



## Ectoparasitism on deep-sea fishes in the western North Atlantic: In situ observations from ROV surveys



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### ABSTRACT

A complete understanding of how parasites influence marine ecosystem functioning requires characterizing a broad range of parasite–host interactions while determining the effects of parasitism in a variety of habitats. In deep-sea fishes, the prevalence of parasitism remains poorly understood. Knowledge of ectoparasitism, in particular, is limited because collection methods often cause dislodgment of ectoparasites from their hosts. High-definition video collected during 43 remotely operated vehicle surveys (2013–2014) provided the opportunity to examine ectoparasitism on fishes across habitats (open slope, canyon, seamount, cold seep) and depths (494–4689 m) off the northeastern U.S., while providing high-resolution images and valuable observations of fish behavior. Only 9% ( $n = 125$  individuals) of all observed fishes (25 species) were confirmed with ectoparasites, but higher percentages (~33%) were observed for some of the most abundant fish species (e.g., *Antimora rostrata*). Ectoparasites included two copepod families (Lernaepodidae, Sphyrriidae) that infected four host species, two isopod families (Cymothoidae, Aegidae) that infected three host species, and one isopod family (Gnathiidae) that infected 19 host species. Hyperparasitism was also observed. As host diversity declined with depth, ectoparasite diversity declined; only gnathiids were observed at depths down to 3260 m. Thus, gnathiids appear to be the most successful group to infect a diversity of fishes across a broad depth range in the deep sea. For three dominant fishes (*A. rostrata*, *Nezumia bairdii*, *Synaphobranchus* spp.), the abundance and intensity of ectoparasitism peaked in different depths and habitats depending on the host species examined. Notably, gnathiid infections were most intense on *A. rostrata*, particularly in submarine canyons, suggesting that these habitats may increase ectoparasite infections. Although ectoparasitism is often overlooked in deep-sea benthic communities, our results demonstrate that it occurs widely across a variety of habitats, depths, and locations and is a significant component of deep-sea biodiversity.

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### 1. Introduction

The importance of parasites in shaping community structure and influencing ecosystem functioning in the marine environment has gained considerable recognition over the past few decades (Dobson and Hudson, 1986; Poulin, 1999; Poulin et al., 2016). Parasites have complex roles in community ecology by influencing population sizes and shifting patterns in both biodiversity and community structure. Parasites can also alter the outcome of competitive interactions, either by enabling rare species to coexist

with dominant ones or by helping to eliminate competitors. Additionally, parasites have become increasingly recognized as important components of trophic pathways (see Demopoulos and Sikkell, 2015). The inclusion of parasites in food webs has revealed higher connections among species (Amundsen et al., 2009) and higher trophic efficiency (Arias-González and Morand, 2006). Although the importance of parasites in marine ecosystems is clear, there is still much to be learned regarding the multiple effects that parasites have in different ecosystems throughout the marine realm.

A recent review regarding the synergy of marine ecology and parasitology highlighted seven key areas to further increase our understanding of the importance of parasites in marine ecosystem functioning (Poulin et al., 2016). Poulin et al. (2016) emphasized the need to discover and identify key parasite species that play pivotal

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roles in ecosystems, while adding new model systems to broaden perspectives on marine parasitism. Because the majority of marine parasitology studies have been conducted in coastal and coral reef ecosystems, it was also suggested that research should be expanded to additional marine habitats. Focusing on a narrow range of habitats can constrain generalizations regarding parasitism in the marine environment (Poulin et al., 2016).

The deep sea is one such understudied ecosystem in which data on parasitism remains limited. For fishes inhabiting the deep sea, knowledge of parasitism is limited to <10% (Klimpel et al., 2006). The few studies on parasitism in deep-sea fishes have focused mainly on the prevalence of endoparasitism (Noble, 1973; Campbell et al., 1980; Klimpel et al., 2006; Palm and Klimpel, 2008), revealing the importance of temperature, depth, and habitat (such as submarine canyons) in influencing the prevalence of endoparasite infections in the deep sea (Manter, 1934; Campbell et al., 1980; Gartner and Zwermer, 1989; Marcogliese, 2002; Klimpel et al., 2006). However, deep-sea fishes are also hosts to ectoparasites, which can adversely affect fishes by causing anemia (Adlard and Lester, 1995; Lester et al., 1995), tissue damage (Adlard and Lester, 1995; Lester et al., 1995), scarring (Ross et al., 2001), and behavioral changes (e.g. Welicky and Sikkel, 2014; Artim et al., 2015), while transmitting other diseases [e.g., blood parasites, (Davies and Smit, 2001), viruses (Lawler et al., 1974)]. Ectoparasitism may thus influence population dynamics of deep-sea fishes and may be important in trophic ecology through direct consumption by other organisms (Johnson et al., 2010; Demopoulos and Sikkel, 2015). Yet, ectoparasitism remains understudied, partly because prior data have been obtained opportunistically from trawling and dredging efforts. These types of gear can dislodge ectoparasites from their hosts during collection (Ross et al., 2001).

To investigate ectoparasitism in the deep sea, direct observations using remotely operated vehicles (ROVs) provide an alternative method to trawling. Visual based surveys have provided a considerable amount of information on ectoparasite-host interactions in shallow waters, while revealing effects of parasitism on fish behavior (e.g., swimming behavior, site fidelity, Barber et al., 2000; Sikkel et al., 2004). Trophic connections have also been determined from *in situ* observations (i.e., cleaner stations on coral reefs, Sikkel et al., 2004). Thus, the value of visual analysis in parasite studies, from shallow waters to the deep-sea, is clear.

Recent expeditions to survey various seafloor features along the continental margin of the northeastern United States (NEUS) provided an opportunity to increase knowledge of ectoparasites infecting demersal fishes in the deep sea. Visual observations from ROV surveys were used in the present study to identify ectoparasites and their hosts and examine whether ectoparasite diversity declines with increasing depth. We also examined whether ectoparasite-host interactions and intensity of infections differ among depths and habitats in each of three common fish species [*Antimora rostrata* (family Moridae), *Nezumia bairdii* (family Macrouridae), and *Synphobranchus* (family Synphobranchidae)]. The high-definition video obtained from these expeditions enabled *in situ* observations of host-parasite interactions while providing unparalleled, high-resolution images of ectoparasites infecting fishes in the deep sea.

## 2. Material and methods

Forty-three remotely operated vehicle (ROV) dives were conducted with the ROV *Deep Discoverer* (D2) along the NEUS continental margin and New England Seamount Chain during two expeditions (9 July to 16 Aug 2013 and 19 Sep to 6 Oct 2014) aboard the NOAA Ship *Okeanos Explorer* (Fig. 1). These expeditions were

telepresence-enabled, with live video feeds transmitted back to shore in real time (<http://oceanexplorer.noaa.gov/okeanos/media/exstream/exstream.html>), allowing scientists on shore and on the ship to interact during the dives via an Internet chat room and satellite teleconference line.

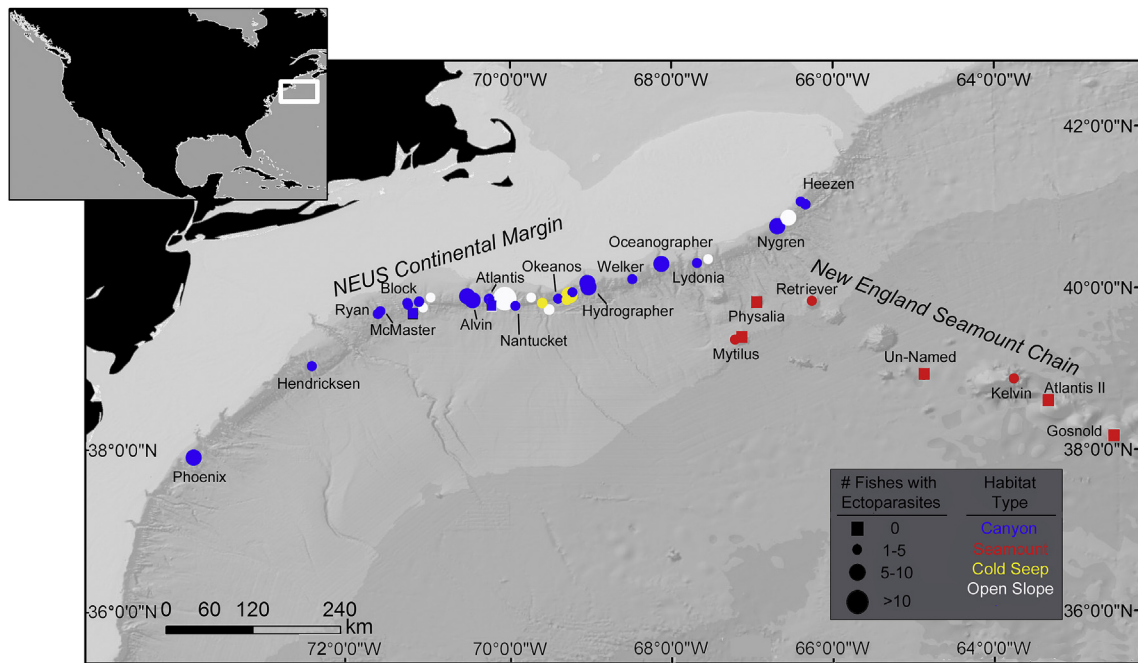
The ROV D2 was equipped with two high-definition cameras and 16,600 lumens of hydraulically positioned LED lights. A Seabird 911+ conductivity-temperature-depth (CTD) logger with a dissolved oxygen (DO) sensor was also attached to the ROV. Paired lasers (10 cm apart) were positioned on the ROV to approximate field of view and sizes of fishes and ectoparasites. The *Okeanos Explorer* followed the vehicles using dynamic positioning and tracked vehicle position with an ultra-short baseline tracking system.

Each ROV dive traversed one broad-scale habitat feature at depths ranging from 494 to 4689 m (Fig. 1). These habitat features included: submarine canyons (25 dives), cold seeps (three dives), open slope/intercanyon areas (seven dives), and seamounts (eight dives). No fishes were observed during one dive at the deepest seamount surveyed (un-named Seamount, 4552–4689 m). As the ROV traversed a habitat feature (~0.1–0.2 knots, 1 knot = 0.514 m s<sup>-1</sup>), the cameras were generally set on wide-angle view, but zooms were frequently conducted to obtain detailed imagery of each previously undocumented species encountered during a given dive survey. The over-ground distance covered by the ROV [measured in ArcGIS v9 (ESRI)] varied across dives (300–2200 m), but the observation time on bottom was approximately the same (5–7 h per dive).

During each dive, video clips (103–191 clips) from the high-definition camera mounted on the ROV D2 were contiguously acquired as part of the mission of the expeditions. These video clips ranged in length from approximately 30 s to 5 min. Frame grabs (112–351 per dive) were subsequently taken from video clips. Sixty-nine demersal fish taxa and three mesopelagic taxa were identified using both frame grab and video observations (see Quattrini et al., 2015). Ectoparasites were identified to the lowest taxonomic level on fishes from all available frame grabs. Ectoparasite type, placement, number and size also ensured that individuals were counted only once. Because we restricted this analysis to using frame grabs only, we calculated frequency of ectoparasite-host interactions to examine general patterns across the region.

Three species of fishes (*Antimora rostrata*, *N. bairdii* and *Synphobranchus* spp.) that were dominant in the region and had ectoparasites were further enumerated using all video clips. The average intensity of infection (number per one side) was estimated for these species using individuals imaged during times when the camera was positioned to permit accurate counts. Although gnathiid parasites were common, these could not be consistently identified on all individuals due to the wide camera view. Thus, estimates provided herein for this taxonomic group are conservative and many parasites labeled as “unknown” may in fact be gnathiids.

For each dominant fish species, abundances of ectoparasite-host interactions were estimated by taking the total number of hosts observed with at least one ectoparasite during a dive and dividing by the product of the total over the ground distance covered by the ROV and the estimated field of view (4.3 m). Abundances were also calculated within particular depth zones per dive. Depth zones were binned into 300 m depth intervals from 500 to 3200 m, except the last depth zone ranged from 2900 to 3262 m. A single dive may have traversed across two depth zones, but only across one broad-scale habitat feature. A Kruskal-Wallis (K-W) test was used to determine if hosts or ectoparasite-host interactions were significantly more abundant within a particular depth range or habitat.



**Fig. 1.** Locations of 43 ROV dives conducted along the northeastern U.S. continental margin and New England Seamount Chain. Circle Size = Number of ectoparasite-host interactions per dive. Square = No ectoparasites observed. Colors denote habitats.

Following other deep-sea studies (e.g., Davies et al., 2008; Doughty et al., 2014), only dives in which each of the dominant species was present were included in these tests. All statistical tests were conducted in R v 3.1 (R Core Team., 2015; <http://www.R-project.org>).

### 3. Results

#### 3.1. Ectoparasite-host interactions

A total of 125 adult fishes [out of 1429 individuals confirmed with or without ectoparasites] representing at least 25 species [out of 69 demersal species (Quattrini et al., 2015) and three mesopelagic species] from 18 families were observed hosting at least five families of ectoparasites (Table 1). The Isopoda (Aegidae, Cymothoidae, Gnathiidae) was the most common group of ectoparasites observed, infecting 74 individual hosts. Siphonostomatoid (Lernaepodidae, Sphyriidae) copepods infected 22 individual hosts. An additional 29 individual hosts were infected with ectoparasites that could not be identified; however, many were possible gnathiids. Gnathiids were the most common ectoparasite observed across species, infecting at least 19 species (Table 1). *Amblyraja radiata* and *N. bairdii* hosted aegid isopods. *Hoplostethus mediterraneus* hosted a cymothoid isopod (Tables 1 and 2). Siphonostomatoid copepod parasites were observed on at least four host species: *A. rostrata*, *Diaphus* sp., *N. bairdii*, and *Synaphobranchus* spp.

Two families of siphonostomatoid copepods were identified on three species of fishes (Fig. 2A–C). Copepods from the family Lernaepodidae, sized at approximately 1–3 cm total length (TL), were observed on *A. rostrata* (Fig. 2A). Copepods were attached to anal fins, below second dorsal fins, and behind the eyes. At least two species (likely *Lophoura* spp.) from the family Sphyriidae infected *Synaphobranchus* spp. (Fig. 2B) and *N. bairdii* (Fig. 2C). The copepods (~2–3 cm TL) infecting *N. bairdii* were attached directly behind the dorsal fin, whereas larger copepods (~4–5 cm TL) infecting

*Synaphobranchus* spp. were attached mid body; either laterally or ventrally. Unidentified siphonostomatoid copepods were observed (~2 cm TL) on mesopelagic fishes, including two *Diaphus* sp. individuals (Fig. 2D) and four unidentified myctophids. Copepods were attached behind the dorsal fins of myctophids. In all cases, only one copepod was observed on a single fish. Hyperparasitism was observed on *N. bairdii*, with each sphyriid copepod infected by at least three to eight leeches (Fig. 2C).

Of the three families of isopods that infected demersal fishes, gnathiids were the most common, with 1 to 45 individuals infecting at least one side of each individual fish. Gnathiids were translucent, attached to all fins, heads, and sides of bodies (Fig. 2H), and ranged in size from 1 to 3 mm TL. Distinct species of aegids infected *A. radiata* and *N. bairdii*. One large (~2.5 cm TL) aegid was attached mid-way on the body of *A. radiata*, at the juncture of the left pectoral wing and the central disk (Fig. 2G). The other fish individual had at least 15 smaller (1–2 mm TL) aegids attached to both the wings and the central disk. Five *N. bairdii* were observed each with an aegid isopod. Each aegid (~2–3 cm TL) was attached behind the dorsal fin (Fig. 2E). One cymothoid isopod (~4 cm TL) was observed attached on the side of the body below the dorsal fin of *H. mediterraneus* (Fig. 2F).

#### 3.2. General patterns across sites and depths

Ectoparasite-host interactions were documented during 36 dives across the entire study region at depths ranging from 494 to 3262 m (temperature 5.6 to 2.6 °C, dissolved oxygen 3.6–5.6 ml L<sup>-1</sup>) (Fig. 1). Observations of host-ectoparasite interactions were more frequent in canyons (66%, n = 23 dives) than in open slope (23% n = 7 dives), cold seep (7%, n = 3 dives), and seamount (4%, n = 3 dives) habitats (Fig. 1). Of the six seamounts where fishes were observed (<20 individuals per dive), ectoparasites (gnathiids) were observed on five individuals, one individual each on Kelvin and Retriever seamounts and three individuals from

**Table 1**  
Number of individuals per species observed with ectoparasites. \* indicates species for which parasites were counted using video clips. Total number of hosts present in video clips but too distant to confirm ectoparasite infections are in parentheses.

	# Hosts Examined	Siphonostomatoid Copepoda			Isopoda			Unknown	# Parasites
		Lernaeopodidae	Sphyriidae	Unknown	Cymothoidae	Aegidae	Gnathiidae		
<b>Etmopteridae</b>									
<i>Centroscyllium fabricii</i>	9						4	5	9
<b>Scyliorhinidae</b>									
<i>Apristurus manis</i>	3						1	1	2
<b>Rajiidae</b>									
<i>Amblyraja radiata</i>	3					2			2
<b>Chimaeridae</b>									
<i>Hydrolagus pallidus</i>	3							2	2
<b>Halosauridae</b>									
<i>Halosauropsis macrochir</i>	3						1	1	2
<b>Notacanthidae</b>									
<i>Notacanthus chemnitzii</i>	2						2		2
<b>Synphobranchidae</b>									
<i>Synphobranchus</i> spp.*	1241 (1785)		8				5	12	25
<b>Myctophidae</b>									
<i>Diaphus</i> sp.	2			2					2
Unidentified	4			4					4
<b>Bathysauridae</b>									
<i>Bathysaurus ferox</i>	2						2		2
<b>Ophidiidae</b>									
? <i>Lamprogrammus</i> sp.	1						1		1
<i>Monomitopus agassizi</i>	1						1		1
Ophidiidae sp.	1							1	1
<b>Macrouridae</b>									
<i>Coryphaenoides armatus</i>	2						2		2
<i>Coryphaenoides rupestris</i>	1							1	1
<i>Nezumia bairdii</i> *	57 (153)		4				5	8	19
<b>Moridae</b>									
<i>Antimora rostrata</i> *	44 (97)	4					28		32
<i>Lepidion guentheri</i>	1						1		1
<b>Phycidae</b>									
<i>Phycis chesteri</i>	17						1	4	5
<i>Urophycis tenuis</i>	1						1		1
<b>Trachichthyidae</b>									
<i>Hoplostethus mediterraneus</i>	3				1				1
<b>Oreosomatidae</b>									
<i>Neocyttus helgae</i>	7						4		4
<b>Sebastidae</b>									
<i>Helicolenus dactylopterus</i>	4						1		1
<i>Sebastes mentella</i>	4						1		1
<b>Psychrolutidae</b>									
<i>Cottunculus thomsonii</i>	12						1		1
<b>Pleuronectidae</b>									
<i>Reinhardtius hippoglossoides</i>	1						1		1
<b>Total Observations</b>	1429 (2122)	4	12	6	1	7	66	29	125

**Table 2**  
Observations of ectoparasite-host interactions by depth. Number of dives (n) occurring within a particular depth range where ectoparasite-host interactions were observed is also listed.

	500–800 m n = 8	800–1100 m n = 11	1100–1400 m n = 12	1400–1700 m n = 9	1700–2000 m n = 3	2000–2300 m n = 3	2900–3300 m n = 1
<b>Copepoda</b>							
Sphyriidae	3	8	1				
Lernaeopodidae		2	2				
Unknown		1	4				
<b>Isopoda</b>							
Aegidae	3	3					
Cymothoidae	1						
Gnathiidae	8	11	18	18	5	4	2
Unknown Ectoparasites	4	10	11	3		1	1
<b>Total No. Observations</b>	19	42	31	20	5	5	3
<b>Total No. Host Spp. Infected</b>	8	10	12	7	2	3	2

Mytilus Seamount, at depths ranging from 2035 to 3260 m (Fig. 1, Table 2). The number of species infected with parasites was similar among open slope (6 spp.), seamount (4 spp.), and cold seep (4 spp.)

habitats, but higher in canyon habitats (21 spp.) Overall, ectoparasite-host interactions peaked at mid-slope depths. Frequencies of ectoparasite-host interactions ranged from 2 to 34%,



**Fig. 2.** Example images of ectoparasites infecting various host species. A) *Antimora rostrata* with a lernaepodid copepod (1059 m, Alvin Canyon); B) *Synaphobranchus* sp. with a sphyriid copepod (820 m, open slope); C) *Nezumia bairdii* with a sphyriid copepod parasitized by eight leeches (1035 m, Phoenix Canyon); D) Black fish, *Diaphus* sp. with an unknown siphonostomatid copepod (1130 m, cold seep) attached behind dorsal fin; E) *N. bairdii* with aegid isopod (780 m, open slope); F) *Hoplostethus mediterraneus* with a cymothoid isopod (744 m, Nygren Canyon); G) *Amblyraja radiata* with aegid isopod (1010 m, Alvin Canyon); and H) *Cottunculus thomsonii* with gnathiids (1210 m, Oceanographer Canyon).

with the most frequent observations in 800–1100 m and 1100–1400 m (Table 2). Few ( $n = 8$ ) ectoparasite-host interactions were observed in the deeper areas ( $>1700$  m) (Table 2). The number of host species infected with parasites was highest at depths of 800–1100 m ( $n = 12$  species), followed by 1100–1400 m ( $n = 11$  species), and then declined with increasing depth (Table 2).

Species richness of ectoparasites was similar among habitats,

but declined with deeper depths (Table 2). Siphonostomatoid copepods were observed in canyon, cold seep, and open slope habitats at depths down to 1400 m. Aegids were observed in open slope and canyon habitats at depths down to 1100 m. One cymothoid isopod was observed in a canyon habitat at a depth of 739 m. Gnathiids were observed in all habitats and at the deepest depths surveyed (down to 3300 m).

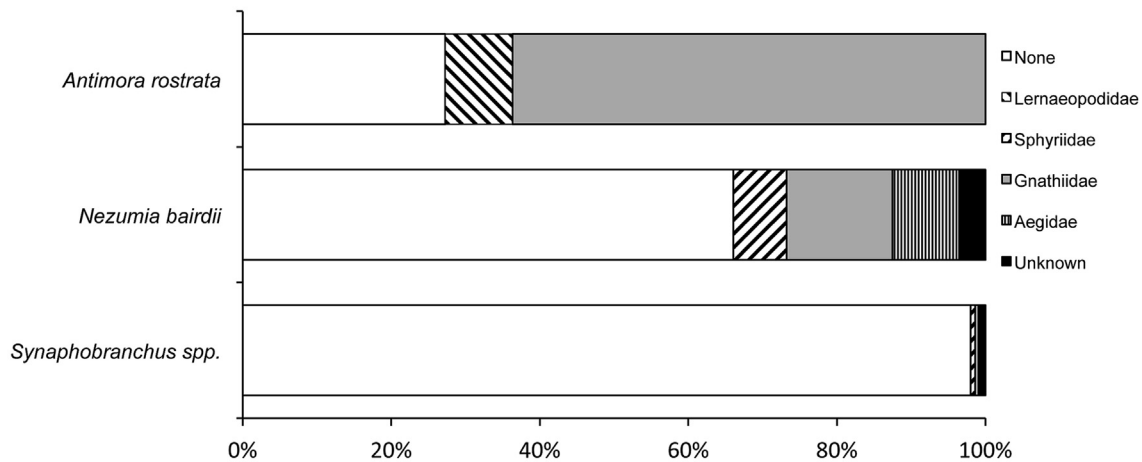


Fig. 3. Percentage of ectoparasites infecting three common demersal fishes. Unconfirmed observations are not included.

### 3.3. Ectoparasitism on three common species

Out of the three common species enumerated on video, *Antimora rostrata* (n = 97 adults, n = 29 dives) was observed with parasites most frequently. We positively identified ectoparasites on 33% of all observed *A. rostrata* (25–40 cm TL). Of the individuals confirmed with parasites, 88% were infected with gnathiids and 12% were infected with lernaepodid copepods (Fig. 3, Table 1). Only 12% of *A. rostrata* individuals did not have ectoparasites (Fig. 3). For the remaining 55% (n = 53) of individuals, it could not be determined whether or not individuals had ectoparasites because individuals in the video were too far from the camera to confirm whether or not ectoparasites were present. The average number of parasites infecting a single side of an individual was  $7.72 \pm 1.89$  SE parasites (n = 26 individuals, 1 to 45 ectoparasites per individual). The most intense infections ( $9.05 \pm 2.39$  SE ectoparasites per side) were observed on individuals in canyon habitats, particularly at depths ranging from 1100 to 2000 m (Table 3). Although prevalence of infections did not differ (K-W,  $\chi^2 = 0.14$ , p = 0.93) among the three dominant species, the infection intensity was significantly higher (K-W,  $\chi^2 = 14.78$ , p = 0.0006) in *A. rostrata* than in the other species.

*Antimora rostrata* was observed at depths ranging from 810 to 2718 m. This species was most abundant at depths of 1100 to 1400 m ( $0.029 \pm 0.010$  SE individuals  $10\text{ m}^{-2}$ ) followed by 1400 to 1700 m ( $0.027 \pm 0.009$  SE individuals  $10\text{ m}^{-2}$ ) (Fig. 4A). Although ectoparasite-host interactions ( $0.010 \pm 0.006$  SE interactions  $10\text{ m}^{-2}$ ) were slightly higher at 800 to 1100 m, there were no significant differences in ectoparasite-host interactions among depth zones (K-W,  $\chi^2 = 4.28$ , p = 0.63, Fig. 4A). Only two individuals were infected with gnathiid parasites depths >2000 m. Among all habitats, *A. rostrata* was most abundant in cold seeps ( $0.020 \pm 0.009$  SE individuals  $10\text{ m}^{-2}$ , Figs. 5 and 6A). *A. rostrata* was most abundant during a single dive at a cold seep site (0.37 individuals  $10\text{ m}^{-2}$ , 1412–1474 m depth). Here, only 0.004 ectoparasite-host interactions  $10\text{ m}^{-2}$  was estimated. The greatest number

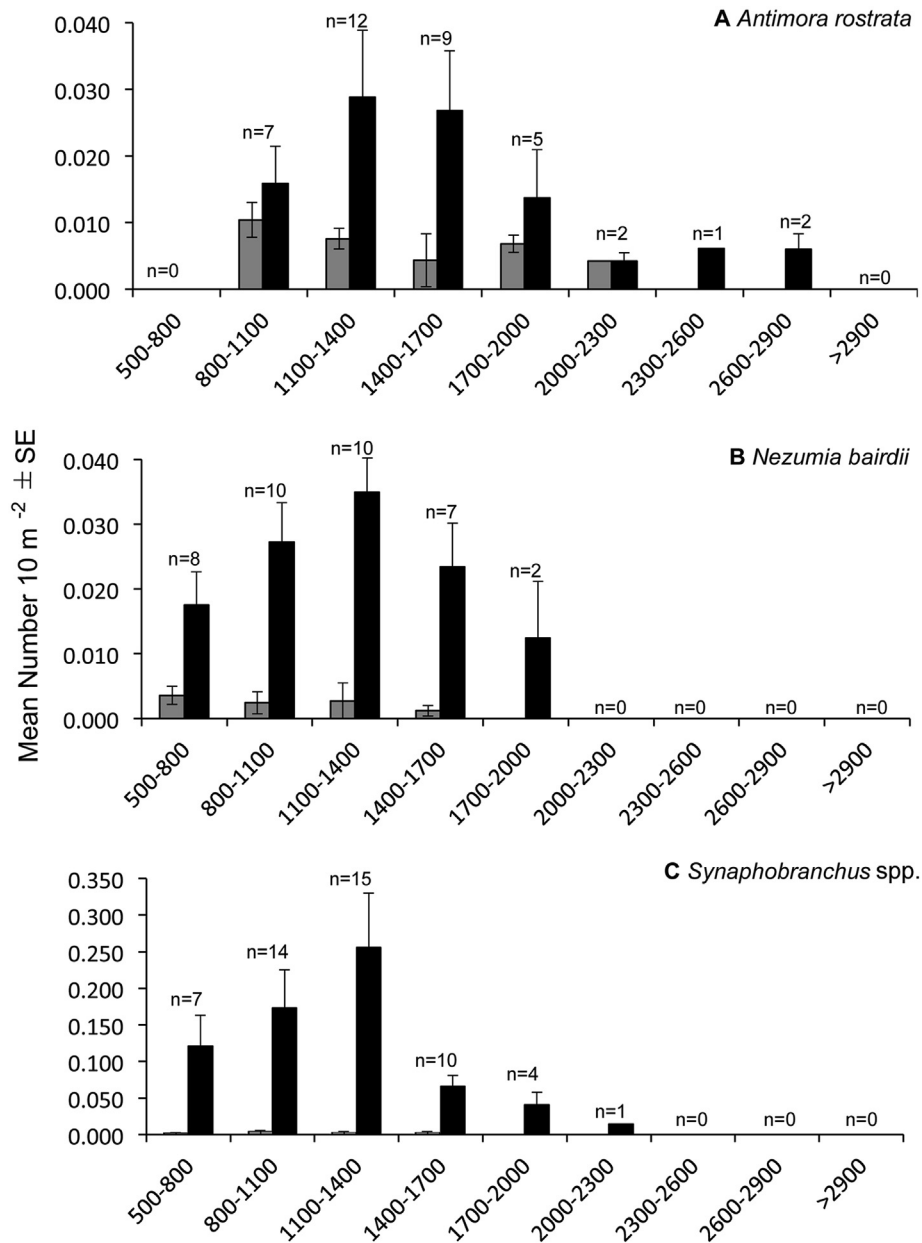
( $0.005 \pm 0.001$  SE interactions  $10\text{ m}^{-2}$ ) of ectoparasite-host interactions was in submarine canyons, but interactions were not significantly different among habitats (K-W,  $\chi^2 = 5.56$ , p = 0.13, Fig. 5A). The highest abundance (0.13 interactions  $10\text{ m}^{-2}$ ) of ectoparasite-host interactions during a single dive was from Heezen Canyon (1694–1722 m), where the abundance of *A. rostrata* was 0.018 individuals  $10\text{ m}^{-2}$ .

For *N. bairdii* (n = 153 individuals, n = 24 dives), we positively identified ectoparasites on 12% of all individuals (15–25 cm TL), while 25% of *N. bairdii* individuals had no ectoparasites. Of the individuals confirmed with parasites, 42% were infected with gnathiids, 26% were infected with aegid isopods, 21% were infected with sphyriid copepods, and 11% had unidentified parasites (Table 1, Fig. 3). For the remaining 63% of individuals, it could not be determined whether or not individuals hosted parasites. The average number of parasites infecting a single side of an individual was  $2.15 \pm 0.52$  SE parasites per side (n = 13 individuals, 1 to 7 ectoparasites per individual). The highest intensity of infections ( $2.67 \pm 0.92$  SE ectoparasites per side) on *N. bairdii* occurred in open slope/intercanyon habitats (Table 3).

While *N. bairdii* was observed at depths of 500 to 1860 m, this species was most abundant ( $0.035 \pm 0.007$  SE individuals  $10\text{ m}^{-2}$ ) between 1100 and 1400 m. However, ectoparasite-host interactions were not significantly different among depth zones (K-W,  $\chi^2 = 7.57$ , p-value = 0.11) (Fig. 4B). Ectoparasite-host interactions also did not differ among habitats (K-W,  $\chi^2 = 1.92$ , p = 0.38, Figs. 5B, 6B). Mean abundances ranged from  $0.014 \pm 0.004$  SE individuals  $10\text{ m}^{-2}$  (n = 6 dives, open slope) to 0.038 individuals  $10\text{ m}^{-2}$  (n = 1 dive, cold seep). During a single dive, *N. bairdii* was most abundant (0.054 individuals  $10\text{ m}^{-2}$ ) in Okeanos Canyon at depths ranging from 1360 to 1500 m; yet no individuals had ectoparasites at this site. The greatest number of individuals with ectoparasites (0.009 interactions  $10\text{ m}^{-2}$ ) was during a single dive in Phoenix Canyon at depths ranging from 1035 to 1172 m. Here, abundance of *N. bairdii* was 0.041 individuals  $10\text{ m}^{-2}$ .

**Table 3**  
Mean  $\pm$  SE (and range) of infection intensity for each dominant species across four general habitat types (seamount, canyon, cold seep, and open slope/intercanyon). Intensity was calculated as the number of ectoparasites observed per one side of the individual. n = number of individuals used in calculations.

Species	Cold seep	Seamount	Open slope/Intercanyon	Canyon
<i>Antimora rostrata</i>	$6.50 \pm 2.00$ (n = 2)	6 (n = 1)	$2.00 \pm 1.00$ (1–4, n = 3)	$9.05 \pm 2.39$ (6–45, n = 8)
<i>Nezumia bairdii</i>			$2.67 \pm 0.92$ (1–7, n = 6)	$1.71 \pm 0.57$ (1–5, n = 7)
<i>Synphobranchus spp.</i>	$1.00 \pm 0.00$ (1, n = 2)		$1.00 \pm 0.00$ (1, n = 5)	$2.00 \pm 0.225$ (2–3, n = 4)

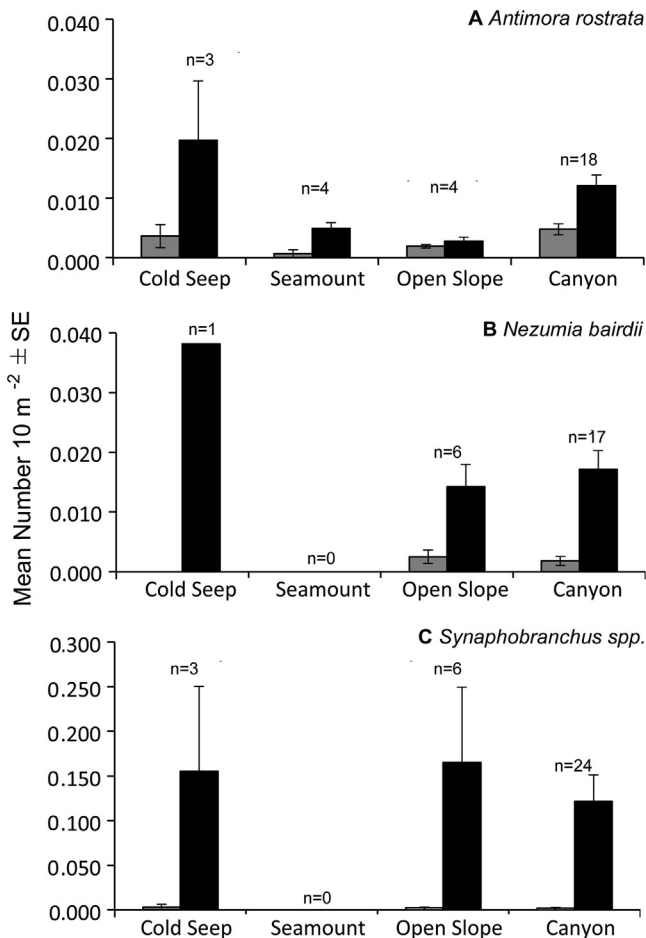


**Fig. 4.** Mean abundance ( $\pm$ SE) of A) *Antimora rostrata*, B) *Nezumia bairdii*, and C) *Synaphobranchus* spp. per depth zone (black bars). Mean abundance ( $\pm$ SE) of ectoparasite-host interactions (grey bars) also included. n = number of dives during which the species was present.

The cutthroat eel, *Synaphobranchus* spp. was the most abundant species observed ( $n = 1785$  individuals, 33 dives) across the study area, but had the fewest ectoparasites. Ectoparasites were observed on only 1.4% of all *Synaphobranchus* spp. (25–50 cm TL), whereas 68.2% of *Synaphobranchus* individuals had no ectoparasites. Of the individuals confirmed with parasites, 32% were infected with sphyriid copepods, 2% were infected with gnathiids, and 48% had unidentified parasites (Fig. 3). For the remaining 30.4% of individuals, it could not be determined whether or not individuals hosted ectoparasites. The average number of parasites infecting a single side of an individual was  $1.45 \pm 0.21$  SE parasites per side (1–3 ectoparasites per individual). The most intense infections ( $2.00 \pm 0.25$  SE ectoparasites per side) were in canyon habitats (Table 3).

*Synaphobranchus* spp. was observed at depths ranging from 500 to 2025 m and was most abundant ( $0.256 \pm 0.074$  SE individuals

$10 \text{ m}^{-2}$ ) at depths of 1100 to 1400 m. Ectoparasitism, however, was slightly more abundant at 800 to 1100 m, but not significantly higher (K-W,  $\chi^2 = 4.20$ ,  $p = 0.52$ ) than other depth ranges (Fig. 4C). None of the *Synaphobranchus* spp. observed >2000 m were infected by ectoparasites. Although *Synaphobranchus* spp. were abundant in open slope habitats ( $0.165 \pm 0.083$  SE individuals  $10 \text{ m}^{-2}$ ), ectoparasite-host interactions did not differ among habitats (K-W,  $\chi^2 = 0.79$ ,  $p = 0.67$ , Figs. 5C, 6C). Ectoparasite-host interactions ranged from  $0.002 \pm 0.001$  to  $0.003 \pm 0.003$  SE individuals  $10 \text{ m}^{-2}$  in open slope, canyon, and cold-seep habitats. During a single dive, both the highest abundances of *Synaphobranchus* spp. ( $0.68$  individuals  $10 \text{ m}^{-2}$ ) and ectoparasite-host interactions ( $0.014$  individuals  $10 \text{ m}^{-2}$ ) were observed in Phoenix Canyon at depths ranging from 1000 to 1170 m.



**Fig. 5.** Mean abundance ( $\pm$ SE) of A) *Antimora rostrata*, B) *Nezumia bairdii*, and C) *Synaphobranchus* spp. per habitat (black bars). Mean abundance ( $\pm$ SE) of ectoparasite-host interactions (grey bars) is also included. n = number of dives during which the species was present.

### 3.4. Behavioral observations

No notable differences in behavior were observed for the majority of fishes infected with ectoparasites, particularly those infected with gnathiids. Most of the individuals appeared to be either resting on the bottom [e.g., *A. radiata*, *Bathysaurus ferox*, *Cottunculus thomsonii*] or swimming normally (e.g., sharks, chimaeras, ophiidiids, morids, macrourids, synaphobranchids) either close to or just a few meters above the seafloor. Only a few of the fishes that had large ectoparasites appeared to be behaving abnormally. One *N. bairdii* individual with a sphyriid copepod hyperparasitized by eight leeches (Fig. 2C) appeared to be underweight than other individuals of similar total lengths (~15 cm TL). This individual was observed swimming in circles and appeared to be leaning towards one side (Suppl. Video). One *Hoplostethus mediterraneus* with a large cymothoid isopod on its left side was observed making short, erratic movements using its pectoral fins. Finally, one *Synaphobranchus* individual with a large (~5 cm TL) sphyriid copepod was swimming so close to the seafloor that both host and copepod were in contact with the sediment, perhaps increasing the chance for parasite removal. Although ROV lights and noise can alter individual fish behavior (Stoner et al., 2008), abnormal swimming behaviors were likely not an effect of the ROV because these behaviors were not observed in numerous uninfected individuals.

Supplementary video related to this article can be found at <http://dx.doi.org/10.1016/j.ijppaw.2016.07.004>.

## 4. Discussion

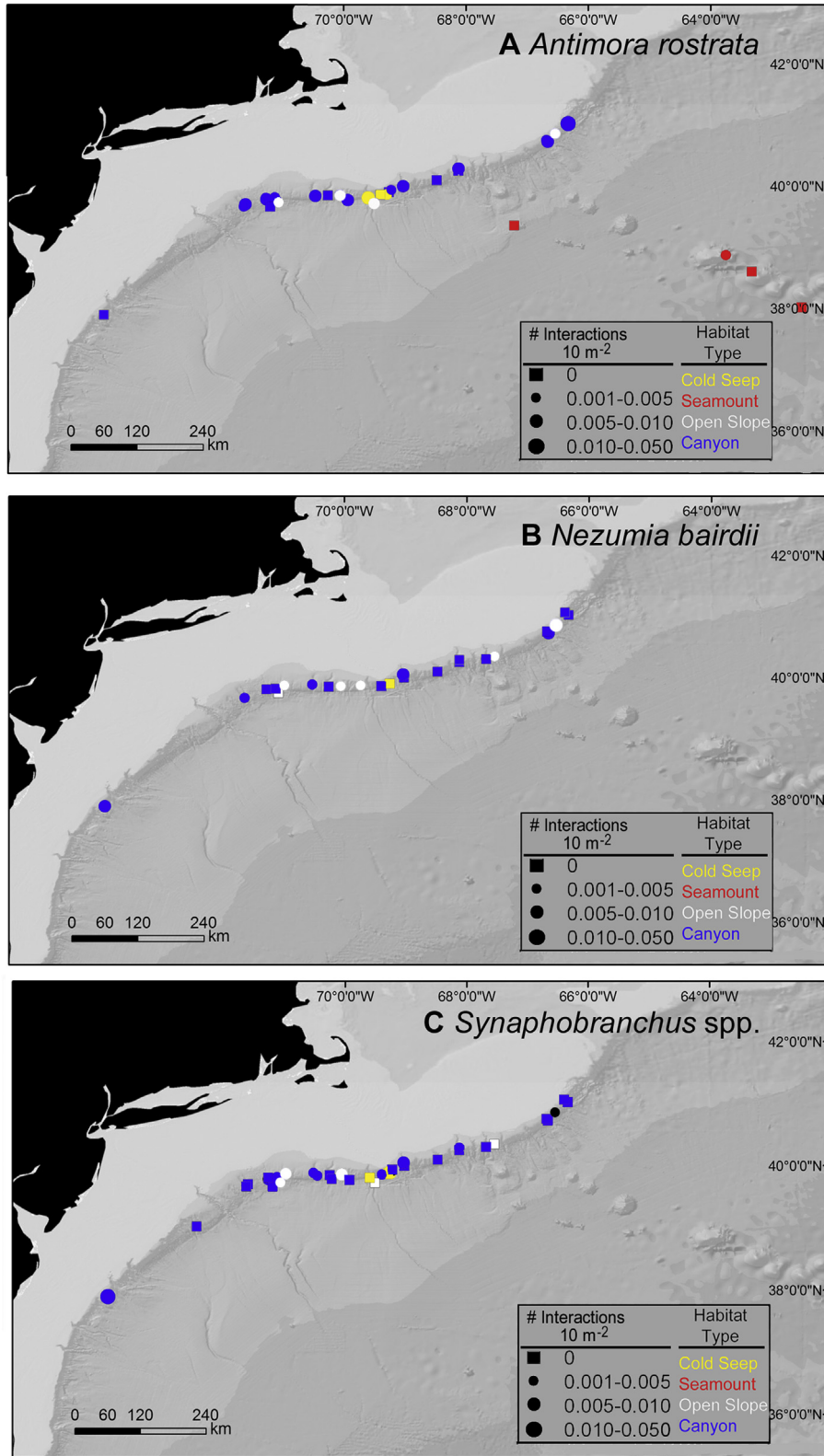
ROV video provided remarkable observations of ectoparasite infections on deep-sea fishes. These observations enabled us to determine that ectoparasitism occurs across a variety of depths (500–3300 m), habitats (seamounts, canyons, cold seeps, open slope), and host species (25 species) along the northeastern U.S. (NEUS) continental margin and New England Seamount Chain. We found that the abundance of ectoparasite-host interactions and intensity of infections peaked within particular depths and habitats depending upon the host species examined, but that submarine canyons may enhance ectoparasitism. We also found that species richness of ectoparasites declined with depth; only gnathiids were observed at the deepest depths surveyed. Thus, our results strengthen the notion that as temperature decreases (Poulin and Rohde, 1997) and the number of host species decline (Campbell et al., 1980) with increasing depth, the diversity of host-ectoparasite interactions decreases as well. We also note that, at least at the family level, ectoparasites infecting demersal fishes appear to be both generalist (gnathiids, infecting 19 host species) and specialist (copepods, aegids, and cymothoids, each infecting 1–2 host species) species, likely due to differences in parasite life cycles. Although our estimates of ectoparasite diversity are conservative, as species cannot be identified without collections, our study demonstrates the utility of using an ROV to observe and count ectoparasite-host interactions across a variety of depths, habitats, and host species, while providing the opportunity to examine *in situ* the impact of ectoparasite infections on fish behavior.

### 4.1. Ectoparasite-host interactions

Ectoparasitism was widespread across fish species, with 18 families of teleosts and chondrichthyans observed with ectoparasite infections. Demersal species were more frequently infected than mesopelagic species. Many ectoparasites have benthic life stages (e.g., Smit and Davies, 2004) and thus would more likely encounter a demersal fish host than a mesopelagic host. The majority of fish species harboring ectoparasites were both relatively abundant in the region and/or were habitat generalists (Auster et al., 1995; Ross et al., 2015; Quattrini et al., 2015). Thus, the number of ectoparasite-host interactions could be a consequence of the host population size or the host adopting a generalist strategy by utilizing a wide range of niches, including food resources and habitats. Other host behaviors, such as spawning (e.g., scyliorhinids) or feeding on the benthos (e.g., *N. bairdii*, Campbell et al., 1980) or aggregating (*A. rostrata*, Iwamoto, 1975), may also increase ectoparasite infections (Boxshall, 1998).

Our study also revealed that demersal lifestyle alone, of hosts, was not sufficient to explain ectoparasite infections. The number of demersal host species (24 species) with ectoparasites constituted approximately one third of all demersal species (69 species) observed across the same depth range in the region (Table S1, Quattrini et al., 2015). Although ectoparasite-host interactions may be underestimated, our results are comparable to those documented from deep-sea fishes (to 1000 m) collected off Australia using surface-deployed gear (e.g., traps, trawls) (Rohde et al., 1995). The absence of ectoparasites on several species might provide evidence of unoccupied niches for the ectoparasites (Rohde et al., 1995). Alternatively, the absence of ectoparasites could be a result of a fish's resistance to infection (e.g. mucous production, skin/scale resiliency, Coile and Sikkell, 2013), rarity of the fish host (Boxshall, 1998) or fish behavior (Boxshall, 1998).





**Fig. 6.** Ectoparasite-host interactions for A) *Antimora rostrata*, B) *Nezumia bairdii*, and C) *Synaphobranchus* spp. across the region for which the presence or absence of ectoparasites could be confirmed. Circle Size = Number of confirmed ectoparasite-host interactions 10 m<sup>-2</sup>. Square = No ectoparasites observed. Colors denote habitats.

The intensity of infections and the abundance of ectoparasite-host interactions was not a function of host abundance. Ectoparasitism was not most abundant where both *N. bairdii* and *A. rostrata*

were locally most abundant. Furthermore, *Synaphobranchus* spp. was the most abundant species observed; yet ectoparasitism was relatively low in this species compared to the others. Additionally,

among the three dominant species, the infection intensity was highest in *A. rostrata*, yet all three species were common across depths and habitats and all are generalist feeders. *A. rostrata* and *Synaphobranchus* spp. scavenge (Collins et al., 1999; Jamieson et al., 2011) or feed on benthopelagic species and *N. bairdii* feeds mainly on benthic invertebrates (Campbell et al., 1980; Houston and Haedrich, 1986). Perhaps the higher intensity of infections on *A. rostrata* relate to movement and/or aggregation of individuals (Boxshall, 1998) for reproduction (Iwamoto, 1975; Wenner and Musick, 1977). Aggregating at a single, dominant spawning site or undergoing periodic re-distribution during reproduction (White et al., 2011) may increase transmission rates of ectoparasites. Higher infection intensity in *A. rostrata* may also be due to reduced resistance to infection. Gnathiids could perhaps more easily penetrate *A. rostrata*, as this species has relatively large, overlapping cydoid scales.

In addition to the ecology and biology of the host species, the ecology and life history traits of the ectoparasites also influence prevalence, specificity, and intensity of infections. Compared to the other ectoparasite families, gnathiids infected a variety of host species (19 spp.) across the entire depth range. A single species of gnathiid is known to infect numerous host species in shallow waters (e.g., Coile and Sikkell, 2013). Life history characteristics of gnathiids likely increase their ability to infect a variety of species and more than one host species in their lifetime (Lafferty and Kuris, 2002; Jones et al., 2007; Grutter et al., 2008). Although the three larval stages of gnathiids are obligate fish parasites, between each stage, larval gnathiids return to the benthos (e.g., sponges, corals, serpulid tubeworms, tunicates, sediments, among rocks, wood) to molt until infecting another species or until the final, non-feeding adult stage (Mouchet, 1928; Stoll, 1962; Upton, 1987; Jacoby and Greenwood, 1988; Klitgaard, 1991; Smit et al., 1999, 2003; Smit and Davies, 2004). Thus, gnathiids may have been so successful at colonizing, with high intensity, a diversity of host fishes from shallow waters to the deep sea because of attributes of their life cycle.

In contrast to gnathiids, siphonostomatoids, aegids, and cymothoids isopods are known to be highly host specific (Wilson, 1919; Ho, 1985; Boxshall, 1998; Bunkley-Williams and Williams, 1998; Ross et al., 2001). In our study, siphonostomatoid copepods and aegid and cymothoid isopods infected four, two, and one species, respectively. For cymothoids and copepods, free-living juvenile stages attach to hosts and remain on the host for life until reproduction (Boxshall, 1998; Bunkley-Williams and Williams, 1998). Although these ectoparasites have reproductive strategies that would help them complete their life cycle in the deep sea [e.g., males parasitizing females (copepods, Boxshall, 1998) and hermaphroditism (cymothoids, Bunkley-Williams and Williams, 1998)], specializing on only a few host species may help increase encounter rates of male and females during periods of sexual reproduction. In contrast, aegids are temporary parasites, changing hosts during their lifetimes by settling on the benthos until infecting another species (Bunkley-Williams and Williams, 1998). This behavior may result in higher infection rates of demersal fishes that feed on the benthos, such as *N. bairdii* and *A. radiata* (e.g., Campbell et al., 1980).

Based on previous research, ectoparasites from the host-specific families observed in this study were most likely different species. *Lophoura* spp. are known to exhibit high host specificity. In the NEUS region, *Leptodactylus gracilis* has been reported from *S. kaupii* (Wilson, 1919) whereas *Leptodactylus pentaloba* and *Leptodactylus bouvieri* have been reported from *N. bairdii* (Wilson, 1919; Ho, 1985). *Parabrachiella pinguis* is the only lernaepodid that has been reported from *A. rostrata* in the NEUS region (Wilson, 1915; Ho, 1985). *Sarcotretes scopeli* (family Pennellidae) is the only

copepod recorded from myctophids in the Atlantic (Gartner and Zwerner, 1989; Boxshall, 1998). As for the isopods, the aegid *Syscenus infelix* has been reported from *N. bairdii* along the NEUS slope (Ross et al., 2001). *Aega psora* is the only aegid recorded from *Antimora radiata*, documented only once in the Bay of Fundy (Wallace and Huntsman, 1919). One cymothoid was observed in this study, and to our knowledge constitutes the first record of ectoparasitism on *H. mediterraneus*. Few cymothoids are known to inhabit deep waters (Brusca, 1981), particularly below 800 m (Poore and Bruce, 2012).

#### 4.2. Patterns across depth and habitat

Ectoparasite-host interactions were observed in all habitats, but our data suggest that submarine canyons may increase abundance of ectoparasite-host interactions, the number of host species infected, and the intensity of infections, at least for some species. Canyons (Alvin, Nygren, Hydrographer, Phoenix) with the highest ectoparasite-host interactions observed contained relatively high numbers of fish species observed (14–20 species per dive) than other sites in the region (see Quattrini et al., 2015). Additionally, for each dominant species, ectoparasite-host interactions were most abundant during a single dive in a canyon habitat. For *A. rostrata*, the mean abundance of ectoparasite-host interactions and the intensity of ectoparasite infections were also higher in submarine canyons than other habitats. Campbell et al. (1980) found a higher endoparasite load in both *A. rostrata* and *N. bairdii* occupying canyon habitats in the same region. Higher intensities of infections in canyon environments may in part be related to increased habitat heterogeneity, including higher abundances of both corals and sponges (Huvenne et al., 2011; Quattrini et al., 2015). Corals and sponges have been noted to house resting stages of gnathiid larvae (Klitgaard, 1991). In fact, all resting larval and adult stages have been previously collected from a single sponge in deep waters (150–487 m, Klitgaard, 1991), suggesting some site fidelity for parasites. Submarine canyons also channel organic matter (Canals et al., 2006; Oliveira et al., 2007), and have been documented with higher abundances of fauna compared to the surrounding slopes (Vetter and Dayton, 1999). It is possible that deep-sea fishes, including *A. rostrata*, are more actively feeding in submarine canyons, and thus these behaviors may increase infection rates of ectoparasites.

Depth was an important factor influencing ectoparasitism. Peaks in both ectoparasite diversity and ectoparasite-host interactions were observed at mid-slope depths. Ectoparasite-host interactions were most abundant at depths of 800 to 1100 m for *A. rostrata* and *Synaphobranchus* spp. and at 500 to 800 m for *N. bairdii*. Ectoparasitism diversity was highest at depths of 500 to 1400 m, and then declined with increasing depth. Siphonostomatoid copepods, aegids, and cymothoids were absent at depths >1400 m; only gnathiids were observed at the deepest depths surveyed (up to 3260 m). Peaks at mid-slope depths appear to correspond to higher species richness of fishes. ROV dives from the 2013–2014 expeditions documented fewer numbers of species (5–12 species per dive) at deeper depths (>1400 m) than in shallower (500–1400 m) depths (9–20 species per dive, see Quattrini et al., 2015). The absence of the host-specific ectoparasites at deeper depths is due to decreased diversity and depth range limits of host species, similar to the endoparasite fauna sampled from fishes in the same region (Campbell et al., 1980). But in contrast to patterns in the endoparasite fauna, the number of ectoparasite-host interactions did not decrease linearly with depth in this region; similar abundances of ectoparasite-host interactions were observed at depths >1100 m (Campbell et al., 1980). In addition to host distribution, environmental conditions, such as temperature,

could also limit the distribution of ectoparasites. Temperature has a significant effect on the species richness of ectoparasite communities (Rohde et al., 1995). In the NEUS region, temperature changes from 4–5 °C to 3–4 °C at a depth boundary of approximately 1300 m, corresponding to a change in deep water masses (Pickart, 1992).

#### 4.3. Sampling considerations

This study was part of a larger expedition that was not focused solely on documenting ectoparasites on deep-sea fishes. Thus, we note a few methodological limitations and suggest modifications for future use of ROVs to fully document ectoparasitism in the deep sea. Due to inadequate camera angles, we were unable to determine whether ectoparasites were present on a portion of the dominant species. Further, we could not quantify ectoparasitism on all fishes observed in this study. Targeted ROV surveys that incorporate frequent zooms and discrete collections, perhaps in combination with museum collections, would be best to elucidate fine-scale patterns of ectoparasitism in the deep sea. We acknowledge that further sampling across similar depths and habitats is necessary to resolve confounding effects of habitat and depth on the distribution of ectoparasites and ectoparasite-host interactions; most effort was conducted at depths of 500 to 1100 m in canyon habitats. Further quantification is necessary to determine whether submarine canyons significantly influence the prevalence, abundance, and infection intensity of ectoparasitism in deep-sea fishes.

#### 4.4. Further considerations

Metazoan parasites are an important, yet overlooked, component of deep-sea communities. Similar to shallow-water communities, an estimated 1.5 metazoan parasite species occur per fish species; thus parasites likely have significant impacts on ecosystem functioning in the deep sea (Klimpel et al., 2001). In the present study, the widespread occurrence of ectoparasitism across a variety of host species, depths, habitats, and locations indicate that ectoparasites are a significant component of deep-sea biodiversity. Because ectoparasitism is widespread and many fishes also have wide-ranging distributions (e.g., Moore et al., 2003), ectoparasites could alter behavior and population dynamics of hosts, while increasing trophic connections (Amundsen et al., 2009; Demopoulos and Sikkkel, 2015) in communities throughout the deep sea. Understanding parasite ecology may thus serve as a proxy for determining healthy ecosystems (Hudson et al., 2006). For example, recent studies in shallow water ecosystems have demonstrated the important connections between fishes, ectoparasites, and cleaner species (Johnson et al., 2010); disruptions to these connections can cause community changes (e.g., Lafferty et al., 2008; Sun et al., 2015). Focused parasitology studies are sorely needed to further our understanding of the roles of parasites in both community and trophic ecology in the deep sea (Poulin et al., 2016). By demonstrating the widespread occurrence of ectoparasitism in the deep sea using visual based surveys, we hope that this study can serve as a basis for testing further hypotheses regarding the role of parasitism throughout the deep sea.

#### Author contribution

AWJD conceived the study. AMQ analyzed the video, conducted analyses, and wrote the text with significant contributions from AWJD.

#### Conflicting interests

We have no competing interests.

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