



Cold-Water Soft Corals (Cnidaria: Nephtheidae) as Habitat for Juvenile Basket Stars (Echinodermata: Gorgonocephalidae)

Bárbara de Moura Neves^{1*}, Vonda Wareham Hayes¹, Erin Herder¹, Kevin Hedges², Cindy Grant³ and Philippe Archambault³

¹ Northwest Atlantic Fisheries Center, Department of Fisheries and Oceans Canada, St. John's, NL, Canada, ² Freshwater Institute, Department of Fisheries and Oceans Canada, Winnipeg, MB, Canada, ³ ArcticNet, Québec Océan, Takuvik, Département de Biologie, Université Laval, Québec, QC, Canada

OPEN ACCESS

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*Correspondence:

Bárbara de Moura Neves
barbara.neves@dfo-mpo.gc.ca

Specialty section:

This article was submitted to
Deep-Sea Environments and Ecology,
a section of the journal
Frontiers in Marine Science

Received: 01 April 2020

Accepted: 25 August 2020

Published: 09 October 2020

Citation:

Neves BM, Wareham Hayes V,
Herder E, Hedges K, Grant C and
Archambault P (2020) Cold-Water
Soft Corals (Cnidaria: Nephtheidae)
as Habitat for Juvenile Basket Stars
(Echinodermata: Gorgonocephalidae).
Front. Mar. Sci. 7:547896.
doi: 10.3389/fmars.2020.547896

Nephtheidae soft corals are a common component of benthic ecosystems in the Northwest (NW) Atlantic and in the Arctic, but little is known about their functional roles. Here we investigated their role as habitat for basket stars (Ophiuroidea). By examining over 4500 soft coral colonies of *Drifa glomerata*, *Duva florida*, *Gersemia* spp., and *Pseudodrifa racemosa* collected during trawl surveys in the regions of Newfoundland, Labrador and West Baffin Bay, we show that Nephtheidae soft corals are habitat for juvenile *Gorgonocephalus* sp. basket stars. Juvenile *Gorgonocephalus* sp. were found on all soft corals species, but *Drifa glomerata* was the soft coral species with the highest occurrence of associated juvenile basket stars (32%), with a maximum of 111 basket stars found on a single 4.8 cm tall (contracted state) colony. Individual basket star disc diameter did not change with colony height, but it varied with season for individuals found on *D. glomerata*. On the other hand, colony height was positively related with maximum disc diameter (*D. glomerata*), and presence and number of basket stars on a colony (*D. glomerata* and *D. florida*). One very young ophiuroid was found within one polyp of a *D. florida* colony collected in July. We also examined bottom trawl survey data from 2011 to 2017 from Newfoundland to Baffin Bay, and other locations in the Eastern Canadian Arctic and found that for our largest database, 45% of trawl sets that contained basket stars also contained corals, of which 67% were Nephtheidae soft corals. In this study we show that all four Nephtheidae soft coral taxa studied act as habitat for juvenile basket stars, which are conspicuous components of benthic communities in cold-water environments. Soft corals are commonly exposed and vulnerable to bottom fishing gear in the North Atlantic. We urge future studies evaluating the nature of this relationship, the potential role of soft corals as nurseries, and the potential degree of dependency/preference between basket stars and soft corals in relation to other organisms.

Keywords: cold-water corals, Nephtheidae, functional role, habitat, basket stars, *Gorgonocephalus*, juveniles

INTRODUCTION

The functional role of an organism can be defined as the functions provided to the ecosystem (Vaughn and Hakenkamp, 2008), such as ecosystem functions related to impacts on substrate, benthopelagic coupling, and associations with other organisms (e.g., provision of microhabitat) (Bell, 2008). The function of habitat provision might also be accompanied by other functions, such as protection against predation, substrate for settlement, and camouflage (Bell, 2008). Cold-water corals are well known for their habitat-provision potential, as they are often reported in association with other organisms. Gorgonians and black corals have drawn particular attention, as they can grow to large sizes and host a variety of organisms in symbiotic, parasitic, or simply epibiotic relationships (Wahl, 1999; Krieger and Wing, 2002; Buhl-Mortensen and Mortensen, 2004a,b, 2005; Mosher and Watling, 2009; Clippele et al., 2015; Girard et al., 2016). With the advent of imagery technologies, *in situ* evidence of conspicuous associations with cold-water corals have become more common. This is especially true for taxa that can attain large sizes like gorgonians, which are more noticeable from imagery than small taxa like Nephtheidae soft corals, which are relatively small (often < 15 cm tall), with flexible, soft bodies. In contrast to other octocorals, soft corals have even been considered unsuitable to host attached species (Buhl-Mortensen et al., 2010), and believed to not host symbionts, in comparison to their warm-water nephtheid counterparts (Watling et al., 2011).

Ophiuroids in the genus *Gorgonocephalus* are a good example of conspicuous organisms commonly reported in association with cold-water corals (Table 1), including the scleractinians *Desmophyllum pertusum* (published as *Lophelia pertusa*) (Jensen and Frederiksen, 1992; Rosenberg et al., 2005; Wheeler et al., 2005) and *Madrepora oculata* (Buhl-Mortensen et al., 2010), the stylasterid *Errina antarctica* (Försterra et al., 2017), the gorgonians *Paragorgia arborea* (Buhl-Mortensen and Mortensen, 2005; Metaxas and Davis, 2005; Buhl-Mortensen et al., 2010; Clippele et al., 2015), *Paramuricea placomus* (Rosenberg et al., 2005; Clippele et al., 2015), *Primnoa* spp. (Jensen and Frederiksen, 1992; Krieger and Wing, 2002; Wild et al., 2008; Clippele et al., 2015), and also sponges (Klitgaard, 1995). Adult *Gorgonocephalus* spp. can have disc diameters of 7–10 cm, and they can also be found as free-living organisms (Mortensen, 1927; Patent, 1970a). Juveniles, on the other hand, have been suggested to be strongly linked to cold-water Nephtheidae soft corals (hereinafter referred to as soft corals), as this association has been reported at several instances (e.g., Fedotov, 1924; Mortensen, 1927; Patent, 1970a; Haedrich and Maunder, 1984; Buhl-Mortensen and Mortensen, 2005; Buhl-Mortensen et al., 2017).

Fedotov (1924) and Patent (1970a) revealed that the relationship between juvenile basket stars and soft corals begins very early in the basket stars' ontogeny. Fedotov (1924) observed juvenile *Gorgonocephalus* sp. (<0.5 mm disc diameter) protruding from polyps of live *Drifa glomerata* colonies from Kola Fjord (Barents Sea, published as *Gersemia glomerata*). Decades later, Patent (1970a) reported the presence of juvenile *Gorgonocephalus eucnemis* inside polyps of live *Gersemia* sp. colonies from Washington State (West coast of North America),

in both August and September 1965. Patent (1970a) suggested that basket star embryos are passively ingested by the soft corals between spawning and 8–9 days of age, and develop within the polyps. Since Patent's work, studies have focused on reporting the association: Haedrich and Maunder (1984) found *Gorgonocephalus lamarckii* individuals entangled with colonies of a Nephtheidae coral in Newfoundland, and young individuals of *Gorgonocephalus* sp. have been reported on *D. florida* (Buhl-Mortensen and Mortensen, 2005) and *D. glomerata* (Buhl-Mortensen et al., 2017). Young basket stars have also been observed *in situ* on colonies of *Gersemia* sp. from coastal areas in Labrador (~50–60 m, personal communication B. M. Neves and R. Rangeley, Oceana Canada).

Both soft corals and basket stars are common in the Northwest (NW) Atlantic and the Eastern Canadian Arctic, being found at wide latitudinal ranges and depths of <10–1287 m (Wareham and Edinger, 2007; this study) and 40–1324 m (Neves and Wareham Hayes, 2019; this study), respectively. Soft coral colonies can be found in high densities, being often the most frequent coral taxa in bottom trawl bycatch samples in this region (Wareham and Edinger, 2007; Wareham, 2009; Murillo et al., 2011). Similarly, basket stars can be found in high densities at some locations (e.g., Neves and Wareham Hayes, 2019).

Despite commonly reported in the literature, the basket star-soft coral association has never been quantified. Considering the potential importance of soft corals in the early stages of basket star development, the objectives of this study are: (1) to describe the relationship between the two taxa in terms of epibiont basket star size ranges, occurrence and position on a colony, and (2) to investigate the potential influence of colony height and environmental variables on epibiont basket star occurrence and abundance by soft coral taxa. We examined over 4500 physical colonies from four soft coral taxa (*Drifa glomerata*, *Duva florida*, *Gersemia* spp., and *Pseudodrifa racemosa*) from the regions of Newfoundland, Labrador, and W Baffin Bay (NW Atlantic). Using 7 years of bottom trawl bycatch data we also investigated the co-occurrence of soft corals and basket stars in the region.

MATERIALS AND METHODS

Sampling

Most soft coral samples were collected during multispecies trawl surveys conducted by the Department of Fisheries and Oceans Canada (DFO) between the years 2003–2015 in the NW Atlantic and Eastern Canadian Arctic (Table 2 and Figure 1A). These surveys are conducted by DFO's Newfoundland and Labrador (NL) and Ontario and Prairie (OP, previously Central and Arctic) Regions. Surveys have a stratified random design, with tow speeds of 3 knots and duration of 15 minutes, although OP tows can range between 15 and 30 min.

The NL Region conducts annual Multispecies Stock Assessment Surveys twice a year, between April-May and October-December. But in some cases, surveys took place during months outside of this range. In this region, surveys use a Campelen 1800 shrimp trawl equipped with rockhopper footgear, with tight rubber disks and spacers mounted along

TABLE 1 | Reported associations between Gorgonocephalidae basket stars and cold-water corals.

Coral group	Specific coral taxa	<i>Gorgonocephalus</i> taxa	Location	Depth (m)	Notes from the publications	Source
Octocorallia	Nephtheidae sp.	<i>G. lamarckii</i>	Newfoundland continental slope	200–1800	Most specimens were entangled with a Nephtheidae coral in an apparently parasitic relationship "as noted by others."	Haedrich and Maunder, 1984
	Nephtheidae sp. (published as <i>Eunephtya</i> spp.)	<i>G. eucnemis</i>	North Atlantic	na	Lives parasitic on polyps of <i>Eunephtya</i> spp. When branching of arms begins they leave the coral and may seek adult specimens.	Mortensen, 1927
	<i>Drifa glomerata</i>	<i>Gorgonocephalus</i> spp.	Russia, Norway	na	Observed juveniles of <i>Gorgonocephalus</i> spp. within the polyps of <i>Drifa glomerata</i> (Published as <i>Gersemia glomerata</i>).	Fedotov, 1924; Buhl-Mortensen et al., 2017
	<i>Duva florida</i>	<i>Gorgonocephalus</i> sp.	Continental shelf and slope, Atlantic Canada	na	Observed younger individuals amongst branches of soft coral <i>Duva florida</i> .	Buhl-Mortensen and Mortensen, 2005
	<i>Gersemia</i> sp.	<i>G. eucnemis</i>	San Juan Islands, Washington State, USA	37–183	Very small (<1 mm disc diameter) specimens found living inside polyps of <i>Gersemia</i> .	Patent, 1970a
	Gorgonians	<i>Gorgonocephalus</i> spp.	na	na	Often found clinging to gorgonians and can reach up to 10 cm (disc diameter)	Mortensen, 1927
	Octocoral sp.	<i>G. eucnemis</i>	Guadalupe Island, Mexico	287.6	One specimen (100 mm) observed lying on remnants of dead octocoral colony.	Herrero-Pérezrul et al., 2014
	<i>Paragorgia arborea</i>	<i>G. caputmedusae</i>	na	na	General information.	Storm, 1901; Mortensen, 1927; referenced in Buhl-Mortensen and Mortensen, 2004a
	<i>Paragorgia arborea</i>	<i>G. lamarckii</i>	na	na	General information.	Storm, 1901; Mortensen, 1927; referenced in Buhl-Mortensen and Mortensen, 2004a
	<i>Paragorgia arborea</i>	<i>G. lamarckii</i>	Continental shelf and slope, Atlantic Canada	300–600	<i>G. lamarckii</i> observed on outer branches of <i>P. arborea</i> . Observed on young parts of colony. Predominantly large individuals with disc diameter of 15–60 mm. Use of host: substrate.	Buhl-Mortensen and Mortensen, 2005; Buhl-Mortensen et al., 2017
	<i>Paragorgia arborea</i>	<i>G. arcticus</i>	Northeast Channel, Northwest Atlantic	380–498	General information.	Metaxas and Davis, 2005
	<i>Paragorgia arborea</i>	<i>G. caputmedusae</i>	na	na	General information.	Buhl-Mortensen et al., 2017
	<i>Paragorgia arborea</i>	<i>G. eucnemis</i>	na	na	General information.	Buhl-Mortensen et al., 2017
	<i>Paragorgia arborea</i>	<i>Gorgonocephalus</i> sp.	Norway	200–400	Young sections of <i>Paragorgia</i> sp. used as a feeding site by <i>Gorgonocephalus</i> sp.	Buhl-Mortensen et al., 2010
	<i>Paragorgia arborea</i>	<i>Gorgonocephalus</i> sp.	Continental margin, Northern Norway	116–863	Use corals as a substrate for attachment and shelter, for feeding, parasitism.	Clippele et al., 2015
	<i>Paragorgia</i> sp.	<i>Gorgonocephalus</i> sp.	West of Faroe Islands	375	<i>Gorgonocephalus</i> sp. found in same trawl catch with <i>Lophelia</i> and <i>Paragorgia</i> .	Bruntse and Tendal, 1999

(Continued)

TABLE 1 | Continued

Coral group	Specific coral taxa	<i>Gorgonocephalus</i> taxa	Location	Depth (m)	Notes from the publications	Source
	<i>Paramuricea placomus</i>	<i>Gorgonocephalus</i> sp.	Continental margin, Northern Norway	116–863	Use corals as a substrate for attachment and shelter, for feeding, parasitism.	Clippelle et al., 2015
	<i>Paramuricea placomus</i>	<i>G. caputmedusae</i>	Oslofjord, Norway	85–120	35 of 90 gorgonocephalids were attached to the gorgonian on one 400 m long transect.	Rosenberg et al., 2005
	<i>Primnoa resedaeformis</i>	<i>G. lamarckii</i>	Continental shelf and slope, Atlantic Canada	300–600	Use of host: substrate.	Buhl-Mortensen and Mortensen, 2005
	<i>Primnoa resedaeformis</i>	<i>Gorgonocephalus</i> sp.	Continental margin, Northern Norway	116–863	Use corals as a substrate for attachment and shelter, for feeding, parasitism	Clippelle et al., 2015
	<i>Primnoa</i> spp.	<i>G. eucnemis</i>	Gulf of Alaska	161–365	<i>G. eucnemis</i> either fed on <i>Primnoa</i> polyps, used the branches for suspension feeding, or sought protection.	Krieger and Wing, 2002
Primnoidae		<i>Gorgonocephalus</i> sp.	Argentina	135	<i>Gorgonocephalus</i> sp. Accompanied by different species of the octocoral family Primnoidae.	Portela et al., 2012
Ellisellidae		<i>G. chilensis</i>	South Brazil	20	One single specimen (28 mm disc diameter) collected associated with the octocoral.	Barboza et al., 2010
Stylasteriidae	<i>Errina antarctica</i>	<i>G. chilensis</i>	Chile	18	<i>Gorgonocephalus chilensis</i> is commonly encountered on <i>E. antarctica</i> .	Häussermann and Fösterra, 2007
Scleractinia	<i>Lophelia pertusa</i> , gorgonians	<i>G. caputmedusae</i>	Norway	na	Facultative, commensal.	Storm, 1901; Mortensen, 1927; Dons, 1944; Burdon-Jones and Tambs-Lyche, 1960; referenced in Buhl-Mortensen and Mortensen, 2004a
	<i>Lophelia banks</i>	<i>Gorgonocephalus</i> sp.	Faroe Islands	na	The ophiuroid <i>Gorgonocephalus</i> sp. is known from trawl hauls on <i>Lophelia banks</i> in the Faroes.	Jensen and Frederiksen, 1992; Reference BIOFAR trawl surveys not conducted as part of this paper – see Bruntse and Tendal, 1999
	<i>Lophelia pertusa</i>	<i>G. caputmedusae</i>	Oslofjord, Norway	85–120	<i>G. caputmedusae</i> were found associated with live and dead <i>L. pertusa</i> and coral rubble.	Rosenberg et al., 2005
	<i>Lophelia pertusa</i>	<i>Gorgonocephalus</i> sp.	Northwest Porcupine Bank, west Ireland	664	Photograph observation.	Wheeler et al., 2005
	<i>Lophelia</i> sp.	<i>Gorgonocephalus</i> sp.	West of Faroe Islands	375	<i>Gorgonocephalus</i> sp. found in same trawl catch with <i>Lophelia</i> , and <i>Paragorgia</i> .	Bruntse and Tendal, 1999
	<i>Madrepora oculata</i>	<i>Gorgonocephalus</i> sp.	Norway	200–400	Submersible observation (photograph) of <i>Gorgonocephalus</i> sp. wrapped around <i>M. oculata</i> .	Buhl-Mortensen et al., 2010
	<i>Oculina varicosa</i>	<i>Asteropora annulata</i>	East-central Florida	56–84	Simple-armed gorgonocephalid, observed on live and dead coral mounds (109–207 mm disc diameter)	Hendler and Miller, 1984

TABLE 2 | Gear (mostly trawls), mean tow duration, number of sets/stations, regions surveyed, years, months, and number of colonies per survey (Ncol) for physical samples and trawl databases.

Source	Gear	Dur	Sets (N)	General region	Years	Depth (m)	Months	Ncol
Physical samples								
DFO-NL	Campelen (STD)	15 min	768	Labrador, Newfoundland	2003–2015	41–1452	Jan, April–Jul, Oct–Dec	2999
DFO-OP	Campelen (MOD)	15 min	1	Ungava Bay	2011	171	Sept	1
DFO-OP	Cosmos	15 min	114	W Baffin Bay, Ungava Bay, West of Hudson Strait (WHS)	2006–2014	104–908	Aug–Nov	323
DFO-OP	Alfredo	30 min	110	W Baffin Bay and Davis Strait	2006–2014	435–1452	Sept–Nov	467
DFO-OP	Gillnet	na	1	Baffin Bay	2006	119	Aug	1
NSRF	Campelen (MOD)	15 min	197	W Baffin Bay and Davis Strait	2005–2013	116–666	April, Jul–Aug	445
Academic	Agassiz	1.5–3	3	Baffin Bay, Hudson Bay	2018	91–309	June–July	33
FOP	Variable	Variable	113	Baffin Bay, Labrador, Newfoundland	2004–2013	46–1320	Jan–Dec	199
CFER ^a	Longline, shrimp trap	Variable	2	Arctic Bay, Resolute	2015	178, 717	Aug–Sept	2
GEAC ^b	Campelen (STD)	15 min	1	S Gulf of St. Lawrence, NE Scotian Shelf, SW Grand Banks	2014	na	na	2
Unknown ^b	na	na	na	na	na	na	na	55
Total			1322					4527
Trawl database								
DFO-NL	Campelen (STD)	15 min	8096	Labrador, Newfoundland	2011–2017	36–1480	Jan–Dec (except Feb)	Na
DFO-OP	Campelen (MOD)	15 min	1494	Davis Strait, Ungava Bay, N Labrador	2011–2017	104–745	Jul–Sept	Na
DFO-OP	Cosmos	15 min	151	W Baffin Bay, Davis Strait, Western Hudson Strait, Ungava Bay	2011–2013	103–950	Aug–Nov	Na
DFO-OP	Alfredo	30 min	854	W Baffin Bay, Davis Strait	2011–2017	298–1492	Aug–Nov	Na
Academic	Agassiz	1.5–3 min	88	Eastern Canadian Arctic (including W Baffin Bay)	2007–2018	35–1453	June–Oct	Na
Total			10,683					

^aExperimental fisheries (CFER, Marine Institute, Memorial University). ^bGroundfish Enterprise Allocation Council (GEAC) samples and source unknown represent samples whose specific origin data was lost. These samples were only included in the descriptive analyses that did not involve environmental data.

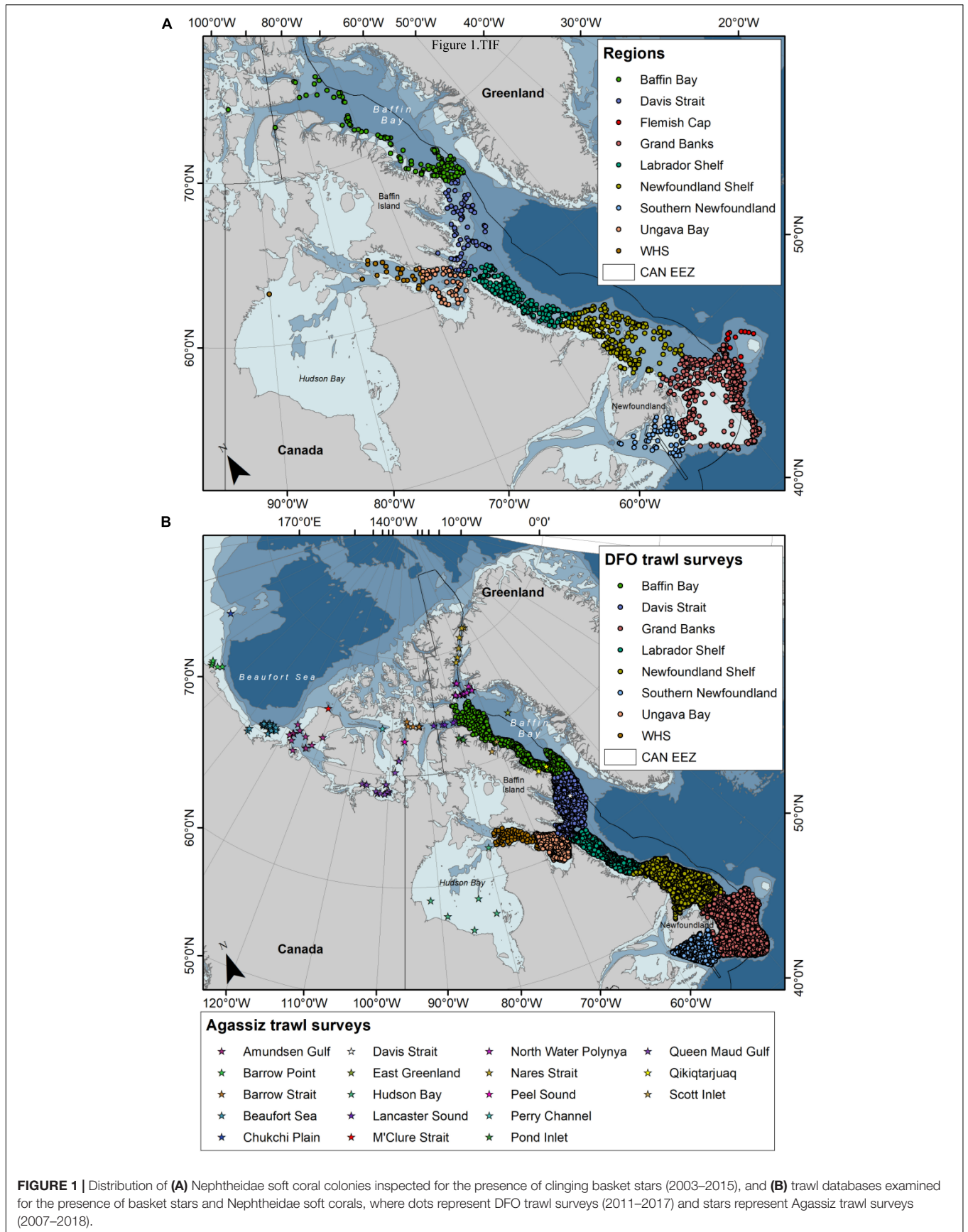
the footrope. The spring survey covers areas within NAFO Divisions 3PL, to a maximum depth of 750 m, while the fall survey covers deep and more northern areas (NAFO Divisions 2HJ, 3KLMNOP) to a maximum depth of 1500 m.

The OP Region conducts annual Groundfish Stock Assessment Surveys twice a year, in August and September, targeting Greenland halibut (*Reinhardtius hippoglossoides*) and shrimp (*Pandalus* spp.). These surveys use different trawl types depending on the area being surveyed. Cosmos and Alfredo trawls are used from Hatton Basin to Baffin Bay (NAFO Div. 0AB), to maximum depths of 1500 m. A Campelen trawl is used to survey SE Baffin Shelf - Hatton Basin area (NAFO Div. 0B).

Samples collected during Northern Shrimp Research Foundation (NSRF)/DFO Stock Assessment Surveys were also analyzed. These surveys are conducted from July to September (2006-present), and target *Pandalus* spp. in Hudson Strait and Ungava Bay, and Eastern Arctic Regions (NAFO Divisions 2G, 0B). This survey uses a modified Campelen 1800 shrimp trawl, sampling at depths < 750 m. A small number of samples from the Baffin Bay region were obtained from miscellaneous surveys, which include the Fisheries Observer Program (FOP), other

fisheries surveys (e.g., GEAC), academic research surveys, and experimental fisheries (Table 2).

Over the years, coral samples collected during these surveys have been kept frozen at -20°C at the Northwest Atlantic Fisheries Center (St. John's, Canada). For this study, soft coral samples were randomly selected from a number of bags containing a miscellaneous of specimens from different trips. Not all specimens from a trip were available, as not all samples caught are kept during the surveys. A total of 4527 soft coral colonies were examined for the presence of clinging epibiont ophiuroids. Samples include colonies of *Duva florida* ($N = 1192$), *Drifa glomerata* ($N = 959$), *Gersemia* spp. ($N = 2154$), and *Pseudodrifa racemosa* ($N = 222$) from Newfoundland, Labrador, and Baffin Bay (Figure 1A), from depths ranging between 41 and 1452 m, sampled between January and December. Only whole colonies were considered in this study. Due to challenges in the current taxonomy of Nephtheidae soft corals, we opted for pooling colonies of *Gersemia*, although we believe to have at least two taxa in this group (*Gersemia rubiformis* and *Gersemia fruticosa*), as per current classification (Utinomi, 1961).



Height was measured for each soft coral colony. Ophiuroid positions on the colony, their mass, and disc diameter were also determined. Ophiuroid position was standardized in relation to colony height due to variation in colony sizes. Position was measured as the distance from the center of the basket star's disc to the colony distal extremity, with relative values of 100% representing individuals found at the very tip of the colony. Position of ophiuroid on a colony was not annotated for 11% of the specimens. This was merely circumstantial, as position was not a variable of interest in the early days of the project. Basket stars were photographed under a stereomicroscope and disc diameters were measured using the image analysis software Image-Pro Plus 7.0. Disc diameters were measured from the distal edge of the radial shields to the edge of the opposite interradial, following Stöhr et al. (2012). A total of 28 ophiuroids (1.4% of measured specimens) could not be measured, as they were deemed too damaged. These individuals were still counted. We provide the final *N* used in all analyses.

To investigate the presence of embryo or juvenile ophiuroids inside the corals, a subset of the studied colonies of *D. glomerata* (*N* = 178) and *D. florida* (*N* = 145) collected between April and December was also dissected and examined internally. A total of 10 polyps from three regions in each colony (i.e., top, middle, and base) were dissected and examined under a stereomicroscope (total 30 polyps per colony). Polyps of only a few *Gersemia* spp. (*N* = 13) and *P. racemosa* (*N* = 11) colonies were examined, as they were often retracted or in a poor physical condition due to their preservation method (i.e., freezing).

Due to the very small size of most ophiuroids, 19 randomly chosen specimens were submitted to the Natural Resources DNA Profiling and Forensic Centre (NRDPFC, Trent University, Canada) for DNA barcoding species identification. COI was the targeted gene, following Layton et al. (2016). Not all samples were amplified using Layton et al.'s primers, so additional primers produced by the NRDPFC (not published) and Kim and Shin (2015) were used.

To gain further insights into the relationship between soft coral and basket stars, we also performed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes analyses and elemental C and N (%) on seven basket stars (disc diameters between 1.3 and 15 mm) and their soft coral hosts (*D. florida* and one *P. racemosa*). Sample preparation followed Sherwood et al. (2008) for both soft corals and basket stars. Briefly, randomly chosen individual soft coral polyps were removed to make a composite sample, while whole basket stars were processed due to their small size (one specimen had an arm sampled). Both dried and crushed basket stars and soft corals were acidified with 5% HCl prior to $\delta^{13}\text{C}$ analyses to remove carbonates. Analysis of C/N ratios indicated that samples might not have been completely decalcified; therefore only results of the $\delta^{15}\text{N}$ analyses are presented. Samples were analyzed at the Stable Isotopes Laboratory at Memorial University (St. John's, Canada) and results are given in ‰.

Although the inspection of colonies for clinging basket stars was done carefully and diligently, we acknowledge that extremely small basket stars could have been missed during inspection, which could have led to false absences. Similarly, the loss of clinging juvenile basket stars during sampling (i.e., trawling)

cannot be excluded. However, basket stars were found strongly intermingled with the corals, such that in some cases it was hard to remove them without breaking their arms. Ultimately, we believe that these potential false absences were not common and should not have largely influenced our analyses. In spite of that, we call for caution on the interpretation of absences.

Trawl Database

We have also examined DFO's multispecies trawl survey and Agassiz trawl Arctic survey databases (**Figure 1B**) to investigate relationships between soft coral and basket star occurrence in trawl sets (**Table 2**). A total of 10595 trawl sets were analyzed for coral and basket star presence/absence using the DFO database (NL and OP), from mean depths ranging between 36 and 1492 m, between 2011 and 2017. For the Agassiz trawl Arctic database, data from 88 stations were analyzed, most of which have been resampled through the years during the months of June to October (2007–2018, with exception of 2012). Mean depth for these surveys ranged between 35 and 1453 m. For the trawl datasets we treated soft corals at the family level (i.e., Nephtheidae) due to difficulties with species identification at lower taxonomic levels in the field. Basket stars are not routinely measured in the field, so information on their ontogeny was not available for this study. Generally, the presence of juvenile basket stars on corals is also not accounted for as basket star presence in a trawl set, as soft corals are not inspected at sea.

Five different bottom trawls were used in the surveys included in the trawl database portion of this study: Alfredo, Campelen standard, Campelen modified, Cosmos, and Agassiz (**Table 2**). These trawls are routinely deployed in different regions, have different dimensions, and can be deployed for different periods of time. For instance, Campelen standard trawls are normally deployed for 15 min during DFO multispecies surveys in the Newfoundland Region, while the much smaller Agassiz trawls are usually deployed for less than 5 min in the Eastern Canadian Arctic as part of academic research surveys. However, our objective was to investigate the presence of soft corals and basket stars in a same set. In this sense, we refrained our analyses to descriptive statistics and considered that any emerging patterns should be relatively consistent across these trawls. Due to a more substantial difference in the gear dimensions, we present the data from the DFO trawls separately from the Agassiz trawl surveys.

Data Analysis

Data analyses were performed using RStudio 1.1.383 (RStudio Team, 2016). *Pseudodrifa racemosa* and *Gersemia* spp. were not included in the statistical analyses because of the small number of basket stars associated with them and/or very unbalanced number of observations per season (in some cases not enough to include co-variables). However, the raw data for these taxa is described and graphically presented. Analyses were performed separately for *D. glomerata* and *D. florida*, as descriptive statistics revealed that basket star occurrence rates between the two taxa were quite distinct.

Our main explanatory variables of interest were colony height and season. However, in the initial models we also

included depth, latitude, year, and interactions (height:depth, height:latitude, season:latitude). We ran different models that included all or some of these variables, and performed model selection by comparing Akaike Information Criteria (AIC) values. Models with the lowest AIC values were selected, except for model 2b shown below, for which the diagnostic plots looked slightly improved than those for the model with the lowest AIC.

The relationship between individual basket star disc diameter (log-transformed) and colony height and season was investigated through Linear Mixed Effects Models (R package nlme, lme function in R, Pinheiro et al., 2020), with colony height and season as fixed effects, and colony id nested in trawl set (station) as random effects (Model 1). Basket star disc diameter was log-transformed to reduce its left-skewed impact on the analyses. We also examined the influence of colony height and season on basket star maximum disc diameter per colony. For *D. glomerata* the selected model also included depth and latitude (Model 2a), while for *D. florida* the simplest model (height and season) was selected (Model 2b). For this analysis, only trawl set was included as a random effect, as in this case there was only one disc diameter measurement per colony.

Basket star presence-absence (PA) on a colony was investigated through binomial Generalized Additive Mixed Models (GAMMs) with a clog-log link, with colony height and season as fixed effects, and trawl set (station) as a random effect (Model 3). The clog-log link function was chosen because there were considerably more zeros than ones (Zuur et al., 2009). We also used GAMMs with a Poisson family to investigate the relationship between number of basket stars per colony (in colonies with basket stars) and colony height and season as fixed effects, and trawl set (station) as a random effect (Model 4a). For *D. glomerata* the selected model also included depth and latitude (Model 4b). We did not include year or interactions in the initial GAMMs, as including these terms generated model convergence errors, likely due to the high complexity of the models for the available data. We used restricted maximum likelihood (REML) as the estimator for the mixed linear models (Zuur et al., 2009). The final models were:

Model 1: $\text{lme}(\text{logdiscdiam} \sim \text{height} + \text{season}, \text{random} = \sim 1 | \text{station/colony}, \text{method} = \text{"REML"})$.

Model 2a (*D. florida*): $\text{lme}(\text{logmaxdd} \sim \text{height} + \text{season}, \text{random} = \sim 1 | \text{station}, \text{method} = \text{"REML"})$.

Model 2b (*D. glomerata*): $\text{lme}(\text{logmaxdd} \sim \text{height} * \text{depth} + \text{latitude} * \text{season} + \text{year}, \text{random} = \sim 1 | \text{station}, \text{method} = \text{"REML"})$.

Model 3: $\text{gamm}(\text{PA} \sim \text{s}(\text{height}) + \text{season}, \text{random} = \text{list}(\text{station} = \sim 1), \text{family} = \text{binomial}(\text{cloglog}))$.

Model 4a (*D. florida*): $\text{gamm}(\text{abundance} \sim \text{s}(\text{height}) + \text{season}, \text{random} = \text{list}(\text{station} = \sim 1), \text{family} = \text{poisson})$.

Model 4b (*D. glomerata*): $\text{gamm}(\text{abundance} \sim \text{s}(\text{height}) + \text{season} + \text{depth} + \text{s}(\text{latitude}), \text{random} = \text{list}(\text{station} = \sim 1), \text{family} = \text{poisson})$.

GAMMs were applied using the gamm function of the R package mgcv (Wood, 2011). When season was identified as a significant source of variation, we used the R function summary to obtain pair-wise comparisons (e.g., between seasons), with

the function relevel used to change the order of the baseline, accordingly.

We tested for the presence of outliers and influential observations using Cook's distance for linear mixed models (CookD function in predictmeans R package). Influential observations were removed as they can have too much influence in the models. For instance, for *D. glomerata*, analysis on the number of basket stars per colony excluded entries with > 100 basket stars ($N = 2$), and only considered basket stars < 15 mm in disc diameter (where disc diameter was included, both species). Assumptions of normality, independence, and homogeneity of residuals were assessed through the visualization of diagnostic plots for the linear mixed models (Kabacoff, 2015). For the GAMMs, validation tools include the examination of normalized residuals versus fitted values and explanatory variables (Zuur et al., 2009). The presence of spatial correlation was assessed by adding a spatial correlation structure to the models, and comparing these to those without a correlation structure using AIC values (Zuur et al., 2009). Significance level for all analyses was set at $\alpha < 0.05$. We included season, depth, and latitude in two selected *D. glomerata* models (Models 2b and 4b); however since DFO trawl surveys per region depend on time of the year, effects of these variables might be confounded.

In terms of the trawl databases, in order to account for the unbalanced number of trawl sets per region and season, data on soft coral and basket star presence per trawl set is presented as relative proportions. For the Newfoundland and Labrador regions, the data is presented by Ecosystem Production Units (EPUs) (Pepin et al., 2014), and by general region where there is no defined EPU (e.g., Davis Strait, Ungava Bay, West of Hudson Bay, and Baffin Bay, **Figure 1B**). For the Agassiz trawl Arctic database, data was grouped in 18 main regions (**Figure 1B**).

RESULTS

Ophiuroid DNA Barcoding

The molecular analysis of 19 basket star specimens yielded 99–100% GenBank matches to *Gorgonocephalus arcticus*. Two brittle stars were also identified: *Ophiopholis aculeata* and *Ophiocten gracilis* (99% matches). Since most specimens were not submitted for molecular analysis ($N = 2003$ specimens in total), we opted for treating the specimens in this study as *Gorgonocephalus* sp., but knowing that all specimens included in the molecular analysis yielded very close matches to *G. arcticus*. GenBank accession numbers for COI sequences of the analyzed specimens can be found in **Supplementary Table S1**.

General Description

A total of 2003 ophiuroids were found on 543 colonies (12% of all examined colonies), although of these only seven were brittle stars, which were found on only five colonies (in some cases both taxa on a same colony). For this reason, we focus the remaining of the study on basket stars only ($N = 1996$).

Basket stars were found clinging on colonies of all four studied soft coral taxa (e.g., **Figure 2**), collected from all studied regions (although limited in Baffin Bay), from depths ranging

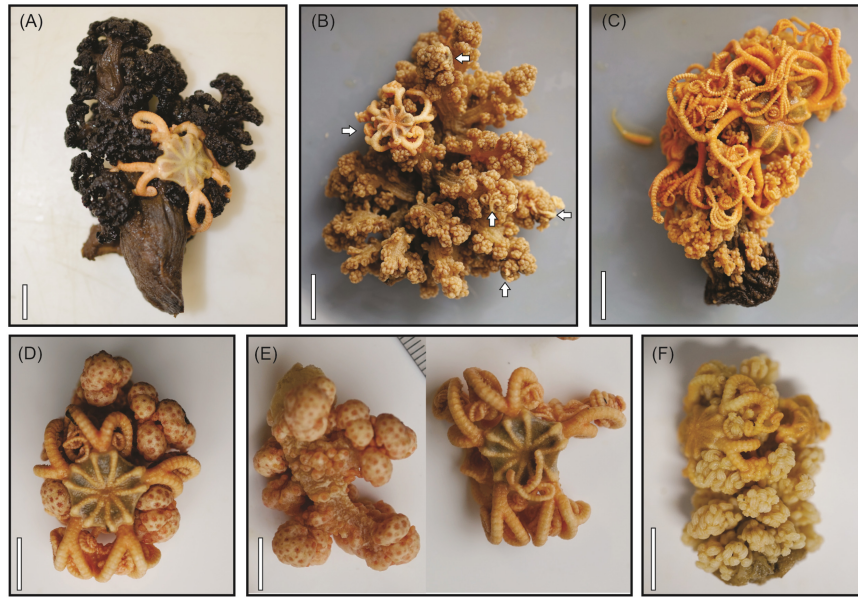


FIGURE 2 | Cold-water Nephtheidae soft corals as hosts for juvenile basket stars (*Gorgonocephalus* sp.). **(A)** *Duva florida*, **(B,C)** *Drifa glomerata*, **(D,E)** *Gersemia rubiformis*, **(F)** *Pseudodrifa racemosa*. Arrows in **(B)** point to some of the individuals found on this colony, which contained 15 juvenile basket stars. **(E)** Shows the colony and basket star seen in **(D)** after being separated. Scale bars = 1 cm.

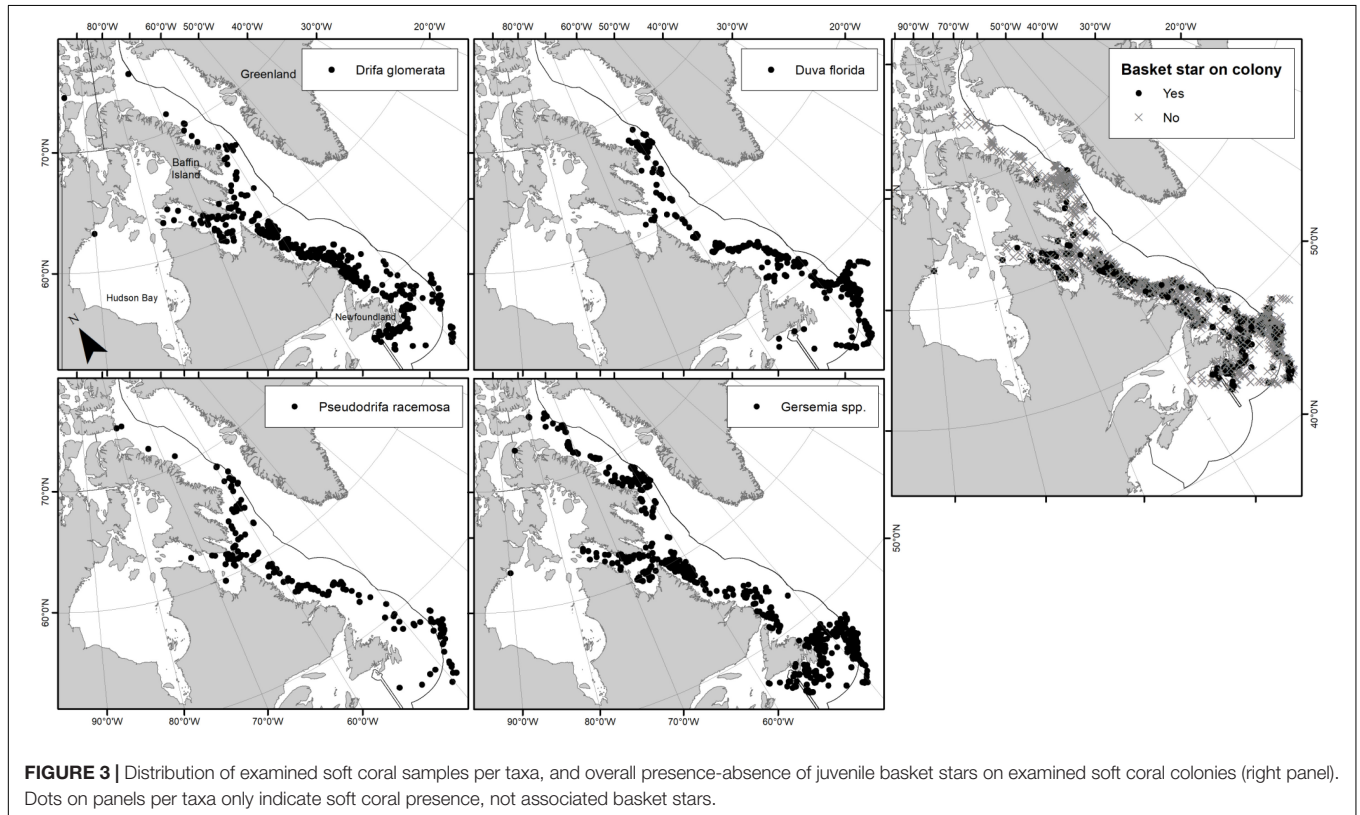
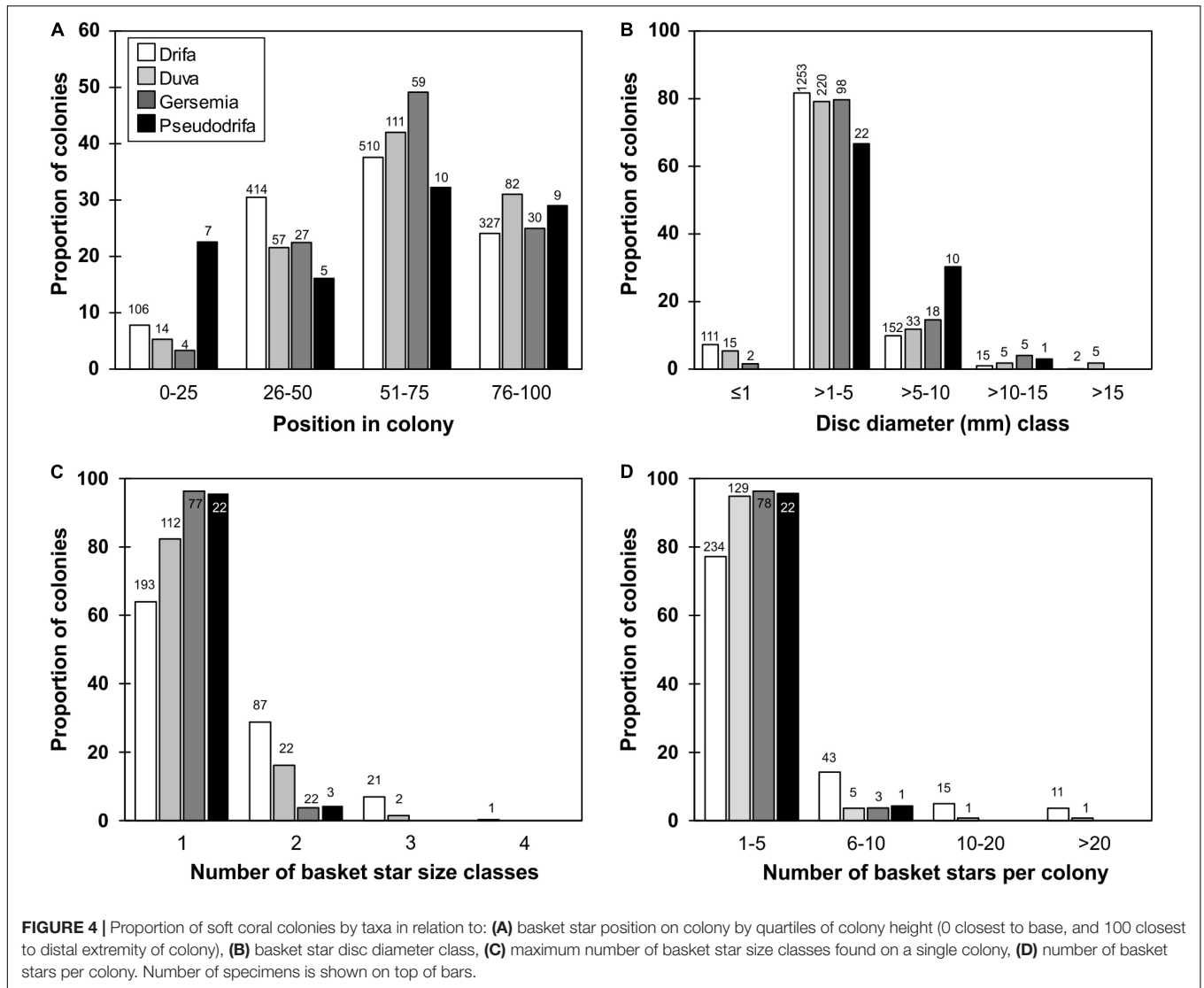


FIGURE 3 | Distribution of examined soft coral samples per taxa, and overall presence-absence of juvenile basket stars on examined soft coral colonies (right panel). Dots on panels per taxa only indicate soft coral presence, not associated basket stars.

between 53 and 1317 m (**Figure 3**). Basket stars were present on colonies collected at every month of the year, except for February when 18 sets were deployed between 2005 and 2006 (one *D.*

glomerata, 24 *D. florida*, and two *Gersemia* sp. colonies). No basket stars < 1 mm in disc diameter were found on colonies collected in February, March, or April. Basket stars were mainly



found between the 2nd and 3rd quartile of colony height (upper half) in all four soft coral taxa (51–75%, **Figure 4A**).

Basket Star Disc Diameter

Disc diameters ranged between 0.42 and 19 mm, however, two basket stars 22.2 and 23.6 mm in disc diameter were found on broken *D. florida* and *D. glomerata* colonies, respectively, which were not included in the analyses. Disc diameters were classified and displayed in five size classes: ≤ 1 , $> 1-5$, $> 5-10$, $> 10-15$, > 15 mm (**Figure 4B**). In most cases, disc diameters ranged between 1 and 5 mm for basket stars found on all soft coral species (**Figure 4B**), and for most colonies basket stars belonged to a single size class, although in *D. florida* and *D. glomerata* basket stars from up to three size classes on a same colony were identified (**Figure 4C**).

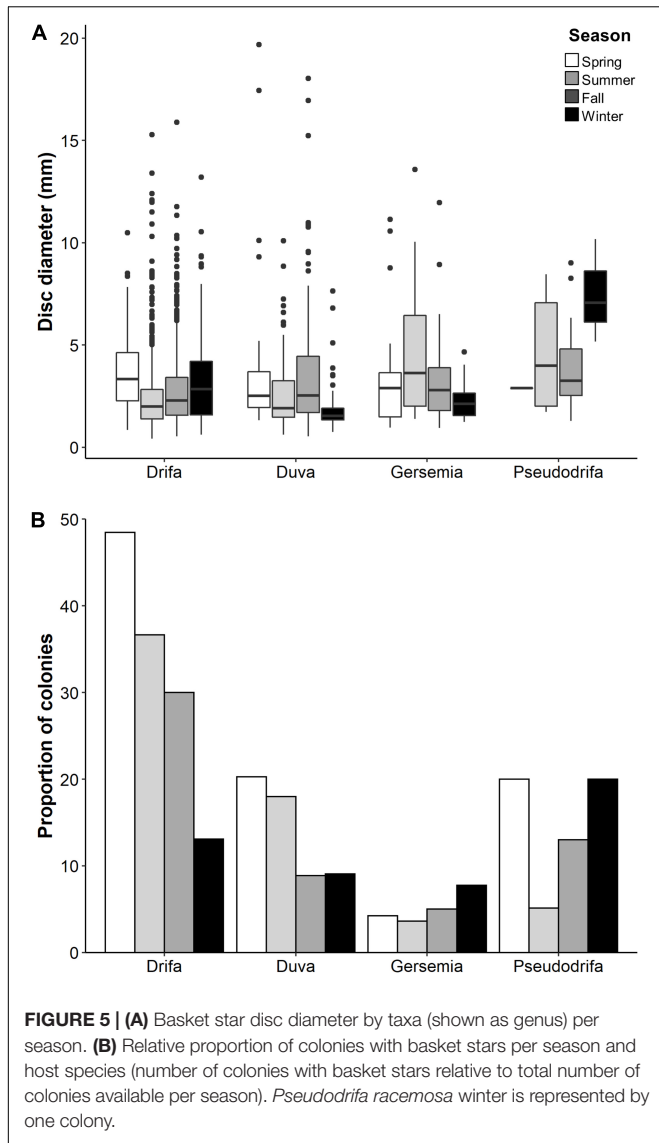
Individual basket star disc diameter did not significantly vary with colony height for both *D. florida* and *D. glomerata*, but it did for season in *D. glomerata* (**Table 3**). For this species,

individual basket star disc diameters were significantly larger in the Spring than in the Summer and Fall (**Figure 5A** and **Supplementary Table S2**).

On the other hand, maximum disc diameter per colony was significantly related to colony height, and latitude in *D. glomerata* (**Table 3**). For *D. florida*, maximum disc diameter was not significantly related to colony height or season (**Table 3**).

Basket Star Presence-Absence on Colonies

Basket stars were present on colonies ranging between 10.5 and 147 mm in height (**Figure 7**). They were more frequent in larger colonies for both *D. glomerata*, *D. florida*, and *Gersemia* spp. (**Table 4** and **Figure 7**). The binomial GAMM indicated that for *D. glomerata* and *D. florida* the probability of having associated basket stars increases with colony height up to ~ 70 mm for both taxa, when it starts to level off for the former and to slightly decrease for the latter (**Figures 6A,B**). Descriptive statistics



corroborate these observations, as the inter-quartile range of colony height – for colonies where basket stars were present – was 38.8–65.6 mm for *D. glomerata* and 44.3–69.9 mm for *D. florida*.

Colonies with basket stars were more frequent during the Spring for *D. glomerata* and *D. florida*, and during the Winter for *Gersemia* spp. and *P. racemosa* (Figure 5B). Basket star presence-absence on *D. glomerata* colonies significantly changed across seasons (Table 4), except for the Summer-Fall pair (Supplementary Table S3 and Figure 5B). For *D. florida*, basket star presence-absence on a colony was also significantly different across seasons (Table 4), except for the pairs Fall-Winter and Spring-Summer (Supplementary Table S3 and Figure 5B).

Examination of at least 10410 dissected polyps from 347 colonies yielded the presence of one juvenile ophiuroid (0.34 mm disc diameter) within a *D. florida* polyp (Figure 8), whose colony was collected in July in the Newfoundland Shelf region, at 306 m. This colony had no epibiont basket stars, and there was no record

TABLE 3 | ANOVA of fixed effects for linear mixed models estimating colony height and season effects on juveniles basket star disc diameter associated with the Nephtheidae soft corals *Drifa glomerata* and *Duva florida* in the Northwest Atlantic.

Response	Effect	Num df	Den df	F-value	p-value	
Log(disc diameter)	<i>Drifa glomerata</i>	Intercept	1	1220	1086.43	<0.0001
		Height	1	107	0.49	0.49
		Season	3	188	5.09	0.002
	<i>Duva florida</i>	Intercept	1	140	322.90	<0.0001
		Height	1	42	0.50	0.48
		Season	3	80	1.62	0.19
Maximum disc diameter	<i>Drifa glomerata</i>	Intercept	1	183	1298.84	<0.0001
		Height	1	106	13.63	<0.0001
		Season	3	183	1.01	0.39
		Depth	1	183	0.77	0.38
		Latitude	1	183	12.59	<0.0001
		Year	1	183	0.58	0.45
		Height:depth	1	106	1.74	0.19
	<i>Duva florida</i>	Intercept	1	81	340.67	<0.0001
		Height	1	45	3.64	0.06
		Season	3	81	1.83	0.15
		Latitude:season	3	183	0.96	0.41
		Height:depth	1	106	1.74	0.19

F-values obtained using the anova function in R. Num df nd Den df = numerator and denominator degrees of freedom, respectively. Values in bold represent significant p-values.

of a basket star collected in that trawl set. The closest set with a basket star reported was at ~34 km from this site.

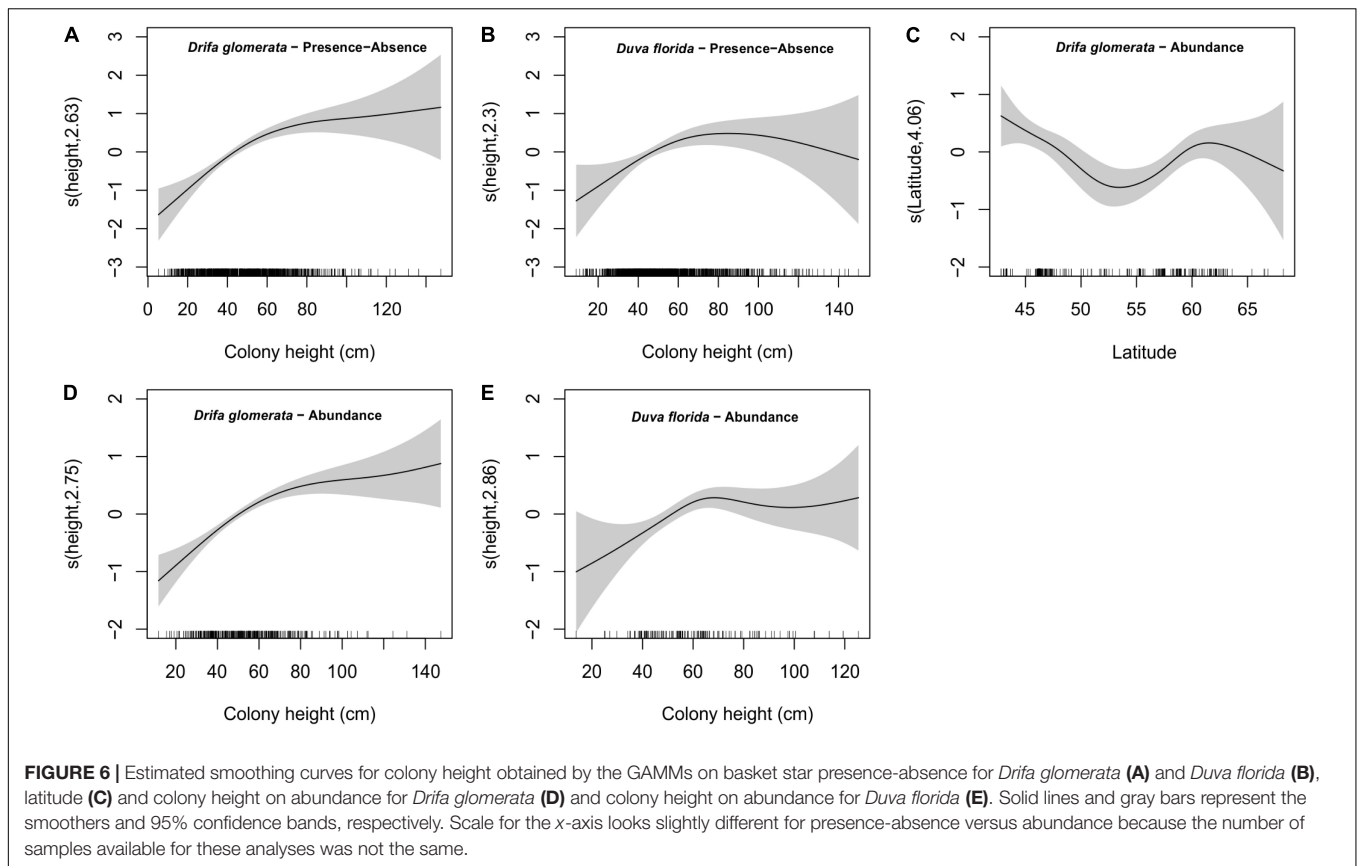
Basket Star Abundance

Most colonies had between 1 and 5 clinging basket stars, and only *D. glomerata* and *D. florida* had > 20 individuals on a single colony (Figure 4D). *Drifa glomerata* had both the highest ophiuroid occurrence (31.5%) and maximum number of ophiuroids per colony (N = 111), followed by *D. florida* and *P. racemosa* (11 and 10.5%, N = 28 and 6, respectively), and *Gersemia* spp. (3.9%, N = 8).

Number of basket stars per colony (in colonies with basket stars) significantly varied with colony height, but not with season for both *D. glomerata* and *D. florida* (Table 4). There was also an effect of latitude for basket star abundance on *D. glomerata* (Figure 6C), but not of depth (variables not tested for *D. florida*). The GAMM for both species indicated that, similarly, to the observed for presence-absence, the number of basket stars per colony increases with colony height up to ~70 mm, when it levels off (Figures 6D,E).

Trawl Data

When examining the DFO-RV database pooled (2011–2017, Figure 9), 45% of trawl sets containing basket stars (N = 2624) also had corals (N = 1186), of which 67% were Nephtheidae soft corals only (N = 796), followed by a mix of coral taxa that could also include soft corals (16%). The total percentage of trawl sets

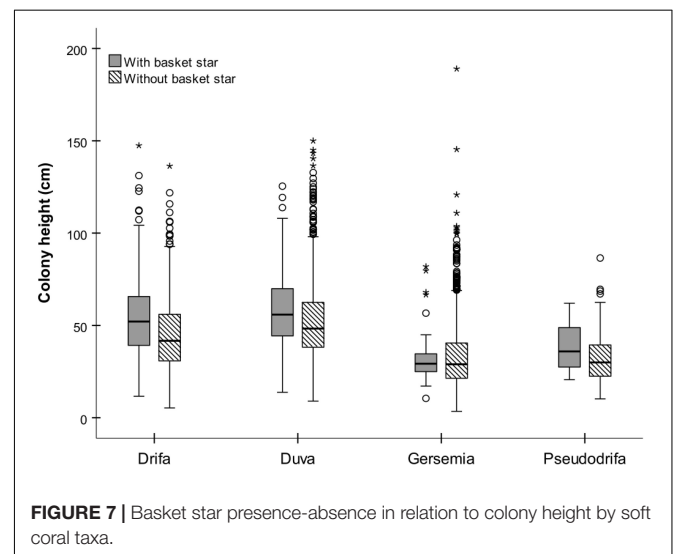


with basket stars that contained soft corals was 35%. Overall, Labrador shelf was the region with the highest co-occurrence of basket stars and soft corals per trawl set (54% of sets, $N = 166$), followed by Newfoundland Shelf (48%, $N = 206$), Grand Banks (36%, $N = 275$), and southern Newfoundland (31%, $N = 120$, **Figure 10A**). Ungava Bay, Davis Strait, and W Baffin Bay had the lowest overall co-occurrence of basket stars and soft corals (18, 19, and 28%, respectively, **Figure 10A**). Maximum co-occurrence across years took place in the Labrador Shelf region in 2012 (84%, $N = 50$), and the lowest co-occurrence was identified in Baffin Bay, Davis Strait, and Ungava Bay, where in some years no soft corals were reported in sets with basket stars.

Since DFO trawl surveys in the different regions are directed by time of the year (e.g., Southern Newfoundland only during Spring), we could not assess the influence of season on basket star-soft coral co-occurrence per region. But in the Grand Banks region, for which there were sets deployed in every season, basket star presence at depths > 100 m was more frequent in the Summer, followed by Winter, Fall, and Spring (**Figure 11**). However, basket star-soft coral co-occurrence was more frequent in the Fall, followed by Winter, Summer, and Spring (**Figure 11**).

Of the 88 stations sampled with the Agassiz trawl in the Eastern Canadian Arctic, 33% contained both basket stars and soft corals, which all together is comparable to the proportions found in Baffin Bay (28%) based on the larger trawls (see **Figure 10**). When examining this database by specific regions in the Arctic, stations (sometimes more than one set) with both

basket stars and soft corals were identified in the Beaufort Sea (32%, $N = 25$), Amundsen Gulf (18%, $N = 11$), Peel Sound ($N = 1$), Queen Maud Gulf (37.5%, $N = 8$), Barrow Strait (100%, $N = 3$), Lancaster Sound (33%, $N = 3$), North Water Polynya (55.6%, $N = 9$), and Scott Inlet (50%, $N = 2$). Unfortunately, physical samples of soft coral colonies from these regions were not inspected for this study and could not be included in



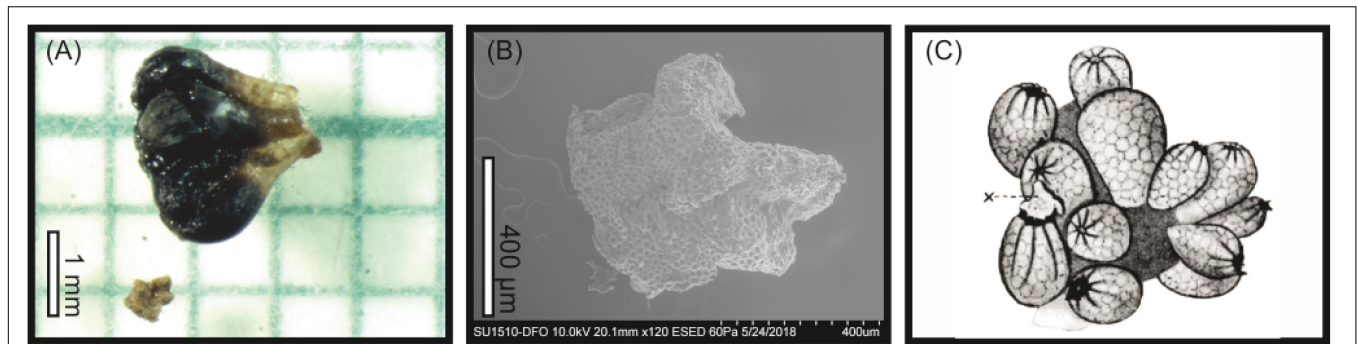


FIGURE 8 | (A) Piece of branch of *Duva florida* colony showing three large polyps and juvenile ophiuroid found within one of the polyps, (B) Scanning Electronic Microscopy (SEM) of the ophiuroid specimen seen in (A), (C) reproduction of Fedotov (1924)'s sketch of a juvenile basket star leaving the polyp of a live *Drifa glomerata* (published as *G. glomerata*) colony in Russia.

TABLE 4 | Statistical outputs of GAMM models on the effects of soft coral colony height (smoother) and season on juvenile basket star abundance and presence-absence on Nephtheidae soft corals in the Northwest Atlantic.

Response	Effect	edf*	F-value	p-value	
Basket star presence-absence	Smoother term				
	<i>Drifa glomerata</i>	s(colony height)	2.57	24.78	<0.0001
		Parametric terms	Df	F-value	p-value
		Season	3	10.79	<0.0001
	<i>Duva florida</i>	Smoother term	edf	F-value	p-value
		S(colony height)	2.30	6.19	0.002
Parametric terms		df	F-value	p-value	
Season	3	4.26	0.005		
Basket star abundance	Smoother term				
	<i>Drifa glomerata</i>	s(colony height)	2.75	24.82	<0.0001
		S(latitude)	4.06	5.13	<0.0001
		Parametric terms	Df	F-value	p-value
		Season	3	2.15	0.09
	<i>Duva florida</i>	Depth	1	1.32	0.25
Smoother term		edf	F-value	p-value	
S(colony height)		2.86	4.51	0.01	
Parametric terms	df	F-value	p-value		
Season	3	0.76	0.52		

*edf = effective degrees of freedom. Approximate significance of smooth terms. Values in bold represent significant p-values.

our analyzes. However, three physical samples from Hudson Bay/Strait area (not included in trawl database), where there was no co-occurrence between the two taxa based on the trawl database had juvenile basket stars associated to them.

Stable Isotope Analyses

Results of the stable isotope analysis indicate that absolute differences in $\delta^{15}\text{N}$ content between basket star and soft coral host (i.e., *D. florida* and one *P. racemosa*) ranged between 0.28 and 1.1‰ (Supplementary Table S4). $\delta^{15}\text{N}$ data show both cases

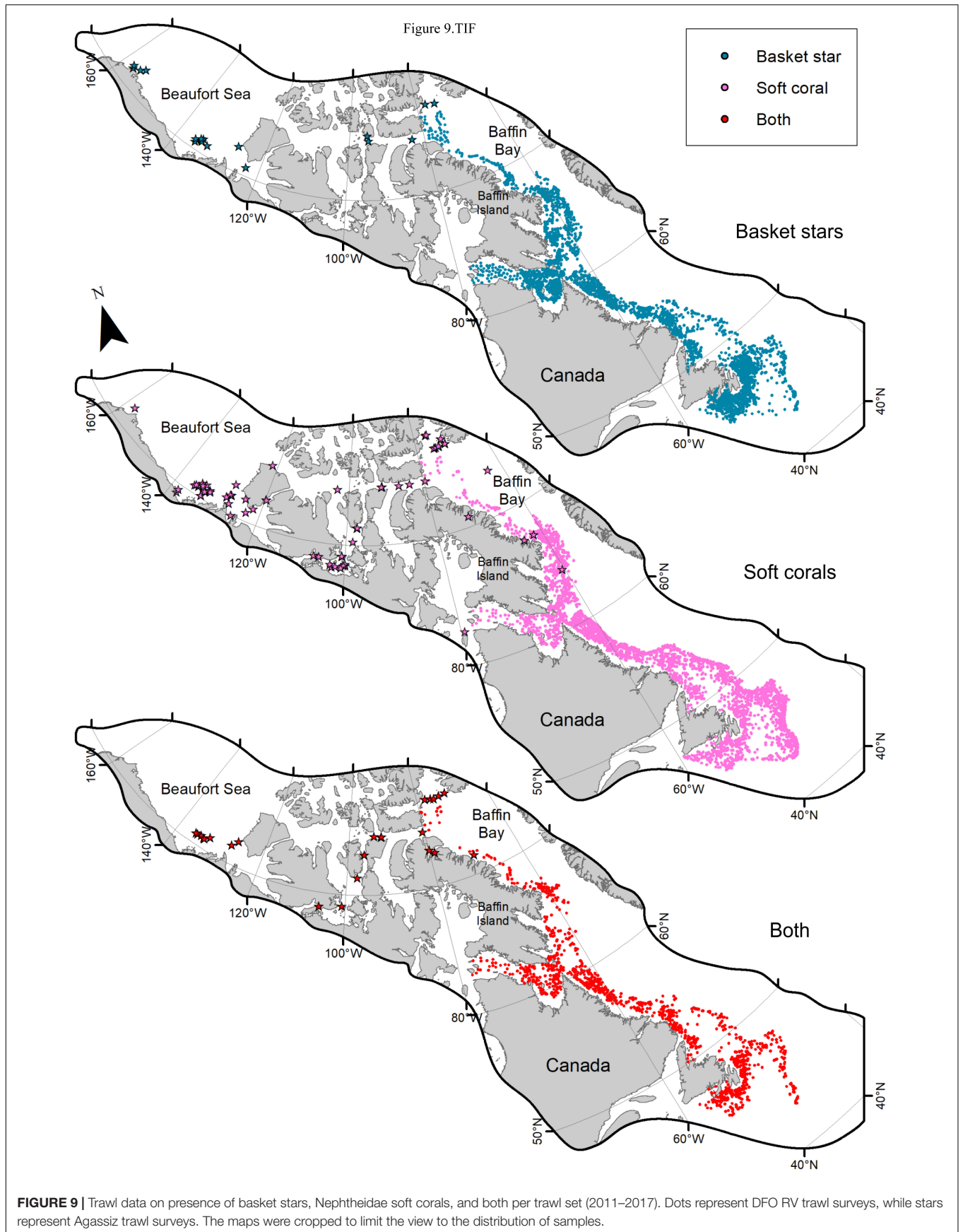
of basket stars with higher and lower $\delta^{15}\text{N}$ than the soft coral hosts (Supplementary Table S4).

DISCUSSION

Basket Star and Soft Coral Co-occurrence

In this study we found juvenile basket stars associated with colonies of all four studied soft coral taxa, from Newfoundland to northern Baffin Bay, at occurrence rates ranging between 4 and 32%, depending on the host taxon. The presence of juvenile basket stars on soft corals is already evidence that the two taxa somehow spatially co-occur. Furthermore, examination of the pooled DFO-RV database showed that 45% of sets with basket stars also had corals, of which 67% were represented by soft corals only. In fact, 35% of the sets with basket stars contained soft corals, which is comparable to the highest proportion of basket star occurrence on physical samples (i.e., 32% in *D. glomerata*). Examination by region showed the highest relative co-occurrence in the Labrador Shelf Region, at 54%. Although this does not necessarily imply that basket star distribution depends on soft coral presence, our data does show a high degree of co-occurrence between the two taxa.

The northern regions (Ungava Bay, Davis Strait, Baffin Bay) had the lowest co-occurrence of soft coral and basket star in a trawl set (DFO trawls). Although we do not show distribution data by genus for the trawl datasets, examination of soft coral genera distribution based on the examined physical samples indicates that the taxa with the highest basket star occurrence on a colony (i.e., *D. glomerata* and *D. florida*) might have their distributions more limited in northern waters. The observation that basket star presence on a colony was limited in Baffin Bay (restricted to latitudes south of 68°N) might be related to the fact that most colonies available/examined from this region were *Gessemia* spp., which had the lowest basket star occurrence rate (i.e., 4%). In addition, for this taxon colonies with basket stars in the southern sites were more frequent during the Winter, when this region is rarely sampled. On the other hand, trawl sets with both basket stars and nephtheid soft corals were identified



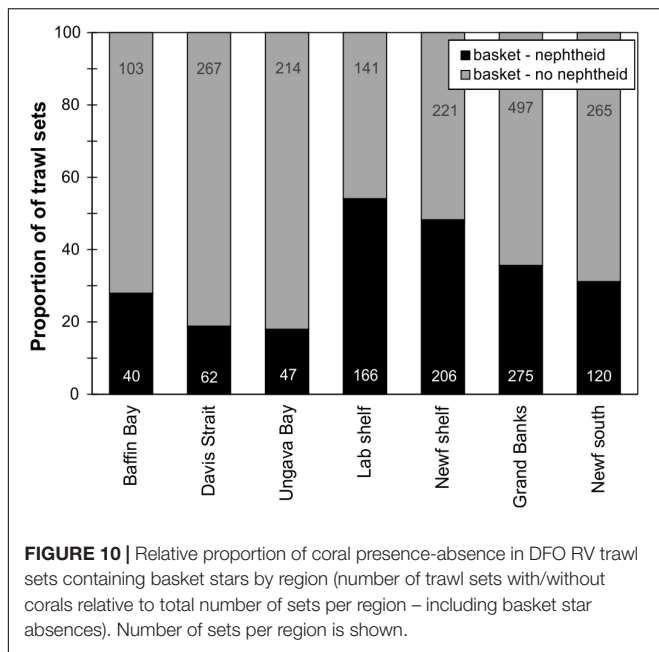


FIGURE 10 | Relative proportion of coral presence-absence in DFO RV trawl sets containing basket stars by region (number of trawl sets with/without corals relative to total number of sets per region – including basket star absences). Number of sets per region is shown.

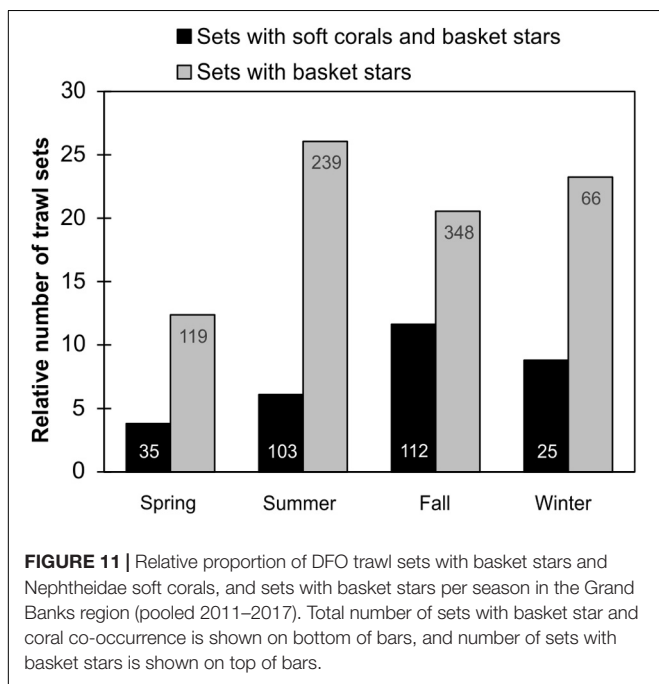


FIGURE 11 | Relative proportion of DFO trawl sets with basket stars and Nephtheidae soft corals, and sets with basket stars per season in the Grand Banks region (pooled 2011–2017). Total number of sets with basket star and coral co-occurrence is shown on bottom of bars, and number of sets with basket stars is shown on top of bars.

in Baffin Bay and elsewhere in the Eastern Canadian Arctic (although at lower rates), indicating that the two taxa do co-occur in this region (even northern of 68°N). The Agassiz trawl data pooled for all sampled Arctic stations indicate a comparable proportion of co-occurrence of the two taxa, in relation to the Baffin Bay data from the larger trawls.

Juvenile basket star occurrence rates on physical colonies were comparable to those found in a study that examined *Gorgonocephalus* spp. *in situ* occurrence (i.e., video data) with gorgonian corals in northern Norway (Clippele et al., 2015). In

that study, *Gorgonocephalus* spp. occurrence rates on colonies of *Paragorgia*, *Paramuricea*, and *Primnoa* spp. were 18, 17, and 3%, respectively. These results are somehow comparable to our findings in terms of occurrence proportion for colonies of *D. florida* (11%), but colonies of *D. glomerata* held a much higher occurrence rate of juvenile basket stars than all three gorgonian species depicted by Clippele et al. (2015), and all other soft coral species included in the present study (i.e., 32%). Although there is no mention of basket star size in the study by Clippele et al. (2015), the authors have limited their analysis to megafauna > 1 cm; furthermore, two photographs indicate that those basket stars were considerably larger than the specimens described in the present study. Therefore, life stages of basket stars associated to soft corals versus other octocorals are likely different.

The preference of juvenile basket stars for colonies of *D. glomerata* might be associated with different factors. First, our trawl database indicates that basket stars are mainly found along the continental shelf. Unpublished information on soft coral distribution (at the species level) in the region indicates that *D. glomerata* seems to follow a more similar distribution to that of basket stars, while *D. florida* is mainly found along the slope break (in preparation, V. Wareham Hayes, personal communication). Therefore, the higher occurrence of basket stars associated with *D. glomerata* could be related to a higher co-occurrence in the distribution of these two taxa.

Colonies of *D. glomerata* have the tissue heavily covered with club-shaped spinous CaCO₃ sclerites (Utinomi, 1961), whose roughness might increase attachment capacity (Dodou et al., 2011), which could be an advantage to juvenile ophiuroids with very short arms. Conversely, the scarce number of basket stars found on colonies of the other soft coral species (especially *Gersemia* spp.) could be related to the production of secondary metabolites by these soft corals, which might function as anti-fouling compounds (Williams et al., 1987; Slattery et al., 1995). To our knowledge, there are no published studies on secondary metabolites produced by *D. glomerata*, *D. florida*, or *P. racemosa*. It should be noted that any potential deterrence produced by these soft corals is obviously not enough to completely repel basket stars, as they were indeed found on all four soft coral taxa.

Basket stars were noticeably blended in color with colonies of *D. glomerata*. The similarity in color between host and basket star could be an advantage for the latter (e.g., camouflage against predators), and protective coloration was also suggested by Patent (1970a). However, colonies of *Gersemia* spp. and *Primnoa resedaeformis* gorgonians are also orange in tone, and had the lowest occurrence rate of *Gorgonocephalus* spp. among the studied colonies in this study and in the study by Clippele et al. (2015). Therefore, protective coloration alone does not seem to be the reason for *Gorgonocephalus* sp. to choose *D. glomerata* more frequently, although it might be an advantage.

Interestingly, young basket stars were commonly observed *in situ* on live colonies of *Gersemia* sp. from coastal areas in Labrador, where other soft coral species were not observed (~50–60 m, personal communication B. M. Neves, and R. Rangeley – Oceana Canada). However, these colonies were observed *in situ*. It is possible that the difference between alive and dead in

the case of this taxon is a factor influencing occurrence rates, since colonies of *Gersemia* spp. can contract considerably more than the other taxa. This might also corroborate our trawl data observations that co-occurrence rates vary regionally.

We found that most colonies had between 1 and 5 clinging basket stars per colony. Patent (1970a) found a maximum of five basket stars per colony on *Gersemia* sp., which is comparable to our numbers for this taxon ($N = 8$). On the other hand, we found a maximum of 111 juvenile basket stars on a single *D. glomerata* colony. Buhl-Mortensen and Mortensen (2005) found 15 *G. lamarckii* individuals on a single large *P. arborea* colony, and up to > 20 individuals per colony have been counted on *P. arborea* colonies collected as trawl bycatch in the Newfoundland region (Wareham-Hayes, unpublished). Clippele et al. (2015) reported a maximum of three basket stars on *P. arborea* and *P. resedaeformis*, and four on *P. placomus*, noting that on colonies of *P. arborea*, single basket stars were more common.

Soft Corals as a Platform for Recruitment and Nature of the Relationship

In this study we showed that most *Gorgonocephalus* sp. specimens found associated with soft corals had disc diameters < 5 mm (86%), characterizing them as juveniles. Our largest specimen was 23.6 mm in disc diameter, but these large individuals were not common, and likely still constitute juvenile basket stars, as Patent (1970a) indicated that most adults are usually between 700 and 850 mm in disc diameter. Our observations indicate that soft corals represent an important host for basket stars in the early stages of their lives.

The observation that for most colonies basket stars were in the same size class indicates that these individuals came from recruitment events that occurred close in time. For instance, in the *D. glomerata* colonies with 111 and 104 individuals, 84 and 76% of them, respectively, had disc diameters between 1 and 5 mm. Fedotov (1924) and Patent (1970a) suggested that basket star embryos are passively ingested by soft corals and develop within polyps, since these authors found very young individuals within live soft coral polyps. In this study we only found one juvenile ophiuroid (0.34 mm dd) within a *D. florida* polyp from a colony collected in July, from ~300 m. Although we could not confirm the taxonomic identity of this individual, the mesh-like structure of its plates is consistent with that of a very young ophiuroid, although it cannot be determined whether it is an euryalid (Stöhrn, personal communication). Noticeably, this colony had no basket stars on it, and there was no record of a basket star present in the trawl set associated with that coral colony.

Our data show that basket stars find their coral hosts at a very young age, and we believe that soft coral passive ingestion and basket star development within polyps, as suggested in those early studies, is still a plausible hypothesis. It is possible that the fact that our samples were not alive when examined had an influence on our lack of success finding additional individuals within polyps. In fact, the trawl vibration, speed and overall stress could have had an influence on basket star expulsion/evacuation.

Furthermore, very few colonies of *Gersemia* spp. or *P. racemosa* were inspected for endobiont basket stars. *Gersemia* sp. was the species studied by Patent (1970a). Soft corals are very small for adult *Gorgonocephalus* spp. to climb on, and it is hard to conceive that individuals as small as 0.4 mm in disc diameter with undeveloped arms would be able to actively swim or crawl from the seafloor to climb on soft corals. The embryology of *Gorgonocephalus* spp. is still not well understood, but Patent (1969) suggested that euryalids might not develop pelagic larvae.

Fedotov (1924) proposed that the stage on *D. glomerata* colonies was a necessary part of the life cycle of *Gorgonocephalus*. Patent (1970b) suggested that embryos of *G. eucnemis* kept in aquarium died < 10 days after spawning because soft corals were absent. If this is the case, it is possible that this relationship has an obligate aspect, as the basket star might depend on the soft coral. Whether the coral also benefits from the presence of juvenile basket stars is still unclear. Mutual benefits of faunal associations are not always evident. The brittle star *Ophiocreas oedipus* lives in a obligate, solitary relationship with the octocoral *Metallogorgia melanotrichos*. Despite this relationship being obligate for the brittle star, no benefits to the coral have been identified (Mosher and Watling, 2009). But in some cases, the meaning of these relationships might come to light under stress. For instance, the euryalid brittle star *Asteroschema clavigerum* appeared to limit impact of the Deepwater Horizon oil spill to colonies of the octocoral *Paramuricea biscaya*, and to have facilitated their recovery after impact (Girard et al., 2016).

Although Fedotov (1924) considered the nature of the juvenile basket star-soft coral relationship to be parasitic, Patent (1970a) noted that the fact that polyps looked healthy is an indication that the basket stars do not harm the coral, although she suggested that basket stars might feed on coral eggs. The case of the *G. rubiformis* colony depicted in **Figure 2** shows a certain degree of “strangling” by the basket star, but we do not know whether/how that might impact the colony. Colonies of *G. rubiformis* have a significant power of contraction, and the “strangling” might therefore seem worse on dead individuals than what it was in fact when the colony was alive. Although the nature of the relationship is still uncertain, the consistent presence of juvenile basket stars on soft corals suggest that they are not ephemeral visitors. We believe that further studies including the monitoring of live organism *in situ* or in laboratory settings are necessary to investigate hypotheses regarding how basket stars reach their soft coral hosts, and the nature of the relationship.

Basket Star Size, Abundance, and Position

Colony height had an effect on maximum disc diameter (*D. glomerata*) and number of basket stars per colony (both species). Although coral size was found not to be a limiting factor in the size of individual juvenile basket stars that it can host, our data indicate that there is a maximum basket star size usually supported by a colony. As mentioned before, larger specimens were found at low frequencies, and our largest specimen was ~24 mm in dd. According to Fedotov (1924), basket stars ~5 mm in dd can leave the soft coral colonies and move to discs of

adult *Gorgonocephalus* sp. Our observation that most individuals were between 1 and 5 mm dd seems to agree with this author in terms of timing (i.e., in ontogeny) when most juveniles leave the colony. The largest juvenile specimen per soft coral colony examined by Patent (1970a) was 3 mm dd, and one free-living individual with a 25 mm dd was also reported by this author. Buhl-Mortensen and Mortensen (2005) reported individuals of *G. lamarckii* ≥ 15 mm in dd on the gorgonian *P. arborea*. These reports show that young basket stars can be found on other habitats. However, it is unknown whether other corals or habitats also host basket stars in their very early stages, like soft corals do. Larvae of the brittle star *Ophiothrix fragilis* settle on the surface of sponges, with recruits doubling their sizes in 3 months (June–September), and leaving for an independent life on other surfaces when they are > 1 mm in disc diameter (Turon et al., 2000). In other cases, adult ophiuroids can host juvenile ophiuroids of different species. Juveniles have been reported to leave the adults at 4.5 mm (Hendler et al., 1999) and 6 mm dd (Fourgon et al., 2007).

Maximum disc diameter also significantly decreased with latitude. Despite the potential for confounding effects between latitude and season, in this case the effect of latitude on maximum disc diameter seems dissociated from season, since there was no significant interaction between latitude and season. Since we do not know whether our *Gorgonocephalus* spp. represent more than one species, we cannot infer on whether changes in disc diameter with latitude might be related to species-specific differences or to other variables.

Number of basket stars per colony was not influenced by seasonality, but rather by colony height (both species) and latitude (*D. glomerata* only). For both taxa, number of basket stars and the probability of basket star presence on a colony increased with colony height up to heights of ~ 70 mm. Maximum *D. glomerata* height among the studied colonies was 147 mm, and the two colonies hosting > 100 basket stars were approximately 100 and 120 mm in height. These colonies were not included in the statistical analyses, as they were rare and had too much influence on the data. The GAMM plot indicated that number of basket stars per colony in *D. glomerata* reaches the lowest point at a latitude of $\sim 55^\circ\text{N}$ (Labrador, Makkovik area). However, in this analysis, season was weakly not significant ($p = 0.09$). Considering that borderline p -values should be taken with extra caution in these types of models (Zuur et al., 2009), it is possible that the effect detected for latitude in this case could be associated to season, because of the survey design previously mentioned (location depends on time of the year).

The presence of more basket stars on larger colonies might be a response to space availability, but also increased distance from the seafloor, as most basket stars were found on the upper half of the colonies (as discussed below), indicating a preference for taller surfaces. However, colonies > 70 mm might not necessarily host more basket stars. Furthermore, no data is available on colony height variation between expanded and contracted states (studied species). A better understanding of these variations, which can be significant in soft corals (e.g., Hellström and Benzie, 2011), might enlighten our interpretation on the role played by colony height on basket star abundance.

Individuals of *Gorgonocephalus* sp. were also found more at the top on the gorgonians *P. placomus* and *P. reseadaeformis*, although nearer the base on *P. arborea* (Clippele et al., 2015). The presence of ophiuroids clinging on corals or other tall structures has been associated with the advantage of being higher in the water column, therefore hiding from predators, and of increasing access to food by benefiting from stronger currents (Buhl-Mortensen and Mortensen, 2005; Clippele et al., 2015; Buhl-Mortensen et al., 2017). The arms of *Gorgonocephalus* spp. individuals start to branch when they are larger than 1 mm in dd (Fedotov, 1924), and individuals > 20 mm in dd are already capable of capturing plankton (Patent, 1970a). Individuals < 20 mm in dd might feed on smaller particles and still benefit from being higher on the water column. Protection against predation is also a plausible hypothesis on their preference for relatively taller portions of the soft coral.

Patent (1970a) suggested that basket stars might be feeding on detritus or food from the polyps, as well as on coral eggs, as Gislén (1924, apud Patent, 1970a) found remnants of soft corals in stomach contents of *G. caputmedusae*. Although limited, our nitrogen stable isotope data indicate that maximum difference in $\delta^{15}\text{N}$ between basket star and host was 1.1‰, indicating that the two organisms share the same trophic level. Average fractionation per trophic level is 3.4‰ for $\delta^{15}\text{N}$ (Vander Zanden and Rasmussen, 2001). A relationship with trophic benefits for the associates has been suggested for other organisms. For instance, juveniles of the brittle star *Ophiothrix fragilis* are believed to take advantage of the currents produced by their sponge hosts (Turon et al., 2000).

Our stable isotopes data showed no indication that increasing size in juvenile basket stars leads to an increase in trophic level. However, this might be the result of our limited sample size, and it might also just indicate that juvenile basket stars of different sizes feed on similar sources. Other studies have yielded enriched $\delta^{15}\text{N}$ values for individuals of *Gorgonocephalus* spp. in Arctic waters, in comparison to our results (Hobson et al., 2002; Iken et al., 2010; Feder et al., 2011). However, it is quite possible that this reflects larger differences in ontogeny, as juveniles and adults live in different habitats. Despite *Gorgonocephalus* spp. usually being considered suspension feeders (Hobson et al., 2002; Iken et al., 2010; Feder et al., 2011), *G. arcticus* has been considered a predatory suspension feeder (Emson et al., 1991), and *G. chilensis* a predator (Mauna et al., 2011), because they extend their arms in a typical suspension feeder position, but trap prey by looping their arms.

Effects of Seasonality

When evaluating the potential effects of seasonality here, it is important to consider that the location of DFO trawl surveys is dependent on time of the year. For instance, Spring surveys take place in southern Newfoundland, while Fall surveys take place in Labrador. Therefore, we cannot exclude that variables affected by season might also be affected by latitude-related dynamics. However, phytoplankton and zooplankton data clearly show the importance of seasonality in this region (Afanasyev

et al., 2001; Pepin et al., 2011). Furthermore, considering that seasonality is expected to play a role on reproductive aspects of many organisms (Gili and Petraitis, 2009), the patterns identified here are discussed in light of this variable, rather than latitude.

Seasonality – with the constraint highlighted above – seems to play a role on the disc diameter of basket stars found on *D. glomerata*, as specimens were significantly larger in the Spring than in the Summer and Fall, but no difference was identified between Spring and Winter. Similarly, the relative number of *D. glomerata* colonies with basket stars peaked during the Spring, with the lowest number of occurrences during Winter. Since we have no information on early growth rates in these ophiuroids, we cannot infer on the timing when most basket stars (embryo/larvae) arrived to the colonies.

In the Grand Banks region, Fall was the season with the highest co-occurrence of basket stars-Nephtheidae soft corals in the trawl sets, followed by Winter, Summer, and Spring. Because soft corals are not mobile organisms, this variation on co-occurrence rates ought to be driven by the basket stars. Seasonality might have an influence on the distribution of adult basket stars, who might migrate seasonally, as do other echinoderms (e.g., Freeman et al., 2001).

In the NE Pacific, *G. eucnemis* (published as *G. caryi*) has a spawning season of 6 months, from June to November (Patent, 1969), but to our knowledge there is currently no published information on reproduction of *Gorgonocephalus* spp. in the NW Atlantic. Our observations that juvenile basket stars (<5 mm in dd) were found on coral colonies collected at every month of the year indicate that the spawning season for *Gorgonocephalus* in this region might be longer than in the Pacific. On the other hand, no basket stars < 1 mm dd were collected in February, March, or April. Reproduction of *Gorgonocephalus* spp. was not in the scope of this study, and therefore more dedicated studies are needed to shed light on the subject.

The lack of a statistically significant influence of seasonality on basket star metrics for *D. florida* (i.e., abundance, disc diameter) could be related to their lower basket star occurrence in comparison to *D. glomerata*. However, despite non-significance, the number of *D. florida* colonies with basket stars followed the same trend as observed for *D. glomerata*, with a peak during the Spring and a low in the Winter time. For *Gersemia* spp., the peak was during Winter time, with the other seasons showing similar trends to one another.

The divergence in co-occurrence per season between physical samples and the trawl sets might be related to the different ontogenetic stages of the basket stars. While physical coral samples contained only juveniles, individuals accounted for in trawl sets are usually large enough to be picked up by hand (Wareham Hayes, personal communication), with sizes not comparable to those found on soft corals. On the other hand, trawl data was considered at the family level, and specific differences by genus (e.g., season of highest frequency of co-occurrence) were not accounted for.

Conservation

Gorgonocephalus arcticus has been found in stomach contents of Greenland sharks (*Somniosus microcephalus*) from Cumberland

Sound, Nunavut (McMeans et al., 2012), and Svalbard, Norway (Leclerc et al., 2012), as well as in stomachs of Northern Wolfish *Anarhichas denticulatus* (Albikovskaya, 1983; Simpson et al., 2013), which is a species protected under the Canadian Species at Risk Act (SARA). Although this does not necessarily mean that basket stars are a common prey item for these fish, stomach content data for these species is limited and additional studies are needed to fully describe their diet. In the Barents Sea, *G. arcticus*, *G. eucnemis*, and *G. lamarckii* are considered “high-risk” species to bottom trawling (Jørgensen et al., 2015). Both soft corals and *Gorgonocephalus* spp. have been considered potential indicators of Vulnerable Marine Ecosystems (VMEs) in that region (e.g., Nadochty et al., 2017), and are listed as indicators in the South Atlantic (as basket stars) by the South East Atlantic Fisheries Organisation – SEAFO CM 30/15 (Food and Agriculture Organization of the United Nations [FAO], 2020). Currently, Nephtheidae soft corals are considered VME indicators in the Northeast Atlantic (i.e., Cauliflower coral fields), South Pacific, and Southern Ocean, but not in the Northwest Atlantic (Food and Agriculture Organization of the United Nations [FAO], 2020). However, recently Long et al. (2020) suggested the inclusion of soft coral gardens from West Greenland as a VME candidate, as they met several of the Food and Agriculture Organization (FAO) VME indicator criteria, such as the structural complexity of the habitat they form.

Basket stars might be relatively long-lived, as some ophiuroids can live for decades (Gage, 1990). Therefore, evidence of the potential impact of the removal of soft corals and their associated juvenile basket stars through fishing on adult basket star populations might be delayed; i.e., the potential impact of high soft coral biomass removal on local adult basket star populations might only be detected several years after the fact. In this sense, our trawl data provided information on distributional patterns between the two taxa. However, temporal synchronicity of catch biomass for basket stars and soft corals cannot be investigated without considering the temporal lag highlighted above.

In this study we showed that in the Northwest Atlantic and Eastern Canadian Arctic juvenile basket stars are consistently found on soft corals, and we believe that further studies are necessary to investigate this association; in particular the potential degree of dependency of basket stars in relation to soft corals and the potential role of the latter as nurseries. This information is paramount to assess the potential impacts that soft coral damage and/or removal (e.g., via bottom-contact fishing) might have on juvenile basket stars, their development, and the success of adult *Gorgonocephalus* populations. Cold-water Nephtheidae soft corals appear to play an essential role as habitat for juvenile basket stars.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repository and accession number(s) can be found in the article/**Supplementary Material**. Data not present in tables is available upon request to the corresponding author.

AUTHOR CONTRIBUTIONS

BMN and VW contributed to conception and design of the study. BMN performed laboratory work, organized the database, performed the statistical analysis, and wrote the manuscript. EH and VW performed laboratory work and literature review. KH, CG, and PA contributed the Arctic databases on trawl data. All authors contributed to manuscript revision, read and approved the submitted version.

ACKNOWLEDGMENTS

We thank the Canadian Coast Guard captains and crew, and the Fisheries and Oceans Canada crew involved in sample collection and processing in the field. Samples collected aboard CCGS *Amundsen* (Agassiz trawl samples and data) were covered by ArcticNet funding. Laura Wheeland and Brynn Devine provided CFER samples. Special thanks to all involved with the Fisheries Observer Program, which provided invaluable material. We also

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thank Paula Hawkins, Sarah Olson, and Rebecca Raymonds (DFO-NL) for assistance in the lab, Alison Pye (Memorial University) for the stable isotope analyses, Matthew Harnden for the DNA barcoding analysis, and Hannah Munro for GenBank submissions. Mr. Klaus Hansen for translating the paper by Fedotov (1924) and Dr. Sabine Stöhrn for her guidance regarding the juvenile ophiuroid found inside of a coral polyp. We also thank three reviewers for their useful comments. The Deep-Sea Biology Society is also thanked for a travel grant provided to BMN to present this study. This study was funded by a DFO International Governance Strategy (IGS) project through a Natural Sciences and Engineering Research Council of Canada (NSERC) Postdoctoral Visiting Fellowship (BMN).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.547896/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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