



# An initial ecological characterization of mesopelagic fauna at Johnston Atoll and Musicians Seamounts

Jason Gronich <sup>a,\*</sup>, Adrienne Copeland <sup>b</sup>, Michael Ford <sup>c</sup>, Amanda N. Netburn <sup>b</sup>

<sup>a</sup> CSU Monterey Bay 100 Campus Center Seaside, CA 93955, United States of America

<sup>b</sup> NOAA Ocean Exploration 1315 East West Hwy Silver Spring, MD 20910, United States of America

<sup>c</sup> NOAA 1315 East-West Highway Silver Spring, MD 20910, United States of America



## ARTICLE INFO

### Article history:

Received 7 December 2022

Received in revised form 27 June 2023

Accepted 27 June 2023

Available online 3 July 2023

### Keywords:

Mesopelagic

Deep scattering layer

ROV

Johnston Atoll

Musicians Seamounts

Gelatinous

## ABSTRACT

The mesopelagic region (200–1000 m) hosts a wide variety of organisms in a concentrated layer known as the deep scattering layer (DSL). Much of the mesopelagic region in the central North Pacific remains unexplored, limiting ecosystem considerations in fisheries management and other applications. The National Oceanic and Atmospheric Administration (NOAA) Office of Ocean Exploration and Research used NOAA Ship Okeanos Explorer to conduct two expeditions in the region, one to Johnston Atoll and the other to Musicians Seamounts. During these expeditions, a remotely operated vehicle collected video and CTD environmental data while the ship collected active acoustics. This project analyzed the video, CTD, and acoustic data to create an ecological characterization of the mesopelagic at Johnston Atoll and Musicians Seamounts. The initial characterization included a full inventory of mesopelagic fauna imaged, the relationship between the abundance of categorical groups (gelatinous, Chaetognatha, Crustacea, and fish) and the environmental variables of salinity, oxygen, and temperature, a comparison between the abundance of mesopelagic fauna below, within, and above the DSL, and a qualitative analysis of the spatial distribution of categorical groups. There was a significant negative relationship between the abundance of the gelatinous organisms and salinity and oxygen concentrations. Overall, there were more sightings per minute of all organisms combined below and within the DSL than above the DSL at Musicians Seamounts, while there was no difference in sightings per minute between the below, within, and above DSL groups at Johnston Atoll. Proportionally, there were more gelatinous organisms than any other single category (fish, Chaetognatha, and Crustacea) at all dive sites in the study. These initial characterizations strive to develop biodiversity concepts and the relationships between the environment and fauna. Progress in these areas can aid the management of marine national monuments and serve as a baseline for future ROV dives.

© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## 1. Introduction

The mesopelagic region of the ocean, as defined by [Gjøsaeter and Kawaguchi \(1980\)](#) and [Sutton \(2013\)](#), typically extends from 200 to 1000 m and receives enough sunlight for organisms to discern diel cycles, but too little light for photosynthesis to occur. Despite containing 20% of the ocean's volume, much of the mesopelagic region or "twilight zone" remains unexplored and poorly understood ([Proud et al., 2017](#)). The direct observation of this region is a relatively new endeavor and as such the general knowledge and trends known about the mesopelagic are based upon observations in a small subset of the ocean.

The non-homogeneous region is further distinguished by sinking marine snow, an increase in hydrostatic pressure, an intermittent food supply, and a diverse assemblage of fauna ([Aldredge and Silver, 1988](#); [Lindsay et al., 2015](#); [Robinson et al., 2010](#)). Fauna within this layer participate in diel vertical migration in which they ascend to the epipelagic zone at dusk and then retreat to the darkness of the twilight zone during the day, contributing to the cycling of carbon and other organic matter ([Hays, 2003](#); [Robinson et al., 2010](#)).

Historically, the biomass of fauna within the twilight zone has been underestimated. The diversity of organisms is also not fully known, with a possibility of one million undescribed species ([Klevjer et al., 2016](#); [Robison, 2004](#)). Biomass for sound reflecting organisms is concentrated in the deep scattering layer (DSL) ([Barham, 1963, 1966](#)). The DSL is a vertically expansive layer (sometimes greater than 200 m) within the mesopelagic and relatively denser (backscatter approximately  $1.59 \times 10^{-5} \text{ m}^2 \text{ m}^{-2}$ ) than the rest of the water column ([Proud et al., 2017](#)). The

\* Correspondence to: 40 Park City Court Apt 5105, Sacramento, CA, 95831, United States of America.

E-mail addresses: [jgronich@csumb.edu](mailto:jgronich@csumb.edu) (J. Gronich), [adrienne.copeland@noaa.gov](mailto:adrienne.copeland@noaa.gov) (A. Copeland), [michael.ford@noaa.gov](mailto:michael.ford@noaa.gov) (M. Ford), [amanda.netburn@noaa.gov](mailto:amanda.netburn@noaa.gov) (A.N. Netburn).

density and position of the DSL are highly influenced by the time of day (due to diel vertical migration patterns), surface primary productivity, ocean temperature, and surface wind stress (Proud et al., 2017). Oxygen minimum zones (OMZs; areas with less than 0.5 ml l<sup>-1</sup>) may be present in mesopelagic regions and the amount of dissolved oxygen can affect both the lower and upper boundaries of the DSL (Netburn and Anthony Koslow, 2015) and the intensity of vertical migration (Perelman et al., 2021). Common mesopelagic fauna found throughout the water column include but are not limited to gelatinous zooplankton like salps, appendicularians (larvaceans), siphonophores, ctenophores, and medusae; crustaceans such as copepods and euphausiids; predatory worms like Chaetognatha; cephalopods; midwater fish such as Myctophidae and Gonostomatidae; and a vast array of microorganisms (Irigoien et al., 2014; Robison, 2004). Due to environmental conditions and ecological relationships, the biomass of non-gelatinous organisms tends to decrease exponentially with depth, while the abundance of gelatinous creatures can increase (Aristegui et al., 2009; Lindsay and Hunt, 2005; Reinhaler et al., 2006; Robison et al., 2010; Yamaguchi et al., 2004).

Understanding the ecology of the mesopelagic is vital because the fauna provide an extensive amount of known and unknown ecosystem services. Mesopelagic fauna serves an important food supply for commercial pelagic species (Robison, 2009). For example, Hoki (New Zealand's largest commercial fishery), is supported by the mesopelagic fishes that serve as their main prey items (McClatchie and Dunford, 2003). Furthermore, mesopelagic micronekton are key prey for larger, deep-diving mammals and thus are a necessary part of the food web. Short-finned pilot whales, beaked whales, and sperm whales have been observed foraging in areas with high micronekton backscatter (Copeland et al., 2019). Mesopelagic fauna also serve as a carbon sink in which they store and transport to depth the carbon captured from the atmosphere by phytoplankton at the surface (Hernández-León et al., 2019; Saba et al., 2021). An estimated average of over 40% of the total carbon export in the oligotrophic North Pacific Subtropical Gyre is facilitated by mesopelagic fish alone (Davison et al., 2013). Gelatinous organisms within the mesopelagic have high pharmaceutical and commercial potential, commonly used for medicine, food, and other products (Robison, 2009; Leone et al., 2015).

The techniques and technology used to study the deep sea have evolved over time. Methods have ranged from the landmark oceanographic expedition on the H.M.S. *Challenger* in the late 1800s that used bottom dredging and open water trawl nets (Wüst, 1964); to the decades after World War II that saw the advent of Nansen bottles and closing trawling nets to collect targeted samples at discrete depths (Johnson et al., 1956); to the adaptation of military sonar technology used to discover the deep scattering layer between the late 1940s and 1960s (Sutton, 2013). More recently, surveys with human operated vehicles (HOVs) and remotely operated vehicles (ROVs) mounted with conductivity, temperature, and depth (CTD) sensors have been routinely implemented in ecological and biological studies due to their ability to make direct in situ observations at depth, discretely collect biological samples, and make environmental observations (Kelley et al., 2016; McLean et al., 2020; Robison et al., 2017; Selig et al., 2019). The use of submersible platforms has led to the documentation of known and unknown species, such as the discovery of an undescribed species from the deep-sea Asteroidea Superorders: Valvatacea, Forcipulatacea, Echinodermata (Mah, 2022) and new higher taxa ctenophores, such as *Duobrachium sparksae* (Ford et al., 2020; Lindsay and Miyake, 2007). ROV imaging can reveal new ecological relationships, for example, range shifts of Humboldt squid and their primary prey items, myctophid fishes, in the Monterey Bay region in response to an expanding OMZ (Stewart

et al., 2014). They can also allow for observations of unique behaviors, such as a previously unknown social entanglement behavior exhibited by mesopelagic *Periphylla periphylla* jellyfish in Lurefjorden, Norway or the inverted swimming behavior of the Ram's Horn Squid (Kaartvedt et al., 2015; Lindsay et al., 2020).

As of 2022, only 23.4% of the world's seafloor has been mapped and even less of the midwater has been explored using remote sensing technologies, leaving large gaps in region-specific ecology (Mapping progress, 2022). Places in the North Central Pacific like Johnston Atoll and Musicians Seamounts have been examined before, but not with ROVs and other remote sensing equipment. Instead, previous biological studies at Johnston Atoll have focused on surveying shallow water biodiversity using SCUBA techniques (Kosaki et al., 1991; Lobel et al., 2020; Wagner et al., 2014), tagging (Economakis and Lobel, 1998), genetic analysis studies (Tenggardjaja et al., 2014; Yabsley et al., 2006), and computer simulations (Kobayashi, 2006). Some studies have examined deep-sea fish fauna at Johnston Atoll, but these studies have been limited and focused on trawl surveys and submersibles that visited depths between 40 and 2000 m (Chave and Mundy, 1995). In contrast, previous studies at Musician Seamounts centered around the geologic history of the seamounts and how they relate to the Hawaiian Islands (Li et al., 2008; Sager and Pringle, 1987). Prior to this study, the mesopelagic macrofauna at Johnston Atoll and Musicians Seamounts had yet to be fully examined.

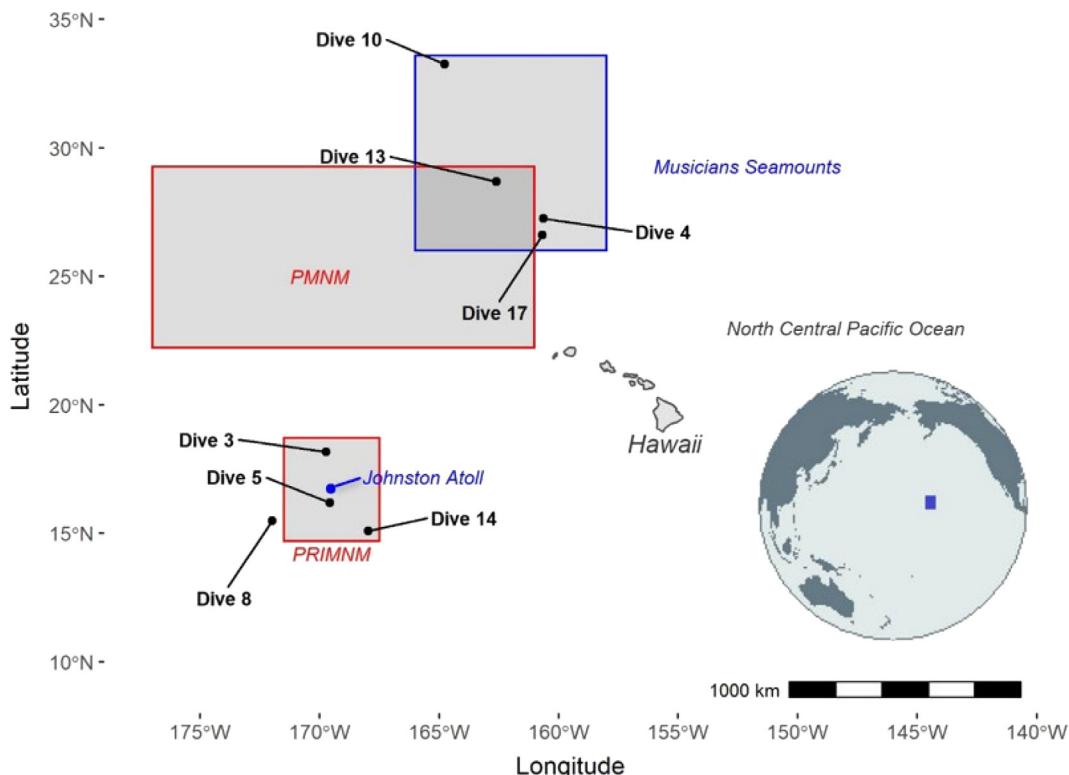
The Campaign to Address Pacific Monument Science, Technology, and Ocean Needs (CAPSTONE), led by the National Oceanic and Atmospheric Administration's (NOAA) Office of Ocean Exploration and Research (OER), was an exploratory mission designed to increase the understanding of the regional biogeography, provide science for management making decisions, and explore mid-water regions (Ford and Netburn, 2017; Netburn et al., 2018; Kennedy et al., 2019). The NOAA Ship *Okeanos Explorer*, collects deep-sea data using ROVs, echosounders, and CTD sensors (Robison et al., 2017; Ford and Netburn, 2017). The purpose of this study was to refine our understanding of the water column distribution of mesopelagic organisms at a regional scale (Johnston Atoll and Musicians Seamounts). This characterization examined the abundance of regional mesopelagic fauna in relation to the environmental conditions of salinity, temperature, and oxygen. Then, the abundance of fauna was compared to the depths of the DSL. Finally, the abundance and proportions of fauna seen was compared spatially across dive sites. These findings were placed in a broader context by comparing patterns seen locally to other mesopelagic studies in the North Central Pacific and across the globe.

## 2. Methods

### 2.1. Study regions

This study focused on two NOAA Ocean Exploration *Okeanos Explorer* missions (Johnston Atoll/EX1706 and Musicians Seamount/EX1708) to two monuments located in the North Central Pacific, Papahānaumokuākea Marine National Monument (PMNM) and Pacific Remote Islands Marine National Monument (PRIMNM) (Fig. 1). PRIMNM and PMNM are especially important as they contain "one million square miles of emergent land, coral reef, ocean, and maritime heritage resources, as well as harbor numerous protected species and likely an abundance of undiscovered resources" (Elliott et al., 2017).

The first expedition, 2017 Laulima O Ka Moana: Exploring Deep Monument Waters Around Johnston Atoll (EX1706), took place from July 7 - August 2, 2017, with the goal of collecting baseline ecological and mapping data around the Johnston Atoll



**Fig. 1.** Depicts the location of the mesopelagic dives for the two study areas: Johnston Atoll (EX1706), denoted by a blue dot, and Musicians Seamounts (EX1708), denoted with a shaded blue rectangle encompassing all seamounts particular to the region. Protected areas within Papahānaumokuākea Marine National Monument (PMNM) and Pacific Remote Islands Marine National Monument (PRIMNM) are represented by red shaded rectangles. The filled blue rectangle on the global inset map indicates the general study area. The ROV dives are indicated by black dots. Each expedition had four ROV dives exploring the mesopelagic zone: EX1706 - dives 3, 5, 8, and 14 and EX1708 - dives 4, 10, 13, and 17. See [Table 1](#) for specific information on the transect depths for each dive. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

A summary of the mesopelagic dives for the Johnston Atoll (EX1706) and Musicians Seamounts (EX1708) expeditions. Includes information about the expedition number, dive number, dive name, date, latitude, longitude, time range (converted from UTC to local Hawaiian standard time) transect depths (meters) and times (mins) in parentheses, and a link to the original SeaTube footage.

Dive #	Dive name	Date	Latitude	Longitude	Time range (local time)	Transect depth (m) for time (min) format: Depth (min)	SeaTube link
<b>Johnston Atoll (EX1706)</b>							
3	Unnamed Seamount	7/14/2017	18.15335	-169.73398	16:18 – 18:18	800 (11), 700 (10), 600 (11), 500 (11), 400 (10), 300 (11)	<a href="https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=603">https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=603</a>
5	Sally Seamount	7/17/2017	16.79496	-169.56541	16:18 – 18:17	900 (10), 700 (9), 550 (10), 500 (10), 400 (10), 350 (10)	<a href="https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=623">https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=623</a>
8	Pierpoint Seamount	7/22/2017	15.47146	-171.99310	15:57 – 18:17	800 (14), 700 (11), 600 (15), 500 (15), 400 (10), 300 (10)	<a href="https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=653">https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=653</a>
14	Keli Ridge	7/28/2017	15.09452	-167.95966	16:17 – 18:15	800 (10), 700 (12), 600 (12), 500 (10), 400 (10), 300 (11)	<a href="https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=713">https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=713</a>
<b>Musicians Seamounts (EX1708)</b>							
4	Sibelius Seamount	9/10/2017	27.24802	-160.63327	16:20 – 18:21	800 (10), 700 (14), 600 (10), 500 (15), 400 (10), 300 (10)	<a href="https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=1470">https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=1470</a>
10	Shostakovich Seamount	9/16/2017	33.25124	-164.76734	16:09 – 17:26	800 (10), 700 (10), 600 (12), 500 (10)	<a href="https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=843">https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=843</a>
13	Paganini Seamount	9/19/2017	28.68279	-162.60977	16:27 – 18:08	800 (10), 700 (10), 500 (10), 300 (10)	<a href="https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=873">https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=873</a>
17	Rapano Ridge	9/23/2017	26.59547	-160.67291	16:06 – 18:01	800 (13), 700 (10), 600 (10), 500 (12), 300 (10)	<a href="https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=913">https://data.oceannetworks.ca/SeaTubeV3?resourceType=600&amp;resourceId=913</a>

Unit (JAU) of the PRIMNM (Kelley et al., 2019). The JAU is located approximately 800 nautical miles southwest of the main Hawaiian Islands chain and includes a wide variety of underwater seamounts that host a diversity of aquatic life (Fig. 1). A total of four exploratory mesopelagic ROV dives were conducted at targeted seamounts and ridges. Six horizontal transects (i.e., at near constant depth) were run for each dive, at depths ranging

from 300 to 900 m, and for durations ranging from 9 to 15 min. For specific information about each dive location, refer to [Table 1](#).

The second expedition, Deep-Sea Symphony: Exploring the Musicians Seamounts (EX1708), occurred from September 6–30, 2017, to the Musicians Seamounts, located approximately 650 nautical miles northwest of the Hawaiian Ridge and near the PMNM (Cantwell et al., 2020) (Fig. 1). This expedition had four

mesopelagic ROV dives at predetermined seamounts and ridges. Dive four had six transects, ranging from depths of 300 to 800 m, and ranging in duration from 10 to 15 min. Due to time constraints and a technical glitch in which the video stream was interrupted, dives 10 and 13 conducted four transects each, covering depths between 300 and 800 m, and durations ranging from 10 to 12 min. Dive 17 had 5 mesopelagic transects, covering depths between 300 and 800 m, and durations from 10 to 13 min. For more specific information on each dive, refer to Table 1. All midwater transects for EX1706 and EX1708 occurred between 1:30 and 4:30 UTC (3:30 to 6:30 pm local time), with sunset occurring between 5:10 and 5:18 UTC (7:10 and 7:18 PM HST) for EX106 and 4:14 and 4:43 UTC (6:14 and 6:43 PM HST) for EX1708.

## 2.2. Video data

During EX1706 and EX1708 the two-part system, the ROV *Deep Discoverer* (D2) and its accompanying camera sled, *Seirios*, used Insite Pacific "Zeus Plus" HD Video Cameras to capture video footage. The video was recorded at a resolution of 1920 x 1080 pixels and using a frame rate of 29.97i. Specifics regarding the lighting and color correction used to produce the video is found in Ford et al. (2020).

The ROV maintained a near constant depth during the mid-water transects and recorded various targets while moving forward for a predetermined amount of time, between 9–15 min. These were exploratory transects that did not have a set transit speed, distance, or camera zoom and were occasionally interrupted to image specific targets. All organisms, including copepods when they could be clearly identified by shape or movement, were counted and identified to the most descriptive taxonomic level possible without compromising accuracy using SeaTube V2 (<https://data.oceanetworks.ca/SeaTubeV2>). The video footage was rigorously reviewed in consultation with experts and then annotated with the World Register of Marine Species (WoRMS). All original comments from offshore participants are preserved within SeaTubeV2 and are available to the public. Consult Table 1 for transect times. See Fig. 2 for examples of organisms encountered on these expeditions.

Once the transect was complete, the ROV would ascend approximately 100 m and repeat the transect process. On most dives the pilots would conduct two transects outside the DSL (800 and 300 m) and four within the DSL (700, 600, 500, and 400 m). The DSL depth was determined by active acoustic data.

## 2.3. Acoustic data

Active acoustic data were collected with a hull mounted calibrated Simrad EK60 multi-frequency echosounder. The echosounder was calibrated using standard techniques (Foote, 1987; Demer et al., 2015). The echosounder began recording data prior to the start of each ROV dive and collected data at 18, 70, 120, and 200 kHz frequencies until the ROV was brought back to the surface. For this paper, the 18 kHz frequency was used instead of 38 kHz frequency, because the 38 kHz caused interference between the ROV USBL navigation and multibeam sonar, which may have led to navigation errors and risked the safety of the ROV. The 18 kHz data was analyzed and cleaned with a power of 2000 W and a pulse length of 8.192 ms in Echoview V11.0.304 (Echoview Software Pty Ltd, 2013), using the impulse noise control and reduced pings operands. The mean volume backscattering strength (mean Sv;  $\text{dB re m}^2/\text{m}^3$ ) minimum threshold was set to  $-80 \text{ dB re m}^2/\text{m}^3$  to better identify the DSL (Colombo et al., 2003). A bottom line was placed to outline the upper boundary of the seafloor. To outline the range of the DSL, a maximum Sv algorithm, with a

minimum Sv value at  $-70 \text{ dB re m}^{-1}$ , was used to mark the lower depth boundary and the upper depth boundary. The maximum Sv algorithm spans the gaps in between the acoustic backscatter to create the boundary line. The upper and lower depth DSL boundary lines were visually inspected and edited to fit the data when the algorithm detection and a visual assessment were not matched. Once the lines sufficiently captured the DSL boundaries, they were exported to a csv file and analyzed in RStudio V4.0.2 (RStudio, 2020).

## 2.4. CTD data

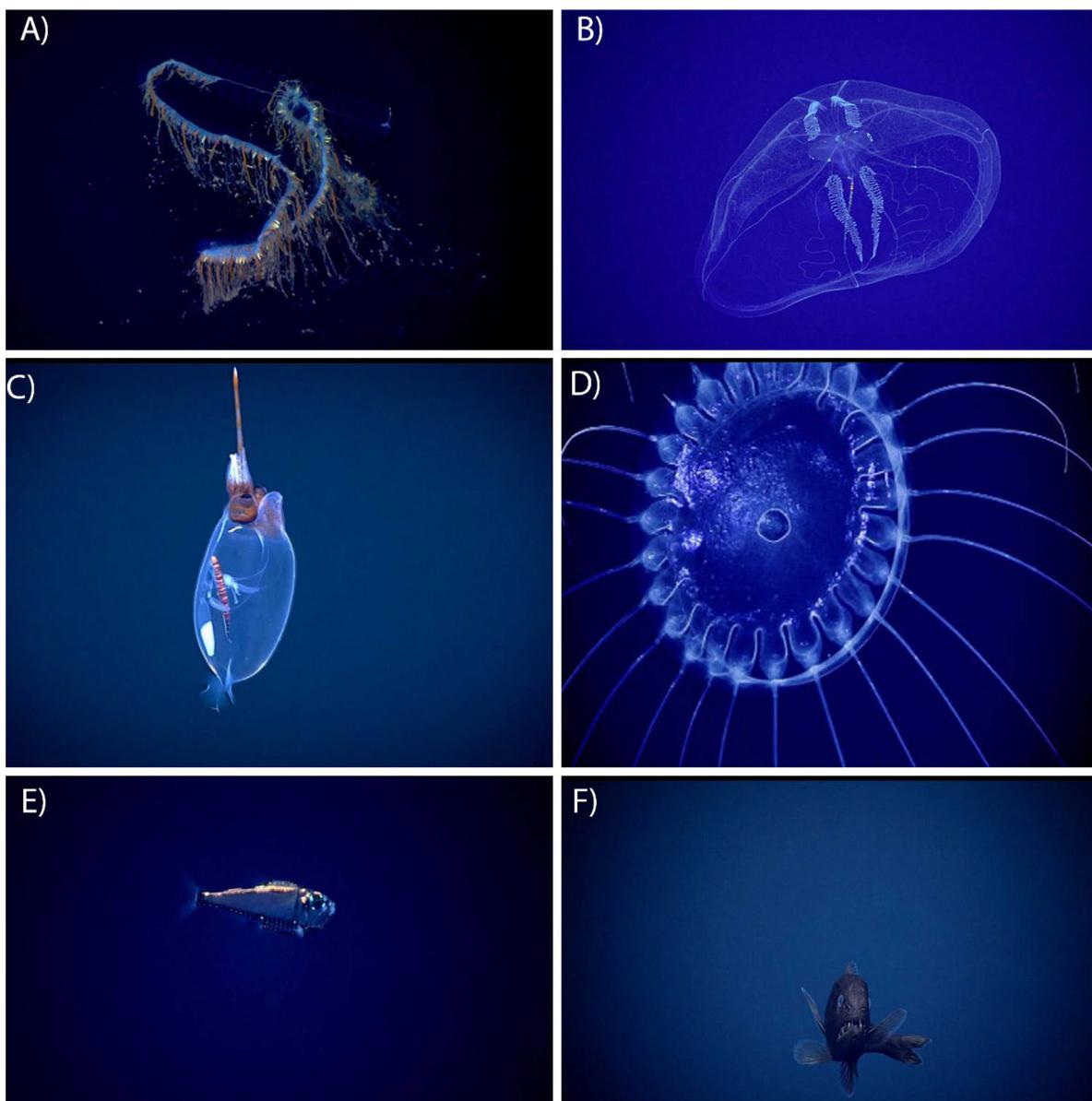
Calibrated SeaBird SBE-911 Plus CTD sensors on ROV D2 and camera sled *Seirios* collected data on conductivity (used to calculate salinity), temperature, depth, and dissolved oxygen at a rate of up to 22 times a second from the start to the end of the dive (Fig. 3). A ROV-mounted Paroscientific 8B7000-I depth sensor was used to record the depth and a Tracklink 10000 Ultra Short Baseline (USBL) Acoustic Tracking System was used to record position. The salinity, temperature, depth, and dissolved oxygen data from D2 and *Seirios* were compared graphically and used in the analysis. D2 data was used preferentially because it is the platform that housed the main video camera. *Seirios* was used as a backup when the D2 data stream was interrupted and recorded incorrect values. The CTD downcast data were converted using SBE data processing software V7.27.2 and decimated by a pressure increment of one (Sea-Bird Scientific, 2017) (see Fig. 3).

## 2.5. Data analysis

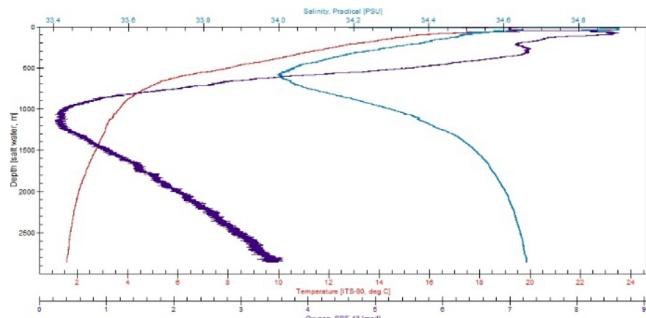
There were four dives (24 transects, 263 total minutes) at Musicians Seamounts and four dives (19 transects, 206 total minutes) at Johnston Atoll (Table 1). The depths of these transects ranged from 300 to 900 m. Transects were nonlinear and conducted for 9 to 15 min. An inventory of mesopelagic organisms was created from the reviewed annotations (Table 2) and the number of sightings for each individual species was totaled. Due to low sample sizes, the individual species were further organized into four categorical groups (example families are in parentheses): Chaetognatha, Crustacea (*Harpacticidae*, *Sergestidae*, and *Euphausiidae*) fish (*Myctophidae*, *Gonostomatidae*, and *Sternopychidae*) and gelatinous (*Salpidae*, *Cuninidae*, *Halicreatidae*, *Agalmatidae*, *Rhopalonemidae*, and *Thalassocalycidae*). These groupings are not functional in nature and instead represent the dominant types of organisms seen. The total number of sightings of each categorical group was averaged across each transect and then standardized by dividing the number of minutes taken to complete the transect (Table 3) (Costello et al., 2005; Söflker et al., 2011). Time, instead of distance, was used to standardize the average sightings because each transect was constrained by an ideal time range, the ROV did not move at a constant speed, and it occasionally stopped. The nonlinear nature of the exploratory transects makes calculating the distance using the latitude and longitude of each point on the transect impractical. The average sightings per minute is used as a proxy for abundance and will be abbreviated as such for the rest of the paper. This proxy method was used in similar studies: Hoving et al. (2019), Hidaka et al. (2021), Lindsay and Hunt (2005), Selig et al. (2019).

### 2.5.1. Abundance in relation to environmental parameters

To evaluate the difference in total abundance of fauna between expeditions, the mean fauna abundance was calculated across all transects for each expedition and then tested with a Wilcoxon rank sum test (RStudio, 2020). If a significant difference was



**Fig. 2.** Screenshots of marine organisms recorded by the ROV *Deep Discover* during midwater transects on expeditions at Johnston Atoll and Musicians Seamounts. (A) Siphonophore – EX1708, Dive 17, 600 m. (B) *Thalassocalyce* sp. – EX1706, Dive 8, 600 m. (C) Cranchiid Squid – EX1708, Dive 8, 700 m. (D) *Solmissus* sp. – EX1708, Dive 17, 700 m. (E) *Argyropelecus* sp. (Hatchet Fish) – EX1708, Dive 4, 500 m. (F) *Anoplogaster* sp. (Fangtooth Fish) – EX1708, Dive 17, 800 m.



**Fig. 3.** Example of CTD collected during each dive. Salinity (light blue), temperature (° C) (red), and dissolved oxygen concentration (mg/l) (purple) are plotted with respect to depth (m). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

found, then the expedition was added to the model as a random effect.

The abundance data for each transect was then combined with the environmental data to build a mixed effects linear model that explains the distribution of organisms in relation to depth and the environmental parameters of oxygen concentration (mg/l), salinity, and temperature (° C) (v1.1-26; (Bates et al., 2015)). A separate model was run for each categorical group. Expedition was used as a random effect in each of the models (when expedition was significant).

The general mixed linear model (Eq. (1)) is as follows:

$$\text{Abundance} = \beta + \mu_{\text{oxygen}} + \mu_{\text{salinity}} + \mu_{\text{temperature}} \quad (1)$$

General mixed effects linear model relating the abundance of fauna to environmental parameters where  $\mu_{\text{oxygen}}$ ,  $\mu_{\text{salinity}}$ ,  $\mu_{\text{temperature}}$  are the average environmental parameter for each transect depth for all dives and both expeditions.

**Table 2**

An inventory of all mesopelagic fauna seen, identified, and annotated using WoRMS during dives at Johnston Atoll (EX1706) and Musicians Seamounts (EX1708). The categorical grouping that each phylum belongs to can be seen on the leftmost column. The total number of sightings for each taxonomic rank is given and is indicative only on the ranking it corresponds to (not additive to lower taxonomic classifications). A blank space indicates that the fauna was not seen.

EX1706 Johnston Atoll										
Categorical group	Phylum	Class	Order	Family	Genus	Species	Dive 3	Dive 5	Dive 8	Dive 14
Gelatinous	Annelida	Polychaeta	Phyllodocida	Tomopteridae	<i>Tomopteris</i>		1			
Crustacea	Arthropoda	Hexanauplia						2	1	
		Malacostraca	Amphipoda				1	1	2	
			Decapoda				2	1	1	
				Sergestidae			1	1	1	
					<i>Sergestes</i>		1	1		
		Euphausiacea	Euphausiidae		<i>Euphausia</i>		1		2	
Chaetognatha	Chaetognatha						4	2	3	2
Fish	Chordata	Actinopterygii					11	12	12	8
		Anguilliformes	Nemichthysidae	<i>Nemichthys</i>			1			
			Nettastomatidae	<i>Leptocephalus</i> (larva)						1
			Serrivomeridae	<i>Serrivomer</i>			2	4	4	
					<i>Serrivomer</i>		1			
					<i>beanii</i>					
		Aulopiformes	Notosudidae				1			
		Mycetophiformes	Myctophidae				2	1		
		Stomiiformes	Gonostomatidae				1	1		
				<i>Cyclothona</i>			6	5	4	6
				<i>Gonostoma</i>			4	3	4	6
					<i>Gonostoma</i>		2	3	3	6
			Sternopychidae	<i>Sigmops</i>			1			
				<i>Argyropelecus</i>						
				<i>Sternopyx</i>						
					<i>Sternopyx</i>		1			
					<i>diaphana</i>					
Gelatinous	Appendicularia						4	6	9	4
	Copelata						4	2	1	2
		Oikopleuridae					1	1		
				<i>Bathochordaeus</i>			1			
				<i>Mesochordaeus</i>						
	Thaliacea	Salpida					3	3	5	1
			Salpidae				1	3	5	1
Gelatinous	Cnidaria	Hydrozoa					17	12	16	15
		Narcomedusae	Aeginidae	<i>Bathykorus</i>			1		2	
			Cuninidae	<i>Solmissus</i>			3		2	
			Solmundaeginidae	<i>Solmundella</i>				1	1	
					<i>Solmundella</i>		1			
		Siphonophorae	Agalmatidae	<i>Agalma</i>			5	5	4	8
			Prayidae				1	1		1
		Trachymedusae	Halicreatidae	<i>Praya</i>			2	2		2
				<i>Halicsera</i>			2			1
				<i>Halitrephe</i>				1		
			Rhopalonematidae	<i>Arctapodema</i>			2	1	1	2
				<i>Colobonema</i>			1	1		
				<i>Tetrorchis</i>					1	2
Gelatinous	Ctenophora	Tentaculata					3	3	7	3
		Lobata	Bathocyroidae	<i>Bathocyroe</i>						1
		Thalassocalycida	Thalassocalycidae	<i>Thalassocalyce</i>					3	
				<i>inconstans</i>						
Gelatinous	Mollusca	Gastropoda	Pteropoda	Cavoliniidae	<i>Diacria</i>			1		
							1			

(continued on next page)

**Table 2** (continued).

B.								EX 1708 Musicians Seamounts			
Categorical group	Phylum	Class	Order	Family	Genus	Species		Dive 4	Dive 10	Dive 13	Dive 17
Gelatinous	Annelida	Polychaeta									1
Crustacea	Arthropoda	Hexanauplia	Harpacticoida	Harpacticidae				1	2	1	1
		Malacostraca	Decapoda					1			
			Euphausiacea	Sergestidae	<i>Sergestes</i>			4	1		
				Euphausiidae				1		1	2
						<i>Euphausia</i>				1	2
Chaetognatha	Chaetognatha							6	7	3	8
Fish	Chordata	Actinopterygii	Beryciformes	Anoplogastridae	<i>Anoplogaster</i>			12	7	5	8
			Myctophiformes	Myctophidae				5	1	2	
			Osmeriformes	Bathylagidae					1		
			Stephanoberyciformes	Microstomatidae	<i>Microstoma</i>					1	
			Stomiiformes	Melamphaidae							1
				Gonostomatidae	<i>Cyclothona</i>			4	5		5
					<i>Gonostoma</i>			5			
				Sternoptychidae	<i>Argyropelecus</i>			2		1	
						<i>Argyropelecus gigas</i>		1			1
Gelatinous	Appendicularia							5		4	5
		Copelata	Oikopleuridae	<i>Bathochordaeus</i>				1		1	3
		Thaliacea	Salpida	<i>Mesochordaeus</i>						1	
				<i>Erythrocephalus</i>						1	
Gelatinous	Cnidaria	Hydrozoa	Narcomedusae	Cuninidae	<i>Solmissus</i>			15	13	10	17
					<i>Solmissus incisa</i>			3	3	1	1
			Siphonophorae	Solmundaeginidae	<i>Solmundella</i>			3			1
								9	5	4	10
			Trachymedusae	Agalmatidae	<i>Agalma</i>	<i>Agalma elegans</i>				1	
					<i>Frillagalma</i>	<i>Frillagalma vityazi</i>				1	2
				Prayidae	<i>Praya</i>			1			1
				Halicreatidae	<i>Halicreas</i>	<i>Halicreas minimum</i>		2		1	
					<i>Halitrephe</i>					1	
				Rhopalonematidae	<i>Arctapodema</i>			1		3	3
					<i>Colobonema</i>			1		1	
		Scyphozoa	Coronatae	Periphyllidae	<i>Periphyllopsis</i>						1
			Semaeostomeae	Ulmaridae	<i>Poralia</i>	<i>Poralia rufescens</i>		2	1	1	
Gelatinous	Ctenophora	Tentculata	Cydippida					2	1	1	
			Lobata	Bathocyroidae	<i>Bathocyroe</i>			1		1	1
			Thalassocalycida	Thalassocalycidae	<i>Thalassocalyce</i>	<i>Bathocyroe fosteri</i>				1	
Gelatinous	Mollusca	Cephalopoda	Oegopsida	Cranchiidae		<i>Thalassocalyce inconsans</i>					1
					<i>Helicocranchia</i>					1	1

### 2.5.2. Abundance in relation to the deep scattering layer (DSL)

We combined the DSL boundary data with the ROV annotations in order to determine the abundance within and outside of the DSL. Since there was a difference in abundance between Johnston Atoll and Musicians Seamounts, we separated each expedition and then subsetted the transects based on their position relative to the DSL: "in", "above", and "below". A Wilcoxon Rank Sum Test was used to determine the difference in abundance within, below, and above DSL (RStudio, 2020).

### 2.5.3. Spatial distribution of categorical groups

To qualitatively assess the spatial distribution of the four categorical groups, sightings per minute of each categorical group were divided by the total sightings per minute of all organisms seen for each ROV dive. The categorical group proportions were graphed as pie charts using Scatterpie (Yu, 2017) and positioned on a map according to their geographic coordinates (RStudio, 2020).

**Table 3**

An abbreviated inventory of all mesopelagic fauna seen, identified, and annotated using WoRMS during dives at Johnston Atoll (EX1706) and Musicians Seamounts (EX1708) used for data analysis. The categorical grouping that each phylum belongs to can be seen on the leftmost column. The total number of sightings per minute for each taxonomic rank is given and is indicative only on the ranking it corresponds to (not additive to lower taxonomic classifications). A blank space indicates that the fauna was not seen.

		EX1706 Johnston Atoll				
Categorical group	Phylum	Class	Dive 3	Dive 5	Dive 8	Dive 14
Gelatinous	Annelida	Polychaeta			0.07	0.07
Crustacea	Arthropoda	Hexanauplia	0.10	0.31	0.28	0.38
		Malacostraca	0.10	0.31	0.14	0.08
Chaetognatha	Chaetognatha		0.39	0.20	0.24	0.30
Fish	Chordata	Actinopterygii	1.60	2.17	1.98	1.18
			1.02	1.23	0.79	0.72
Gelatinous		Appendicularia	0.38	0.62	0.76	0.37
		Thaliacea	0.29	0.31	0.43	0.10
Gelatinous	Cnidaria		1.59	1.23	1.29	1.40
		Hydrozoa	1.59	1.23	1.29	1.40
Gelatinous	Ctenophora		0.30	0.20	0.50	0.28
		Tentaculata			0.23	0.10
		EX 1708 Musicians Seamounts				
Categorical group	Phylum	Class	Dive 4	Dive 10	Dive 13	Dive 17
Gelatinous	Annelida	Polychaeta			0.10	0.10
Crustacea	Arthropoda	Hexanauplia	0.54	0.30	0.20	0.38
		Malacostraca	0.10	0.10	0.10	0.28
			0.44	0.10	0.10	
Chaetognatha	Chaetognatha		0.57	0.65	0.30	0.75
Fish	Chordata	Actinopterygii	1.45	0.75	1.00	1.11
			1.01	0.65	0.50	0.67
Gelatinous		Appendicularia	0.44		0.40	0.44
		Thaliacea		0.10	0.10	
Gelatinous	Cnidaria		1.42	1.27	1.10	1.64
		Hydrozoa	1.22	1.17	1.00	1.56
		Scyphozoa	0.20	0.10	0.10	0.08
Gelatinous	Ctenophora		0.24	0.10	0.30	0.46
		Tentaculata	0.10		0.20	0.26
Gelatinous	Mollusca				0.10	0.10
		Cephalopoda			0.10	0.10

### 3. Results

#### 3.1. Abundance in relation to environmental parameters

There was a total of 43 transects used to assess the relationship between abundance (average sightings per minute) of the four categorical groups and environmental parameters. (Table 1). There was a significantly higher abundance of organisms sighted at Musicians Seamounts when compared to Johnston Atoll ( $W = 2903$ ,  $p$ -value = 0.01943) (Fig. 4) and so the expedition was added as a random effect to the mixed effects linear model.

The abundance of gelatinous organisms was negatively correlated with oxygen concentration ( $p = 0.010$ ) and salinity ( $p = 0.001$ ); temperature was not significantly related ( $p = 0.249$ ). As the average oxygen concentration (mg/l) increased, the abundance of gelatinous organisms decreased (Fig. 5 A). Similarly, as the average salinity increased, the abundance of gelatinous organisms decreased (Fig. 5B). The nonsignificant relationship between temperature and abundance of gelatinous organisms is not shown. The gelatinous categorical group mixed model accounts for 29.5% of the variation found in the abundance of gelatinous fauna (Table 4). Neither Crustacea, fish, nor Chaetognatha abundance had significant relationships with the environmental variables of oxygen ( $p = 0.823$ , 0.591, 0.084), salinity ( $p =$

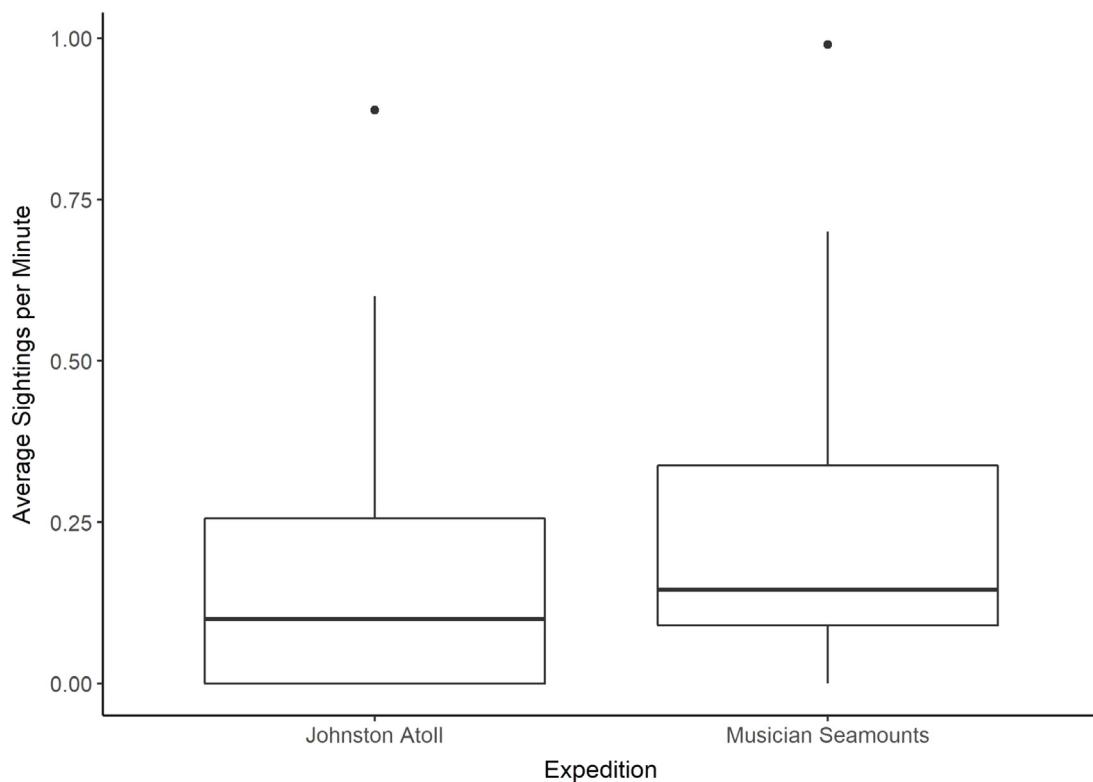
0.885, 0.388, 0.262), and temperature ( $p = 0.305$ , 0.631, 0.401) (Table 4).

#### 3.2. Abundance in relation to the deep scattering layer

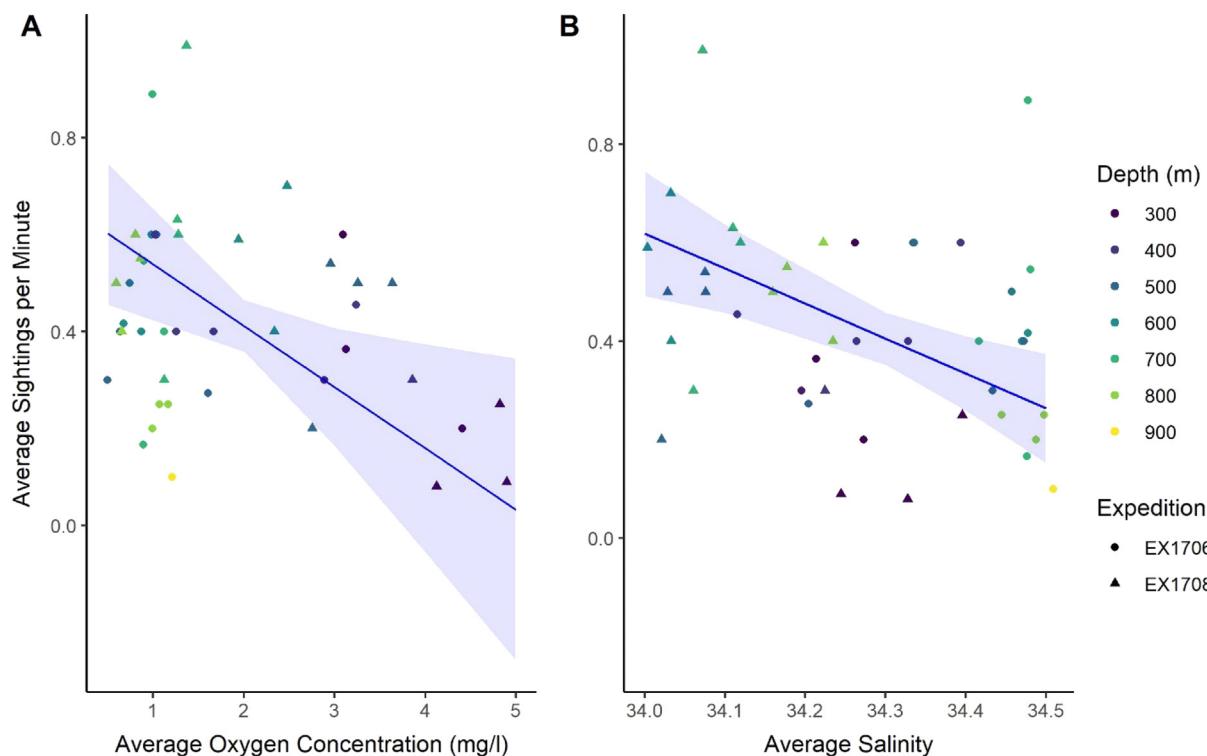
At Johnston Atoll, there were 14 transects within the DSL and 10 transects outside of the DSL (6 below and 4 above); Musicians Seamount had 10 transects within the DSL and 9 transects outside the DSL (6 below and 3 above). For Johnston Atoll, there was no significant difference between the overall median sightings per minute within the DSL compared to below the DSL ( $W = 736$ ,  $p = 0.246$ ), above the DSL ( $W = 535$ ,  $p = 0.110$ ), nor between the above and below DSL groups ( $W = 217$ ,  $p = 0.240$ ) (Fig. 6 A). In contrast, Musicians Seamount had higher median sightings per minute within and below the DSL when compared to above ( $W = 377.5$ ,  $p = 0.001$ ;  $W = 204$ ,  $p = 0.022$ ), while there was no significant difference between the below and within group ( $W = 541.5$ ,  $p$ -value = 0.197) (Fig. 6B).

#### 3.3. Spatial distribution of categorical groups

Johnston Atoll ROV dives to Unnamed Seamount (Dive 3), Sally Seamount (Dive 5), Pierpont Seamount (Dive 8), and Keli Ridge (Dive 14) had total average fauna sightings per minute



**Fig. 4.** Differences between the average sightings per minute of all observed organisms between the two expedition locations: Johnston Atoll and Musicians Seamounts. There were significantly more average sightings per minute at Musicians Seamount when compared to Johnston Atoll. The horizontal lines in the boxplot represent the median, the boxes represent the interquartile range, the whiskers represent the data values between the interquartile range and either the minimum/maximum, and the dots represent outliers.

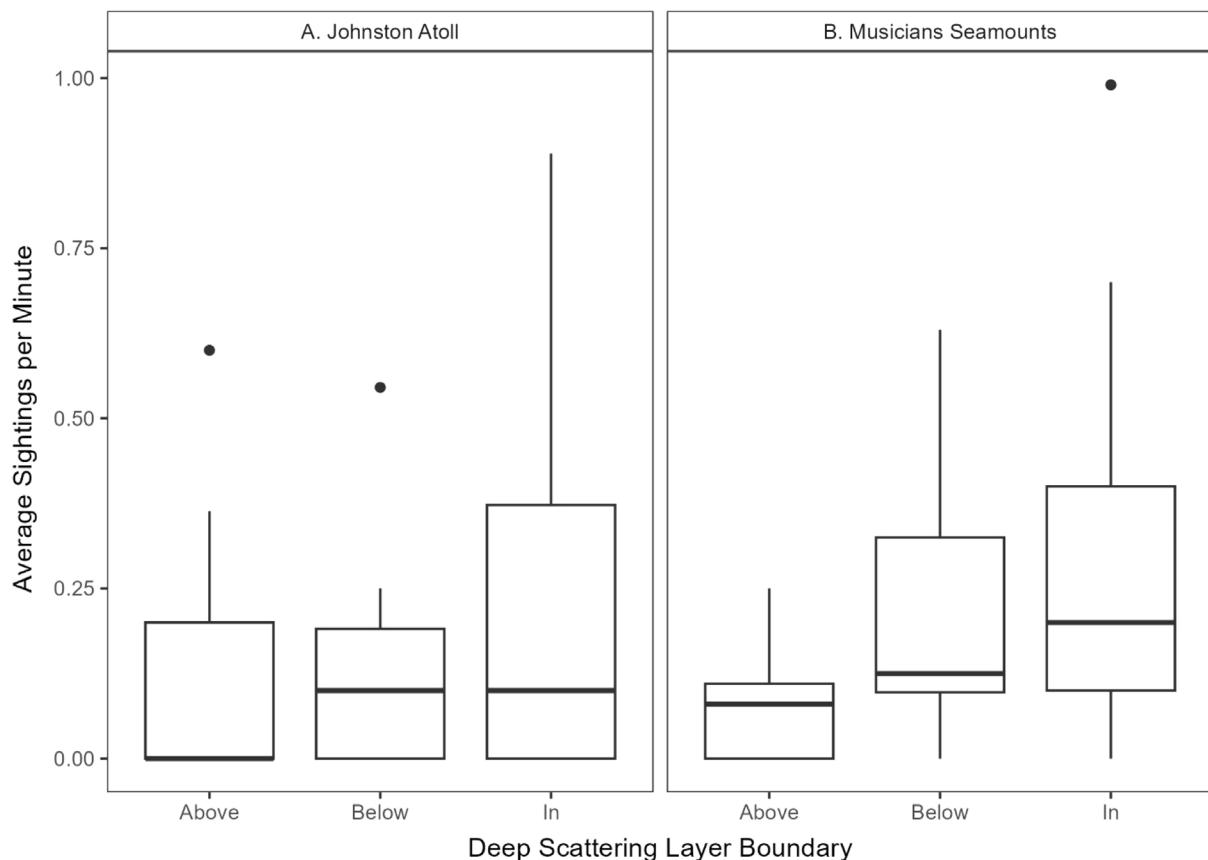


**Fig. 5.** A & B. Relationship between the abundance of gelatinous organisms when compared to (A) average oxygen concentration levels and (B) average salinity levels. The points depict the abundance of gelatinous organisms in comparison to the average oxygen concentration or average salinity of each transect and the depth (m) and location is denoted by color and shape respectively. The blue line demonstrates the fitted regression model. The shaded blue area represents the 95% confidence interval. As average oxygen levels and average salinity increased, the average sightings per minute of gelatinous organisms decreased. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 4**

Summary of environmental mixed linear regressions for the Crustacea, Gelatinous, Fish, and Chaetognatha categorical groups. The models for the Crustacea, Fish, and Chaetognatha categorical groups were not significant. The average sightings per minute for the Gelatinous group decreased as the oxygen concentration (mg/l) and salinity increased.

Predictors	Crustacea			Gelatinous			Fish			Chaetognatha		
	Estimates	CI	p value	Estimates	CI	p value	Estimates	CI	p value	Estimates	CI	p value
(Intercept)	0.93	8.61 – 10.46	0.849	24.79	10.55 – 39.03	<b>0.001</b>	5.38	–6.17 – 16.93	0.361	3.51	–2.48 – 9.49	0.251
Oxygen (mg/l)	–0.01	–0.07 – 0.05	0.823	–0.13	–0.22 – 0.03	<b>0.01</b>	–0.02	–0.10 – 0.06	0.591	0.04	–0.00 – 0.07	0.084
Salinity	–0.02	–0.30 – 0.26	0.885	–0.71	–1.13 – 0.29	<b>0.001</b>	–0.15	–0.49 – 0.19	0.388	–0.1	–0.28 – 0.08	0.262
Temperature (C°)	–0.01	–0.30 – 0.04	0.305	0.03	–0.02 – 0.07	0.249	–0.01	–0.05 – 0.03	0.613	–0.01	–0.03 – 0.01	0.401
<b>Random Effects</b>												
$\sigma^2$	0.01			0.03			0.02			0		
N (Expedition)	2			2			2			2		
Observations	43			43			43			43		
Marginal R <sup>2</sup>	0.117			0.295			0.114			0.257		



**Fig. 6.** A & B. Sightings per minute of all organisms above, below, or within the deep scattering layer for Johnston Atoll, plotted on the left, and for Musicians Seamounts, plotted on the right. The median of the sample is represented by the bold horizontal line, the interquartile range is represented by the non-bold box. The lines extending from the box demonstrate the outer quartiles while the black dots show outliers. The above group was not significantly different in median sightings per minute, compared to the below or within group for Johnston Atoll. For Musicians Seamounts, the abundances of the below and within group were significantly higher than for the above group.

of 0.6455, 0.7056, 0.6754, 0.5245 respectively (Table 5). Musicians Seamounts ROV dives to Sibelius Seamount (Dive 4), Shostakovich Seamount (Dive 10), Paganini Seamount (Dive 13), and Rapano Ridge (Dive 17) had total average fauna sightings per minute of 0.9450, 0.8775, 0.7250, 0.9000 respectively (Table 5). Musician Seamounts had higher total fauna sightings per minute overall when compared to Johnston Atoll (Fig. 7). Johnston Atoll had a higher average proportion of gelatinous (63.06%) and

fish (23.52%) fauna when compared with Musicians Seamounts (53.41% and 18.45%). Conversely, Musicians Seamounts had a higher proportion of Crustacea (15.29%) and Chaetognatha (12.85%) when compared to Johnston Atoll (7.59% and 5.83%).

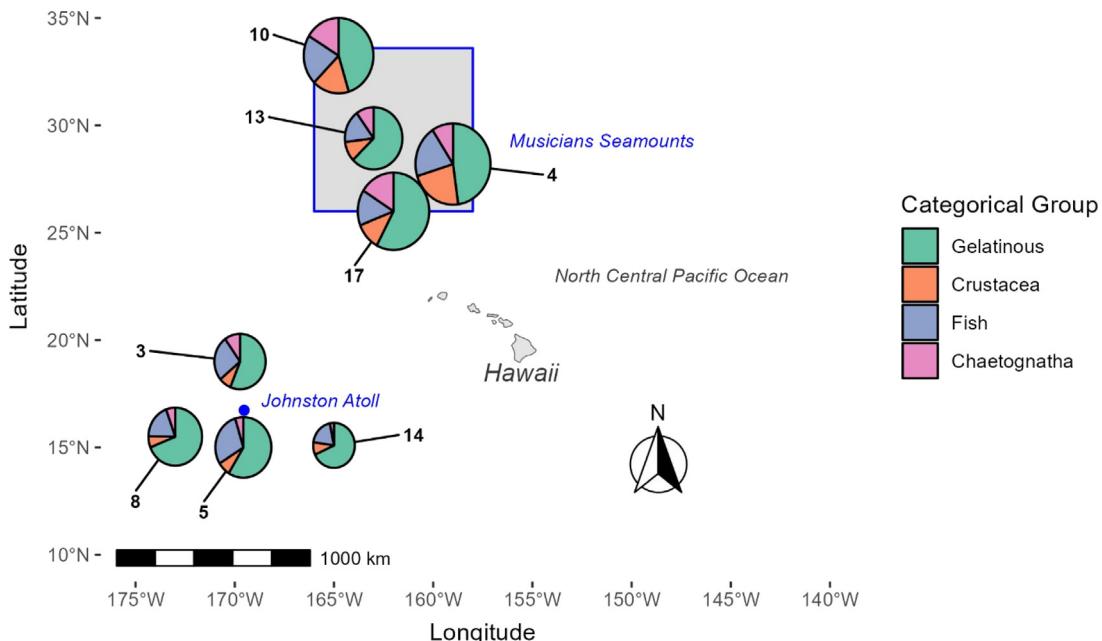
#### 4. Discussion

The ROV transects for Johnston Atoll and Musicians Seamounts took place two months and approximately 700nm (12 degrees in

**Table 5**

Proportion of average sightings per minute for each categorical group across dives from the Johnston Atoll and Musicians Seamounts expeditions.

Expedition	Date	Latitude	Longitude	Dive	Depth range (m)	Average sightings per minute	Proportion of total average sightings per minute			
							Gelatinous	Crustacea	Fish	Chaetognatha
EX1706	7/14/2017	18.15335	-169.734	3	300-800	0.645455	0.562207	0.077465	0.261737	0.098592
EX1706	7/17/2017	16.79496	-169.565	5	350-900	0.705556	0.587927	0.073491	0.291339	0.047244
EX1706	7/22/2017	15.47146	-171.993	8	300-800	0.675379	0.689849	0.062722	0.191905	0.055524
EX1706	7/28/2017	15.09452	-167.96	14	300-800	0.524495	0.682234	0.090034	0.195956	0.031777
EX1708	9/10/2017	27.24802	-160.633	4	300-800	0.945	0.477954	0.223986	0.206349	0.091711
EX1708	9/16/2017	33.25124	-164.767	10	500-800	0.8775	0.452991	0.17094	0.213675	0.162393
EX1708	9/19/2017	28.68279	-162.61	13	300-800	0.725	0.627586	0.103448	0.168966	0.1
EX1708	9/23/2017	26.59547	-160.673	17	300-800	0.9	0.577778	0.113333	0.148889	0.16



**Fig. 7.** Abundance and proportion of the four categorical groups at each dive location. All dives were located on either seamounts or ridges. The blue-outline shaded box represents the area covered by Musicians Seamounts while the blue dot represents Johnston Atoll. Each pie chart represents a dive location with each color representing a different categorical group. The center point of each pie chart indicates the dive locations, while the numbers extending from the chart designate the dive number. The size of the pie chart is proportional to the total average sightings per minute for the dive. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

latitude) apart. To limit bias in the linear regression model, where the data from the two study regions were combined, a random effects term accounted for the difference in location.

The two study regions have a difference in productivity regimes, which could explain why Musicians Seamounts had a higher total abundance of fauna seen in comparison to Johnston Atoll. Primary productivity is positively related to Chlorophyll *a* concentration, and generally where primary productivity is high, there is a high abundance of plankton and marine microneuston (Irigoin et al., 2014). Between September 10–19, 2017 Musicians Seamounts had a higher Chlorophyll *a* concentration ( $0.05\text{mg m}^{-3}$ ) when compared to Johnston Atoll ( $0.02\text{mg m}^{-3}$ ) on July 14–July 28, 2017 (ERDDAP, 2017). These trends are consistent with documented trends; Johnston Atoll is located within oligotrophic waters in the Hawaiian Island Zone, ranging from  $10^{\circ}\text{N}$  and  $18^{\circ}\text{N}$  latitude (Morel et al., 2010), while Musicians Seamounts is northward and near the more productive subtropical Transition Zone Chlorophyll Front, between  $32^{\circ}\text{N}$  and  $42^{\circ}\text{N}$  latitude (Polovina et al., 2017).

While we did not find relationships between oxygen concentration, salinity, nor temperature and the Crustacea, Chaetognatha, and fish categorical groups, there was a significant negative relationship between oxygen concentration and salinity and the occurrence of gelatinous organisms. Gelatinous fauna require oxygen, but generally have lower metabolism and higher

swimming efficiency, allowing them to live in more hypoxic conditions than other organisms (Thuesen et al., 2005) & (Purcell et al., 2001). Gelatinous zooplankton like Medusozoa and Ctenophora may be more abundant in the mesopelagic as the oxygen concentration generally decreases with depth in the Pacific Ocean, thus allowing them to outcompete or avoid predation from other organisms that cannot tolerate hypoxic conditions (Boero et al., 2016). Similarly, our results align with Luo et al. (2014) who found a negative relationship between salinity and the distribution of mesopelagic gelatinous organisms. Salinity, used as a metric for defining fronts, was an important factor in determining the distribution of mesopelagic gelatinous organisms, but it did not rank as high as oxygen or depth for most species (Luo et al., 2014). *Colobonema* may be especially negatively affected by an increase in salinity, as seen when an El Niño event in Monterey Bay caused a warmer and saltier water mass to penetrate the mesopelagic and decrease the sightings of the normally abundant *Colobonema sericeum* (Raskoff, 2001). Shallow-occurring ( $\leq 150\text{ m}$ ) Scyphozoan jellyfish in the Gulf of Mexico, Yellow Sea, and East China Sea have similarly been found to be negatively correlated with lower salinity concentrations (Heim-Ballew and Olsen, 2019; Zhang et al., 2012). Conversely, in another study located in the Western Pacific Ocean, the individuals (or sightings) per minute of Ctenophore, Hydromedusae, and Siphonophore either increased with an increase in salinity or

had a negligible effect (Hidaka et al., 2021). More investigation into the variable effects salinity and various water masses on abundance of gelatinous fauna will need to be conducted to continue to better understand these relationships.

Given the limited number of observations that we could make during these opportunistic exploratory surveys, we grouped the biological observations into the broad taxonomic classifications of Crustacea, Chaetognatha, and fish categorical groups in order to investigate relationships with potential environmental drivers. However, these groupings may have limited our ability to detect relationships at lower taxonomic levels. For example, some opportunistic predators, such as Myctophidae, perform extensive diel vertical migrations to support their feeding and thus their distributions may be additionally responsive to their prey distributions (Kinzer and Schulz, 1985), in addition to environmental factors (Brodeur and Yamamura, 2005) Other fish such as most Sternopychidae do not conduct DVM and thus their distribution could be based more heavily on environmental factors (Olivar et al., 2017). In Eduardo et al. (2020), the abundance of *Argyropelecus hemigymnus* was constrained to depths of 300–400 m and at 700–800 m while other studies conducted in colder water (Merrett and Roe, 1974) found their distribution's upper range to reach 150 m depth, indicating that some Sternopychidae may only tolerate specific temperature ranges. Distributions of fish and other non-gelatinous organisms may also be responsive to light intensity (Klevjer et al., 2016) and reproductive period (Sassa, 2019) neither of which were accounted for in this study.

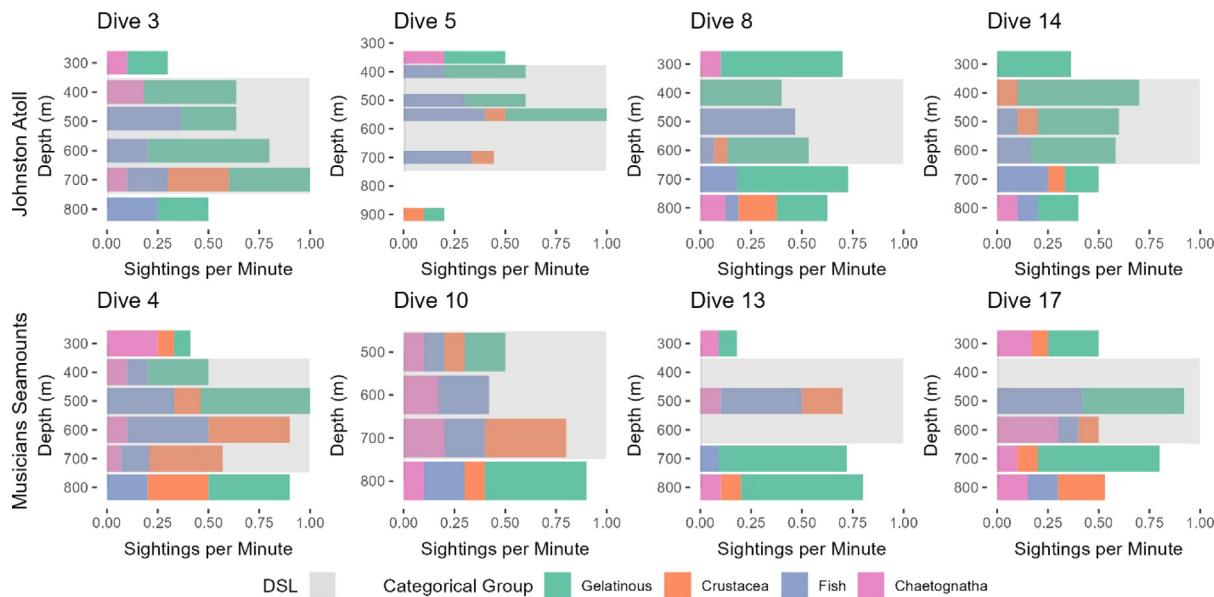
Gelatinous organisms were seen in greater abundance than any other categorical group which could possibly be due to avoidance of the ROV by mobile organisms. Fish and other faster moving organisms may flee from a source that outputs sound or light (Kaartvedt et al., 2012). Significant avoidance patterns have been observed on other Deep Discoverer dives (Leavitt et al., 2019) and other ROVs in general (Stoner et al., 2008). This pattern suggests that ROVs may be more effective in studying slower moving organisms and that acoustics and midwater trawls should possibly be used in conjunction with ROVs to get a more complete picture of the abundance of life in the mesopelagic.

The predominance of gelatinous organisms and visual avoidance patterns at higher depths could have led to the inconsistent patterns of abundance results in relation to the DSL. The total abundance of fauna was significantly higher within and below the DSL when compared to above the DSL at Musicians Seamounts, while there was no significant difference between the below, above, and within groups at Johnston Atoll. Gelatinous organisms, aside for some exceptions like siphonophores, are weak acoustic targets (Colombo et al., 2003). Qualitatively, there was a greater proportion of gelatinous organisms compared to any other category within and outside the DSL for most transects at Johnston Atoll (Fig. 8). No statistics were run on these data as the sample size is too small to determine meaningful results. Some fish can also be missed entirely by the ROV in the upper depth ranges due to visual avoidance, and thus not counted, resulting in an underestimation of the population (Stoner et al., 2008). The methods used by NOAA Ship *Okeanos Explorer* may also disturb the natural location of the DSL. Since the ship collects acoustic data at the same time the ROV is completing the midwater transects, the DSL boundaries may shift as organisms move to avoid the ROV.

There are no ROV mesopelagic studies that have occurred at Johnston Atoll and Musicians Seamounts, making localized comparisons difficult. A survey conducted in 1994 at Johnston Atoll used a submersible to image benthic fish and while a few Actinopterygii were documented in the midwater, the study largely ignored the mesopelagic (Chave and Mundy, 1995). A trawl survey performed 25 km off the coast of Oahu (1200 km away from both Johnston Atoll and Musicians Seamounts) at

depths between 0 m and 1,200 m found *Cyclothona* had the highest proportional abundance of daytime abundance in relation to Myctophidae, Sternopychidae and Anguilliformes (Maynard, 1975). In our study, Cyclothona similarly occupied the highest proportional abundance of the fish categorical group (Table 2). Maynard (1975) encountered a low number of Anguilliformes compared to Myctophidae and Sternopychidae, while at Johnston Atoll there was a much higher proportion of Anguilliformes compared to Myctophidae and Sternopychidae. We did not encounter any Anguilliformes at Musicians Seamounts. A study at Cross Seamount (1,150 km away from Johnston Atoll and 1,350 km away from Musicians Seamounts), between 500 m and 1500 m depth, found genera/species similar to our study: *Cyclothona*, *Gonostoma atlanticum*, *Argyropelecus*, *Sigmops*, and *Sternopyx* (De Forest and Drazen, 2009). The Japan Agency for Marine-Earth Science and Technology (JAMSTEC) uses methodology similar to our study and paired a ROV and CTD to the study the distribution of gelatinous fauna at the Sumsi Caldera – located 430 km southeast of Japan and approximately 6,200 km away from our study region. They observed several gelatinous species similar to our study, including: *Bathocyroe fosteri*, *Agalma elegans*, *Halicereas minimum*, *Colobonema sericeum*, and *Solmissus incisa* (Hidaka et al., 2021). The GEOMAR Helmholtz Centre for Ocean Research Kiel also paired a ROV and CTD to explore the mesopelagic a Senghor Seamount (550 km west of Mauritania's coast). Despite being located 13,500 km from our study region, their Pelagic In situ Observation System (PELAGIOS) ROV observed similar fauna: Narcomedusae (*Solmundella* and *Solmissus*), Trachymedusae (*Halicereas*, *Halitrophes*, and *Colobonema*), Siphonophorae (*Praya*), Ctenophora (*Bathocyroe* and *Thalassocalyce*), Chaetognatha, Phyllodocida (*Tomopteris*), Decapoda, Euphausiacea, Oegopsida (*Helicocranchia*), Anguilliformes, Myctophiformes, and Stomiiformes (Hoving et al., 2019). Unlike our survey, Hoving et al. (2019) found that there were higher proportions of fish, chaetognaths, and crustaceans during the day when compared to gelatinous fauna. This difference could be attributed to varying vertical diel migration patterns differences in towing speed, or higher rates of ROV avoidance although further study will be needed to confirm its validity.

This study provides a new baseline understanding of the diversity and frequency of organisms observed at Johnston Atoll and Musicians Seamount, in conjunction to how these organisms relate to their environment. Localized knowledge of the organisms that exist in a particular region combined with ecological context is an important step in properly managing the marine environment (Day et al., 2015). A lack of proper management in the mesopelagic could have devastating impacts economically and biologically, especially in the face of changing ocean conditions. Proud et al. (2017) predicts that as the ocean warms, mesopelagic biomass of fish will increase in Pacific gyres by the year 2100. Conversely, abundance of 46% of individual fish stocks are trending downward and 40% are exploited above sustainable rates (Britten et al., 2021). Select mesopelagic fish may become a possible replacement and are currently being investigated as a potential source of protein and oil for animal feed and human consumption (Grimaldo et al., 2020). Gelatinous zooplankton (especially Scyphozoa and Ctenophora) are known to thrive in disturbed ecosystems and may increase with hotter and more acidic oceans (Richardson et al., 2009). Outbreaks of gelatinous zooplankton could have negative consequences on the ecosystem through the potential exclusion of fish stocks (Richardson et al., 2009). Background knowledge and an ecological understanding of mesopelagic gelatinous organisms can allow for decisive management action and potentially help prevent infestations. Since this study is only an initial investigation, a final consideration is to improve upon this study and construct long-term monitoring systems. The potential of marine monuments to conserve and protect marine organisms and resources is vast - if only we take the time to properly understand the local ecology.



**Fig. 8.** Sightings per minute composition of categorical groups in relation to depth for all dives. The DSL is represented by the light gray box. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

## CRediT authorship contribution statement

**Jason Gronich:** Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Adrienne Copeland:** Resources, Data curation, Writing – review & editing, Supervision, Project administration. **Michael Ford:** Resources, Data curation, Writing – review & editing, Supervision. **Amanda N. Netburn:** Resources, Writing – review & editing, Supervision.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

## Acknowledgments

I would like to give special thanks to my co-authors and mentors for their continuous guidance and support. I would also like to thank the NOAA Office of Ocean Exploration and Research, National Marine Fisheries Service, and the NOAA Ernest F. Hollings Undergraduate Scholarship for supporting this work. Thank you to the mission team, officers, and crew of NOAA Ship *Okeanos Explorer* and the shoreside scientists who collected the data used in this project. Finally, a thank you to Tracey T. Sutton for his help with fish identification, Corey Garza for his insightful comments and authorship support, Cara Wilson for her satellite database help, Jon Gronich and Lynda Gronich for their proofreading, and Jeffrey Gronich, Rosa Nelson, and Dawn Gronich for their technical support.

## Funding sources

This work was supported through the NOAA's Ernest F. Hollings Undergraduate Scholarship Program, the NOAA Office of Ocean Exploration and Research, and the NOAA National Marine Fisheries Service. Data collection was supported by the officers, crew, and mission personnel onboard NOAA Ship *Okeanos Explorer*.

## References

Alldredge, A.L., Silver, M.W., 1988. Characteristics, dynamics and significance of marine snow. *Prog. Oceanogr.* 20 (1), 41–82. [http://dx.doi.org/10.1016/0079-6611\(88\)90053-5](http://dx.doi.org/10.1016/0079-6611(88)90053-5).

Arístegui, J., Gasol, J.M., Duarte, C.M., Herndld, G.J., 2009. Microbial oceanography of the dark ocean's pelagic realm. *Limnol. Oceanogr.* 54 (5), 1501–1529. <http://dx.doi.org/10.4319/lo.2009.54.5.1501>.

Barham, E.G., 1963. Siphonophores and the deep scattering layer. *Science* 140 (3568), 826–828. <http://dx.doi.org/10.1126/science.140.3568.826>.

Barham, E.G., 1966. Deep scattering layer migration and composition: Observations from a diving saucer. *Science* 151 (3716), 1399–1403. <http://dx.doi.org/10.1126/science.151.3716.1399>.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), <http://dx.doi.org/10.18637/jss.v067.i01>.

Boero, F., Brotz, L., Gibbons, M.J., Piraino, S., Zampardi, S., 2016. 3.10 Impacts and Effects of Ocean Warming on Jellyfish. *Explaining Ocean Warming: Causes, Scale, Effects and Consequences*. IUCN, Gland, pp. 213–237. <http://dx.doi.org/10.2305/iucn.ch.2016.08.en>.

Britten, G.L., Duarte, C.M., Worm, B., 2021. Recovery of assessed global fish stocks remains uncertain. *Proc. Natl. Acad. Sci.* 118 (31), e2108532118. <http://dx.doi.org/10.1073/pnas.2108532118>.

Brodeur, R., Yamamura, O., 2005. *Micronekton of the north Pacific*. PICES Sci. Rep. 30 (30), 1–115.

Cantwell, K., Smith, J.R., Putts, M., White, M.P., Cantelas, F., Bowman, A., 2020. EX-17-08 Expedition Report: Deep-Sea Symphony: Exploring the Musicians Seamounts (ROV/Mapping). OER Expedition Cruise Report. EX-17-08, Office of Ocean Exploration and Research, Office of Oceanic and Atmospheric Research, NOAA, Silver Spring, MD 20910, p. 64. <http://dx.doi.org/10.25923/pvw9-b391>.

Chave, E.H., Mundy, B.C., 1995. Deep-sea benthic fish of the Hawaiian archipelago, cross seamount, and johnston atoll. *Oceanograph. Lit. Rev.* 6 (42), 486.

Colombo, G.A., Mianzan, H., Madriolas, A., 2003. Acoustic characterization of gelatinous plankton aggregations: Four case studies from the Argentine continental shelf. *ICES J. Mar. Sci.* 60 (3), 650–657. [http://dx.doi.org/10.1016/S1054-3139\(03\)00051-1](http://dx.doi.org/10.1016/S1054-3139(03)00051-1).

Copeland, A.M., Whitlow, W.L.Au., Polovina, J., 2019. Influences of temporal changes in pelagic scattering layers on short-finned pilot whales behavior. *Oceanogr. Fish. Open Access J.* 9 (2), <http://dx.doi.org/10.19080/foaj.2019.09.555758>.

Costello, M.J., McCrea, M., Freiwald, A., Lundälv, T., Jonsson, L., Bett, B.J., et al., 2005. Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: *Cold-Water Corals and Ecosystems*. pp. 771–805. [http://dx.doi.org/10.1007/3-540-27673-4\\_41](http://dx.doi.org/10.1007/3-540-27673-4_41).

Davison, P.C., Checkley, Jr., D.M., Koslow, J.A., Barlow, J., 2013. Carbon export mediated by mesopelagic fishes in the northeast Pacific ocean. *Prog. Oceanogr.* 116, 14–30. <http://dx.doi.org/10.1016/j.pocean.2013.05.013>.

Day, J.C., Laffoley, D., Zischka, K., Gilliland, P., Gjerde, K., Jones, P.J.S., Knott, J., McCook, L., Milam, A., Mumby, P.J., Wilhelm, A., 2015. Marine protected area management. In: Worboys, G.L., Lockwood, M., Kothari, A., Feary, S., Pulsford, I. (Eds.), *Protected Area Governance and Management*. ANU Press, pp. 609–650. <http://dx.doi.org/10.22459/pagm.04.2015.20>.

De Forest, L., Drazen, J., 2009. The influence of a Hawaiian seamount on mesopelagic micronekton. *Deep Sea Res. I* 56 (2), 232–250. <http://dx.doi.org/10.1016/j.dsr.2008.09.007>.

Demer, D.A., Berger, L., Bernasconi, M., Bethke, E., Boswell, K., Chu, D., Domokos, R., et al., 2015. Calibration of Acoustic Instruments. ICES Cooperative Research Report No. 326, p. 133. <http://dx.doi.org/10.25607/OBP-185>.

Echoview Software Pty Ltd, 2013. *Echoview® Version (11.0.304)*. Echoview Software Pty Ltd, Hobart, Australia.

Economakis, A.E., Lobel, P.S., 1998. Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific ocean. *Environ. Biol. Fishes* 51 (2), 129–139. <http://dx.doi.org/10.1023/A:1007416813214>.

Eduardo, L.N., Bertrand, A., Mincarone, M.M., Santos, L.V., Frédu, T., Assunção, R.V., et al., 2020. Hatchetfishes (Stomiiformes: Sternopychidae) biodiversity, trophic ecology, vertical niche partitioning and functional roles in the western Tropical Atlantic. *Prog. Oceanogr.* 187, 102389. <http://dx.doi.org/10.1016/j.pocean.2020.102389>.

Elliott, K., Kelley, C., Mah, C., Malik, M., 2017. NOAA ship Okeanos explorer: 2017 Laulima O Ka Moana: Exploring deep monument waters around Johnston Atoll: Background information: Mission plan: NOAA office of ocean exploration and research. <https://oceanexplorer.noaa.gov/okeanos/explorations/ex1706/background/plan/welcome.html>.

ERDDAP, 2017. Chlorophyll, NOAA S-NPP VIIRS, science quality, global 4km, level 3, 2012 – present, weekly [data set]. NOAA NESDIS CoastWatch. [https://coastwatch.pfeg.noaa.gov/erddap/griddap/nedisVHNSQchlawaWeekly.graph?chl\\_a\[\(2017-06-04T12:00:00Z\):\(2017-10-01T12:00:00Z\)\]\[\(0.0\)\]\[\(35.0625\):\(9.993747\)\]\[\(-163.9937\)\]&draw=surface&vars=time%7Clatitude%7Cchl\\_a&colorBar=%7C%7Clinear%7C0%7C3%7C&timeRange=23,day\(s\)&bgColor=0xffffccff](https://coastwatch.pfeg.noaa.gov/erddap/griddap/nedisVHNSQchlawaWeekly.graph?chl_a[(2017-06-04T12:00:00Z):(2017-10-01T12:00:00Z)][(0.0)][(35.0625):(9.993747)][(-163.9937)]&draw=surface&vars=time%7Clatitude%7Cchl_a&colorBar=%7C%7Clinear%7C0%7C3%7C&timeRange=23,day(s)&bgColor=0xffffccff).

Foote, K.G., 1987. Fish target strengths for use in echo integrator surveys. *J. Acoust. Soc. Am.* 82 (3), 981. <http://dx.doi.org/10.1121/1.395298>.

Ford, M., Bezio, N., Collins, A., 2020. *Duobrachium sparksae* (incertae sedis Ctenophora Tentaculata Cydippida): A new genus and species of benthopelagic ctenophore seen at 3, 910 m depth off the coast of Puerto Rico. *Plankton Benthos Res.* 15 (4), 296–305. <http://dx.doi.org/10.3800/pbr.15.296>.

Ford, M., Netburn, A., 2017. The 2016 midwater exploration of the Mariana region. *Oceanography* <http://dx.doi.org/10.5670/oceanog.2017.supplement.01>, supplement.

Gjøsaeter, J., Kawaguchi, K., 1980. *A Review of the World Resources of Mesopelagic Fish*. Food & Agriculture Org.

Grimaldo, E., Grimsø, L., Alvarez, P., Herrmann, B., Møen Tveit, G., Tiller, R., Slizyte, R., Aldanondo, N., Guldberg, T., Toldnes, B., Carvajal, A., Schei, M., Selnes, M., 2020. Investigating the potential for a commercial fishery in the Northeast Atlantic utilizing mesopelagic species. *ICES J. Mar. Sci.* 77 (7–8), 2541–2556. <http://dx.doi.org/10.1093/icesjms/fsaa114>.

Hays, G.C., 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503 (1), 163–170. <http://dx.doi.org/10.1023/B:HYDR.0000008476.23617.b0>.

Heim-Ballew, H., Olsen, Z., 2019. Salinity and temperature influence on scyphozoan jellyfish abundance in the Western Gulf of Mexico. *Hydrobiologia* 827 (1), 247–262. <http://dx.doi.org/10.1007/s10750-018-3771-0>.

Hernández-León, S., Olivar, M.P., Fernández de Puelles, M.L., Bode, A., Castellón, A., López-Pérez, C., Tuset, V.M., González-Gordillo, J.I., 2019. Zooplankton and micronekton active flux across the tropical and subtropical Atlantic ocean. *Front. Mar. Sci.* 6, <http://dx.doi.org/10.3389/fmars.2019.00535>.

Hidaka, M., Nishikawa, J., Lindsay, D.J., 2021. Gelatinous zooplankton community around a hydrothermally active deep-sea caldera: results from ROV video records. *Plankton Benthos Res.* 16 (1), 40–58. <http://dx.doi.org/10.3800/pbr.16.40>.

Hoving, H.J., Christiansen, S., Fabrizius, E., Hauss, H., Kiko, R., Linke, P., Neitzel, P., Piatkowski, U., Körtzinger, A., 2019. The pelagic in situ observation system (PELAGIOS) to reveal biodiversity, behavior, and ecology of elusive oceanic fauna. *Ocean Sci.* 15 (5), 1327–1340. <http://dx.doi.org/10.5194/os-15-1327-2019>.

Irigoien, X., Klevjer, T.A., Røstad, A., Martínez, U., Boyra, G., Acuña, J.L., Bode, A., Echevarría, F., González-Gordillo, J.I., Hernández-León, S., Agustí, S., Aksnes, D.L., Duarte, C.M., Kaartvedt, S., 2014. Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Commun.* 5 (1), 3271. <http://dx.doi.org/10.1038/ncomms4271>.

Johnson, H.R., Backus, R.H., Hersey, J.B., Owen, D.M., 1956. Suspended echosounder and camera studies of midwater sound scatterers. *Deep Sea Research* (1953) 3 (4), 266–272. [http://dx.doi.org/10.1016/0146-6313\(56\)90016-8](http://dx.doi.org/10.1016/0146-6313(56)90016-8).

Kaartvedt, S., Staby, A., Aksnes, D., 2012. Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Mar. Ecol. Prog. Ser.* 456, 1–6. <http://dx.doi.org/10.3354/meps09785>.

Kaartvedt, S., Ugland, K.I., Klevjer, T.A., Røstad, A., Titelman, J., Solberg, I., 2015. Social behaviour in mesopelagic jellyfish. *Sci. Rep.* 5 (1), 11310. <http://dx.doi.org/10.1038/srep11310>.

Kelley, C., Kerby, T., Sarradin, P.M., Sarrazin, J., Lindsay, D.J., 2016. Submersibles and remotely operated vehicles. In: *Biological Sampling in the Deep Sea*. pp. 285–305. <http://dx.doi.org/10.1002/9781118332535.ch13>.

Kelley, C., Mah, C., Elliott, K., Malik, M., 2019. 2017 Laulima O Ka Moana: Exploring Deep Monument Waters Around Johnston Atoll Expedition Report. OER Expedition Rep.17-06, Office of Ocean Exploration and Research, Office of Oceanic & Atmospheric Research, NOAA, Silver Spring, MD 20910, p. 195. <http://dx.doi.org/10.25923/h9p9-d266>.

Kennedy, B.R.C., Cantwell, K., Malik, M., Kelley, C., Potter, J., Elliott, K., Lobecker, E., Gray, L.M., Sowers, D., White, M.P., France, S.C., Auscavitch, S., Mah, C., Moriwake, V., Bingo, S.R.D., Putts, M., Rotjan, R.D., 2019. The unknown and the unexplored: Insights into the Pacific deep-sea following NOAA CAPSTONE expeditions. *Front. Mar. Sci.* 6, <http://dx.doi.org/10.3389/fmars.2019.00480>.

Kinzer, J., Schulz, K., 1985. Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic: I. Myctophidae. *Mar. Biol.* 85 (3), 313–322. <http://dx.doi.org/10.1007/BF00393252>.

Klevjer, T.A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V.M., Kaartvedt, S., 2016. Large scale patterns in vertical distribution and behaviour of mesopelagic scattering layers. *Sci. Rep.* 6 (1), 19873. <http://dx.doi.org/10.1038/srep19873>.

Kobayashi, D.R., 2006. Colonization of the Hawaiian Archipelago via Johnston Atoll: A characterization of oceanographic transport corridors for pelagic larvae using computer simulation. *Coral Reefs* 25 (3), 407–417. <http://dx.doi.org/10.1007/s00338-006-0118-5>.

Kosaki, R.K., Pyle, R.L., Randall, J.E., Irons, D.K., 1991. *New records of fishes from Johnston Atoll, with notes on biogeography*.

Leavitt, H., Copeland, A., Netburn, A.N., Ford, M., 2019. Abstract: Using remotely operated vehicles and active acoustics to study the distribution of mesopelagic fauna. In: *Ocean Sciences Meeting 2020*. <https://agu.confex.com/agu/osm20/preliminaryview.cgi/Paper642367.html>.

Leone, A., Lecci, R.M., Durante, M., Meli, F., Piraino, S., 2015. The bright side of gelatinous blooms: Nutraceutical value and antioxidant properties of three Mediterranean jellyfish (Scyphozoa). *Mar. Drugs* 13 (8), 4654–4681. <http://dx.doi.org/10.3390/mdl304654>.

Li, C., Pan, Y., Li, A., Rodey, B., 2008. Geochemistry of the lava and its implications in Musicians Seamounts. *Chin. J. Oceanol. Limnol.* 26 (4), 459–468. <http://dx.doi.org/10.1007/s00343-008-0459-8>.

Lindsay, D.J., Hunt, J.C., 2005. Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan sea and north-western Pacific. *J. Mar. Biol. Assoc. U.K.* 85 (3), 503–517. <http://dx.doi.org/10.1017/S0025315405011434>.

Lindsay, D.J., Hunt, J.C., McNeil, M., Beaman, R.J., Vecchione, M., 2020. The first in situ observation of the Ram's horn squid *Spirula spirula* turns “common knowledge” upside down. *Diversity* 12 (12), 449. <http://dx.doi.org/10.3390/d12102049>.

Lindsay, D.J., Miyake, H., 2007. A novel benthopelagic ctenophore from 7, 217 m depth in the Ryukyu Trench, Japan, with notes on the taxonomy of deepsea cydippids. *Plankton Benthos Res.* 2 (2), 98–102. <http://dx.doi.org/10.3800/pbr.2.98>.

Lindsay, D., Umetsu, M., Grossmann, M., Miyake, H., Yamamoto, H., 2015. The gelatinous macroplankton community at the Hatoma Knoll hydrothermal vent. In: *Subseafloor Biosphere Linked to Hydrothermal Systems: TAIGA Concept*. pp. 639–666. [http://dx.doi.org/10.1007/978-4-431-54865-2\\_51](http://dx.doi.org/10.1007/978-4-431-54865-2_51).

Lobel, P., Schreiber, A.E., McCloskey, G., O’Shea, L., 2012. *An Ecological Assessment of Johnston Atoll*.

Lobel, P.S., Lobel, L.K., Randall, J.E., 2020. Johnston Atoll: Reef fish hybrid zone between Hawaii and the equatorial Pacific. *Diversity* 12 (2), 83. <http://dx.doi.org/10.3390/d12020083>.

Luo, J.Y., Grassian, B., Tang, D., Irisson, J.-O., Greer, A.T., Guigand, C.M., McClatchie, S., Cowen, R.K., 2014. Environmental drivers of the fine-scale distribution of a gelatinous zooplankton community across a mesoscale front. *Mar. Ecol. Prog. Ser.* 510, 129–149. <http://dx.doi.org/10.3354/meps10908>.

Mah, C.L., 2022. New genera, species and occurrences of deep-sea asteroidea (Valvatacea, Forcipulatacea, Echinodermata) collected from the north Pacific ocean by the CAPSTONE expedition. *Zootaxa* 5164 (1), 1–75. <http://dx.doi.org/10.1116/46/zootaxa.5164.1.1>.

Mapping progress, 2022. The Nippon foundation-GEBCO seabed 2030 project. <https://seabed2030.org/mapping-progress>.

Maynard, S.D., 1975. Mesopelagic micronekton in Hawaiian waters: faunal composition, standing stock, and diel vertical migration. *Fish. Bull.* 73, 726–736.

McClatchie, S., Dunford, A., 2003. Estimated biomass of vertically migrating mesopelagic fish off New Zealand. *Deep Sea Res. I* 50 (10–11), 1263–1281. [http://dx.doi.org/10.1016/s0967-0637\(03\)00128-6](http://dx.doi.org/10.1016/s0967-0637(03)00128-6).

McLean, D.L., Parsons, M.J.G., Gates, A.R., Benfield, M.C., Bond, T., Booth, D.J., Bunce, M., Fowler, A.M., Harvey, E.S., Macreadie, P.I., Pattiariatchi, C.B., Rouse, S., Partridge, J.C., Thomson, P.G., Todd, V.L.G., Jones, D.O.B., 2020. Enhancing the scientific value of industry remotely operated vehicles (ROVs) in our oceans. *Front. Mar. Sci.* 7, <http://dx.doi.org/10.3389/fmars.2020.00220>.

Merrett, N.R., Roe, H.S.J., 1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. *Mar. Biol.* 28 (2), 115–126. <http://dx.doi.org/10.1007/BF00396302>.

Morel, A., Claustré, H., Gentili, B., 2010. The most oligotrophic subtropical zones of the global ocean: similarities and differences in terms of chlorophyll and yellow substance. *Biogeosciences* 7 (10), 3139–3151.

Netburn, A.N., Anthony Koslow, J., 2015. Dissolved oxygen as a constraint on daytime deep scattering layer depth in the southern California current ecosystem. *Deep Sea Res. I* 104, 149–158. <http://dx.doi.org/10.1016/j.dsr.2015.06.006>.

Netburn, A.N., Ford, M., Lindsay, D., 2018. 2017 Midwater exploration on Okeanos explorer. *Oceanography* <http://dx.doi.org/10.5670/oceanog.2018.supplement.01>, supplement.

Olivar, M.P., Hulley, P.A., Castellón, A., Emelianov, M., López, C., Tuset, V.M., Contreras, T., Molí, B., 2017. Mesopelagic fishes across the tropical and equatorial Atlantic: Biogeographical and vertical patterns. *Prog. Oceanogr.* 151, 116–137. <http://dx.doi.org/10.1016/j.pocean.2016.12.001>.

Perelman, J.N., Firing, E., van der Grient, J.M.A., Jones, B.A., Drazen, J.C., 2021. Mesopelagic scattering layer behaviors across the Clarion-Clipperton Zone: Implications for deep-sea mining. *Front. Mar. Sci.* 8 (492), 632764. <http://dx.doi.org/10.3389/fmars.2021.632764>.

Polovina, J.J., Howell, E.A., Kobayashi, D.R., Seki, M.P., 2017. The transition zone chlorophyll front updated: advances from a decade of research. *Prog. Oceanogr.* 150, 79–85. <http://dx.doi.org/10.1016/j.pocean.2015.01.006>.

Proud, R., Cox, M.J., Brierley, A.S., 2017. Biogeography of the global ocean's mesopelagic zone. *Curr. Biol.* 27 (1), 113–119. <http://dx.doi.org/10.1016/j.cub.2016.11.003>.

Purcell, J., Breitburg, D., Decker, M., Graham, W., Youngbluth, M., Raskoff, K., 2001. Pelagic cnidarians and ctenophores in low dissolved oxygen environments: A review. In: *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*, Vol. 58. pp. 77–100. <http://dx.doi.org/10.1029/CE058p0077>.

Raskoff, K.A., 2001. The impact of El Niño events on populations of mesopelagic hydromedusae. In: *Jellyfish Blooms: Ecological and Societal Importance: Proceedings of the International Conference on Jellyfish Blooms*. Gulf Shores, Alabama, 12–14 January 2000, Springer Netherlands, pp. 121–129.

Reinthal, T., Van Aken, H., Veth, C., Aristegui, J., Robinson, C., Williams, P.J.L.B., et al., 2006. Prokaryotic respiration and production in the meso- and bathypelagic realm of the eastern and western north Atlantic basin. *Limnol. Oceanogr.* 51 (3), 1262–1273. <http://dx.doi.org/10.4319/lo.2006.51.3.1262>.

Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: Causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.* 24 (6), 312–322. <http://dx.doi.org/10.1016/j.tree.2009.01.010>.

Robinson, C., Steinberg, D.K., Anderson, T.R., Aristegui, J., Carlson, C.A., Frost, J.R., Ghiglione, J.-F., Hernández-León, S., Jackson, G.A., Koppelman, R., Quéguiner, B., Ragueneau, O., Rassoulzadegan, F., Robison, B.H., Tamburini, C., Tanaka, T., Wishner, K.F., Zhang, J., 2010. Mesopelagic zone ecology and biogeochemistry – a synthesis. *Deep Sea Res. II* 57 (16), 1504–1518. <http://dx.doi.org/10.1016/j.dsr2.2010.02.018>.

Robison, B.H., 2004. Deep pelagic biology. *J. Exp. Mar. Biol. Ecol.* 300 (1), 253–272. <http://dx.doi.org/10.1016/j.jembe.2004.01.012>.

Robison, B.H., 2009. Conservation of deep pelagic biodiversity. *Conserv. Biol.* 23 (4), 847–858. <http://dx.doi.org/10.1111/j.1523-1739.2009.01219.x>.

Robison, B.H., Reisenbichler, K.R., Sherlock, R.E., 2017. The coevolution of mid-water research and ROV technology at MBARI. *Oceanography* 30 (4), 26–37. <http://dx.doi.org/10.5670/oceanog.2017.421>.

RStudio Team, 2020. RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA, URL <http://www.rstudio.com/>.

Saba, G.K., Burd, A.B., Dunne, J.P., Hernández-León, S., Martin, A.H., Rose, K.A., et al., 2021. Toward a better understanding of fish-based contribution to ocean carbon flux. *Limnol. Oceanogr.* 66 (5), 1639–1664. <http://dx.doi.org/10.1002/lno.11709>.

Sager, W.W., Pringle, M.S., 1987. Paleomagnetic constraints on the origin and evolution of the musicians and south Hawaiian Seamounts, Central Pacific ocean. In: *Seamounts, Islands, and Atolls*. American Geophysical Union (AGU), pp. 133–162. <http://dx.doi.org/10.1029/GM043p0133>.

Sassa, C., 2019. Reproduction and early life history of mesopelagic fishes in the Kuroshio region: a review of recent advances. In: *Kuroshio Current: Physical, Biogeochemical, and Ecosystem Dynamics*. pp. 273–294.

Sea-Bird Scientific, 2017. SBE data processing (Version 7.27.7) [Computer software]. <https://www.seabird.com/software>.

Selig, G.M., Netburn, A.N., Malik, M., 2019. Distributions of the pelagic holothurian pelagothuria in the Central Pacific ocean as observed by remotely-operated vehicle surveys. *Front. Mar. Sci.* 6, <http://dx.doi.org/10.3389/fmars.2019.00684>.

Söffker, M., Sloman, K.A., Hall-Spencer, J.M., 2011. In situ observations of fish associated with coral reefs off Ireland. *Deep Sea Res. I* 58 (8), 818–825. <http://dx.doi.org/10.1016/j.dsr.2011.06.002>.

Stewart, J.S., Hazen, E.L., Bograd, S.J., Byrnes, J.E.K., Foley, D.G., Gilly, W.F., Robison, B.H., Field, J.C., 2014. Combined climate- and prey-mediated range expansion of Humboldt squid (*Dosidicus gigas*), a large marine predator in the California current system. *Global Change Biol.* 20 (6), 1832–1843. <http://dx.doi.org/10.1111/gcb.12502>.

Stoner, A.W., Ryer, C.H., Parker, S.J., Auster, P.J., Wakefield, W.W., 2008. Evaluating the role of fish behavior in surveys conducted with underwater vehicles. *Can. J. Fish. Aquat. Sci.* 65 (6), 1230–1243. <http://dx.doi.org/10.1139/F08-032>.

Sutton, T.T., 2013. Vertical ecology of the pelagic ocean: Classical patterns and new perspectives. *J. Fish Biol.* 83 (6), 1508–1527. <http://dx.doi.org/10.1111/jfb.12263>.

Tenggardjaja, K.A., Bowen, B.W., Bernardi, G., 2014. Vertical and horizontal genetic connectivity in *Chromis verater*, an endemic damselfish found on shallow and mesopelagic reefs in the Hawaiian archipelago and adjacent Johnston Atoll. *PLoS One* 9 (12), <http://dx.doi.org/10.1371/journal.pone.0115493>.

Thuesen, E., Rutherford, L., Brommer, P., 2005. The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachei*, *Bolinopsis infundibulum* and *Mnemiopsis leidyi*. *J. Mar. Biol. Assoc. U.K.* 85, <http://dx.doi.org/10.1017/S0025315405011550>.

Wagner, D., Kosaki, R.K., Spalding, H.L., Whitton, R.K., Pyle, R.L., Sherwood, A.R., Tsuda, R.T., Calcina, B., 2014. Mesopelagic surveys of the flora and fauna at Johnston Atoll, Central Pacific ocean. *Mar. Biodivers. Rec.* 7, <http://dx.doi.org/10.1017/S1755267214000785>.

Wüst, G., 1964. The major deep-sea expeditions and research vessels 1873–1960. *Prog. Oceanogr.* 2, 1–52. [http://dx.doi.org/10.1016/0079-6611\(64\)90002-3](http://dx.doi.org/10.1016/0079-6611(64)90002-3).

Yabsley, M.J., Work, T.M., Rameyer, R.A., 2006. Molecular phylogeny of *Babesia poelea* from brown boobies (*Sula leucogaster*) from Johnston Atoll, Central Pacific. *J. Parasitol.* 92 (2), 423–425. <http://dx.doi.org/10.1645/ge-617r.1>.

Yamaguchi, A., Watanabe, Y., Ishida, H., Harimoto, T., Furusawa, K., Suzuki, S., et al., 2004. Latitudinal differences in the planktonic biomass and community structure down to the greater depths in the western north Pacific. *J. Oceanogr.* 60 (4), 773–787. <http://dx.doi.org/10.1007/s10872-004-5770-1>.

Yu, G., 2017. Creates scatterpie plots using scatterpie. <https://CRAN.R-project.org/package=scatterpie>.

Zhang, F., Sun, S., Jin, X., Li, C., 2012. Associations of large jellyfish distributions with temperature and salinity in the yellow sea and east China sea. *Hydrobiologia* 690 (1), 81–96. <http://dx.doi.org/10.1007/s10750-012-1057-5>.