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Distributions of the Pelagic Holothurian *Pelagothuria* in the Central Pacific Ocean as Observed by Remotely-Operated Vehicle Surveys

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Pelagothuria is the only known genus of holothurian that is considered to be holopelagic. There is thought to be only one species, *Pelagothuria natatrix*, and little is known about its abundance and distribution throughout the global ocean. Most documented observations of *Pelagothuria* are in tropical regions with many in or near water masses with low dissolved oxygen concentrations, suggesting that *Pelagothuria* may be associated with oxygen minimum zone regions. During the spring 2017 NOAA Ship *Okeanos Explorer* Mountains in the Deep Expedition, scientists onboard the ship and participating through telepresence noted seeing an exceptional number of *Pelagothuria* during ROV dives conducted at sites along a transit from Pago Pago, American Samoa to Honolulu, Hawaii. Video from all dives was later reviewed using the video replay and annotation tool SeaTube and *Pelagothuria* were seen at 9 of the 12 ROV dive sites explored. A total of 97 *Pelagothuria* were observed in depths ranging from 196 to 4,440 m, temperatures of 1.3–15.4°C, salinities of 34.5–35.2, and oxygen concentrations of 0.17–3.77 mg L^{-1}. The vertical distribution of *Pelagothuria* averaged 865 m depth, and their observations occurred at means of 5.24°C, 34.56, 1.71 mg L^{-1} for temperature, salinity, and dissolved oxygen, respectively. In 30 percent ($n = 27$) of the occurrences of *Pelagothuria*, the organism was observed at or within site of the seafloor, suggesting that the species may not actually be entirely holopelagic. A literature review was also conducted to look at the biogeography of the taxon. Results suggest that the horizontal distributions of *Pelagothuria* may extend to the Equatorial Pacific region, and the relatively high occurrence of *Pelagothuria* in oxygen minimum zones indicates they may be particularly hypoxia-tolerant. There is some indication that *Pelagothuria* may also be associated with areas of high particle flux. The strong El Niño event that occurred shortly before the expedition and anomalously warm conditions throughout much of the Pacific could have provided conditions favorable to a *Pelagothuria* bloom, however the high abundances of the organism seen on a nearby 2015 expedition and a later 2019 expedition suggest that this may be a persistent feature. The water column in this region has never before been explored with ROVs, and this study demonstrated use of an archived and publicly-accessible exploratory dataset to make novel discoveries.

Keywords: ***Pelagothuria,*** **oxygen minimum zone, eastern tropical pacific, equatorial pacific, water column exploration, Echinodermata, Holothuroidea**

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INTRODUCTION

The deep (>200 m) pelagic ocean contains more than 90% of the Earth's habitable volume for multicellular organisms (Robison, 2009; Haddock et al., 2017). Also referred to as the midwater, this environment contains a high abundance and diversity of organisms, yet remains one of the least understood ecosystems on Earth due to the logistical challenges of accessing the deep sea (Robison, 2004; Webb et al., 2010; Netburn et al., 2018). With relatively few direct observations in the pelagic ocean, there is likely a significant amount of undescribed biodiversity of mesopelagic organisms (Webb et al., 2010). It was long thought that the deep pelagic ocean was entirely void of life, but midwater trawling conducted on the HMS Challenger expedition in the 1870s revealed that there is a ubiquitous assemblage of animals inhabiting these depths throughout the global ocean. While trawling continued to reveal the diversity of uniquely-adapted organisms living in the deep pelagic ocean, it was not until William Beebe and Otis Barton began to explore the water column environment with submersibles in the 1930s that the fine-scale spatial distribution and behaviors of midwater organisms could be observed *in situ* (Robison, 2004). While early submersible-based exploration included midwater observations (e.g., Barham, 1966), the focus of deep submergence studies soon largely shifted to seafloor environments. The greatest exception to this was the Johnson Sea-Link program, based at Harbor Branch Oceanographic Institute, which supported significant midwater exploration from the 1970s through the early 2000s (Greene et al., 1988; Widder et al., 1992; Frank and Widder, 1997; Liberatore et al., 1997). In 2016, the human-occupied vehicle (HOV) *Alvin* was used for the first time in decades to survey the pelagic environment in a study of the distribution of water column organisms at Hydrographer Canyon in the northwest Atlantic Ocean (Netburn et al., 2017). The success of this operation in making novel observations and collections demonstrated the value of bringing people directly into the midwater environment. However, HOVs are expensive to operate and their operational endurance is constrained (National Research Council, 1996).

Beginning in the 1980s, remotely operated vehicles (ROVs)—initially developed for industrial uses—were recognized as potential tools for conducting scientific observations in the deep sea. The Monterey Bay Aquarium Research Institute (MBARI), founded in 1987, developed a ROV-based research program to observe and survey midwater environments. Since 1989, MBARI researchers have conducted depth-stratified ROV transects through the upper kilometer of the water column at a reference station in Monterey Canyon (Robison et al., 2017), providing the longest and most comprehensive time series of visual observations in the deep pelagic environment. New taxa are still regularly discovered (e.g., Matsumoto et al., 2003; Dunn et al., 2005; Osborn et al., 2011) and MBARI's annotated and quality-controlled database provides an unprecedented time series (Schlining and Stout, 2006; Schlining et al., 2013) to investigate the relationships between abundance and distributions of organisms in response to environmental variability, as well as a video archive that can be mined for observations such as trophic interactions (Choy et al., 2017) and distributions of bioluminescent organisms (Martini and Haddock, 2017). While limited work has been done in other locations, such as Hawaii, the Gulf of California, and Japan, much of the ocean remains unexplored for water column organisms.

The National Oceanic and Atmospheric Administration's Office of Ocean Exploration and Research (OER) supports ocean exploration to address both current and emerging science and management needs in unexplored areas of the ocean, with a focus on the U.S. Exclusive Economic Zone (EEZ). OER achieves these goals by conducting seafloor mapping, water column acoustic data collection, and ROV surveys with NOAA Ship *Okeanos Explorer* to provide baseline habitat characterizations and sharing the data with the public (Eakins et al., 2019). Standard operations have generally focused on the seafloor, however the *Okeanos Explorer* began conducting water column ROV surveys in 2012 on select dives to collect baseline information on the pelagic environment in response to expressions of interest from the water column scientific community (Ford and Netburn, 2017; Netburn et al., 2018).

During the 2017 Mountains in the Deep Expedition in the Central Pacific ocean, the *Okeanos Explorer* encountered an unexpected abundance of the pelagic holothurian (Class: Holothuroidea), *Pelagothuria*, while conducting both midwater and seafloor ROV surveys (**Figure 1**). There is some disagreement on whether the genus *Pelagothuria* is comprised of multiple species or a single species, *Pelagothuria natatrix* (Ludwig, 1893). Since no specimens were collected during the Mountains in the Deep Expedition for genetic or morphological species confirmation, we refer to these observations by genus only. *Pelagothuria* is the only holothurian that is considered to be holopelagic (Miller and Pawson, 1990) and thus a member of the plankton. Consequently, *Pelagothuria* have an unusual morphology for a holothurian, which Miller and Pawson (1990) described as resembling "an umbrella turned inside out by a gusting wind."

While *Pelagothuria* is anecdotally a cosmopolitan genus, there are only a limited number of confirmed observations in the scientific record and the global abundance and distributions of the taxon remain poorly documented (**Figure 2**). Through a review of published literature and online resources archiving publicly-available data, we identified a total of 428 specimens collected or observed by video (**Figure 2**; **Table S1**; Ludwig, 1893; Chun, 1900; Clark, 1920; Heding, 1940, 1950; Gebruk, 1989; Miller and Pawson, 1990; Jones et al., 2009; Buglass et al., 2019; Morris, 2019; National Museum of Natural History, 2019; Natural History Museum, 2019; OBIS, 2019; Orrell, 2019; Seid, 2019), including 151 specimens collected in the central Pacific in 2015 (Drazen, unpublished data) and 143 *Pelagothuria* seen on a 2019 E/V Nautilus expedition to the same region as our study. *Pelagothuria* are well-documented across tropical regions, however they have been observed in a range of geographies and conditions, such as in the Southern Ocean. The locations of all confirmed *Pelagothuria* observations are available in **Table S1** and **Figure 2**.

Sutton et al. (2017) defined 33 ecoregions—areas with geographically-distinct faunal assemblages (Spalding et al.,

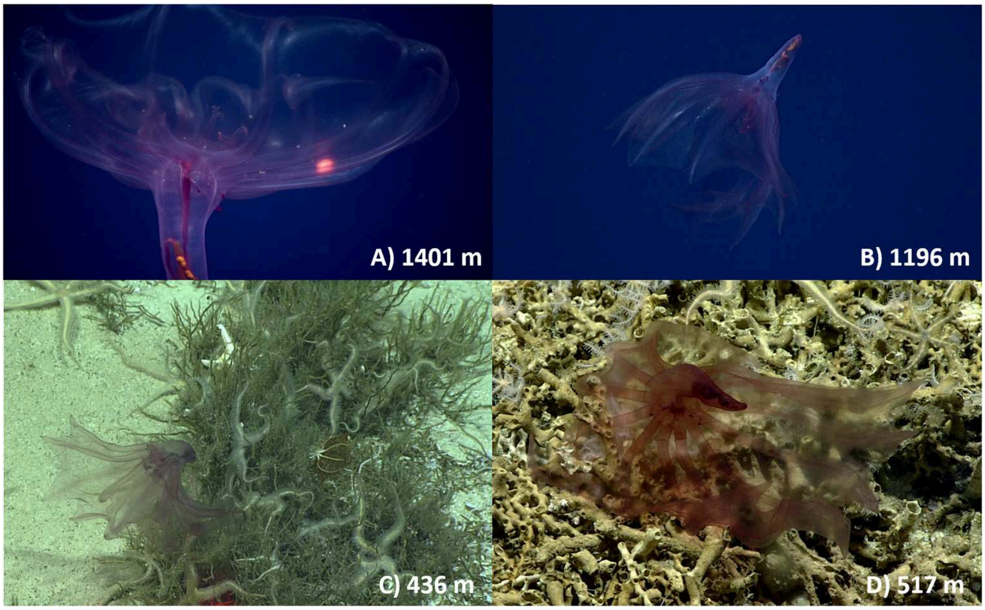

FIGURE 1 | Images of *Pelagothuria* encountered on the NOAA Ship *Okeanos Explorer* Mountains in the Deep Expedition. Depths are indicated in the lower right corner of each image. The images were taken by the ROV *Deep Discoverer* in the water column on: **(A)** Dive 6—Keli'ihananui **(B)** Dive 3—Te Kawhiti a Maui Potiki and at the seafloor: **(C)** Dive 5—Jarvis Island, and **(D)** Dive 5—Jarvis Island. Image credit: NOAA Office of Ocean Exploration and Research, Mountains in the Deep 2017.

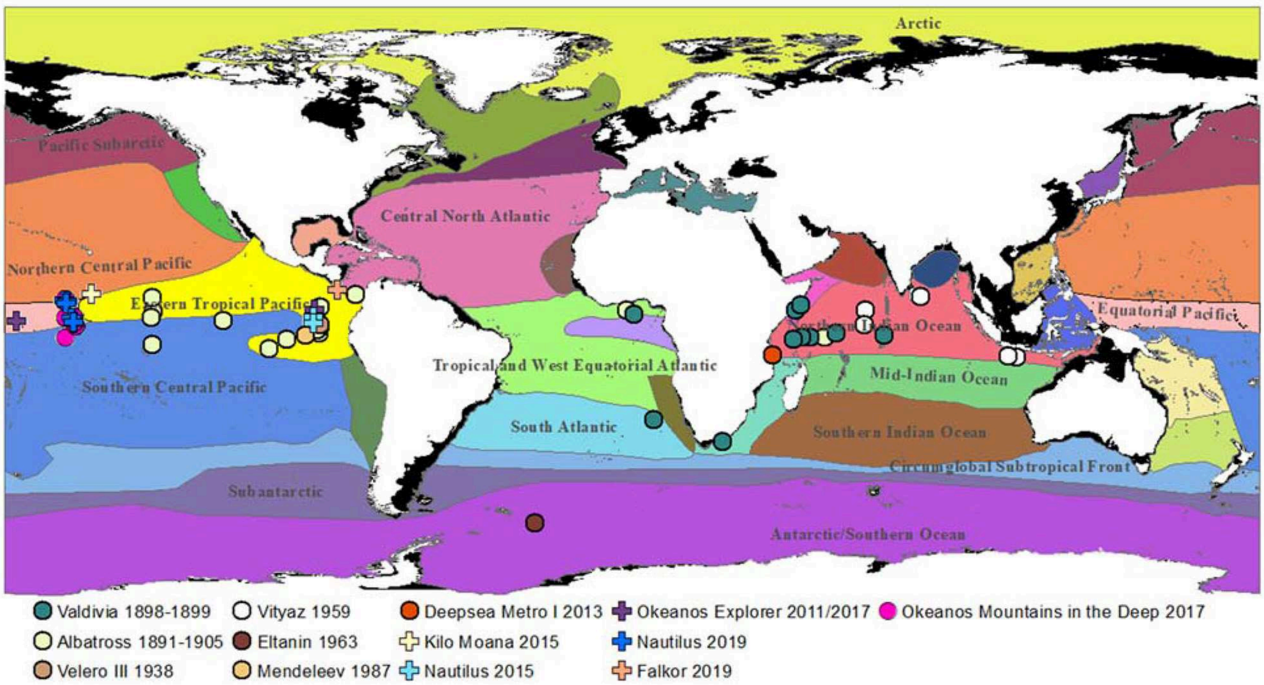

FIGURE 2 | Confirmed observations of *Pelagothuria* overlaid on map of ecoregions as defined by Sutton et al. (2017). Further details on the expeditions are in **Table S1**.

2007)—based on daytime distributions of mesopelagic communities, water masses, presence of an oxygen minimum zone, surface productivity, temperature extremes, and biotic partitioning (**Figure 2**). The limited data available indicate that although *Pelagothuria* likely have a global distribution, they may be especially concentrated at tropical latitudes with high numbers in the Eastern Tropical Pacific (ETP), Equatorial Pacific, and Northern Indian Ocean ecoregions. Most Pacific observations are associated with the ETP, which is characterized by high primary productivity and strong layering of water masses, indicated by a shallow and abrupt thermocline (Sutton et al., 2017). The circulation of the equatorial Pacific ecoregion is complex, with a westward surface current, an eastward undercurrent within the thermocline, and strong upwelling (Kessler, 2006). This upwelling causes high primary production year round (Sutton et al., 2017). As a result, the assemblage of the mesopelagic fauna of the Equatorial Pacific has been found to differ significantly from those of both the Northern and Southern Central Pacific (Barnett, 1983). The ETP also has an oxygen minimum layer which is notable for both its size and the degree of hypoxia (Fiedler and Talley, 2006). The Northern Indian Ocean has a more broad and homogeneous OMZ than that of the Eastern Pacific margin with localized areas of upwelling (Helly and Levin, 2004; Sutton et al., 2017). Because animals differ greatly in their tolerances to hypoxia (Levin, 2003; Seibel, 2011), the apparent association of *Pelagothuria* with the ETP, Equatorial Pacific, and Northern Indian Ocean ecoregions suggests that the species may be particularly hypoxia-tolerant and thus able to thrive in oxygen minimum zone regions.

While we did not intentionally set out to study *Pelagothuria*, they were observed in high numbers and at multiple sites during ROV-based video surveys conducted on the Mountains in the Deep Expedition (EX1705). The aim of this study was to review video to quantify these observations to describe both geographic and vertical distributions of the poorly understood genus, *Pelagothuria*, examine their distributions in relation to environmental variables to try to identify possible drivers of the high concentrations of *Pelagothuria* observed in the region, and provide a baseline characterization of their habitat. An ancillary goal was to more broadly demonstrate how data collected in an exploratory context can inform understanding of a rare or rarely-observed taxon. Finally, we evaluated the real-time annotation software that was used during this expedition.

METHODS

Shipboard Observations

The Mountains in the Deep Expedition (EX1705) took place on NOAA Ship *Okeanos Explorer* from 27 April to 19 May 2017, as part of NOAA's 2015–2017 Campaign to Address Pacific monument Science, Technology, and Ocean NEeds (CAPSTONE). CAPSTONE was an initiative to collect deepwater baseline information to support science and management decisions in and around the U.S. marine protected areas in the central and western Pacific, areas which include some of the least explored deep waters on Earth (Leonardi et al., 2019). Goals of the Mountains in the Deep Expedition were to collect geological and ecological data in and around two units of the Pacific Remote Islands Marine National Monument—the Jarvis Island Unit and the Kingman Reef and Palmyra Atoll Unit, as well as at Marae Moana in the Cook Islands (Bohnenstiehl et al., 2018). The *Okeanos Explorer* is a 68.3 m vessel equipped with a Kongsberg EM302 30 kHz multibeam sonar for seafloor mapping, Knudsen 3.5 kHz sub-bottom profiler to map geological characteristics below the seafloor, and Simrad 5-frequency EK60 echosounders to detect midwater organisms and features (e.g., gas bubbles). The 6,000 m-rated ROV *Deep Discoverer* (D2) is the primary platform for making *in situ* observations and collections. D2 is tethered to a secondary ROV, *Seirios*, which helps dampen the effects of ship heave, and provides a broad view of operations (Quattrini et al., 2015; Gregory et al., 2016). The forward-facing Insite Pacific Zeus Plus high-definition video Camera on D2 was used as the main scientific camera to direct the mission. Forward-facing illumination was provided by LEDs capable of providing 96,000 lumens of light, some of which were mounted on D2's four adjustable swing arms (D. Rogers, GFOE, pers. comm.). D2 was equipped with two mechanical manipulator arms to sample rocks, corals, and sponges, however at the time of this study, the ROV had no capability to collect pelagic organisms (Gregory et al., 2016). Both D2 and *Seirios* are equipped with SeaBird SBE-911 Plus CTDs with dissolved oxygen, turbidity, and oxygen reduction potential sensors.

All shipboard scientific sonars were typically operating throughout the night and during transits. ROV operations were conducted during the daytime, and the Simrad EK60 echosounders were run during the midwater ROV transects. The ROVs were typically launched at 0830 local time, and recovered after 8 h. Twelve ROV dives were conducted during the expedition between Pago Pago, American Samoa and Honolulu, Hawai'i (**Figure 3**, **Table 1**).

At the beginning of each dive, the ROVs descended to the seafloor, where D2 conducted visual benthic surveys and collected sessile organisms and rocks. At three sites, "Te Kawhiti a Maui Potiki" (Dive 3), "Keliihananui" (Dive 6), and "Kingman Deep" (Dive 12), the total ROV time was extended by 2 h, and exploratory midwater transects were conducted following the seafloor surveys at depths from 300 to 1,800 m during the ascent. While midwater ROV transects should ideally be conducted on descent to minimize known avoidance effects, the dual-body system on the Okeanos Explorer limited operations to ascent only. The *Pelagothuria* did not exhibit notable avoidance behavior, so it is likely that the data were not biased by this limitation. Scientists participating through telepresence selected depths for the midwater transects based on EK60 backscatter (e.g., to target deep scattering layers), ROV CTD profiles (e.g., to target the oxygen minimum), and an interest in surveying across a range of depths. During midwater transects, the ROV proceeded slowly through the water column at 0.1–0.4 kts while maintaining constant depth (within ± 2 m of target depth). Direction of the transects was determined by currents and other conditions to optimize the likelihood of being able to stop the vehicles and take close-up video of target organisms in order to aid species identifications and observe the organisms' behaviors. Exploratory transects were typically conducted for 10 min at each target depth, which included time spent stopped and imaging organisms. Ascent speed between transect depths was on average 30 m min^{-1}. Depths at which the midwater transects were conducted at each site are indicated in **Table 2**.

Seafloor survey locations were selected based on prior knowledge of the region, existing and newly-collected mapping

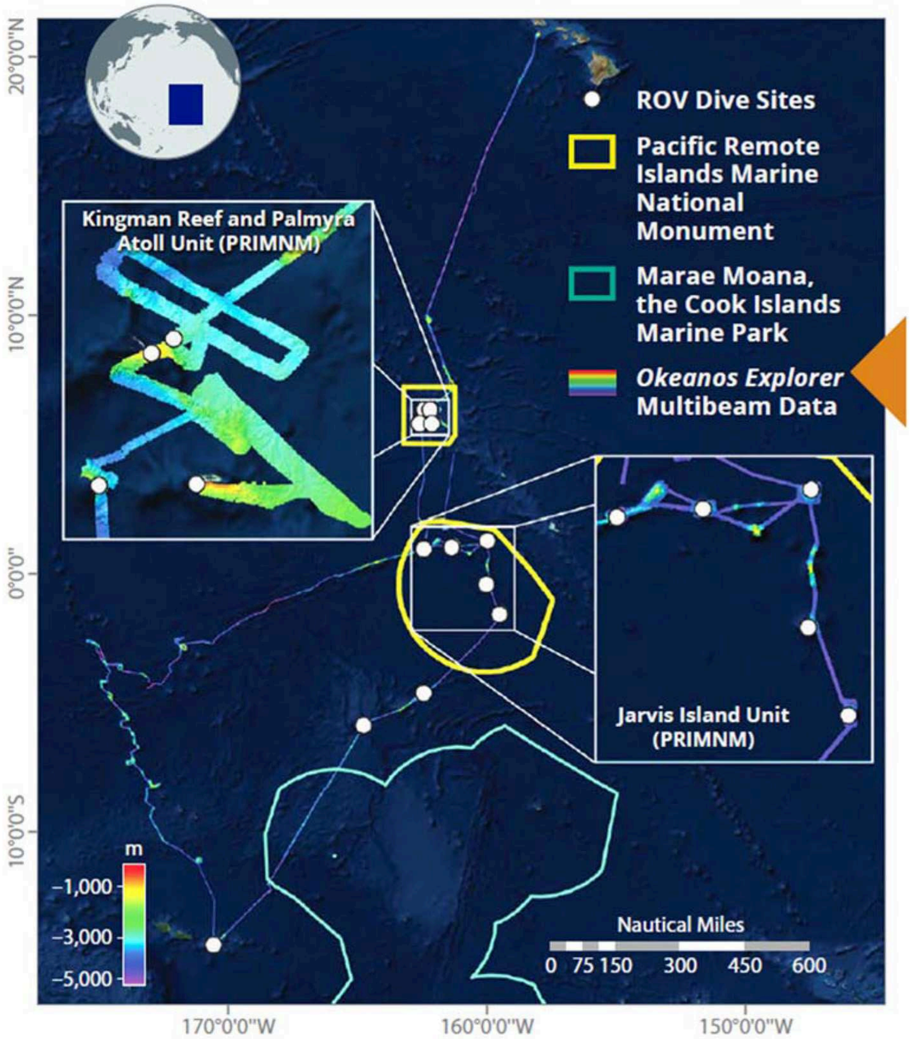

FIGURE 3 | Mountains in the Deep Expedition on NOAA Ship *Okeanos Explorer*, conducted from 27 April to 19 May 2017. The cruise track shows the multibeam bathymetry and the white points are sites where seafloor ROV surveys were conducted. Midwater transects were conducted at three of these sites. *Image courtesy of the NOAA Office of Ocean Exploration and Research*.

data, and science and management interests (e.g., potential for high coral and sponge cover). Seafloor surveys started at the deepest end of the target feature and moved upslope until the dive was complete. D2 transited the seafloor at an average speed of 0.2 kts ($\sim$0.1 m s^{-1}) and intermittently stopped to focus in on or collect samples of characterization targets. The dives had an average ascent and descent rate of 25–30 m min^{-1} (Kennedy et al., 2019).

A unique aspect of *Okeanos Explorer* operations is the use of telepresence technologies to engage a broad range of scientists in expeditions (Peters et al., 2019). Onboard and shore-based scientists collaborated through the use of live-streaming video, a shared conference phone line, a text chatroom, and the SeaScribe annotation system. Live video was broadcast in real time and could be accessed at low-latency through Internet 2 or with a several second delay through standard internet. Scientists from 94 national and international institutions and organizations, as well as 8 divisions within NOAA, participated in the Mountains in the Deep Expedition, providing input on planning, real-time mission guidance, and interpretation of the ROV dives.

Annotations

A new capability introduced to *Okeanos Explorer* in the 2017 field season is the web-based annotation tool, SeaScribe, developed by Ocean Networks Canada (ONC). SeaScribe allows scientists both onshore and onboard the ship to annotate ROV operations (e.g., start and end of midwater transects), organisms observed, and seafloor characteristics (Jenkyns et al., 2013; Gomes-Pereira et al., 2016; Etnoyer et al., 2018). The real-time annotations provide valuable information to researchers and scientists analyzing the video post cruise, however there is currently no standardized process for quality control and assurance, and organism sightings

TABLE 1 | ROV dive locations explored during the Mountains in the Deep expedition.

Dive #	Site #/name	Site description	Date	Latitude	Longitude	Bottom depth (m)	*Total # Pelago.*
1	Aunu'u Unit	NMSAS[a]	4/27/2017	14.28159° S	170.50145° W	239	0
2	Te Tekunga o Fakahotu[†]	Eastern ridge of a mesa in the northern Manikiki Plateau	4/30/2017	5.85984° S	164.69764° W	2,456	0
3*	Te Kawhiti a Maui Potiki[†]	Large ridge structure of Manikiki Plateau	5/2/2017	4.58109° S	162.39475° W	2,179	2
4	Kahalewai[†]	Seamount in Jarvis Island unit of PRIMNM[b]	5/4/2017	1.51171° S	159.45684° W	1,701	20
5	Jarvis Island	Ridge on southeastern slope of Jarvis Island	5/5/2017	0.39815° S	159.96582° W	820	18
6*	Keli'ihananui[†] (proposed name)	Flat topped seamount in Jarvis Island unit of PRIMNM[b]	5/6/2017	1.32337° S	159.93126° W	1,934	14
7	Whaley Seamount[†]	Flat topped seamount in Jarvis Island unit of PRIMNM[b]	5/7/2017	1.08175° N	161.28324° W	1,105	23
8	Fracture Zone	Westernmost edge of Clipperton Fracture Zone	5/8/2017	0.97625° N	162.37959° W	4,572	6
9	West Palmyra Seamount	Unnamed seamount west of Palmyra Atoll	5/10/2017	5.8527° N	162.51034° W	2,172	8
10	South Palmyra Slope	Southwest margin of Palmyra atoll	5/11/2017	5.85802° N	162.13323° W	493	0
11	Kingman Cone	Small cone on flat-topped platform SE of Kingman Reef	5/12/2017	6.36538° N	162.30568° W	1,031	3
12*	Kingman Deep	Small cone NE of Kingman Reef	5/13/2017	6.41887° N	162.22115° W	2,253	3

[*] Sites where midwater transects were conducted.
[†] Proposed name.
[a] National Marine Sanctuary of American Samoa.
[b] Pacific Remote Islands Marine National Monument.

TABLE 2 | For each site, the depths of exploratory water column transects are marked with an X.

Depth (m)	Te Kawhiti a Maui Potiki (Dive 3)	Keli'ihananui (Dive 6)	Kingman deep (Dive 12)
1,800	**X** (13 min)	–	–
1,500	**X** (8)	–	**X** (11 min)
1,400	–	**X** (11 min)	–
1,200	**X** (11)	–	**X** (11)
1,000	–	**X** (11)	–
900	**X** (16)	–	–
750	–	–	–
710	**X** (11)	–	–
600	**X** (11)	–	**X** (12)
475	–	**X** (9)	–
450	**X** (7)	–	–
300	**X** (9)	**X** (9)	**X** (15)

Time (in minutes) spent at each depth is listed in parentheses.

may have been missed or incorrectly annotated during real-time annotations. Detailed review and *post hoc* analysis of the video imagery was therefore required to assure the completeness and accuracy of the real-time annotations.

Within 5–10 min after annotations are made in SeaScribe, they are made publicly available along with streaming video capabilities through a second ONC tool called SeaTube, available at the website: https://data.oceannetworks.ca/SeaTubeV2. OER began beta testing SeaTubeV2 for video playback and annotations in 2017. SeaTube has a function to search the video annotations by text for targets of interest, and has the capability to capture screenshots and video clips, and to bookmark video of interest. An additional capability exists to create and edit new annotations. This function is restricted to registered users in order to track the source of annotations and edit history. We used SeaTube to review and annotate all 12 dives of the *Mountains in the Deep* expedition for *Pelagothuria*, including during midwater transects, seafloor surveys, and the initial descents and final ascents at each site. For each *Pelagothuria* observation entered as an annotation in SeaTube, the position, depth, temperature, salinity, and dissolved oxygen were recorded as measured by sensors on the ROV. The video review and annotations were completed in June–July 2018. A complete list of annotations made during the project is available in **Table S2**.

Analysis/Visualization

We plotted the locations and relative abundances of *Pelagothuria* over the ecoregions defined by Sutton et al. (2017) to qualitatively evaluate whether the taxon is associated with a particular ecoregion within the vicinity of our 2017 study. We also plotted the locations of all known global *Pelagothuria* sightings as identified through literature and database review on a global map of the ecoregions. The depths of the *Pelagothuria* observations were plotted and overlaid with profiles of salinity, temperature, and dissolved oxygen to inspect for associations with depth, hypoxic waters, and other physical-chemical features throughout the water column. We made frequency histograms of the temperature, salinity, and dissolved oxygen values where *Pelagothuria* were found. The locations of all known *Pelagothuria* observations—including from this study—were plotted over dissolved oxygen at 200 m to qualitatively evaluate for a possible association of *Pelagothuria* with oxygen minimum zone regions (Garcia et al., 2018). We also investigated a possible affinity of *Pelagothuria* for areas with high particle flux by plotting the observations over modeled mean particulate organic carbon flux at 500 m for years 2000–2009 (data provided by A. Yoole; Yoole et al., 2007). Finally, to assess how well the real-time annotations captured occurrences of the taxon, we compared the number of real-time annotations and post-cruise annotations of *Pelagothuria*.

RESULTS

Data from the expedition can be found at the Ocean Exploration Digital Atlas (https://www.ncddc.noaa.gov/website/google_maps/OE/mapsOE.htm; Cantwell et al., 2017). Streaming video can be accessed through SeaTube and higher-resolution clips are available at the OER Video Portal (https://www.nodc.noaa.gov/oer/video/). Video from all 12 ROV dives was reviewed, totaling 96 h of video replay. *Pelagothuria* were observed at 9 of the 12 dive sites, with a total of 97 individuals observed throughout the expedition (**Figure 4**, **Tables 1**, **2**). The last column of **Table 1** lists the total number of *Pelagothuria* observed at each ROV dive site. The ROV dive sites spanned three different ecoregions as defined by Sutton et al. (2017)—Southern Central Pacific, Eastern Tropical Pacific, and the edge of the Northern Central Pacific. Seventy-one percent of the observations of *Pelagothuria* were found in the Equatorial Pacific ecoregion just west of the Eastern Tropical Pacific, 20% were just south of the boundary between the Equatorial Pacific and the Southern Central Pacific ecoregions, and the remainder just north of the boundary between the Equatorial Pacific and the Northern Central Pacific (**Figure 4**).

Pelagothuria were found in depths ranging from 197 to 4,441 m (**Figures 5**, **6**, **Table 3**), temperatures ranging from 1.30 to 15.40°C (**Figures 5–7**, **Table 3**), salinities from 34.6 to 35.2 (**Figures 5**, **6**, **8**, **Table 3**), and dissolved oxygen concentrations from 0.18 to 3.8 mg L^{-1} (**Figures 5**, **6**, **9**, **Table 3**).

DISCUSSION

Biogeography

The data collected from the Mountains in the Deep Expedition, along with the inclusion of other recent unpublished data, significantly increases the number of confirmed direct observations of *Pelagothuria* in the midwater environment, and contributes data points to fill in the global biogeography of the taxon (**Figures 2**, **10**, **11**). While *Pelagothuria* have previously been documented across tropical latitudes, our results add to the known range southerly into the central portion of the Southern Central Pacific and westward into the Equatorial Pacific, which was also corroborated by the observation from the *Okeanos Explorer* Discovering the Deep Expedition (**Figures 2**, **10**, **11**, **Table S1**). However, while the observations made in this study were mostly within the Equatorial Pacific and waters just north and south of this ecoregion, the locations were close to the ETP, where the majority of observations of *Pelagothuria* in the Pacific have previously been made. It is possible that the ETP water mass extended into the Equatorial Pacific ecoregion due to seasonal variation at the time of the Mountains in the Deep Expedition. Sutton et al. (2017) acknowledged that the ecoregion boundaries are not static. We did not see any *Pelagothuria* during dives (sites 1 and 2) in the southernmost portion of the expedition, which are further from the influence of the ETP water mass.

The increased knowledge of the biogeography of a poorly-documented organism demonstrates the value of making exploratory observations in understudied parts of the ocean. Further observations throughout the global ocean are required to fill in the biogeographic gaps in the distribution of *Pelagothuria*. Publicly-available ROV video that was not originally collected for these purposes may be leveraged to observe and document pelagic organisms.

The high numbers of *Pelagothuria* we saw in the Central Pacific begets the question of whether there were environmental parameters that set up conditions favorable to a *Pelagothuria* bloom or whether high abundance of the taxon is a perennial feature of the region. There were some anomalous climatic events in the region in the couple of years before our observations took place that may have put the ocean in an atypical state to support high numbers of these animals (Di Lorenzo et al., 2015). The unusually warm conditions of 2013-15 throughout much of the Pacific (aka "the warm blob"; Bond et al., 2015; Di Lorenzo and Mantua, 2016) and the strong El Niño event of 2015–2016 (Jacox et al., 2016; Chen et al., 2017) had effects on organisms throughout the north Pacific (Cavole et al., 2016; Racault et al., 2017; Brainard et al., 2018), and could have provided conditions favorable for a *Pelagothuria* bloom. The high abundances of the organism seen on a nearby 2015 expedition (J. Drazen, pers. comm.; points labeled "RV Kilo Moana" in **Figures 2**, **10**, **11** and listed in **Table S1**) occurred during the peak of the warming event which supports this hypothesis, but they were also seen in abundance during a 2019 EV Nautilus expedition that occurred after the warm blob/El Niño events. We suggest that dominance of *Pelagothuria* is a persistent, or at least common, feature in the region. Repeat observations in the region across different climatic conditions would continue to provide data to distinguish between these possibilities and understand the factors that are conducive to large populations of this unique organism in this region.

Vertical Distributions

Some notable environmental features were detected in the vertical profiles of temperature, salinity, and dissolved oxygen. The temperature profiles have a stepwise structure at ∼200–300 m at some stations (Dives 4, 5, 6, 7, and 11), indicating there may be submerged mixed layer waters (**Figure 7**). At all but one site (Dive 4), the *Pelagothuria* were found below this

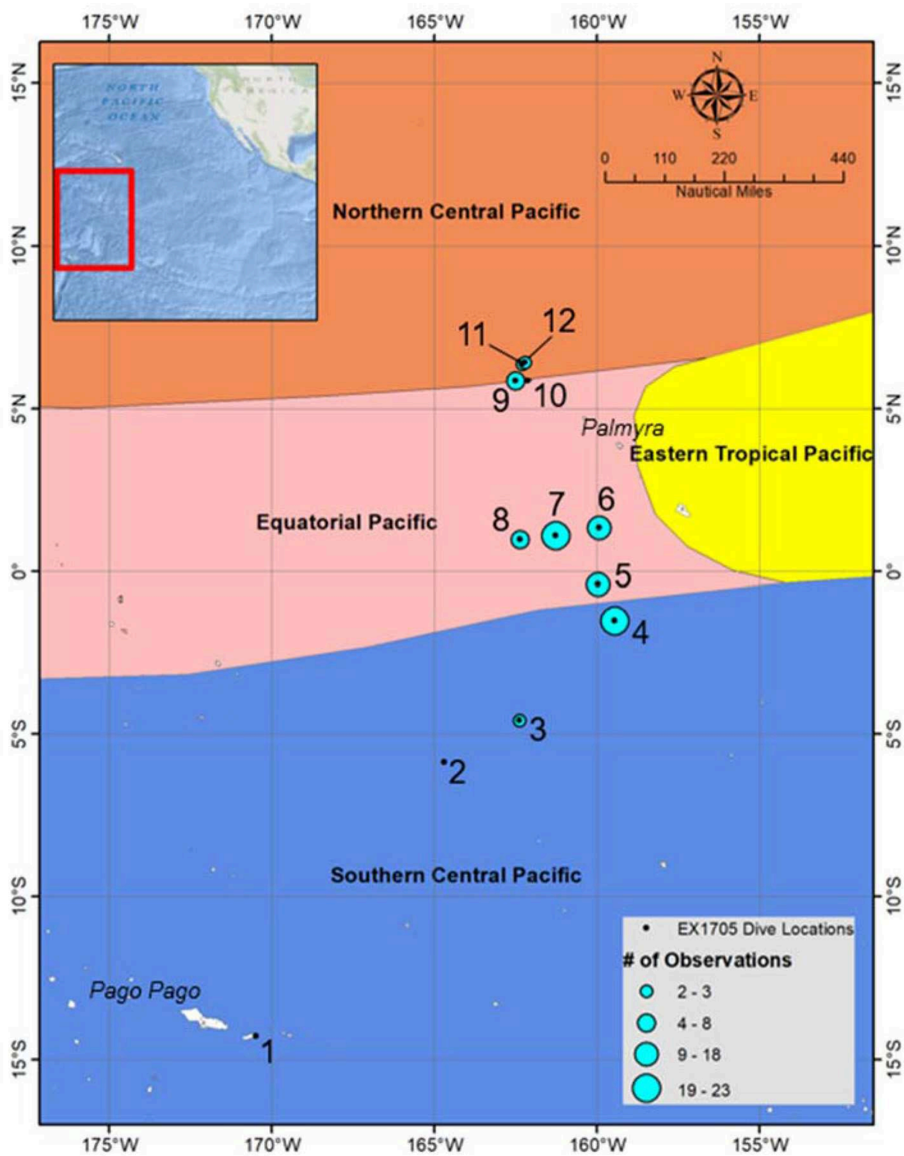

FIGURE 4 | Locations of all dives conducted during the Mountains in the Deep Expedition are marked in black, and labeled by Dive number (refer to **Table 1** for site details). Sites where *Pelagothuria* were observed are indicated by blue circles, sized according to the number of observations. The background is color-coded by ecoregions as defined by Sutton et al. (2017).

layer. At Dive sites 5, 6, 7, 9, 11, and 12 there was a sharp salinity inversion around 200 m (**Figure 8**). The *Pelagothuria* were all observed well below this feature. A pronounced oxygen minimum, with values below (and in some cases, well below) 1.0 mg L^{-1} were observed at stations 4, 5, 9, 11, and 12 (**Figure 9**). At all sites except one (Dive 4), the *Pelagothuria* were found within or below the oxygen minimum, supporting the hypothesis that they are hypoxia tolerant. There was an oxygen inversion between ∼350 and 500 m at Dive sites 3, 4, 5, 7, 9, 11, and 12 that suggest there may be an intrusion at these depths of the more highly-oxygenated Equatorial Pacific water mass into the hypoxic Eastern Tropical Pacific waters. At all but one of these sites, the *Pelagothuria* were encountered either above or below this intrusion, again suggesting that they associate with the ETP. The one site where *Pelagothuria* were found within this layer is at Dive 5, where all individuals encountered were at or very near the seafloor, an anomalous observation we discuss below.

Because all ROV dives were conducted during the daytime, it is not possible to say whether *Pelagothuria* conduct diel vertical migration (DVM), however J. Drazen (pers. comm.) did see distribution patterns suggesting that they *do* based on paired day-night MOCNESS sampling during his nearby expedition off of the R/V *Kilo Moana* in 2015. The depths of peak abundance of *Pelagothuria* as observed by depth-stratified MOCNESS trawls

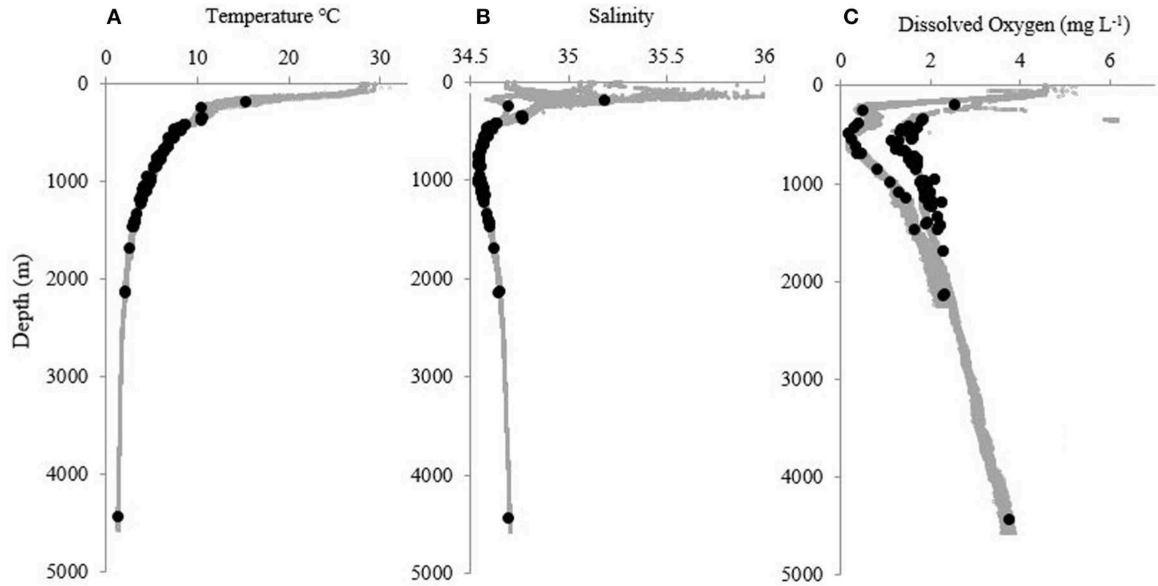

FIGURE 5 | Profiles of **(A)** temperature (°C), **(B)** salinity, and **(C)** dissolved oxygen (mg L^{-1}) at all sites where at least one *Pelagothuria* was observed during the *Mountains in the Deep* expedition. Black points indicate the depth of *Pelagothuria* observations.

were 700–1,500 m during the day with bimodal peaks at night at 100–400 m and 1,000–1,500 m. We suggest that vertically-stratified exploratory transects be conducted throughout the global ocean in order to provide enough data to quantitatively investigate the factors that affect the vertical distributions of *Pelagothuria* and other rarely-observed organisms in the water column. Paired day-night surveys at the same location would not only allow us to look for evidence of DVM, but provide an opportunity to observe the mechanism *Pelagothuria* use to migrate between depths.

Horizontal Distribution

Pelagothuria are broadly distributed across the ocean, and are not limited only to low oxygen regions (**Figure 10**). For example, a documented observation of the animal in the southern ocean suggests they survive in well-oxygenated and cool, high-latitude waters (**Figure 1**, **Table S1**) and they are also seen in relatively well-oxygenated waters off the east coast of Africa. Though observations across the full globe remain limited, we suggest that *Pelagothuria* is cosmopolitan, but may be more common in hypoxic waters because they may be able to outcompete more active animals in these zones.

Another factor that could determine where *Pelagothuria* are found in high abundances is related to their feeding habits. As suspension feeders, they are thought to rely heavily on marine snow and other particulate carbon sources. Numerous benthic deep-sea holothurians are known to be reliant on incoming marine snow (organic particle flux); for example, *Scotoplanes* sp. aggregate toward dead and decaying fish on the seafloor (Miller and Pawson, 1990). A significant correlation between holothurian abundance and organic carbon flux to the seafloor was also found by Sibuet (1985) in the tropical Atlantic. A *Pelagothuria* found in the Indian Ocean had exclusively pelagic components in its gut, such as pelagic diatoms, radiolaria, foraminifera, and copepod feces (Gebruk, 1990). We examined global patterns of organic particle flux from measurements (Mouw et al., 2016) and models (Yoole et al., 2007; Agostini et al., 2009; DeVries and Weber, 2017). There appears to be an association between areas of high carbon flux and *Pelagothuria* sightings, particularly in the Pacific Ocean and in coastal areas, though the association is less clear in the Indian Ocean (**Figure 11**).

Seafloor Observations

Thirty percent ($n = 27$) of the *Pelagothuria* seen on the Mountains in the Deep Expedition were encountered at or within sight of the seafloor. Four individuals were observed directly on the seafloor at Jarvis Island (Dive 5, **Figure 1**), at 517, 473, 436, and 363 m. It was not clear if they were intentionally utilizing the seafloor as habitat or had gotten caught on coral rubble. This benthic survey focused on a small ridge on the southeastern slope of the Jarvis Island Unit of PRIMN which are part of the Line Islands linear volcanic chain (Davis et al., 2002). A high abundance and diversity of marine organisms were observed in this dive compared to others in the expedition which is most likely due to the shallower depth range of 349–820 m. Dead and broken scleractinian coral branches were first encountered at 820 m where the ROV reached bottom. Large carbonate sections of rocks created overhangs that provided a habitat for suspension-feeding fauna. At 415 m bamboo colonies were overgrown by a yellow zoanthid and at 385 m, an area of low relief dense with primnoid fans and urchins was observed (Cantwell et al., 2019).

Pelagothuria are generally described as holopelagic, living and feeding entirely in the water column (Miller and Pawson, 1990). However, there is some evidence that *Pelagothuria* have been

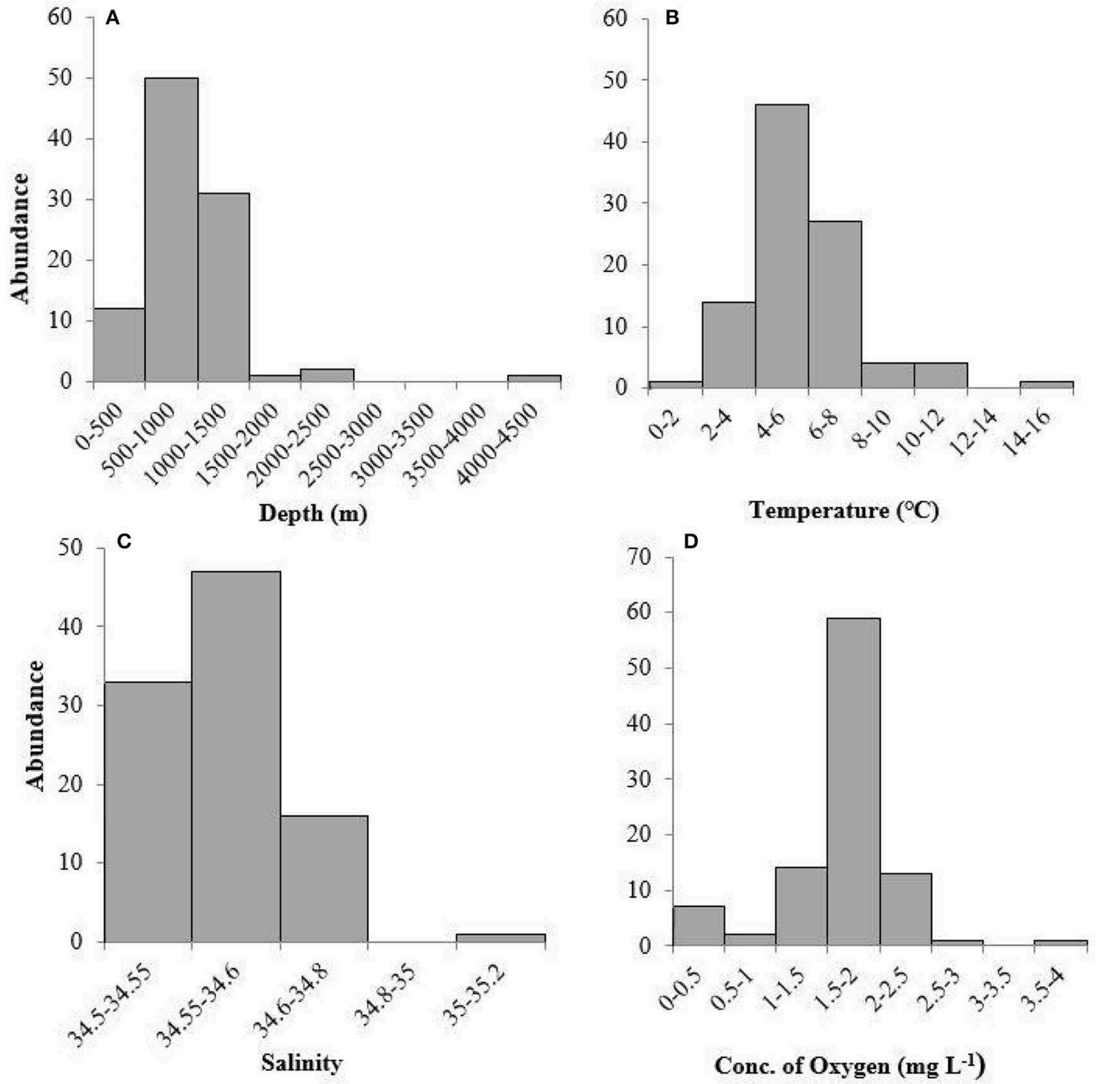

FIGURE 6 | Frequency histograms of **(A)** depth, **(B)** temperature, **(C)** salinity, and **(D)** dissolved oxygen measurements where *Pelagothuria* were observed during the 2017 Mountains in the Deep Expedition.

TABLE 3 | Summary statistics for environmental data where *Pelagothuria* were observed in the 2017 mountains in the Deep Expedition.

	Depth (m)	Temp (°C)	Salinity	Dissolved oxygen (mg L^{-1})
Minimum	197	1.30	34.54	0.17
Maximum	4,441	15.42	35.19	3.77
Mean	929	5.65	34.58	1.65
Standard deviation	503	2.11	0.08	0.53
Median	865	5.24	34.56	1.71

encountered near the seafloor in the past. Lemche et al. (1976) described a *Pelagothuria* from a blurred image that has since been discounted as being a cnidarian (Miller and Pawson, 1990). Miller and Pawson (1990) described the swimming behavior of a *Pelagothuria* that was encountered just meters from the seafloor, but did not consider that the organism may have been associating with the seafloor environment. Though they found only pelagic organisms and unidentifiable organisms in the guts, they only collected a single individual, so there was not a lot of data. It is possible that *Pelagothuria* do settle on the seafloor for periods of time, perhaps related to feeding, reproduction, or shelter. There are thousands of hours of video data available from various deep submergence programs (e.g., Woods Hole Oceanographic Institution's National Deep Submergence Facility, NOAA OER's *Okeanos Explorer* and grant-funded projects, E/V *Nautilus*, etc.) that have been collected over several decades for seafloor investigations. It is likely that numerous individuals of *Pelagothuria* have been imaged but not documented in the literature or available databases. A review of these videos specifically for *Pelagothuria* would help to understand both the prevalence and purpose of their presence on the seafloor. Targeted studies where

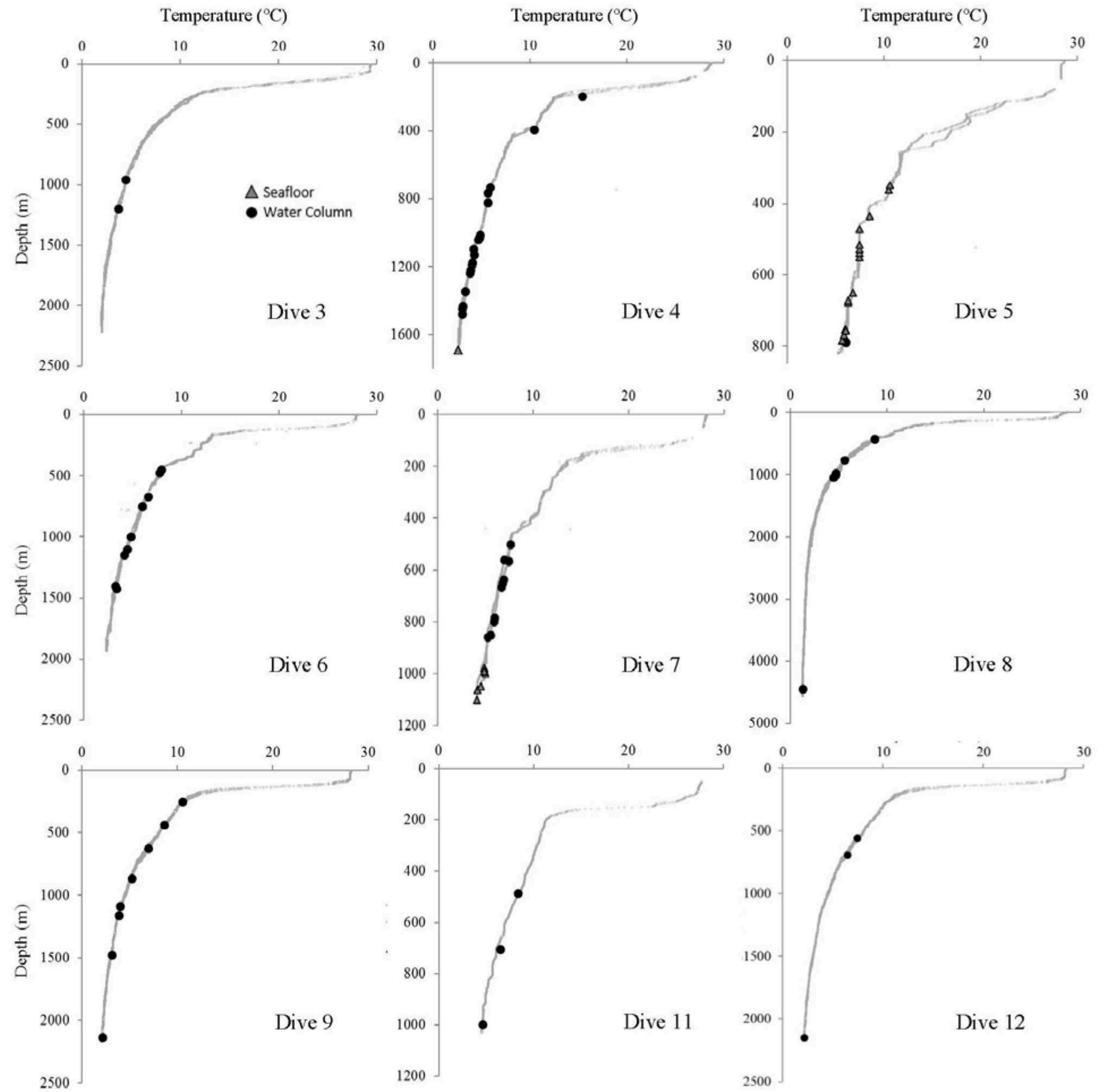

FIGURE 7 | Temperature at every site where at least one *Pelagothuria* was observed during the Mountains in the Deep Expedition. Black points indicate the depth of water column *Pelagothuria* observations and gray triangles represent the depth of *Pelagothuria* seen at the seafloor.

Pelagothuria are known to be abundant, such as in the ETP, could provide an opportunity to make longer observations of the organisms in order to examine their behavior at the seafloor.

Evaluation of Real-Time Annotations

The dataset generated from the real-time annotations and available through SeaTube included 33 annotations of *Pelagothuria*, only about a third of the 97 individuals that were annotated through methodical *post hoc* review of the ROV dives. The accuracy and completeness of the real-time annotations is limited primarily by two factors: (1) available expertise—the researchers annotating the video must have significant expertise to be able to make accurate identifications of a range of different taxa in real time, and (2) limited observation time—organisms in the water column often move past the camera very quickly and multiple organisms may be seen simultaneously, requiring a very fast response time to input all of the annotations. An inherent challenge of the community-based approach to exploration is the

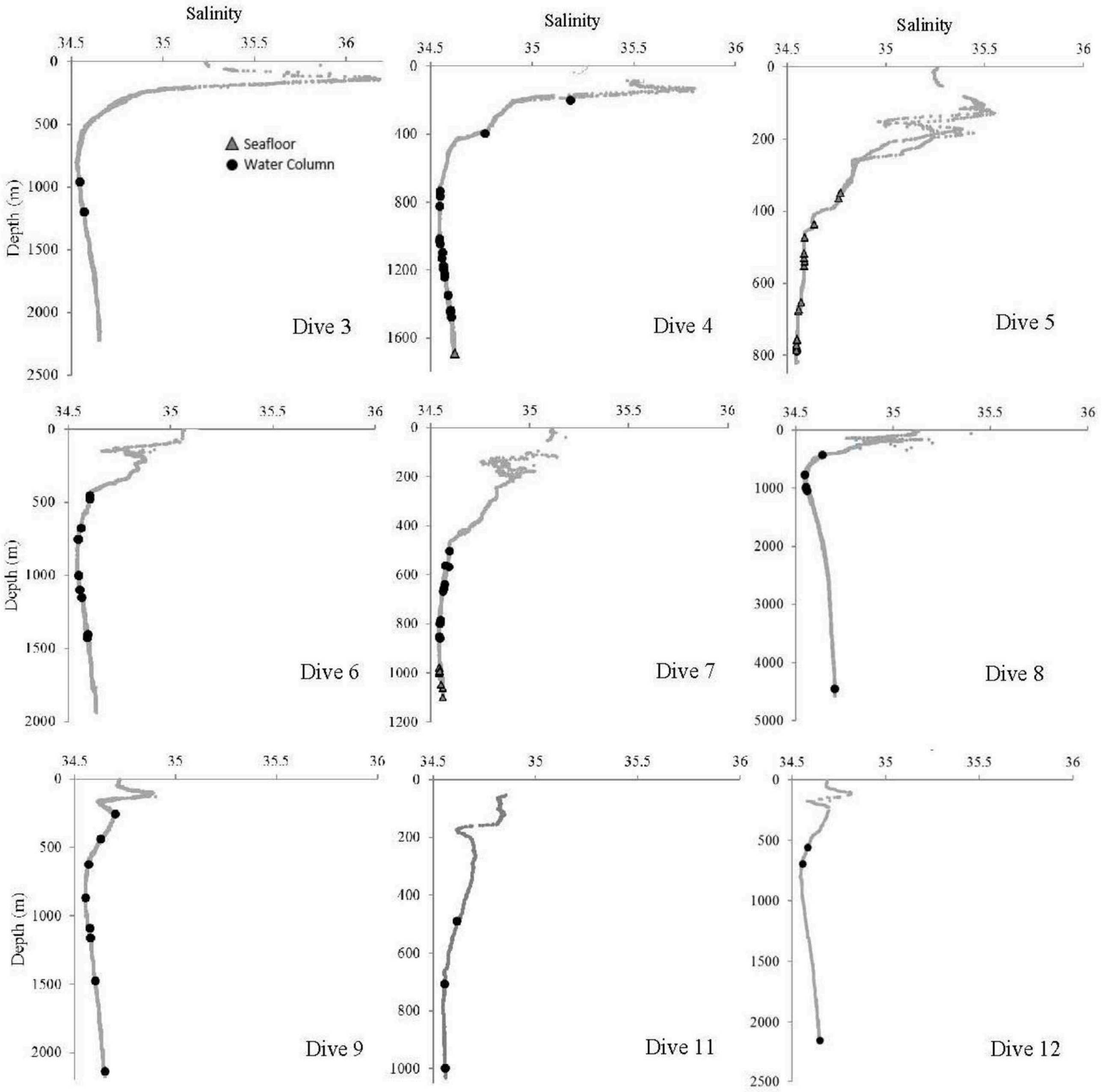

FIGURE 8 | Salinity at each site where at least one *Pelagothuria* was observed during the Mountains in the Deep Expedition. Black points indicate the depth of water column *Pelagothuria* observations and gray triangles represent the depth of *Pelagothuria* seen at the seafloor.

willingness of participating scientists to consistently annotate the video and share these annotations. NOAA Office of Ocean Exploration and Research has started to address this challenge by providing SeaTube as an annotation tool that enables participants to annotate both in real-time and after the dive is complete. However, if the annotations are made only in personal notebooks, in chatrooms, or in individually-managed databases, as often occurs, they will not be available to the broader community.

Creating a quality-controlled database of annotations is a challenge for any operation that utilizes a distributed network of scientists and is committed to providing publicly-available data (e.g., Ocean Exploration Trust's E/V *Nautilus*, Schmidt Ocean Institute's R/V *Falkor*). While some powerful tools exist for making both real-time and *post hoc* annotations, such as Monterey Bay Aquarium Research Institute's Video Annotation and Reference System, such tools are designed for a traditional research expedition, where the onboard team has the needed

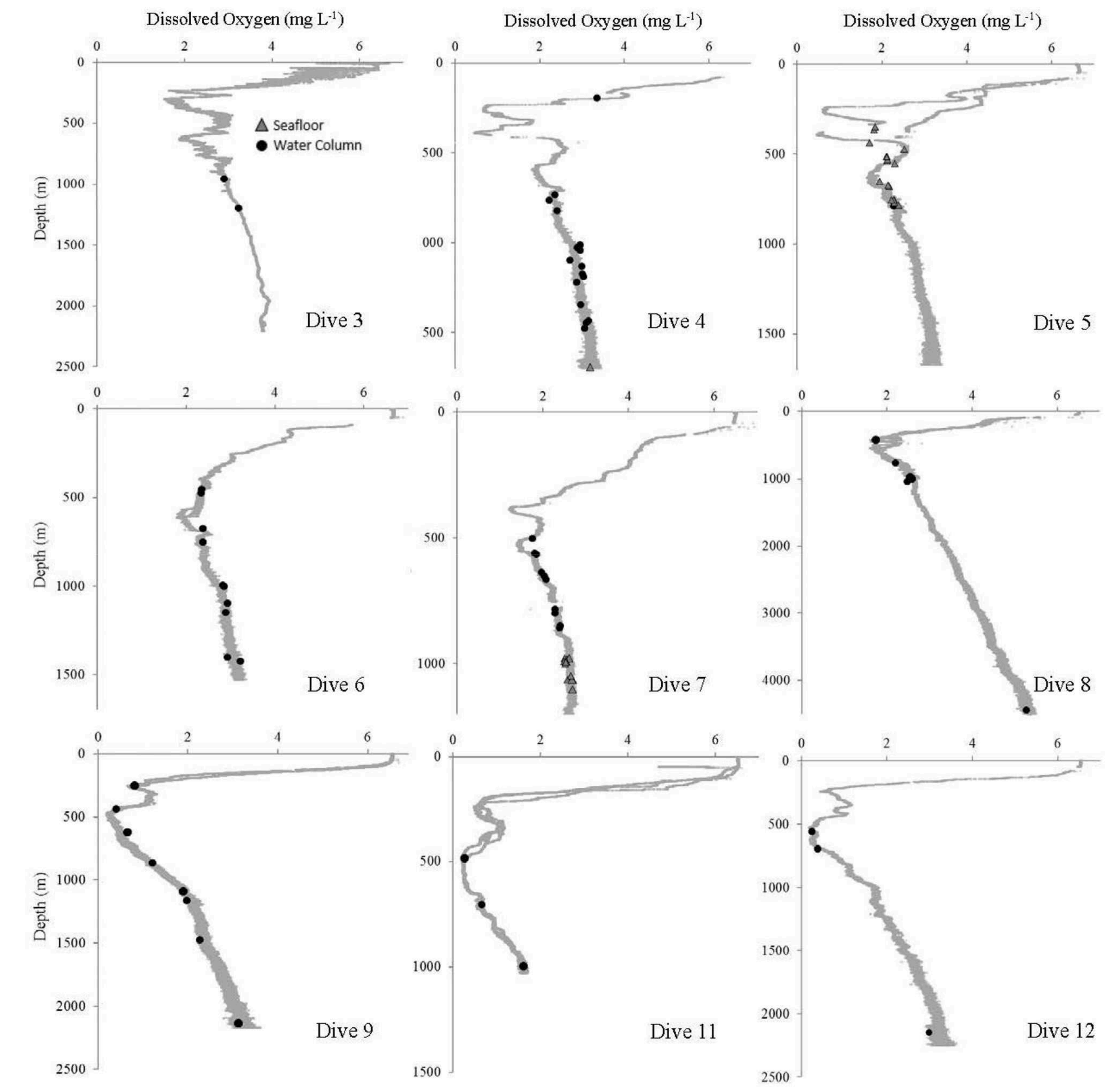

FIGURE 9 | Dissolved oxygen at each site where at least one *Pelagothuria* was observed during the Mountains in the Deep Expedition. Black points indicate the depth of water column *Pelagothuria* observations and gray triangles represent the depth of *Pelagothuria* seen at the seafloor.

expertise. Okeanos Explorer operations sail with a limited science team, and rely on a distributed network of experts for annotations.

Tools like SeaTube make the video and environmental data accessible to interested researchers in an online collaborative environment, which alleviates some issues with accessing and integrating the datasets following an expedition. However, reviewing and annotating video remains extremely labor and time intensive. Reviewing the video to build a complete and accurate dataset of *Pelagothuria* observations for this study required a significant time commitment, around 10 h beyond the 96 h of video reviewed, and this was for a study for just a single target. Though we know of multiple publicly-available video archives, including from other *Okeanos Explorer* expeditions, this study was limited to a single expedition because of this constraint.

Recommendations to improve the completeness and accuracy of real-time annotations include taxonomic training and delegating individuals to make the annotations. These

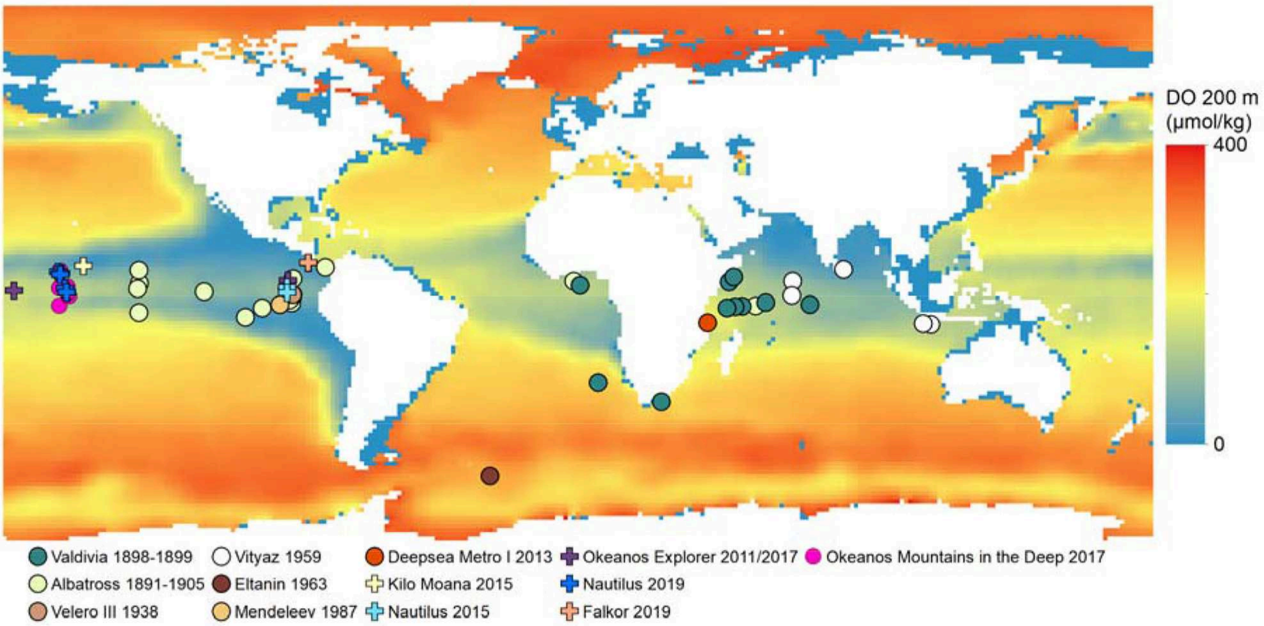

FIGURE 10 | Observations of *Pelagothuria* overlaid on map of dissolved oxygen (μmol kg^{-1}) at 200 m from the NOAA National Center for Environmental Information (NCEI) World Ocean Atlas 2018 (Garcia et al., 2018). Further details on the expeditions are in **Table S1**.

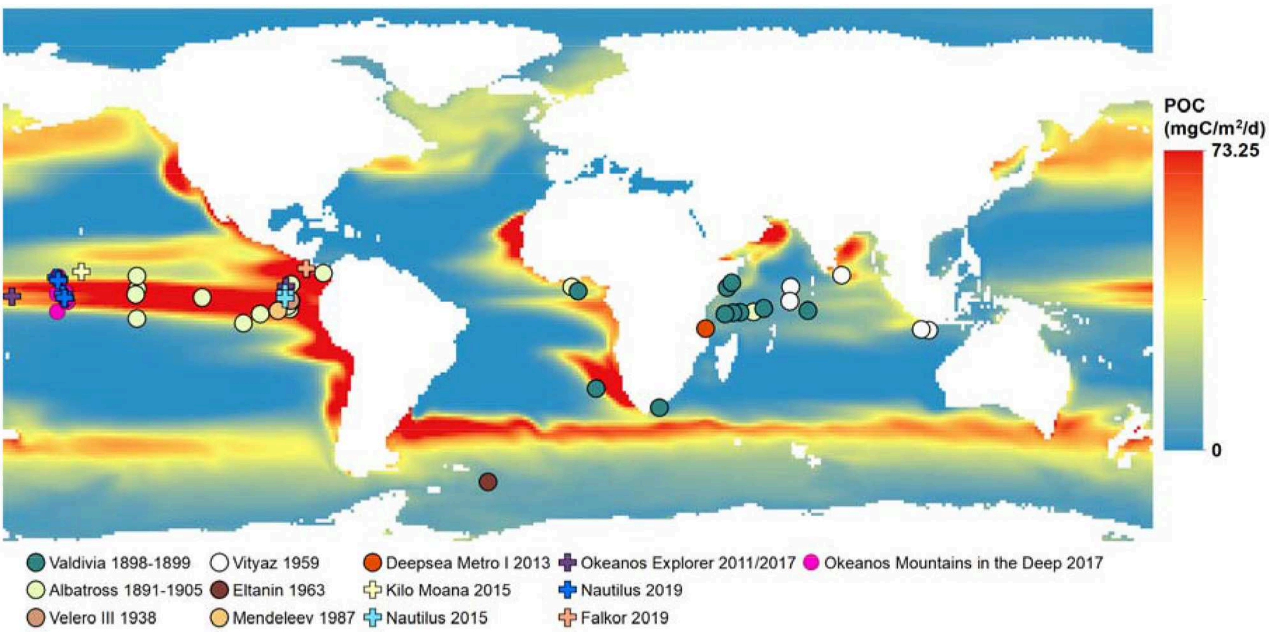

FIGURE 11 | Observations of *Pelagothuria* overlaid on a map of mean particulate organic carbon flux at 500 m as modeled by Yoole et al. (2007, and Yoole, pers. comm.) for years 2000–2009. Further details on the expeditions are in **Table S1**.

recommendations would aid scientists across taxonomic interests and disciplines, and apply to *post hoc* annotations as well. Though there would be costs involved with these approaches (both in money and time), the benefit of having quality-controlled annotations would save scientists significant time in the post-cruise analysis as they would be able to find the video of organisms and features of interest.

A promising opportunity to significantly reduce the time and labor required to make video annotations is to apply machine learning algorithms to image classification. However, many complete and accurate annotations are required in order to train the machine learning algorithms. Other challenges to using machine learning for image classification exist such as the orientation of the marine organism and turbidity of the water (Margolis et al., 2019). Complete and accurate annotations of the whole range of taxa encountered on exploratory expeditions would greatly improve our understanding of biogeography, and provide baseline characterization data at every explored site that can be used to make comparisons between locations and over time.

CONCLUSION

Documented observations of *Pelagothuria* are relatively rare throughout the global ocean, however it is clear from this and several other studies that they are not exactly uncommon. Through this study, we contributed substantially to the number of known encounters with *Pelagothuria*, found evidence that they are able to tolerate highly hypoxic waters, and discovered they associate with the seafloor in fairly significant numbers. Observations throughout the global ocean and over time are required to test whether *Pelagothuria* exist in high abundances in other water masses and conditions and to understand the nature of their association with the seafloor. While this study focused on just a single taxon, we emphasize the value of conducting similar studies on a range of water column organisms in order to provide a comprehensive understanding of abundances and distributions of deep pelagic organisms.

There has been recent interest in increasing understanding of processes and life in the water column (Netburn, 2018). The water column has historically been overlooked by exploration initiatives, despite the outsize role of the deep pelagic environment in supporting marine food webs and fisheries production, and regulating climate through carbon transport to the deep seafloor (Robinson et al., 2010). Data on the diversity and distributions of the organisms living in the water column provide baseline characterizations which may be used to monitor the responses of this community to both natural climate variability and anthropogenic climate change, marine pollution, and overfishing (Ramirez-Llodra et al., 2011). Though *Pelagothuria* are not likely to be the direct targets of fisheries, the high numbers we observed in the Central Pacific Ocean and their circumglobal distributions indicate that they may have a critical role in the marine environment. Thus, understanding their distributions and the factors that support their populations is relevant to understanding the marine environment as a whole. This study demonstrates how dedicating survey time and *post hoc* analysis for water column exploration can fill gaps in our understanding of this underexplored portion of the marine environment. It will take many such studies, as well as a persistent, expansive, and coordinated community effort to achieve the goals of knowing, understanding, and monitoring the distributions and behaviors of the full diversity of fauna in the deep pelagic environment.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

AN led the conceptualization and design of the work, acquisition of data, interpretation of the data, and the writing and editing the paper. GS led the analysis and initial draft of the manuscript, created figures, and contributed to design, writing, and editing of the manuscript. MM contributed to the conceptualization and design of the work, figure generation, and interpretation of the data, particularly with regards to the evaluation of the real-time annotations. He also contributed to writing and editing of the manuscript. All authors approved the final content for submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00684/full#supplementary-material

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