28.8 km from the head of the fjord. The change in community structure was similar to that observed in the 2 arms of Glacier Bay, and many of the same species were present, including the sea stars (*Lethasterias nanimensis*, *Leptasterias* sp., *Henricia* sp., *Pteraster tesselatus*), the common basket star, the feather star *Florometra serratissima*, and the sea cucumber *Synallactes challengeri*. Observations were geographically limited in Endicott Arm (3.7–10 km from the head of the fjord), but the species observed were consistent with those seen at the sites in Tracy Arm at similar distances from the head of the fjord.

Growth rates—Glacier Bay

The chronosequence provided by the known glacial retreat in the East Arm (Fig. 2) allowed us to calculate the minimum (i.e., slowest) growth rate for red tree corals present there (Table 2). Assuming that corals settled the year the habitat was deglaciated, we calculated minimum growth rates for corals at each site where they were present; minimum growth rates were 0.31–2.39 cm/year (Table 2). In addition, we used the growth rate (1.60–2.32 cm/year) estimated by Andrews et al. (2002) for the species in presumably optimal open-ocean habitat to calculate a range of potential years of recruitment (Table 2). We suggest that the higher growth rates we estimated from the year of deglaciation corroborate those estimated by Andrews et al. (2002) and represent recruitment to the substrate soon after deglaciation and that the smaller colonies (i.e., those for which we suggest a slower growth rate) are from variable or delayed recruitment events thereafter. We do note, however, that this scenario assumes that growth rates for all colonies would be the same, a reasonable assumption given that all colonies would be equally subjected to the variables that presumably constrain growth (i.e., temperature and food supply).

Oceanography—Glacier Bay

Average daily temperatures for the entire deployment period (from 22 April 2005 to 14 June 2006) of the temperature logger at Site 5 in the East Arm ranged from 4.5°C (27 April 2006) to 7.8°C (8 August 2005) (Fig. 9A). The range for all temperatures measured during the deployment of the logger at Site 5 was 4.1°C (19 March 2006) to 7.8°C (17 September 2005). The mean annual temperature (from 22 April 2005 to 21 April 2006) at Site 5 in the East Arm was 6.4°C. General seasonal trends were 1) cooling in early November at the time of an obvious water column mixing event and 2) warming beginning in early May. The CTD casts made during surveys (Table 3) confirmed these temperatures at a depth of 18 m at Site 5. The CTD data (Table 3) from the late-April 2004 survey indicated that temperatures were stable in the East Arm and slightly cooler at depths below ~15 m in central Glacier Bay and Icy Strait. The CTD data (Table 3) from the survey conducted in late-April 2005 indicate unstable temperatures at depths shallower than 20 m in both the East and West arms and slightly cooler temperatures in surface waters in comparison with temperatures in central Glacier Bay and Icy Strait. Below a depth of ~15 m, temperature slightly decreased with depth. No major temperature gradient was apparent from the head to mouth of either fjord during the survey periods.

The CTD data (Table 4) from the survey conducted in 2004 indicate slightly lower salinity in surface waters within the East Arm, stable salinities at depths below ~15 m, and slightly higher salinities at all depths at stations outside the fjord. The CTD data (Table 3) from the survey conducted in 2005 indicate slightly lower salinity in surface waters (depths <20 m) within the East and West arms, stable salinities at depths below ~15 m, and higher salinity at all depths at the station in Icy Strait. No major salinity gradient was apparent from the head to mouth of either fjord during the survey periods.

The CTD data (Table 5) from the survey completed in 2004 indicate high oxygen saturation levels (Table 5) at all depths at stations within the East Arm and central Glacier Bay. Very high saturation levels in shallow water at some stations, particularly at Station 1, were likely due to localized phytoplankton blooms. Saturation

[3] Reiswig, H. 2008. Personal commun. Dep. Biol., Univ. Victoria and Nat. Hist. Sect., R. B.C. Mus., P.O. Box 3020, Stn. CSC, Victoria, BC, Canada V8W 3N5.

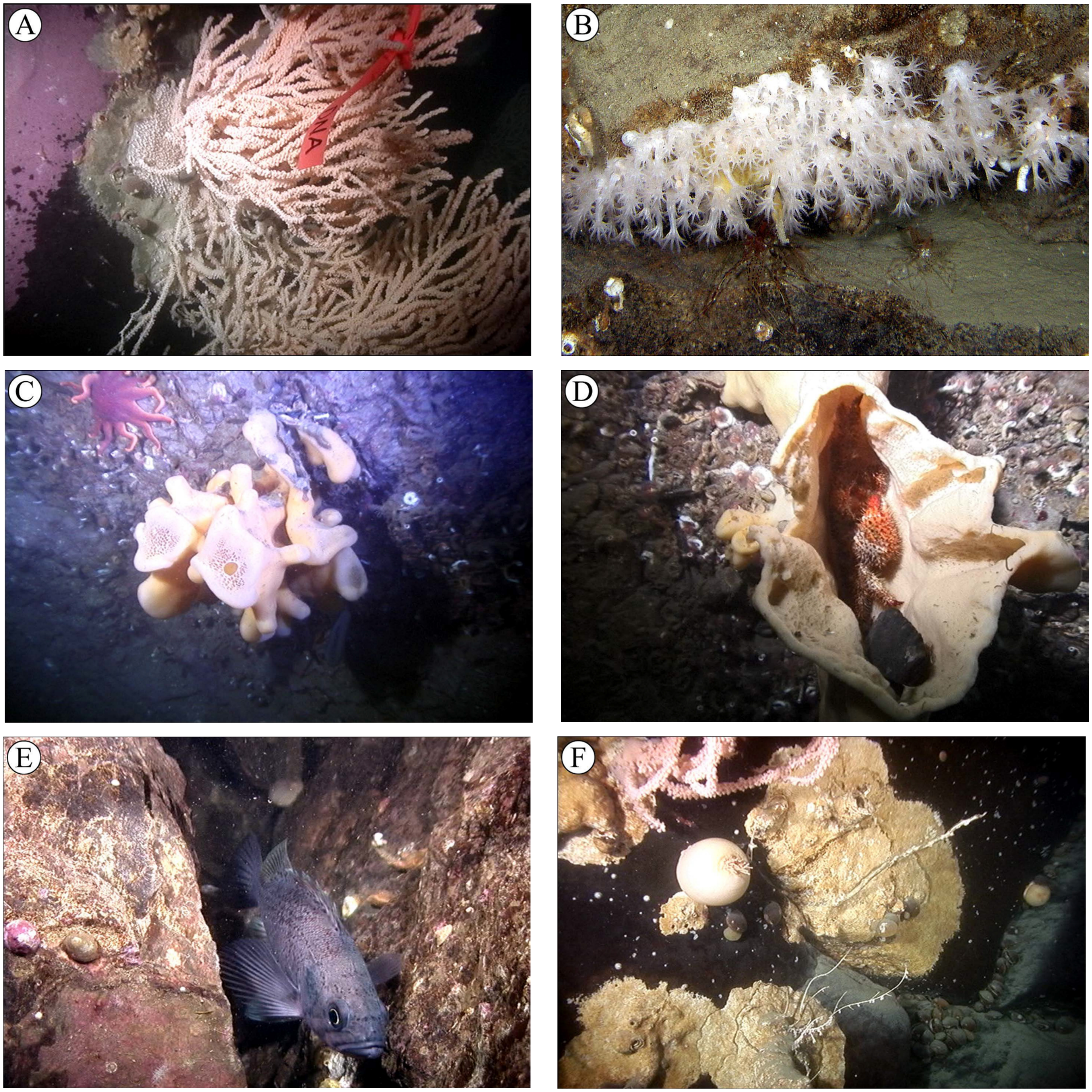

Figure 8

(**A**) A large patch (upper left) of coralline algae (*Lithothamnion* sp.) growing near a colony of red tree coral (*Primnoa pacifica*) at a depth of 18 m in Tracy Arm, Holkam Bay, Southeast Alaska. (**B**) A patch of a stoloniferan coral, *Sarcodictyon incrustans*, at a depth of 22 m in the East Arm (Muir Inlet), Glacier Bay, Southeast Alaska. (**C**) The glass sponge *Aphrocallistes vastus* at a depth of 24 m in the East Arm. (**D**) The glass sponge *Heterochone calyx* at a depth of 24 m in the East Arm. A spiny lithode crab (*Acantholithodes hispidus*) takes refuge in the sponge's atrium. (**E**) Juvenile light dusky rockfish (*Sebastes variabilis*) were observed in shallow water (17 m depth in this photo) only at Site 14 near the mouth of the East Arm. (**F**) A group of heavily calcified basal plates and stumps of red tree corals at a depth of 20 m in Tracy Arm. The colonies were likely removed as a result of iceberg scour. Small coral recruits are visible on some of the plates. (**G**) A school of capelin (*Mallotus villosus*) at a depth of 75 m in Tracy Arm. (**H**) Juvenile walleye pollock (*Gadus chalcogrammus*), which were sometimes associated with red tree corals during the winter months in Tracy Arm (20 m depth). (**I**) Egg mass of a great sculpin (*Myoxocephalus polyacanthocephalus*) at a depth of 18 m in the East Arm. The sculpin, not pictured, was guarding several egg masses deposited on the colony. (**J**) A blue king crab (*Paralithodes platypus*) using a large red tree coral as cover at a depth of 18 m in Tracy Arm.

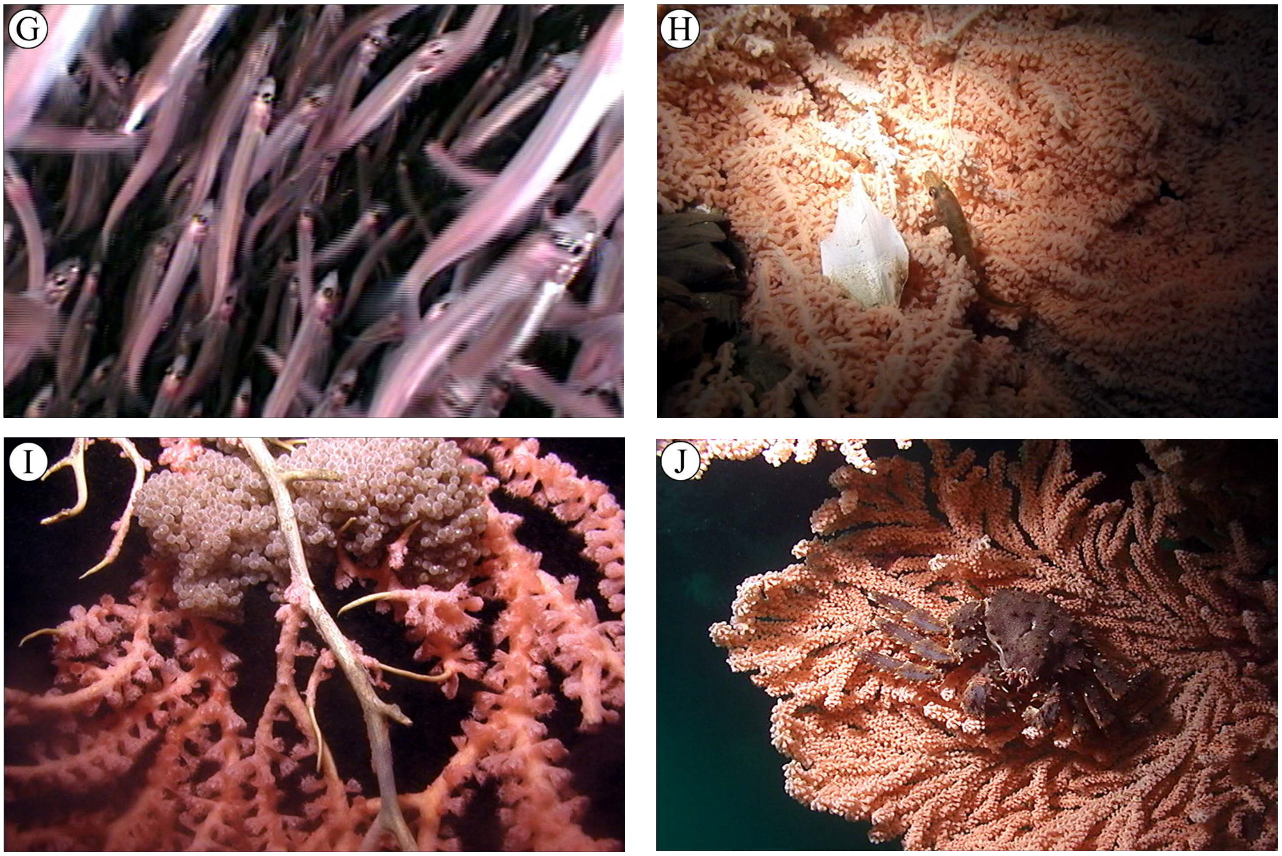

Figure 8 (continued)

levels steadily decreased with depth, particularly to 50 m, and were highest in central Glacier Bay and in Icy Strait. The CTD data (Table 5) from the survey conducted in 2005 indicate very different scenarios in the 2 fjords. Saturation levels were much lower, but stable, in shallow water (depths <15 m) in the East Arm than in the West Arm, central Glacier Bay, and Icy Strait (Table 5). The high saturation levels measured in shallow water outside the East Arm were undoubtedly due to localized phytoplankton blooms. Contrastingly, saturation levels in deeper waters (depths >20 m) were consistently higher in the East Arm than at other stations within Glacier Bay. No major oxygen saturation gradient was apparent from the head to mouth of either fjord during the survey periods.

The CTD data (Table 6) from the survey conducted in 2005 indicate a strong gradient of decreasing euphotic depth from the head to mouth of the East Arm. Euphotic depth near the head of the fjord was only 2.8 m and increased steadily to 12.7 m near the mouth of the fjord (Table 6). The CTD data for the West Arm indicate a complicated scenario with unusually deep euphotic depths in the upper reaches of the fjord (Stations 8, 9, 10, and 11). Beginning at Site 12, the same pattern observed in the East Arm continued with increasing euphotic depth farther out the fjord. The euphotic depth at the stations in central Glacier Bay and Icy Strait was considerably deeper than the euphotic depth in either fjord.

Oceanography—Holkham Bay

Water currents were generally bidirectional with the strongest currents (up to 12 cm/s) flowing out-fjord with a weaker reciprocal current flowing in-fjord. The mean annual temperature (from 10 September 2010 to 09 September 2011) at Site 15 in Tracy Arm was 4.4°C, considerably colder than for a 1-year period in the East Arm of Glacier Bay. Average daily temperatures for the entire deployment period (from 9 September 2010 to 4 January 2012) ranged from 3.1°C to 6.3°C (Fig. 9B). The range for all temperatures measured during the deployment was from 2.8°C (18 February 2011) to 6.5°C (28 November 2011). General seasonal trends were 1) cooling in early December and 2) warming beginning in early May. The CTD casts made during survey periods

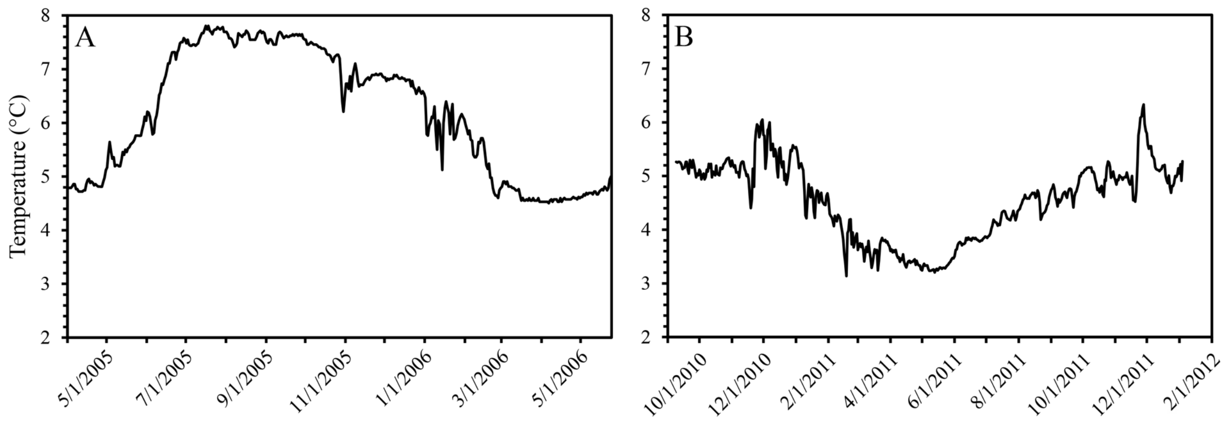

Figure 9

(**A**) Mean daily water temperature recorded between 22 April 2005 and 14 June 2006 at a depth of 18 m at Site 5 in the East Arm (Muir Inlet) of Glacier Bay, Southeast Alaska, and (**B**) mean daily water temperature recorded between 9 September 2010 and 4 January 2012 at a depth of 15 m at Site 15 in the Tracy Arm, Holkham Bay, Southeast Alaska. Water temperature was recorded every 6 h with a temperature logger attached to a coral colony at both sites.

Table 2

Estimated minimum growth rate and years of recruitment of the largest red tree corals (*Primnoa pacifica*) observed at sites in the East Arm (Muir Inlet) of Glacier Bay, Southeast Alaska. Divers measured colony lengths during the survey conducted in 2004. Minimum growth rate was calculated on the basis of the coral recruiting to the substrate in the year of deglaciation. Estimates of the years of recruitment are based on the published growth rate of 1.60–2.32 cm/year (Andrews et al., 2002) for corals in presumably optimal open-ocean habitat.

Site	Maximum colony length (cm)	Year of deglaciation	Minimum growth rate (cm/y)	Years of recruitment
1	55	1978	2.12	1970–1980
3	40	1961	0.93	1979–1987
4	20	1960	0.45	1991–1995
5	144	1942	2.32	1914–1942
6	89	1942	1.44	1948–1966
7	153	1940	2.39	1908–1938
8	21	1937	0.31	1991–1995

(Table 7) confirmed these temperatures at a depth of 15 m at Site 15.

The CTD data (Table 7) from the survey conducted in 2006 indicate that temperature was stable in Tracy Arm but warmer at depths below 15 m, particularly near the head of the fjord. There was a gradient of increasing temperature in surface waters (depths <20 m) from the head to the mouth of the fjord. The CTD data (Table 7) from the survey completed in March 2007 indicate much colder water temperatures at all stations and depths in Tracy Arm in comparison with temperatures recorded in 2006. The CTD data (Table 7) from the survey conducted in 2008 indicate cooler temperatures at depths shallower than 40 m, relatively stable temperatures in deeper water, and an obvious gradient of increasing temperature in surface waters (depths <40 m) from the head to the mouth of the fjord. The CTD data from the survey performed in 2014 indicate a mixing water column with cooler surface waters at all stations, except for obvious warming at Station 10 nearest the mouth of the fjord. Again, there was a gradient of slightly higher temperature in surface waters (depths <40 m) from the head to the mouth of the fjord.

In Endicott Arm, CTD data (Table 7) from the surveys conducted in 2006 and 2007 indicate a well-mixed water column with stable temperatures. No major temperature gradient was observed from the head to mouth of the fjord during either year. The CTD data (Table 7) from the survey completed in 2008 are very similar to those from Tracy Arm and indicate cooler surface waters (depths <40 m), relatively stable temperatures in deeper water, and an obvious gradient of increasing temperature in surface waters from the head to the mouth of the fjord. The CTD data (Table 7) from the survey performed in 2014 are also similar to data recorded in Tracy Arm and indicate a mixing water column with cooler surface waters at the uppermost station only (Station 11). A strong gradient of increasing temperature in surface waters (depths <20 m) from the head to the mouth of the fjord was evident.

Table 3

Water temperature (°C) measured at stations in Glacier Bay, Southeast Alaska, during surveys conducted in 2004 (24–27 April) and 2005 (17–22 April). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 6 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2004	1	5.21	5.04	4.88	4.75	4.70	4.68	4.65	4.64	4.64	4.63	4.63	4.64	4.64	4.64
2004	4	4.85	4.80	4.74	4.69	4.65	4.64	4.64	–	–	–	–	–	–	–
2004	5	4.90	4.84	4.80	4.76	–	–	–	–	–	–	–	–	–	–
2004	7	4.88	4.82	4.78	4.75	4.71	4.69	4.65	4.64	4.64	4.67	4.70	4.68	4.69	4.71
2004	17	5.19	4.88	4.85	4.82	4.79	4.75	4.82	4.91	4.97	4.98	5.00	5.01	5.02	5.00
2004	18	4.85	4.81	4.77	4.79	4.80	4.76	4.75	4.74	4.76	4.79	4.89	4.89	4.92	4.96
2005	1	5.42	5.23	5.05	4.85	4.79	4.78	4.78	4.78	4.78	4.79	4.79	4.79	4.79	4.79
2005	2	4.88	4.85	5.02	4.85	4.78	4.78	4.78	4.79	4.79	4.79	4.79	4.79	4.79	4.80
2005	3	5.48	5.19	5.01	4.81	4.78	4.78	4.78	4.78	4.78	4.78	4.78	4.79	4.79	4.79
2005	6	5.53	5.19	5.06	4.89	4.80	4.78	4.77	4.78	4.78	4.78	4.79	4.79	4.79	4.80
2005	7	5.12	5.02	4.97	4.88	4.86	4.78	4.78	4.79	4.79	4.80	4.80	4.80	4.81	4.81
2005	8	4.73	4.73	4.76	4.76	4.79	4.77	4.80	4.80	4.79	4.79	4.78	4.77	4.76	4.74
2005	9	4.86	4.84	4.76	4.75	4.79	4.80	4.81	4.81	4.80	4.79	4.78	4.76	4.75	4.75
2005	10	4.29	4.38	4.70	4.79	4.81	4.81	4.81	4.80	4.80	4.77	4.76	4.76	4.75	4.75
2005	11	4.77	4.79	4.74	4.77	4.80	4.81	4.81	4.81	4.80	4.79	4.78	4.77	4.76	4.76
2005	12	5.01	5.01	4.98	4.80	4.75	4.78	4.80	4.80	4.80	4.77	4.76	4.75	4.75	4.75
2005	13	5.02	4.94	4.88	4.82	4.79	4.79	4.78	4.77	4.77	4.76	4.76	4.76	4.77	4.76
2005	14	5.21	5.10	5.01	4.86	4.78	4.79	4.78	4.78	4.77	4.77	4.77	4.77	4.77	4.76
2005	15	5.35	5.12	4.95	4.90	4.83	4.80	4.80	4.79	4.78	4.78	4.78	4.78	4.78	4.79
2005	16	5.23	5.07	4.93	4.86	4.79	4.78	4.77	4.77	4.77	4.76	4.76	4.77	4.77	4.77
2005	17	5.44	5.14	5.02	4.99	5.00	4.81	4.81	4.84	4.88	4.90	4.90	4.97	5.02	5.04
2005	18	4.67	4.67	4.66	4.66	4.66	4.53	4.47	4.47	4.49	4.43	4.48	4.51	4.52	4.57

The salinity cell on the DST CTD recorder failed during the first month of deployment, possibly as a result of fouling; consequently, no long-term (i.e., year-round) salinity data were recorded. The CTD data (Table 8) from the surveys conducted in 2006 and 2007 indicate that salinity was slightly lower in surface waters (depths <15 m) of Tracy Arm then relatively stable to a depth of 120 m. There was a slight gradient of increasing salinity from the head to the mouth of the fjord. The same general pattern was observed during the survey completed in 2008, although salinity was slightly lower at all depths to 120 m. The CTD data (Table 8) from the survey performed in 2014 indicate steadily increasing salinity to a depth of 120 m. There was no obvious gradient from the head to the mouth of the fjord.

Salinity in Endicott Arm followed the same general pattern observed in Tracy Arm during all 4 surveys but generally was slightly higher at all depths. The CTD data (Table 8) from the surveys conducted in 2006 and 2007 indicate that salinity was slightly lower in the immediate surface waters (depths <5 m) of Endicott Arm then relatively stable to a depth of 120 m. Salinity at all stations in Endicott Arm and at all depths were higher than salinity values recorded in Tracy Arm. The CTD data (Table 8) from the survey completed in 2014 indicate steadily increasing salinity to a depth of 120 m. There was no obvious gradient from the head to the mouth of the fjord during any survey.

The CTD data (Table 9) from the survey conducted in 2006 indicate low oxygen saturation levels at all stations and at all depths in Tracy Arm except for the immediate surface waters (depths <5 m) at the lower fjord stations. Saturation levels steadily decreased with depth, and a gradient of increasing saturation levels from the head to the mouth of the fjord was not evident. Contrastingly, saturation levels were high at all stations and at all depths during the surveys completed in 2007 and 2008. The same general patterns of oxygen saturation were found in Endicott Arm during all 3 surveys.

Measurements of PAR were recorded during the surveys conducted in 2008 and 2014 (Table 10). The PAR data from the survey completed in 2008 indicate an apparent gradient of decreasing euphotic depth from the head to mouth of Tracy Arm. Euphotic depth near the head of the fjord was only 8.6 m with highly fluctuating measurements, likely due to localized plankton blooms, throughout the fjord. However, the euphotic depth was greatest near the mouth of the fjord (22.3 m). The PAR data for Endicott Arm indicate an even more complicated scenario—with shallow euphotic depths in the upper

Table 4

Salinity measured at stations in Glacier Bay, Southeast Alaska, during surveys conducted in 2004 (24–27 April) and 2005 (17–22 April). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 6 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2004	1	30.33	30.56	30.71	30.76	30.80	30.81	30.82	30.83	30.83	30.84	30.84	30.85	30.85	30.85
2004	4	30.47	30.62	30.73	30.77	30.81	30.83	30.83	–	–	–	–	–	–	–
2004	5	30.51	30.61	30.68	30.73	–	–	–	–	–	–	–	–	–	–
2004	7	30.52	30.65	30.72	30.75	30.80	30.81	30.83	30.84	30.85	30.86	30.87	30.87	30.87	30.88
2004	17	30.37	30.67	30.74	30.78	30.84	30.89	30.95	30.97	30.99	31.00	31.00	31.00	31.01	31.01
2004	18	31.08	31.18	31.19	31.22	31.27	31.39	31.47	31.68	31.72	31.83	32.01	32.06	32.11	32.14
2005	1	29.91	30.16	30.46	30.90	30.96	30.98	30.99	31.00	31.01	31.02	31.02	31.02	31.02	31.02
2005	2	29.91	30.36	30.52	30.80	30.96	30.98	30.99	30.99	31.00	31.00	31.01	31.01	31.02	31.03
2005	3	29.79	30.42	30.64	30.89	30.97	30.99	31.00	31.01	31.01	31.02	31.02	31.02	31.03	31.04
2005	6	29.81	30.31	30.64	30.84	30.97	30.99	31.01	31.02	31.03	31.03	31.04	31.04	31.04	31.05
2005	7	30.55	30.68	30.75	30.85	30.87	30.99	31.00	31.02	31.02	31.03	31.03	31.03	31.04	31.04
2005	8	30.44	30.55	30.65	30.68	30.87	30.96	31.03	31.06	31.07	31.08	31.09	31.09	31.10	31.11
2005	9	30.41	30.53	30.73	30.84	30.94	31.02	31.05	31.07	31.08	31.09	31.10	31.11	31.11	31.12
2005	10	30.14	30.64	30.86	30.94	31.01	31.04	31.05	31.06	31.07	31.08	31.10	31.10	31.11	31.11
2005	11	30.45	30.64	30.73	30.85	30.98	31.03	31.04	31.05	31.07	31.07	31.09	31.09	31.10	31.10
2005	12	30.46	30.64	30.73	30.86	30.95	31.01	31.05	31.06	31.08	31.11	31.11	31.12	31.12	31.12
2005	13	30.62	30.77	30.88	30.96	31.02	31.05	31.07	31.08	31.09	31.09	31.10	31.11	31.11	31.12
2005	14	30.17	30.50	30.78	30.92	31.02	31.03	31.05	31.07	31.08	31.09	31.09	31.09	31.10	31.11
2005	15	29.89	30.56	30.80	30.88	30.94	30.99	31.02	31.03	31.05	31.06	31.07	31.08	31.09	31.11
2005	16	30.34	30.61	30.85	30.97	31.02	31.06	31.08	31.08	31.09	31.10	31.11	31.12	31.12	31.12
2005	17	30.49	30.68	30.79	30.87	30.98	31.00	31.03	31.06	31.08	31.08	31.10	31.11	31.12	31.13
2005	18	30.93	30.96	30.96	30.97	31.00	31.15	31.23	31.29	31.33	31.45	31.54	31.67	31.77	31.87

reaches of the fjord (Stations 12 and 13) but also at Station 15 farther out the fjord near the mouth, again likely as a result of a localized phytoplankton bloom. The PAR data from the survey conducted in 2014 are more straightforward with a clear gradient of deeper euphotic depth from the head to the mouth of both fjords (Table 10).

Measurements of turbidity (the degree to which light is scattered by particles suspended in seawater) were recorded during only the cruise that occurred in 2014 (Table 11). Because high concentrations of particulate matter affect light penetration, measurements of turbidity are relevant to euphotic depth. A moderately strong decreasing turbidity gradient from the head to mouth of both fjords was evident, and a consistent decrease in turbidity with depth at all stations was observed.

Measurements of pH also were recorded during the cruise that occurred in 2014 (Table 12). The pH was stable (7.77–8.34) at all depths and at all stations in both fjords but slightly higher in Tracy Arm. The pH was slightly higher in surface waters (depths <5 m) from the head to mouth of both fjords and steadily decreased with depth at all stations.

Discussion

Our observations of red tree corals thriving at shallow depths in fjords in Southeast Alaska represent a major depth range extension for this keystone species. Distributional data for *Primnoa* in Alaska waters were first summarized by Cimberg et al. (1981), and on the basis of limited data available at the time they reported that *Primnoa* ranged from Amchitka Island in the Aleutian Archipelago to Dixon Entrance on the border with British Columbia, Canada. They also reported a very broad bathymetric distribution for *Primnoa* in Alaska waters ranging from 10 to 800 m. We now know from expert examination of specimens, including those collected during this study, that red tree corals are distributed at depths between 6 and 573 m in Alaska waters (Stone and Cairns, 2017). Furthermore, we know from extensive research surveys conducted with submersibles and from bycatch records of fisheries surveys completed in the eastern GOA and the Inside Passage of Southeast Alaska that red tree corals typically occur at depths between 127 and 365 m (Krieger and Wing, 2002; Stone et al., 2014) and are extremely rare at shallower depths

Table 5

Oxygen saturation (%) measured at stations in Glacier Bay, Southeast Alaska, during surveys conducted in 2004 (24–27 April) and 2005 (17–22 April). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 6 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2004	1	136.8	114.9	102.6	94.4	91.4	93.2	94.0	94.7	95.1	95.4	95.5	95.9	95.9	96.1
2004	4	94.1	96.6	93.4	92.6	94.3	94.9	95.2	–	–	–	–	–	–	–
2004	5	99.8	94.8	93.2	91.3	–	–	–	–	–	–	–	–	–	–
2004	7	115.9	100.3	94.7	92.7	92.7	91.9	92.4	92.9	93.6	94.1	94.4	94.6	94.6	94.5
2004	17	122.1	114.6	105.5	101.5	97.8	96.4	96.9	97.8	98.3	98.7	99.0	99.3	99.3	99.3
2004	18	110.6	105.6	100.2	97.9	95.1	91.9	85.9	80.7	75.9	71.8	66.6	64.9	63.8	62.7
2005	1	64.4	67.6	72.1	72.3	71.7	71.3	71.0	70.7	70.3	69.6	69.4	68.2	68.2	67.3
2005	2	66.8	68.0	68.7	70.1	65.6	64.9	64.7	65.0	65.1	65.1	65.1	65.6	66.0	66.3
2005	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2005	6	70.1	74.7	76.9	76.6	76.4	76.1	75.9	75.8	75.6	75.5	75.3	75.3	75.2	75.0
2005	7	75.1	76.7	77.0	76.9	76.5	75.6	75.4	75.0	74.7	74.6	74.6	74.4	74.4	74.3
2005	8	113.4	86.9	76.9	70.3	67.0	64.4	63.4	63.1	63.1	63.2	63.2	63.2	63.3	63.3
2005	9	110.0	86.6	73.8	66.7	62.8	61.5	60.7	60.7	60.6	60.7	60.7	60.7	60.8	60.8
2005	10	113.8	86.1	69.3	62.8	60.7	60.5	60.5	60.5	60.3	60.3	60.3	60.3	60.3	60.3
2005	11	146.7	99.8	76.5	67.9	63.1	61.5	61.3	61.3	61.3	61.3	61.3	61.3	61.2	61.2
2005	12	156.1	101.9	83.0	68.9	63.3	61.2	60.7	60.6	60.6	60.7	60.7	60.6	60.8	60.8
2005	13	180.0	104.2	83.9	66.9	62.5	61.6	61.0	60.9	60.9	60.8	60.9	61.0	61.2	61.2
2005	14	170.0	114.9	96.6	71.6	63.4	61.5	60.7	60.6	60.3	60.3	60.3	60.3	60.3	60.3
2005	15	135.4	107.7	86.7	74.4	67.0	64.8	63.4	62.9	62.9	62.9	62.9	62.9	63.1	63.5
2005	16	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2005	17	180.9	178.7	110.5	91.2	77.2	72.1	69.6	68.6	68.6	68.5	68.8	69.2	69.3	69.7
2005	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–

aside from those observations reported here for the emerged populations in the glacial fjords.

The results of extensive research through surveys conducted by scuba divers in the shallow waters of Southeast Alaska and elsewhere (senior author, personal observ.) indicate that deep-sea emergence of red tree corals is a rarity in Alaska and is limited to a few glacial fjords where oceanographic conditions are unusually optimal to support corals. The validity of the shallow (<127 m) depth records reported by Cimberg et al. (1981) are questionable. Many of these records are based on anecdotal information, nonexpert identifications, and collections made with spatially imprecise sampling equipment (i.e., fishing gear).

Several gorgonian species closely resemble each other superficially and can be easily mistaken for red tree corals. This problem is particularly the case with the shallow-water acanthogorgiid gorgonian *Calcigorgia spiculifera*, which is the most common shallow-water gorgonian in Alaska (Stone et al., 2017). Additionally, some records reported by Cimberg et al. (1981) are based on fisheries bycatch specimens that may have been collected at their original location and discarded at sea only to be recollected as bycatch at a new location. Such a translocation was apparently the case for one specimen reported in Cimberg et al. (1981) that was collected in shallow water and identified by an acknowledged expert in octocoral taxonomy. The specimen in question was collected during the 1940s near Petersburg, Alaska, by a shrimp trawler at a depth of 21–30 m. In July 1999, scuba divers (senior author, personal observ.) determined that the collection site was a vast, sandy seafloor with high current — habitat that red tree corals do not inhabit. The location was, however, in an area where local fishermen reportedly cleaned their nets of debris after fishing in nearby deeper water. There is one confirmed record of a red tree coral collected at a depth of 64 m in Jack Bay, Prince William Sound (Cairns and Bayer, 2005), which was strongly glacially influenced when the specimen was collected in 1941. However, we propose that the majority of the 30 records of *Primnoa* compiled by Cimberg et al. (1981) for shallow water (depths <127 m) were likely *C. spiculifera*.

Deep-sea emergence has been reported previously for only a few coral species worldwide. The gorgonians *Paramuricea placomus* and red trees (*Primnoa resedaeformis*) emerge from deep waters to depths of 28 and 32 m, respectively, in Norwegian fjords (Strömgren, 1970). The spider hazards (*Lophelia pertusa*), a colonial azooxanthellate scleractinian coral, also emerges in these

Table 6

Photosynthetically active radiation and euphotic depth (the depth where light intensity falls to 1% of that at the sea surface) measured at stations in Glacier Bay, Southeast Alaska, during a survey conducted in 2005 (17–22 April). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 6 and Appendix Table 2.

	Depth (m)								
Station	0	5	10	15	20	30	40	50	Euphotic depth
1	141.00	0.50	0.08	0.05	0.04	0	0	0	2.85
2	357.70	7.33	0.92	0.26	0.04	0	0	0	3.30
3	278.51	7.18	1.34	0.42	0.19	0.06	0.04	0	7.70
6	103.00	1.39	0.24	0.09	0.05	0.04	0	0	5.40
7	136.50	2.44	0.84	0.35	0.08	0.04	0	0	12.72
8	200.00	20.32	4.72	1.70	0.72	0.15	0.05	0	14.20
9	176.20	14.77	3.28	1.16	0.54	0.14	0.05	0	12.76
10	13.71	2.21	0.58	0.27	0.14	0.54	0	0	20.40
11	26.59	2.93	0.51	0.17	0.08	0	0	0	12.60
12	84.69	0.87	0.13	0.05	0	0	0	0	5.15
13	32.96	1.11	0.24	0.09	0.05	0	0	0	8.55
14	31.91	0.29	0.04	0	0	0	0	0	4.85
15	147.40	4.18	0.40	0.12	0.06	0	0	0	6.88
16	84.70	5.05	0.73	0.24	0.18	0.05	0	0	9.64
17	37.19	5.65	2.30	1.08	0.46	0.13	0.06	0.04	23.47
18	417.40	14.36	13.33	12.21	10.62	2.46	0.60	0.16	28.30

same fjords to minimum depths of 52 m (Strömgren, 1971). Deep-sea emergence has also been observed for black corals (Antipatharia) in the southern fjords of New Zealand (Grange et al., 1981; Grange, 1985), where an endemic species, *Antipathes fiordensis*, is also found at unusually shallow depths (5–40 m), and for the cocks-comb cup coral (*Desmophyllum dianthus*), a solitary azooxanthellate scleractinian coral, to depths of 8 m in the fjords of southern Chile (Försterra and Häusser-mann, 2003). None of these studies specifically mention the roles, or even the presence, of tidewater glaciers and fjord bathymetry (e.g., sills) in deep-sea emergence of the corals, but several do implicate oceanographic controls, such as unusual stenothermal and stenohaline conditions, a shallow maximum extension of the surface low salinity layer, and reduced transparency of the water.

The emerged populations of red tree corals found in this study appear to be disjunct from populations outside the fjords but likely extend into much deeper waters within the fjords. We confirmed the presence of red tree corals to depths of more than 100 m in Tracy and Endicott arms in Holkham Bay, and they have been observed at depths of more than 100 m in lower Glacier Bay (Waller[4]). Therefore, it is likely that these populations have crept into the fjords and only emerge to shallow depths near the heads of the fjords where oceanographic conditions are favorable.

Red tree corals that have emerged in glacial fjords are likely living at the edge of their physiological tolerance to the environmental conditions there, and this condition is likely particularly true for colonies residing 1) nearest the glacier face where siltation and turbidity are seasonally very high and 2) at the shallowest depths where the water mass can reach temperatures above 7.5–8.0°C for extended periods. During our early surveys, we noted 2 obvious ecomorphs that were identified as “typical” and “atypical” growth forms of *P. pacifica* (Cairns[5]). The atypical form differs from the typical form described by Cairns and Bayer (2005) and further examined by Cairns (2011) in that “it has very slender branches and sometimes whorled calyces.” Our observations indicate that the atypical colonies appear to be in relatively poor health with much less coenenchyme and far fewer polyps. We found atypical colonies in all 3 fjords where red tree corals were present in shallow water, sometimes interspersed with typical colonies, but atypical colonies were generally more common at shallower depths and at sites nearer the heads of the fjords. Furthermore, atypical forms have never been observed at the deepwater sites studied in the eastern GOA (Stone et al., 2014). We suggest that atypical colonies are ecomorphs responding phenotypically to the physiological stress of residing at the edge of optimal or tolerable habitat.

[4] Waller, R. 2016. Personal commun. Sch. Mar. Sci., Darling Mar. Cent., Univ. Maine, 193 Clarks Cove Rd., Walpole, ME 04573.

[5] Cairns, S. D. 2005. Personal commun. Dep. Invert. Zool., Natl. Mus. Nat. Hist., Smithson. Inst., P.O. Box 37012, MRC 163, Washington, DC 20013-7012.

Table 7

Water temperature (°C) measured at stations in Holkham Bay, Southeast Alaska, during surveys conducted in 2006 (22–27 March), 2007 (26–28 March), 2008 (1–3 May), and 2014 (7–9 June). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 7 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2006	1	3.10	4.02	4.64	4.90	5.07	5.23	5.31	5.28	5.23	5.19	5.17	5.11	5.10	5.09
2006	2	3.56	4.34	4.62	4.87	5.25	5.28	5.26	5.22	5.19	5.15	5.13	5.08	5.07	5.04
2006	3	3.69	4.38	4.92	5.16	5.31	5.32	5.28	5.24	5.20	5.16	5.10	5.08	5.07	5.06
2006	6	4.38	4.90	5.08	5.22	5.29	5.26	5.22	5.20	5.17	5.14	5.11	5.09	5.07	5.06
2006	7	4.86	5.23	5.28	5.29	5.29	5.24	5.21	5.18	5.16	5.15	5.12	5.08	5.06	5.04
2006	8	4.81	5.20	5.28	5.27	5.24	5.20	5.14	5.14	5.12	5.04	5.02	4.99	4.96	4.96
2006	9	4.66	4.91	5.25	5.27	5.23	5.20	5.18	5.16	5.13	5.08	5.06	4.97	4.97	4.91
2006	10	4.90	4.97	5.00	5.11	4.79	4.74	4.72	4.75	4.75	4.75	4.75	4.78	4.81	4.83
2006	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2006	12	5.06	5.42	5.59	5.58	5.57	5.55	5.54	5.53	5.51	5.50	5.49	5.49	5.48	5.47
2006	13	5.45	5.58	5.60	5.60	5.58	5.52	5.50	5.47	5.45	5.44	5.44	5.43	5.43	5.42
2006	14	5.59	5.62	5.62	5.63	5.63	5.53	5.52	5.49	5.47	5.46	5.44	5.41	5.40	5.35
2006	15	5.54	5.58	5.61	5.54	5.54	5.49	5.49	5.49	5.47	5.43	5.32	5.32	5.31	5.28
2006	16	5.40	5.26	5.11	5.08	5.06	5.03	4.96	4.94	4.94	4.92	4.92	4.92	4.91	4.91
2007	1	2.43	3.04	3.31	3.56	3.73	4.04	4.02	3.97	3.95	3.95	3.94	3.92	3.90	3.89
2007	2	3.07	3.30	3.32	3.74	3.89	4.00	4.03	3.97	3.95	3.94	3.94	3.93	3.92	3.89
2007	3	3.13	3.29	3.70	3.75	3.89	4.03	3.98	3.95	3.94	3.92	3.93	3.93	3.92	3.87
2007	6	2.99	3.43	3.70	3.87	4.04	3.96	3.95	3.95	3.93	3.92	3.91	3.90	3.89	3.88
2007	7	3.14	3.41	3.92	3.98	4.02	4.01	3.97	3.94	3.93	3.90	3.89	3.86	3.86	3.85
2007	8	3.20	3.51	3.76	3.93	4.04	4.01	3.97	3.94	3.92	3.86	3.89	3.89	3.85	3.84
2007	9	2.99	3.56	3.83	3.88	3.88	3.97	3.88	3.83	3.81	3.79	3.76	3.76	3.77	3.73
2007	10	3.63	3.66	3.76	3.88	3.85	3.85	3.77	3.75	3.75	3.74	3.72	3.72	3.73	3.75
2007	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2007	12	4.16	4.46	4.56	4.51	4.47	4.44	4.40	4.36	4.35	4.34	4.33	4.24	4.22	4.16
2007	13	4.22	4.36	4.53	4.57	4.48	4.43	4.39	4.36	4.23	4.18	4.13	4.11	4.08	4.06
2007	14	4.37	4.53	4.52	4.32	4.15	4.12	4.09	4.07	4.03	4.02	4.03	4.01	3.99	3.98
2007	15	4.40	4.44	4.47	4.47	4.42	4.35	4.28	4.21	4.14	4.11	4.06	4.04	4.03	4.02
2007	16	4.37	4.35	4.17	4.09	4.02	3.95	3.92	3.91	3.91	3.91	3.91	3.90	3.90	3.90
2008	1	2.29	2.95	3.02	3.18	3.46	3.60	3.78	3.88	3.91	3.93	3.95	3.95	3.96	3.97
2008	2	2.62	2.95	3.13	3.28	3.57	3.75	3.86	3.90	3.92	3.94	3.95	3.98	3.99	3.99
2008	3	2.53	2.98	3.11	3.30	3.58	3.82	3.89	3.92	3.93	3.94	3.95	3.96	3.97	3.98
2008	6	2.94	3.14	3.28	3.46	3.68	3.83	3.92	3.93	3.94	3.94	3.95	3.96	3.97	3.98
2008	7	2.92	3.17	3.31	3.47	3.68	3.87	3.92	3.94	3.94	3.95	3.96	3.97	3.98	3.98
2008	8	2.94	3.16	3.31	3.52	3.71	3.78	3.89	3.94	3.95	3.95	3.96	3.96	3.97	3.98
2008	9	4.41	4.09	3.99	3.96	3.93	3.94	3.95	3.95	3.95	3.95	3.97	3.98	4.00	4.01
2008	10	4.43	4.15	4.11	4.11	4.02	4.01	4.05	4.06	4.08	4.13	4.26	4.26	4.31	4.32
2008	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2008	12	3.54	3.58	3.65	3.85	3.95	4.04	4.12	4.12	4.12	4.12	4.12	4.12	4.12	4.12
2008	13	3.77	3.61	3.75	3.93	3.97	4.09	4.12	4.12	4.12	4.12	4.12	4.12	4.12	4.13
2008	14	4.36	4.27	4.15	4.15	4.15	4.14	4.14	4.13	4.11	4.12	4.13	4.13	4.13	4.13
2008	15	4.75	4.26	4.18	4.14	4.15	4.14	4.13	4.13	4.13	4.14	4.14	4.15	4.15	4.15
2008	16	4.87	4.74	4.57	4.49	4.41	4.39	4.34	4.33	4.32	4.26	4.21	4.23	4.24	4.27
2014	1	4.13	4.21	4.34	4.48	4.67	4.84	5.08	5.20	5.17	5.15	5.11	5.07	5.04	4.98
2014	2	4.19	4.26	4.47	4.53	4.71	4.76	5.18	5.20	5.16	5.12	5.08	5.06	5.04	4.97
2014	3	4.19	4.23	4.35	4.49	4.64	4.84	5.17	5.17	5.13	5.08	5.08	5.02	5.01	4.97
2014	6	4.23	4.33	4.37	4.43	4.55	4.55	4.91	5.18	5.15	5.10	5.08	5.05	5.01	4.99
2014	7	4.28	4.23	4.32	4.40	4.48	4.70	5.16	5.20	5.16	5.11	5.06	5.03	5.01	4.99
2014	8	4.23	4.26	4.31	4.31	4.58	5.13	5.20	5.12	5.10	5.04	5.01	4.97	4.93	4.90
2014	9	4.25	4.24	4.28	4.35	4.71	5.21	5.22	5.16	5.12	5.08	5.02	4.99	4.97	4.95
2014	10	6.52	6.44	5.80	5.42	5.22	5.33	5.33	5.23	5.08	5.05	5.02	4.98	4.95	4.91
2014	11	4.87	4.94	5.15	5.36	5.68	5.58	5.49	5.39	5.34	5.18	4.97	4.81	4.71	4.72
2014	12	4.92	5.03	5.07	5.43	5.75	5.68	5.54	5.38	5.32	5.26	5.12	4.94	4.82	4.74
2014	13	4.94	5.01	5.46	5.68	5.75	5.60	5.50	5.45	5.38	5.30	5.21	5.07	4.88	4.79
2014	14	–	–	5.85	5.86	5.72	5.54	5.48	5.41	5.30	5.21	5.13	5.04	4.88	4.80
2014	15	5.52	5.73	5.87	5.74	5.61	5.45	5.39	5.32	5.22	5.10	5.01	4.93	4.76	4.74
2014	16	6.91	6.38	6.13	5.99	5.45	5.32	5.18	5.15	5.12	5.07	5.06	5.04	5.01	5.02

Table 8

Salinity measured at stations in Holkham Bay, Southeast Alaska, during surveys conducted in 2006 (22–27 March), 2007 (26–28 March), 2008 (1–3 May), and 2014 (7–9 June). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 7 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2006	1	30.40	30.67	30.80	30.91	31.01	31.00	31.05	31.08	31.11	31.13	31.14	31.16	31.17	31.18
2006	2	30.36	30.65	30.81	30.91	31.03	31.05	31.09	31.12	31.13	31.15	31.16	31.18	31.18	31.19
2006	3	30.41	30.65	30.88	30.96	31.02	31.05	31.08	31.10	31.13	31.16	31.18	31.18	31.19	31.19
2006	6	30.60	30.88	30.91	30.98	31.05	31.07	31.11	31.12	31.13	31.15	31.16	31.17	31.18	31.18
2006	7	30.91	30.99	31.04	31.05	31.06	31.11	31.12	31.14	31.15	31.16	31.17	31.17	31.18	31.19
2006	8	30.80	31.00	31.03	31.05	31.07	31.10	31.14	31.15	31.16	31.18	31.18	31.18	31.18	31.19
2006	9	30.70	30.84	31.03	31.05	31.09	31.12	31.13	31.15	31.15	31.16	31.16	31.16	31.17	31.16
2006	10	30.89	30.97	31.03	31.05	31.00	31.03	31.05	31.06	31.08	31.08	31.10	31.12	31.15	31.16
2006	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2006	12	31.13	31.25	31.30	31.32	31.35	31.36	31.37	31.37	31.38	31.40	31.40	31.40	31.41	31.42
2006	13	31.23	31.28	31.32	31.34	31.35	31.37	31.39	31.41	31.42	31.44	31.44	31.44	31.44	31.44
2006	14	31.17	31.26	31.29	31.31	31.34	31.35	31.37	31.40	31.41	31.42	31.42	31.42	31.43	31.43
2006	15	31.14	31.24	31.26	31.29	31.33	31.35	31.38	31.39	31.40	31.40	31.40	31.40	31.41	31.41
2006	16	30.90	31.06	31.22	31.25	31.27	31.30	31.39	31.41	31.42	31.44	31.44	31.45	31.46	31.49
2007	1	30.82	31.07	31.20	31.28	31.38	31.43	31.45	31.47	31.49	31.49	31.49	31.50	31.50	31.49
2007	2	31.03	31.17	31.16	31.34	31.39	31.43	31.44	31.47	31.49	31.49	31.50	31.50	31.50	31.50
2007	3	31.07	31.16	31.29	31.32	31.36	31.44	31.46	31.48	31.49	31.49	31.50	31.50	31.50	31.49
2007	6	31.00	31.17	31.30	31.35	31.44	31.47	31.48	31.49	31.49	31.49	31.49	31.49	31.49	31.49
2007	7	31.03	31.13	31.35	31.38	31.43	31.45	31.47	31.48	31.49	31.49	31.49	31.49	31.49	31.49
2007	8	31.04	31.16	31.29	31.35	31.42	31.45	31.46	31.47	31.46	31.47	31.48	31.48	31.48	31.49
2007	9	30.69	31.16	31.30	31.24	31.41	31.45	31.45	31.46	31.46	31.46	31.47	31.47	31.47	31.48
2007	10	31.17	31.19	31.27	31.35	31.39	31.43	31.45	31.46	31.47	31.47	31.48	31.48	31.48	31.49
2007	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2007	12	31.41	31.54	31.59	31.59	31.59	31.60	31.60	31.60	31.60	31.60	31.60	31.60	31.60	31.59
2007	13	31.48	31.51	31.57	31.58	31.59	31.60	31.60	31.60	31.59	31.59	31.59	31.59	31.59	31.59
2007	14	31.19	31.42	31.56	31.56	31.56	31.56	31.56	31.57	31.57	31.57	31.57	31.57	31.57	31.57
2007	15	31.28	31.44	31.54	31.58	31.59	31.59	31.58	31.58	31.58	31.58	31.57	31.57	31.57	31.57
2007	16	31.26	31.42	31.49	31.50	31.52	31.53	31.56	31.57	31.57	31.57	31.58	31.58	31.58	31.59
2008	1	30.35	30.84	30.89	30.94	31.09	31.16	31.23	31.26	31.27	31.30	31.31	31.32	31.33	31.34
2008	2	30.68	30.84	30.92	31.00	31.15	31.22	31.25	31.26	31.28	31.30	31.32	31.34	31.35	31.36
2008	3	30.58	30.87	30.93	30.99	31.14	31.22	31.26	31.27	31.29	31.31	31.32	31.33	31.34	31.35
2008	6	30.86	30.95	31.00	31.08	31.17	31.22	31.27	31.28	31.30	31.31	31.32	31.33	31.34	31.35
2008	7	30.80	30.95	31.01	31.07	31.16	31.23	31.25	31.27	31.29	31.30	31.32	31.33	31.34	31.35
2008	8	30.72	30.80	30.96	30.99	31.10	31.16	31.22	31.26	31.29	31.30	31.32	31.32	31.33	31.34
2008	9	30.87	31.01	31.03	31.12	31.21	31.23	31.26	31.29	31.30	31.30	31.32	31.33	31.34	31.35
2008	10	30.87	31.09	31.19	31.23	31.26	31.28	31.29	31.30	31.31	31.34	31.36	31.37	31.38	31.38
2008	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2008	12	30.95	31.03	31.13	31.24	31.29	31.34	31.38	31.39	31.40	31.40	31.40	31.41	31.42	31.42
2008	13	30.95	31.06	31.15	31.25	31.31	31.36	31.39	31.39	31.40	31.41	31.42	31.42	31.43	31.43
2008	14	30.77	30.93	31.19	31.24	31.32	31.35	31.36	31.39	31.40	31.42	31.42	31.43	31.43	31.43
2008	15	30.65	31.00	31.12	31.23	31.33	31.35	31.38	31.39	31.40	31.41	31.41	31.42	31.42	31.42
2008	16	30.94	31.13	31.23	31.28	31.35	31.38	31.40	31.41	31.42	31.45	31.47	31.49	31.50	31.51
2014	1	29.14	29.40	29.67	29.94	30.29	30.69	31.07	31.17	31.25	31.30	31.38	31.44	31.49	31.56
2014	2	28.99	29.56	29.95	30.03	30.44	30.72	31.03	31.20	31.29	31.36	31.42	31.46	31.49	31.57
2014	3	29.07	29.35	29.71	30.11	30.38	30.88	31.03	31.23	31.29	31.36	31.40	31.48	31.52	31.58
2014	6	29.08	29.65	29.74	29.93	30.56	30.58	30.78	31.04	31.20	31.29	31.35	31.39	31.46	31.51
2014	7	28.64	29.35	29.70	30.00	30.36	30.69	30.93	31.06	31.19	31.28	31.35	31.41	31.44	31.47
2014	8	29.03	29.58	29.83	29.87	30.51	30.84	31.08	31.23	31.28	31.36	31.41	31.48	31.52	31.57
2014	9	29.25	29.53	29.82	30.19	30.61	30.91	31.03	31.17	31.24	31.31	31.39	31.42	31.46	31.51
2014	10	28.99	29.24	29.94	30.56	30.74	30.89	30.95	31.07	31.32	31.35	31.39	31.44	31.48	31.52
2014	11	29.44	29.71	30.12	30.63	31.13	31.27	31.38	31.49	31.55	31.61	31.67	31.70	31.74	31.75
2014	12	29.41	30.01	30.07	30.63	30.94	31.15	31.33	31.50	31.56	31.59	31.64	31.69	31.73	31.76
2014	13	29.36	30.02	30.52	30.70	31.03	31.24	31.37	31.43	31.50	31.57	31.61	31.65	31.72	31.74
2014	14	–	–	30.61	30.76	31.07	31.28	31.56	31.44	31.53	31.59	31.64	31.67	31.72	31.74
2014	15	29.80	30.48	30.79	30.97	31.19	31.37	31.42	31.48	31.58	31.65	31.69	31.71	31.76	31.76
2014	16	28.14	30.03	30.40	30.59	31.17	31.33	31.48	31.53	31.56	31.60	31.62	31.64	31.68	31.70

Table 9

Oxygen saturation (%) measured at stations in Holkham Bay, Southeast Alaska, during surveys conducted in 2006 (22–27 March), 2007 (26–28 March), and 2008 (1–3 May). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 7 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2006	1	37.06	36.79	36.12	33.24	33.40	33.36	33.32	33.29	33.26	33.22	33.22	33.19	33.30	33.16
2006	2	53.23	51.82	50.17	50.09	50.72	50.90	51.04	52.38	51.36	50.67	50.76	50.57	51.40	51.76
2006	3	94.09	65.14	58.66	55.27	54.01	53.87	66.30	60.69	55.84	56.06	54.90	55.27	54.85	54.71
2006	6	92.94	79.87	69.09	64.51	62.28	58.39	55.70	60.14	52.33	51.86	51.72	51.54	51.40	51.26
2006	7	83.99	70.18	65.05	63.39	60.61	57.09	55.14	52.19	51.36	50.94	50.76	50.57	50.57	50.38
2006	8	89.99	65.20	61.72	60.47	64.02	59.94	56.29	54.35	53.80	53.42	53.83	53.09	53.04	52.89
2006	9	81.52	68.62	67.62	61.17	59.03	58.34	56.76	53.02	51.72	51.67	51.35	51.25	51.25	51.20
2006	10	94.23	78.31	66.68	63.14	61.15	59.80	60.35	56.30	54.65	53.83	53.42	53.06	52.42	52.20
2006	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2006	12	78.40	62.72	56.81	53.87	62.41	53.87	49.95	48.92	48.92	49.34	49.34	48.78	48.88	48.88
2006	13	86.97	66.88	61.91	57.42	56.95	54.38	52.14	50.13	49.85	49.44	49.30	49.11	48.41	48.27
2006	14	80.80	61.63	57.00	53.78	54.96	50.74	51.30	49.34	48.88	48.60	48.46	47.85	48.13	43.32
2006	15	80.02	62.82	57.42	54.24	53.96	51.25	51.39	48.51	47.90	47.99	47.99	48.13	47.57	47.57
2006	16	81.85	75.73	65.55	63.20	61.62	58.44	58.66	54.19	53.37	52.54	52.54	52.54	51.85	51.44
2007	1	100.10	100.10	100.10	100.10	100.00	100.10	100.10	100.00	100.10	100.10	100.00	100.00	100.10	100.10
2007	2	100.20	100.10	100.10	100.20	100.00	95.96	96.10	96.00	100.10	100.10	100.10	100.10	100.10	100.10
2007	3	100.30	100.00	100.20	100.20	100.10	100.10	100.00	100.10	100.10	100.10	100.10	100.10	100.10	100.10
2007	6	100.20	100.10	100.10	100.10	100.10	100.10	100.10	100.10	100.10	100.10	100.10	100.10	100.10	100.10
2007	7	100.10	100.00	100.10	100.10	100.10	100.10	100.00	100.10	100.10	100.10	100.10	100.00	100.00	100.10
2007	8	100.10	100.20	100.00	100.00	100.00	100.00	100.00	100.10	100.10	100.00	100.10	100.10	100.10	100.10
2007	9	100.10	100.10	100.10	100.00	100.10	100.10	100.00	100.00	100.00	100.10	100.00	100.00	100.10	100.10
2007	10	100.20	100.10	100.20	100.10	100.00	100.10	100.10	100.00	100.10	100.10	100.10	100.10	100.10	100.00
2007	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2007	12	100.00	100.20	100.00	100.10	100.10	100.10	100.20	100.10	100.10	100.10	100.00	100.10	100.00	100.00
2007	13	100.00	100.00	100.20	100.00	100.10	100.00	100.10	100.10	100.10	100.00	100.10	100.00	100.10	100.00
2007	14	100.10	100.10	100.10	100.10	100.10	100.10	100.10	100.00	100.10	100.10	100.10	100.10	100.10	100.10
2007	15	100.10	100.30	100.00	100.10	100.10	100.10	100.10	100.00	99.93	100.00	100.00	100.10	100.10	100.10
2007	16	100.20	99.91	100.10	100.00	100.10	100.00	100.10	100.10	100.10	100.10	100.10	100.10	100.10	100.10
2008	1	100.00	100.10	100.10	100.10	100.10	100.10	100.00	100.00	100.10	100.10	100.10	100.10	100.10	100.10
2008	2	100.10	100.00	100.10	100.10	100.10	100.10	100.20	100.10	100.00	100.10	100.10	100.10	100.10	100.10
2008	3	100.10	100.10	99.89	100.10	100.10	100.10	100.00	99.99	100.10	100.10	100.10	100.10	100.10	100.10
2008	6	100.10	99.98	99.95	100.10	100.00	100.20	99.99	100.10	100.10	100.10	100.10	100.10	100.10	100.10
2008	7	99.73	100.10	100.10	99.85	99.87	100.00	99.99	100.10	100.10	100.10	100.10	100.10	100.10	100.10
2008	8	100.00	100.10	100.10	100.20	100.10	100.00	100.00	100.10	100.10	100.10	100.10	100.10	100.10	100.10
2008	9	100.10	100.00	100.10	99.99	99.99	99.99	100.10	100.10	100.10	100.10	100.10	100.10	100.00	100.00
2008	10	100.10	100.10	100.20	100.10	100.10	100.00	100.10	100.10	100.10	100.00	100.10	100.10	100.10	100.10
2008	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2008	12	100.10	100.10	100.10	100.10	100.10	100.10	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00
2008	13	100.10	100.10	100.20	100.10	100.10	100.10	100.00	100.00	100.00	100.00	100.00	100.00	100.10	100.10
2008	14	100.10	100.10	100.20	100.00	100.00	100.00	100.10	100.10	100.00	100.00	100.10	100.10	100.10	100.10
2008	15	100.10	100.10	100.20	100.20	100.30	100.20	100.20	100.30	100.30	100.30	100.30	100.30	100.00	100.00
2008	16	100.10	100.00	100.10	100.10	100.00	100.00	100.10	100.10	100.10	100.00	100.00	100.10	100.10	100.20

Glaciated fjords in Southeast Alaska typically have different oceanographic and physical properties than non-glaciated inlets, including lower temperatures, smaller ranges in salinity and dissolved oxygen, higher sedimentation levels (Pickard, 1967; Carney et al., 1999), and seasonal events of enhanced carbonate mineral saturation (Reisdorph and Mathis, 2014). The environmental conditions found in emerged populations of shallow-water red tree corals in the glacial fjords are similar to those in deeper water on the continental shelf where large populations of red tree corals are located. The optimal temperature range for red tree corals in Alaska appears to be between 3.0°C and 7.5°C. Cimberg et al. (1981) suggested that the lower depth limit and geographical distribution for red tree corals corresponded with a mean spring temperature (typically March, April, and May) of 3.7°C (i.e., they prefer or are tolerant of temperatures above 3.7°C). We measured annual mean

Table 10

Photosynthetically active radiation and euphotic depth (the depth where light intensity falls to 1% of that at the surface) measured at stations in Holkham Bay, Southeast Alaska, during surveys conducted in 2008 (1–3 May) and 2014 (7–9 June). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 7 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)								
Year	Station	0	5	10	15	20	30	40	50	Euphotic depth
2008	1	206.63	4.99	0.72	0.13	0	0	0	0	8.60
2008	2	493.55	13.56	3.12	0.86	0.21	0	0	0	12.18
2008	3	416.13	9.03	1.97	0.47	0.08	0	0	0	10.37
2008	6	371.55	27.69	7.62	2.31	0.72	0	0	0	16.72
2008	7	214.06	3.03	0.88	0.28	0.05	0	0	0	10.55
2008	8	263.15	6.41	1.30	0.50	0.16	0	0	0	8.40
2008	9	140.61	7.29	1.43	0.40	0.10	0	0	0	11.31
2008	10	195.02	27.82	9.02	4.41	2.19	0.51	0.06	0	22.30
2008	11	–	–	–	–	–	–	–	–	–
2008	12	531.63	2.81	0.39	0	0	0	0	0	8.08
2008	13	451.72	4.24	0.58	0.18	0	0	0	0	9.22
2008	14	153.77	22.59	4.65	1.35	0.51	0.03	0	0	15.84
2008	15	129.35	0.98	0.01	0	0	0	0	0	6.12
2008	16	91.56	5.67	0.76	0.16	0	0	0	0	11.65
2014	1	22.18	0	0	0	0	0	0	0	4.45
2014	2	172.20	0	0	0	0	0	0	0	4.25
2014	3	211.37	0.38	0	0	0	0	0	0	4.66
2014	6	468.94	3.75	0.10	0	0	0	0	0	7.20
2014	7	455.95	3.40	0.55	0.02	0	0	0	0	7.35
2014	8	369.07	1.95	0.40	0.03	0	0	0	0	7.75
2014	9	285.56	3.97	0.86	0.13	0	0	0	0	10.62
2014	10	325.50	3.48	0.74	0.17	0.01	0	0	0	9.00
2014	11	383.81	0.65	0	0	0	0	0	0	5.49
2014	12	163.82	2.85	0.02	0	0	0	0	0	9.27
2014	13	90.30	1.84	0.16	0	0	0	0	0	10.19
2014	14	–	–	–	–	–	–`	–	–	–
2014	15	424.03	11.29	5.27	2.59	0.66	0.13	0.13	0	18.98
2014	16	545.92	79.09	17.18	6.54	2.59	0.51	0.07	0	17.95

spring temperatures of 4.9–5.1°C and 3.5°C in Glacier Bay (2005–2006) and Tracy Arm (2011), respectively. Matsumoto (2007), however, found red tree corals thriving in deepwater areas of the Sea of Japan with summer temperatures of 0.2–1.1°C; therefore, they obviously can tolerate very cold water.

Red tree corals at Site 5 in the East Arm of Glacier Bay were subjected to temperatures between 4.1°C (March 2006) and 7.8°C (August and September 2005) (Fig. 9A). The average annual temperature at that site was 6.4°C. Red tree corals at Site 15 in Tracy Arm were subjected to temperatures between 2.8°C (February 2011) and 6.5°C (late November 2011). The average annual temperature at that site was 4.4°C. Results from this study indicate that red tree corals can tolerate temperatures between 2.8°C and 7.8°C, although corals held in the laboratory quickly die when the water temperature consistently holds (i.e., one week or more) near 8.0°C (senior author, unpubl. data). These observations agree with data recorded at deepwater thicket sites in the eastern GOA where water temperatures ranged from 5.3°C to 7.7°C (200 m depth) during the period from August 2013 to June 2015 (senior author, unpubl. data). The average annual temperature at that site was 5.8°C. Conversely, water temperature recorded at non-glacial sites at the same depth in Southeast Alaska ranged from 4.4°C to 10.7°C during the period from July 1999 to June 2004 (Stone et al., 2017) and average annual temperature ranged from 7.1°C to 7.4°C.

Red tree corals are more tolerant of a wider salinity range than expected. Salinity from CTD casts made every 3 months in 2010 and 2011 at 15 m depth at Site 15 in Tracy Arm (Waller et al., 2014) showed a high of 31.41 in March 2011 and a low of 26.86 in September 2011. Salinity ranged from 32.97 to 33.76 at the deepwater thicket sites in the eastern GOA (Stone et al., 2014).

Bare, exposed bedrock is an abundant resource in the path of retreating glaciers and a major requirement of

Table 11

Turbidity measured in nephelometric turbidity units at stations in Holkham Bay, Southeast Alaska, during a survey conducted in 2014 (7–9 June). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 7 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2014	1	7.02	7.32	8.67	8.70	6.93	3.69	2.60	1.50	1.32	1.46	1.46	1.12	1.12	1.56
2014	2	9.86	8.56	6.53	6.84	4.35	2.53	2.07	1.69	1.36	1.30	1.11	1.06	1.60	1.08
2014	3	5.72	6.73	6.47	5.44	4.04	2.52	2.12	1.47	1.24	1.12	1.08	0.98	0.99	0.91
2014	6	4.17	4.85	3.80	4.03	2.74	2.32	1.98	1.34	0.92	0.82	0.87	0.87	0.70	0.68
2014	7	2.89	3.22	3.11	3.11	2.30	1.96	1.21	1.00	0.79	0.86	0.65	0.66	0.60	0.57
2014	8	2.67	2.40	2.16	2.13	1.62	1.15	0.80	0.70	0.55	0.57	0.51	0.52	0.57	0.49
2014	9	2.41	2.22	2.14	1.97	1.49	0.84	0.67	0.59	0.60	0.57	0.57	0.50	0.46	0.50
2014	10	1.07	1.00	0.79	0.72	0.57	0.48	0.50	0.45	0.41	0.40	0.40	0.41	0.44	0.41
2014	11	10.62	12.34	10.91	5.55	3.32	2.51	2.01	1.86	1.64	1.85	1.45	1.81	1.28	1.53
2014	12	5.25	5.56	5.39	4.97	2.36	1.96	1.34	1.03	0.78	0.82	0.83	0.94	1.03	1.09
2014	13	4.79	3.47	1.90	1.81	1.23	0.83	0.83	0.95	0.78	0.75	0.88	0.77	0.78	0.86
2014	14	–	–	0.90	0.60	0.55	0.47	0.46	0.47	0.45	0.46	0.50	0.45	0.45	0.50
2014	15	2.01	0.92	0.60	0.56	0.48	0.47	0.47	0.49	0.45	0.44	0.47	0.45	0.47	0.46
2014	16	1.55	0.89	0.72	0.67	0.47	0.44	0.44	0.44	0.44	0.46	0.49	0.46	0.46	1.55

Table 12

Levels of pH measured at stations in Holkham Bay, Southeast Alaska, during a survey conducted in 2014 (7–9 June). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 7 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2014	1	8.06	7.99	7.96	7.93	7.91	7.90	7.90	7.89	7.88	7.88	7.87	7.86	7.86	7.86
2014	2	7.97	7.93	7.92	7.91	7.90	7.95	7.90	7.89	7.88	7.87	7.86	7.86	7.86	7.86
2014	3	7.90	7.90	7.89	7.88	7.88	7.88	7.88	7.88	7.87	7.86	7.86	7.85	7.85	7.84
2014	6	8.00	7.96	7.95	7.94	7.92	7.92	7.91	7.92	7.91	7.90	7.89	7.88	7.87	7.86
2014	7	8.09	7.96	7.96	7.94	7.91	7.90	7.91	7.91	7.90	7.89	7.88	7.87	7.87	7.86
2014	8	8.12	8.03	7.99	7.97	7.94	7.94	7.93	7.92	7.91	7.90	7.89	7.88	7.87	7.86
2014	9	8.10	8.02	7.98	7.95	7.93	7.94	7.94	7.92	7.91	7.90	7.89	7.88	7.87	7.87
2014	10	8.34	8.27	8.17	8.09	8.01	7.98	7.98	7.96	7.93	7.91	7.90	7.89	7.88	7.87
2014	11	7.90	7.89	7.89	7.89	7.89	7.88	7.87	7.86	7.85	7.84	7.82	7.80	7.78	7.77
2014	12	7.91	7.90	7.89	7.89	7.90	7.89	7.88	7.85	7.84	7.84	7.83	7.81	7.79	7.78
2014	13	7.91	7.90	7.89	7.89	7.89	7.88	7.87	7.86	7.85	7.84	7.83	7.82	7.80	7.78
2014	14	–	–	7.87	7.88	7.88	7.87	7.87	7.86	7.85	7.84	7.83	7.82	7.81	7.80
2014	15	7.94	7.95	7.94	7.92	7.91	7.90	7.88	7.87	7.86	7.84	7.83	7.82	7.81	7.80
2014	16	8.00	7.99	8.00	7.99	7.93	7.90	7.87	7.86	7.85	7.84	7.84	7.83	7.83	7.82

red tree corals and many other corals for initial settlement (Stone et al., 2014). The upper depth limit of red tree corals was often nearly coincident with the lower depth limit of coralline algae, and this pattern was often conspicuous (e.g., Fig. 8A). Algae may outcompete the corals for settling substrate and even use allelopathic agents (Rasher et al., 2011) to do so; however, we suspect that the sharp delineation in bathymetric distribution observed in this study is due to preferences for or tolerances to light conditions.

Species of *Lithothamnion* have been reported to grow to depths of 30 m at other locations (Lamb and Hanby, 2005), but the only sites where the algae were observed at similar depths in this study were at the sites farthest from the heads of the fjords where corals were absent. Coralline algae, like all primary producers, require sunlight for life processes. Red tree corals, unlike most of their tropical counterparts, are azooxanthellate; that is, they lack intracellular symbiotic dinoflagellates that fix carbon through photosynthesis and have no requirements for sunlight. To the contrary, our observations of laboratory held octocorals indicate that they are quickly killed when covered with brown filamentous algae, possibly as a result of tissue suffocation by mucilage produced by the algae (Mistri and Ceccherelli, 1993; Tsounis et al., 2012). Therefore, the demarcation between the depth distributions of the 2 groups may represent the critical light levels for the algae (i.e., not enough) and the coral (i.e., too much). We believe this observation implicates the important role of reduced ambient radiation, caused by high siltation rates and possibly shading by steep walls (*sensu* Blockley and Chapman, 2006) in the upper reaches of the fjords, in deep-sea emergence of red tree corals.

Glacial fjords are very dynamic environments with disturbances from above (e.g., rock and ice slides) and upstream (iceberg scour) that affect the persistence of red tree coral populations in some areas. At several sites, particularly at Sites 5 and 7 in the East Arm of Glacier Bay (Fig. 10A), the rock forming the steep cliffs above is heavily weathered and unstable. There is evidence of frequent slides in some areas, and we observed several colonies encapsulating captured small shot rock with coenenchyme. Red tree corals in shallow-water habitats of the fjords also are subjected to the seasonal onslaught of iceberg scour. Some areas, particularly at depths less than 30 m at Sites 14 and 15 in Tracy Arm (Fig. 10B), had extensive iceberg scour as evidenced by coral stumps and bleached calcified basal plates (Fig. 8F). We found evidence of iceberg scour to a depth of 67 m at these 2 sites.

Our observation that red tree corals occur in areas of Glacier Bay that were deglaciated as recently as 26 years ago clearly indicates that it is a pioneer species in certain settings. On the basis of the reported growth rates of red tree corals (Andrews et al., 2002), this species may have colonized bedrock areas that had been exposed only for a few years. Gorgonians, species of *Primnoella* and *Primnoisis (Primnoisis) antarctica*, were also early colonizers following iceberg disturbance in Antarctic benthic habitats, but *Primnoa resedaeformis* (later confirmed as *P. notialis;* Cairns and Bayer, 2005), a closely related species to *P. pacifica,* was a later colonizer in disturbed habitats (Teixidó et al., 2004).

Glacier Bay has a well-documented history of rapid glacial retreat during the past 2 centuries with subsequent emergence of an extensive fjord system and adjacent terrestrial uplands (Sharman et al., 1995). Consequently, Glacier Bay has been an important site for studies of primary succession in terrestrial, lake, stream, and marine intertidal habitats (Sharman et al., 1995). Primary succession in the subtidal marine habitat has not yet been studied, and although not the principal focus of this study, our observations do support some of the hypotheses set forth by Sharman et al. (1995) regarding succession in marine environments. The pattern of increased species richness at sites farther from the heads of the fjords illustrates classic successional processes of benthic communities as new oceanographic and physical habitats become available in the path of retreating glaciers.

The glacial fjords, particularly the upper reaches, do not support the diverse and abundant demersal resources found in the climax communities in deepwater areas of the continental shelf and upper slope of the eastern GOA (Stone et al., 2014). The fjords are, however, noteworthy for rich stocks of forage fishes and schooling species, such as capelin (*Mallotus villosus,* Fig. 8G) and walleye pollock (*Gadus chalcogrammus*), that use the fjords as important spawning and overwintering habitat (Arimitsu et al., 2007; Arimitsu et al., 2008).

Given the paucity of demersal fish species, particularly shelter-seeking species like rockfish, we were not surprised to find few species using the shallow-water thickets of red tree corals as habitat. However, we did document a few cases of the corals providing seasonally important habitat for some species. Young-of-the-year walleye pollock (~95 mm total length), up to 3–4 fish per colony, use the shallow-water corals as nursery habitat in Tracy Arm during some winter months (Fig. 8H). These fish were so strongly associated with the corals that divers could actually catch them by hand. Sculpins (Cottidae) also were observed using the corals as cover, and several great sculpin (*Myoxocephalus polyacanthocephalus*) were observed guarding egg masses attached to colony branches (Fig. 8I). This behavior may be similar to that in which the goldeneye snailfish (*Allocareproctus unangas*) deposits its adhesive eggs on *Primnoa* in the Aleutian Islands (Busby et al., 2006). We also observed blue king crabs (*Paralithodes platypus*) occasionally using red tree corals as cover (Fig. 8J) and a single blackspotted rockfish (*Sebastes melanostictus*) using a large red tree coral as cover at a depth of 25 m in Tracy Arm. This fish was the only rockfish observed in Holkham Bay during this study.

Some commercial fisheries have historically existed within Glacier and Holkham bays, principally longline fisheries for Pacific halibut (*Hippoglossus stenolepis*) and sablefish (*Anoplopoma fimbria*) and pot fishing for Dungeness (*Cancer magister*) and king crabs (*Paralithodes* spp. and *Lithodes aequispinus*) (Taylor and Perry, 1990; Taggart et al., 2003; Mondragon et al., 2007). These fisheries target species that seldom actively associate with red tree corals (Stone et al., 2014); therefore, fishing gear effects are of minimal concern for the coral habitat there. Shallow-water populations

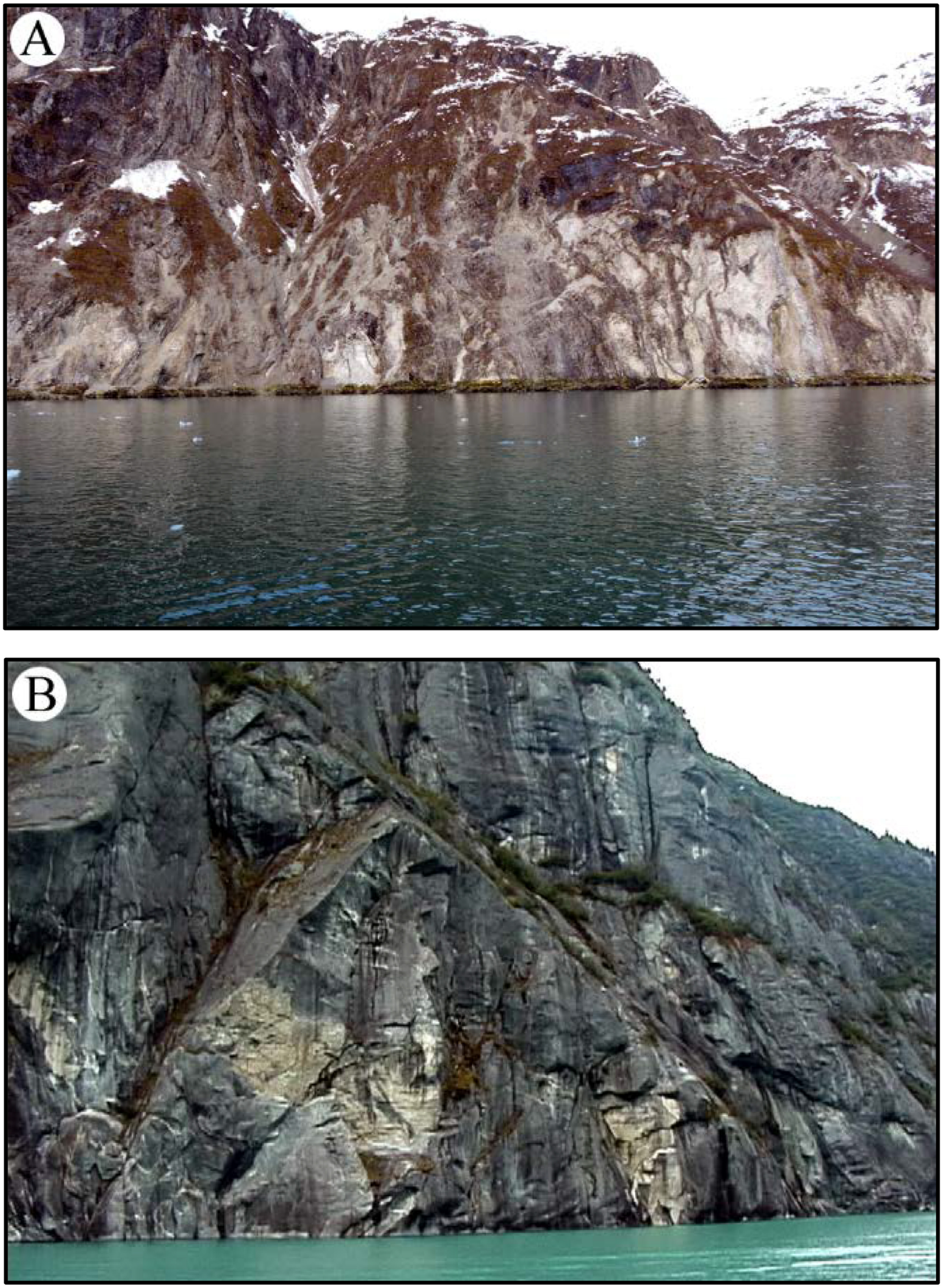

Figure 10

(**A**) Photograph of Sites 5 and 7 at East Arm (Muir Inlet), Glacier Bay, Southeast Alaska, showing the heavily weathered and relatively unstable steep cliffs of vertical walls, both above and below sea level, that consist of well-worn schist and areas of plutonics. (**B**) Photograph of Sites 14 and 15 at Tracy Arm, Holkham Bay, Southeast Alaska, showing the relatively stable, steep vertical walls, both above and below sea level, that consist principally of well-worn graywacke and granodiorite.

have provided researchers the opportunity to study important aspects of the ecology of this important keystone species. Ready access to populations through the use of relatively simple techniques has facilitated studies on reproductive ecology (Waller et al., 2014), population-level genetics studies (Morrison et al., 2015), and ongoing studies on the physiological effects of ocean acidification. These studies will provide important information for appropriate designation of protective measures for populations at risk to human activities in deepwater areas of the GOA.

Glacial retreat and the unique oceanographic conditions created by tidewater glaciers promote the emergence of red tree corals in shallow water. Further, their proximity to tidewater glaciers makes them prime candidates to monitor the potential effects of global climate change, particularly ocean warming and acidification. The results of our study indicate that continued glacial retreat will ultimately lead to the demise of red tree corals in shallow water when tidewater glaciers ground in the valleys they formed, forcing red tree corals to retreat to deeper water, awaiting the next glacial advance.

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Appendix Table 1

Location of sites where surveys were conducted by scuba divers and with a remotely operated vehicle at the 4 study areas in Southeast Alaska to examine the distribution of red tree corals (*Primnoa pacifica*). Note that the distance from the head of fjord for all sites in the West Arm, Glacier Bay, was measured to the head of Johns Hopkins Inlet except for Sites 15, 16, and 17, where the distance was measured to the head of Tarr Inlet. Also note that the distance from the head of fjord for all sites in Tracy Arm, Holkham Bay, was measured to the face of South Sawyer Glacier except for Sites 1, 2, and 3, where the distance was measured to the face of Sawyer Glacier. An asterisk (*) indicates sites surveyed with a remotely operated vehicle.

Site	Distance from head of fjord (km)	Red tree corals present	Latitude (N)	Longitude (W)
East Arm, Glacier Bay				
1	1.32	Yes	59°05.0930′	136°21.8142′
2	5.24	No	59°03.6000′	136°19.1400′
3	11.40	Yes	59°03.4105′	136°12.7715′
4	11.63	Yes	59°03.3505′	136°12.4700′
5	15.98	Yes	59°01.4625′	136°10.4025′
6	17.66	Yes	59°01.2600′	136°08.4000′
7	17.67	Yes	59°00.7180′	136°09.6160′
8	22.58	Yes	58°58.6190′	136°08.6565′
9	24.41	No	58°57.5400′	136°07.5600′
10	26.00	No	58°56.7215′	136°08.0675′
11	27.21	No	58°56.1640′	136°07.4180′
12	33.13	No	58°53.1555′	136°04.1130′
13	35.71	No	58°51.8550′	136°03.2660′
14	47.62	No	58°46.0490′	136°02.4080′
West Arm, Glacier Bay				
15	3.44	No	59°01.6800′	137°03.0600′
16	5.44	No	59°01.0200′	137°00.4200′
17	12.30	No	58°58.0200′	136°56.3400′
18	16.76	No	58°55.6800′	136°55.5300′
19	4.57	No	58°52.4635′	137°04.7030′
20	7.00	No	58°53.3810′	137°03.8510′
21	11.22	No	58°54.1800′	136°59.4900′
22	15.45	No	58°54.0600′	136°55.3200′
23	22.59	No	58°54.3600′	136°47.7900′
24	23.15	No	58°52.6800′	136°47.7900′
25	30.10	No	58°53.5800′	136°40.0500′
26	36.91	No	58°55.2000′	136°36.1500′
27	38.19	No	58°49.9800′	136°33.7500′
28	41.69	No	58°50.1600′	136°29.1000′
Tracy Arm, Holkham Bay				
1	1.07	No	57°54.5490′	133°09.5470′
2	2.06	No	57°53.9950′	133°10.3280′
3	3.28	Yes	57°53.5660′	133°11.3830′
4	4.90	Yes	57°52.5000′	133°09.9160′
5	5.33	Yes	57°52.2640′	133°10.8590′
6	5.82	Yes	57°52.9320′	133°10.3160′
7	6.06	Yes	57°53.0490′	133°10.4390′
8*	6.23	Yes	57°52.7890′	133°11.3050′
9*	6.43	Yes	57°52.6320′	133°11.7700′
10	6.40	Yes	57°52.6260′	133°11.7700′
11	9.38	Yes	57°53.2010′	133°14.2790′
12	9.36	Yes	57°53.1740′	133°14.2630′
13*	13.43	Yes	57°53.4600′	133°17.9820′
14*	14.33	Yes	57°53.3460′	133°18.9730′
15	14.51	Yes	57°53.2740′	133°19.0850′

Table continued

Appendix Table 1 (continued)

Site	Distance from head of fjord (km)	Red tree corals present	Latitude (N)	Longitude (W)
16	15.96	Yes	57°53.6810′	133°20.2610′
17	17.71	Yes	57°53.5620′	133°22.1480′
18	19.68	Yes	57°54.3990′	133°23.5870′
19*	21.94	Yes	57°54.6820′	133°25.8240′
20*	24.03	Yes	57°54.5760′	133°27.8190′
21*	24.40	Yes	57°55.1830′	133°28.1510′
22	24.39	Yes	57°55.1700′	133°28.1390′
23*	25.75	No	57°55.0800′	133°29.5790′
24*	26.02	Yes	57°55.1960′	133°29.7590′
25*	27.42	Yes	57°55.4580′	133°32.6400′
26	27.67	No	57°54.9350′	133°33.1800′
27	27.81	No	57°55.5920′	133°33.3000′
28	32.14	No	57°54.5320′	133°34.8020′
29	37.17	No	57°51.8860′	133°36.0470′
30	48.45	No	57°46.1050′	133°38.8320′
Endicott Arm, Holkham Bay				
31	3.70	No	57°29.9530′	132°56.4960′
32*	6.80	Yes	57°30.9160′	132°59.2810′
33	7.80	Yes	57°30.7520′	133°00.4970′
34*	7.90	Yes	57°30.8000′	133°00.5460′
35*	8.60	Yes	57°31.3750′	133°00.7880′
36*	10.00	Yes	57°30.8180′	133°02.3950′

Appendix Table 2

Location of sampling sites where conductivity, temperature, and depth (CTD) instruments were used to collect oceanographic data in Glacier and Holkham Bays, Southeast Alaska, in 2004, 2005, 2006, 2008, and 2014. Depth is the typical maximum depth of each CTD cast. Station numbers refer to those in Figures 6 and 7.

Station	Latitude (N)	Longitude (W)	Depth (m)
Glacier Bay			
1	59°04.7700′	136°21.2200′	200
2	59°03.0000′	136°11.0400′	200
3	59°01.6000′	136°09.8700′	200
4	59°01.5170′	136°10.4550′	60
5	59°01.2480′	136°08.3970′	30
6	58°58.5100′	136°08.1700′	160
7	58°52.6600′	136°05.3600	275
8	59°00.2000′	136°59.1800	290
9	58°58.3050′	136°55.0750′	290
10	58°53.8350′	137°02.8600′	290
11	58°53.9300′	136°50.4700′	300
12	58°53.8150′	136°44.1950′	300
13	58°55.0750′	136°36.6000′	150
14	58°51.9800′	136°35.5700′	300
15	58°48.6850′	136°28.3700′	300
16	58°45.2400′	136°19.6540′	290
17	58°39.8100′	136°07.6500′	275
18	58°11.4100′	135°01.5900′	300
Holkham Bay			
1	57°52.8180′	133°10.7760′	150
2	57°53.1000′	133°12.7080′	180
3	57°54.0300′	133°17.2560′	200
4	57°53.3460′	133°18.9480′	100
5	57°53.2440′	133°18.7500′	100
6	57°53.8140′	133°21.7320′	200
7	57°54.9420′	133°27.0660′	200
8	57°55.3560′	133°31.1460′	200
9	57°55.2660′	133°35.0040′	200
10	57°49.0200′	133°36.2460′	200
11	57°30.0840′	132°54.6300′	150
12	57°30.8100′	132°59.8980′	150
13	57°31.1160′	133°02.9220′	200
14	57°36.4740′	133°12.1620′	200
15	57°38.3160′	133°16.8000′	200
16	57°43.6140′	133°30.9540′	200

Appendix Table 3

Dissolved oxygen (mL/L) measured at stations in Glacier Bay, Southeast Alaska, during research cruises in 2004 (24–27 April) and 2005 (17–22 April). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 6 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2004	1	9.93	8.36	7.48	6.90	6.69	6.83	6.89	6.94	6.97	7.00	7.01	7.03	7.03	7.04
2004	4	6.88	7.06	6.84	6.78	6.91	6.96	6.98	–	–	–	–	–	–	–
2004	5	7.29	6.93	6.81	6.68	–	–	–	–	–	–	–	–	–	–
2004	7	8.47	7.33	6.92	6.78	6.78	6.73	6.77	6.81	6.86	6.89	6.91	6.92	6.92	6.91
2004	17	8.86	8.36	7.70	7.41	7.15	7.04	7.07	7.12	7.14	7.17	7.19	7.21	7.21	7.21
2004	18	8.05	7.69	7.31	7.14	6.92	6.69	6.25	5.87	5.52	5.21	4.82	4.69	4.61	4.52
2005	1	4.66	4.91	5.25	5.27	5.23	5.20	5.18	5.16	5.13	5.08	5.06	4.97	4.97	4.91
2005	2	4.90	4.97	5.00	5.11	4.79	4.74	4.72	4.75	4.75	4.75	4.75	4.78	4.81	4.83
2005	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2005	6	5.06	5.42	5.59	5.58	5.57	5.55	5.54	5.53	5.51	5.50	5.49	5.49	5.48	5.47
2005	7	5.45	5.58	5.60	5.60	5.58	5.52	5.50	5.47	5.45	5.44	5.44	5.43	5.43	5.42
2005	8	8.32	6.37	5.63	5.14	4.89	4.70	4.62	4.60	4.60	4.61	4.61	4.61	4.62	4.62
2005	9	8.05	6.33	5.40	4.88	4.59	4.48	4.43	4.42	4.42	4.43	4.43	4.43	4.44	4.44
2005	10	8.45	6.36	5.07	4.59	4.43	4.41	4.41	4.41	4.40	4.40	4.40	4.40	4.40	4.40
2005	11	10.75	7.30	5.60	4.96	4.60	4.48	4.47	4.47	4.47	4.47	4.47	4.47	4.47	4.47
2005	12	11.37	7.41	6.04	5.03	4.62	4.47	4.43	4.42	4.42	4.43	4.43	4.43	4.44	4.44
2005	13	13.09	7.59	6.11	4.88	4.56	4.49	4.45	4.44	4.44	4.44	4.45	4.45	4.46	4.46
2005	14	12.35	8.35	7.02	5.22	4.63	4.48	4.43	4.42	4.40	4.40	4.40	4.40	4.40	4.40
2005	15	9.82	7.82	6.31	5.42	4.89	4.73	4.62	4.59	4.59	4.59	4.59	4.59	4.60	4.63
2005	16	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2005	17	13.04	12.96	8.03	6.63	5.60	5.26	5.08	5.00	4.99	4.98	5.00	5.02	5.03	5.05
2005	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Appendix Table 4

Dissolved oxygen (mL/L) measured at stations in Holkham Bay, Southeast Alaska, during 3 research cruises in 2006 (22–27 March), 2007 (26–28 March), and 2008 (1–3 May). Depths are adjusted to mean lower low water. Station numbers refer to those in Figure 7 and Appendix Table 2. En dashes (–) indicate no measurements.

		Depth (m)													
Year	Station	5	10	15	20	30	40	50	60	70	80	90	100	110	120
2006	1	2.83	2.74	2.65	2.42	2.42	2.41	2.40	2.40	2.40	2.40	2.40	2.40	2.41	2.28
2006	2	4.02	3.83	3.68	3.65	3.66	3.67	3.68	3.78	3.71	3.66	3.67	3.66	3.72	3.75
2006	3	7.08	4.81	4.27	4.00	3.89	3.88	4.78	4.38	4.03	4.05	3.97	4.00	3.97	3.96
2006	6	6.87	5.82	5.01	4.66	4.49	4.21	4.02	4.34	3.78	3.75	3.74	3.73	3.72	3.71
2006	7	6.12	5.07	4.69	4.57	4.37	4.12	3.98	3.77	3.71	3.68	3.67	3.66	3.66	3.65
2006	8	6.57	4.71	4.45	4.36	4.62	4.33	4.07	3.93	3.89	3.87	3.90	3.85	3.85	3.84
2006	9	5.98	5.00	4.88	4.41	4.26	4.21	4.10	3.83	3.74	3.74	3.72	3.72	3.72	3.72
2006	10	6.86	5.69	4.84	4.57	4.46	4.37	4.41	4.11	3.99	3.93	3.90	3.87	3.82	3.80
2006	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2006	12	5.68	4.50	4.06	3.85	4.46	3.85	3.57	3.50	3.50	3.53	3.53	3.49	3.50	3.50
2006	13	6.24	4.78	4.42	4.10	4.07	3.89	3.73	3.59	3.57	3.54	3.53	3.52	3.47	3.46
2006	14	5.78	4.40	4.07	3.84	3.92	3.63	3.67	3.53	3.50	3.48	3.47	3.43	3.45	3.47
2006	15	5.73	4.49	4.10	3.88	3.86	3.67	3.68	3.47	3.43	3.44	3.45	3.46	3.42	3.42
2006	16	5.89	5.46	4.74	4.57	4.46	4.23	4.25	3.93	3.87	3.84	3.81	3.81	3.76	3.73
2007	1	7.75	7.62	7.56	7.51	7.47	7.42	7.42	7.42	7.43	7.43	7.43	7.43	7.44	7.44
2007	2	7.62	7.57	7.56	7.48	7.44	7.42	7.42	7.42	7.43	7.43	7.43	7.43	7.43	7.44
2007	3	7.60	7.56	7.49	7.48	7.45	7.42	7.42	7.43	7.43	7.43	7.43	7.43	7.43	7.44
2007	6	7.64	7.54	7.48	7.45	7.41	7.43	7.43	7.43	7.43	7.43	7.43	7.44	7.44	7.44
2007	7	7.60	7.54	7.44	7.43	7.42	7.42	7.42	7.43	7.43	7.44	7.44	7.44	7.44	7.45
2007	8	7.59	7.53	7.47	7.44	7.41	7.42	7.42	7.43	7.43	7.44	7.44	7.44	7.45	7.45
2007	9	7.65	7.52	7.46	7.45	7.45	7.43	7.44	7.45	7.45	7.46	7.46	7.46	7.46	7.47
2007	10	7.51	7.50	7.48	7.45	7.45	7.45	7.46	7.46	7.47	7.47	7.47	7.47	7.47	7.46
2007	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2007	12	7.39	7.34	7.31	7.32	7.33	7.33	7.34	7.35	7.35	7.35	7.35	7.37	7.37	7.38
2007	13	7.38	7.35	7.33	7.31	7.33	7.33	7.34	7.35	7.37	7.38	7.39	7.39	7.40	7.40
2007	14	7.37	7.33	7.32	7.36	7.39	7.40	7.40	7.40	7.41	7.41	7.41	7.41	7.42	7.42
2007	15	7.36	7.35	7.33	7.33	7.34	7.35	7.36	7.37	7.38	7.39	7.40	7.41	7.41	7.41
2007	16	7.37	7.35	7.39	7.40	7.41	7.42	7.43	7.43	7.43	7.43	7.43	7.43	7.43	7.43
2008	1	7.80	7.65	7.63	7.60	7.54	7.51	7.47	7.45	7.45	7.44	7.44	7.44	7.43	7.43
2008	2	7.72	7.64	7.61	7.58	7.52	7.48	7.46	7.45	7.44	7.44	7.44	7.43	7.43	7.43
2008	3	7.74	7.64	7.60	7.57	7.52	7.47	7.45	7.44	7.44	7.44	7.44	7.43	7.43	7.43
2008	6	7.65	7.60	7.57	7.54	7.49	7.47	7.44	7.44	7.44	7.44	7.44	7.43	7.43	7.43
2008	7	7.63	7.60	7.57	7.52	7.48	7.45	7.44	7.44	7.44	7.44	7.43	7.43	7.43	7.43
2008	8	7.65	7.61	7.57	7.54	7.49	7.47	7.45	7.44	7.44	7.44	7.43	7.43	7.43	7.43
2008	9	7.38	7.42	7.45	7.44	7.44	7.44	7.44	7.44	7.44	7.44	7.43	7.43	7.42	7.42
2008	10	7.37	7.41	7.42	7.41	7.43	7.42	7.42	7.42	7.41	7.40	7.38	7.38	7.37	7.37
2008	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2008	12	7.53	7.52	7.50	7.46	7.44	7.42	7.40	7.40	7.40	7.40	7.40	7.40	7.40	7.40
2008	13	7.49	7.51	7.49	7.45	7.43	7.41	7.40	7.40	7.40	7.40	7.40	7.40	7.40	7.40
2008	14	7.39	7.40	7.41	7.40	7.40	7.40	7.40	7.40	7.40	7.40	7.40	7.40	7.40	7.40
2008	15	7.33	7.40	7.41	7.41	7.40	7.40	7.40	7.40	7.40	7.40	7.40	7.40	7.39	7.39
2008	16	7.29	7.30	7.33	7.34	7.35	7.35	7.36	7.36	7.36	7.37	7.38	7.38	7.38	7.38