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Abyssal Scavenging Communities attracted to *Sargassum* and fish in the Sargasso Sea

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ABSTRACT

Deep-sea communities rely on epipelagic surface production as a primary source of energy and food. The flux of phytodetritus drives many abyssal ecological processes but the flux of large particles such as nekton carcasses, macroalgae, and wood may also be important. Recent baited camera experiments noted that some abyssal fish consumed spinach and phytoplankton placed on the seafloor. To evaluate if fish or other scavengers would consume natural plant or macroalgal material falling to the deep-sea floor we conducted camera experiments using *Sargassum* or mackerel bait in the Sargasso Sea. A benthic community of invertebrates was attracted to *Sargassum*, which naturally falls to the seafloor in this area. In five instances it was observed that an isopod *Bathyopsurus* sp. removed a piece of *Sargassum* from the main clump and left the field of view with it. An ophiuroid is also observed handling a piece of *Sargassum*. The group of scavengers attracted to mackerel bait was very different and was dominated by large ophidiid fish. In contrast to studies elsewhere in the abyssal North Atlantic, only a small number of rattails are observed, which could be related to water depth or an ichthyofaunal zonal change between oligotrophic and eutrophic regions.

1. Introduction

The abyssal ecosystem is an allochthonous environment dependent on organic matter from the euphotic zone. The vertical flux of organic matter primarily consists of phytodetritus but large particles such as nekton carcasses, macroalgae and wood may also be important food sources for some organisms (Britton and Morton, 1994; Drazen et al., 2008; Kobayashi et al., 2012). Communities scavenging nekton carcasses are most frequently studied (Smith and Baco, 2003; King et al., 2008) perhaps because baited cameras have become a common tool for ecological investigations (Bailey et al., 2007). Baited camera studies on the abyssal plains have shown a scavenging community primarily consisting of macrourid fish and amphipods (Jones et al., 1998; Witte, 1999; Henriques et al., 2002; Jones et al., 2003; Kemp et al., 2006; Drazen et al., 2008; Yeh and Drazen, 2009, 2011). Studies have found depth and latitudinal differences in dominant scavenging species (Merrett, 1987; Priede et al., 1990; Thurston et al., 1995; Witte, 1999; Janssen et al., 2000) and scavenger composition can be influenced by finer scale geographic features such as canyons and trenches (King et al., 2008; Jamieson et al., 2011).

The primary bait used in most camera studies is fish, usually mackerel or a similar scombrid. This has helped to standardize experiments between ocean basins, depths, and investigators. Dead fish attracts both vertebrates and invertebrates that rapidly consume the bait (Jones et al., 1998), which is an advantage to time-limited deployments. Furthermore, stomach content, isotope, and lipid biomarker studies of deep-sea fish suggest that carrion, principally epipelagic fish and squid, can be a major component of their diets (Gartner et al., 1997; Drazen et al., 2001, 2008; Yeh and Drazen, 2009; Boyle et al., 2012). The dominance of carrion in the diets of *C. armatus* in the North Pacific led Drazen et al. (2008) to suggest that this species bypasses the conventional benthic food web fueled by phytodetritus relying on carrion for most of its nutrition.

A number of studies (Wolff, 1976, 1979a, 1979b; Suchanek et al., 1985; Bernardino et al., 2010; Kobayashi et al., 2012) show that animals consume wood and plant remains on the deep-sea floor including holothurians, bivalves, and polychaetes but these are not the same animals attracted to dead fish or squid. Certainly plant and algal material is less easily digested and has a lower caloric density than most animal remains. However, previous stomach analyses of macrourids have shown that their diets may include small amounts of plant remains (Haedrich and Henderson, 1974; Martin and Christiansen, 1997; Drazen et al., 2001). These observations led Jeffreys et al. (2010) to use a camera system baited with spinach blocks to study scavengers on the Iberian margin of the

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North Atlantic at 3000 m. The spinach blocks attracted both the ophidiid *Spectrunculus* sp. and the macrourid *Coryphaenoides mediterraneus*. A similar first arrival time for *C. mediterraneus* was recorded for both spinach and carrion baits; indicating plant material may create an odor plume attracting the macrourid. *C. mediterraneus* was observed to actually ingest the spinach, sometimes as a feeding frenzy (Jeffreys et al., 2010). When simulated phytodetritus was used, abyssal fish were attracted to and ate it in the North Atlantic where phytodetritus patches are common on the seafloor. However, in the Balearic Sea, where carpets or patches of phytodetritus are not observed, *C. mediterraneus* was not attracted to the simulated phytodetritus (Jeffreys et al., 2011). Stable isotope data showed that phytodetritus is not a primary source of food for these fish at either site (Jeffreys et al., 2011). The situation may be different for invertebrates. In the Balearic Sea amphipods and the crab *Chaceon mediterraneus* responded quickly to and ingested the simulated phytodetritus, and isotopic and fatty acid biomarker results suggested that phytodetritus could be important to its diet and to that of amphipods. One conclusion of these studies was that plant remains could be important to fish and other scavengers if plant detritus commonly occurred on the seafloor (Jeffreys et al., 2010).

The Sargasso Sea, bounded by the North Atlantic subtropical gyre, hosts the floating macroalgae, *Sargassum*, which naturally sinks as detritus to the abyssal seafloor (Schoener and Rowe, 1970; Roper and Brundage, 1972). The algae form mats which in summer can cover vast areas of the oceanic surface out to the mid-Atlantic Ridge (Butler et al., 1983; Niermann, 1986). However, *Sargassum* only accounts for 0.5% of the total regional primary production of the Western Sargasso Sea (Stoner, 1983). Pieces of *Sargassum* sink to the benthos when storms, strong swells, or feeding macrozooplankton puncture the air bladder (Altabet, 1988). It sinks at a rate between 50 and 200 m d^{-1} (Siegel and Deuser, 1997). Photographic evidence of *Sargassum* on the abyssal seafloor was found in about 22% of photographs in the western North Atlantic suggesting widespread occurrence (Schoener and Rowe, 1970; Roper and Brundage, 1972). An invertebrate community has been reported in association with plant material collected from the deep seabed including *Sargassum* and it has been found in the guts of ophiuroids and isopods (Wolff, 1962, 1979a; Schoener and Rowe, 1970). Amphipods have also been observed to be attracted to *Sargassum* via trapping methods on the upper continental slope (Lawson et al., 1993). In these studies in situ observations of the animals around the plant remains were not available and because most of the nutrients in the plant/algal material are thought to be made available through bacterial and fungal degradation (Wolff, 1979a) it is not clear if animals are rapidly attracted to falls of naturally occurring plant or macroalgae in the same way that scavengers are attracted to falls of nekton carcasses.

To further evaluate the importance of macroalgal remains to deep-sea scavenging communities we described the scavenging communities of the Sargasso Sea abyssal plain using cameras baited

Table 1
Summary of deployment information.

Deployment	Bait type	Deployment date	Deployment time (hh:mm)	Latitude (N)	Longitude (W)	Depth (m)	Duration (hh:mm)
S3-07	1.5 kg Mackerel	13-Feb-11	11:19	29 36.49	66 32.20	5160	24:32
S5-01	1.5 kg Mackerel	15-Feb-11	12:18	26 44.481	69 42.004	5200	39:24
S6-10	1.5 kg Mackerel	22-Feb-11	14:01	25 30.860	71 20.899	5440	26:02
S6-01	1 kg *Sargassum*	18-Feb-11	8:17	25 37.4	70 52.54	5460	39:26
S6-06	1 kg *Sargassum*	20-Feb-11	14:05	25 30.1	71 10.5	5550	39:20

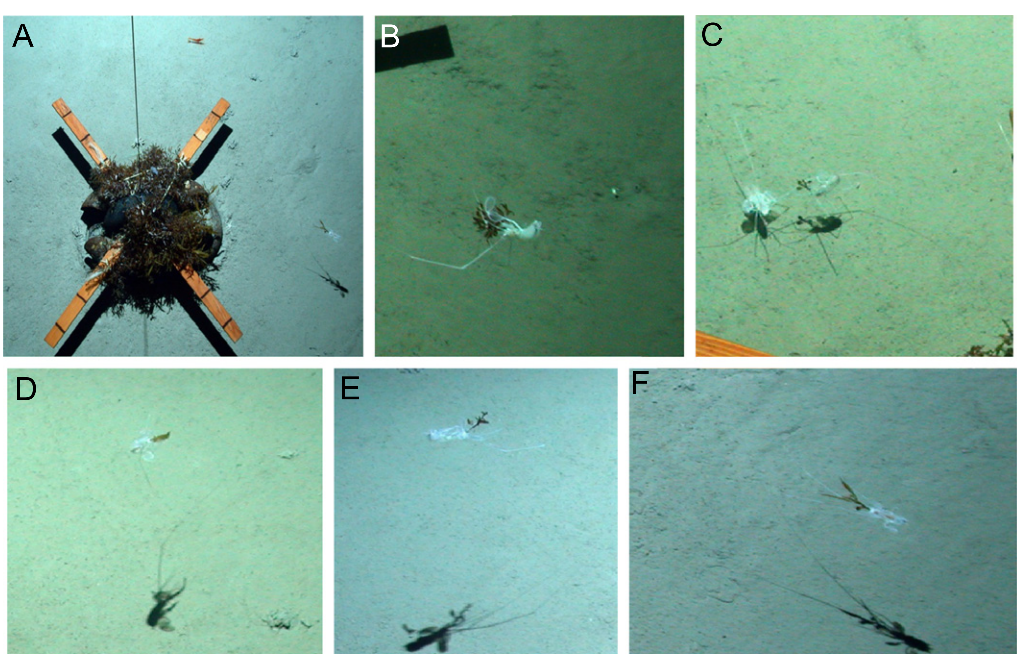

Fig. 1. *Bathyopsurus* sp. with pieces of *Sargassum* leaving the bait field of view in two deployments. Photograph A shows the 1 kg *Sargassum* bait. Photographs B and C were taken from S6-01. Photographs D, E, and F were taken from S6-06.

with both naturally occurring macroalgal remains (*Sargassum*) and mackerel carcasses. The objectives of this research are: (1) identification of the scavenging communities on the abyssal plain attracted to fish and *Sargassum* baits, (2) comparison of the relative abundances and behavioral characteristics of each community.

2. Material and methods

2.1. Data collection

Free-vehicle, time-lapse baited camera systems (described in Yeh and Drazen (2009, 2011)) were dropped to the seafloor to photograph scavenging communities. All deployments occurred in the central Sargasso Sea between Bermuda and the Bahamas during February 2011 (Table 1). The camera system consisted of a 4.0 Megapixel digital still camera and strobe (Scorpio Plus, Insite Pacific) suspended 2 m above the bait and seafloor. Photographs were taken at 2 min intervals for 24 to 40 h. The field of view averaged approximately 1.75 m^2.

Deployments were baited either with ~1.5 kg of mackerel or with ~1 kg of *Sargassum* (Fig. 1A). Mackerel was previously frozen and represents the standard bait used in many previous studies (Bailey and Priede, 2002; Yeh and Drazen, 2009; Jamieson et al., 2011; Martinez et al., 2011). *Sargassum* was netted at the sea surface in the area of operation. It was placed in flow through aquaria on deck in full sunlight until it was used for deployment, within 48 h. The *Sargassum* was not cleaned of attached invertebrates so that it closely mimicked its natural state upon sinking. It was tied to the anchor and scale bar using twine. The scale bars were made of thin wooden boards and had lines 10 cm apart for approximation of animal sizes.

2.2. Data quantification

Species were identified to their lowest taxonomic level based on morphological characteristics with the assistance of various taxonomic specialists (see acknowledgements). Amphipods were observed on the bait (both types) in all deployments; however, only amphipods greater than 1 cm were counted, but not identified. It was not possible to accurately count the amphipods smaller than 1 cm due to their small size and the wide field of view of the camera.

The two principal variables used for analysis of the photographs were the same as in past studies. First arrival time, the time required for the first individual of each species to enter the field of view after vehicle touchdown, was recorded for each scavenging species present. Peak abundance, n_{max}, the maximum number of a given species observed in a single image throughout the deployment, was determined for all scavenging species present. The relative abundance for all species, $\sum n_{max}$, which is the conservative minimum number of animals attracted to the bait, was determined for each deployment. Cluster analysis was employed to compare scavenging communities between bait types. The analysis was carried out on a Bray–Curtis similarity matrix of the square-root transformed n_{max} data for all species and deployments, using group-average linkage method. Significance of cluster nodes was performed using the similarity profile (SIMPROF) routine in the PRIMER statistical package (Anderson et al., 2008).

3. Results

Data was collected from five deployments in the Sargasso Sea between February 13 and February 22, 2011 with depths ranging

Table 2
Scavenger peak abundance (n_{max}) and time of first arrival ($_{min}$) in parentheses.

Deployment	Bait type	Fish					Invertebrate							
		Barathrites iris	*Barathrites* sp.	*Bassozetus* sp.	*Coryphaenoides armatus*	Small Unidentified Ophidiid	Amphipod (> 1 cm)	*Alicella gigantea*	*Bathyopsurus* sp.	cf *Hymenopenaeus*	Galatheid crab	*Plesiopenaeus armatus*	Polychaete	Ophiuroid
S3-07	Mackerel	2 (740)		9 (300)	1 (730)		2 (148)	1 (730)		1 (80)		2 (158)	1 (1016)	
S5-01	Mackerel	4 (96)	1 (1438)	12 (188)	1 (1594)	2 (488)	2 (60)			3 (38)		2 (44)	2 (1174)	
S6-10	Mackerel	2 (194)	1 (64)	3 (430)	1 (724)		2 (110)		1 (952)	5 (16)		2 (8)	2 (900)	3 (10)
S6-01	*Sargassum*		1 (214)			1 (1516)			6 (296)	1 (1032)		1 (196)	1 (2130)	1 (908)
S6-06	*Sargassum*								6 (224)	2 (134)	1 (1508)	1 (594)	1 (478)	4 (8)

5160 m to 5550 m (Table 1). Three utilized mackerel bait and two *Sargassum* bait. The cameras remained on the seafloor for durations of 24:32 to 39:26 (hr:mm). The mackerel bait deployment S3-07 inadvertently had its focal length set too high resulting in a narrower field of view (0.25 m^2). As a result n_{max} for S3-07 may have been underestimated in comparison to the other deployments.

A total of 12 different species were attracted to the mackerel bait, deployments S3-07, S5-01, and S6-10 (Table 2), with four seen feeding on the bait: amphipods (> 1 cm), *Barathrites iris*, *Barathrites* sp., and *Coryphaenoides armatus* (Fig. 2). The ophidiid, *Bassozetus* sp., was the most abundant (n_{max}) fish attracted to the bait reaching a peak abundance of 12. *Bassozetus* sp. was always observed swimming above or around the bait but never actually eating it. The second most abundant scavenger was another ophidiid *Barathrites iris*, which was seen regularly tearing at the underside of the bait and removing large chunks from the ventral region. The macrourid, *C. armatus*, was rarely seen and never more than one at a time. It was observed in 18 nonconsecutive photographs, though within a small time frame, in S3-07. It was observed only three times in S5-01 and once in S6-10. On average *C. armatus* arrived at a later time than the other fish species. *Barathrites* sp., a smaller fish one-sixth the size of the ~60 cm *B. iris*, appeared in only two of the mackerel baited deployments with a peak abundance of one. The *Barathrites* sp. was observed feeding on the bait in the presence of *B. iris* suggesting it was not deterred by the larger fish.

Seven species of invertebrates were observed in the mackerel baited deployments (Table 2). Upon touchdown on the seafloor, small amphipods were observed feeding on the carrion within approximately 30 min and larger amphipods (> 1 cm) arrived soon after. The decapod *cf Hymenopenaeus* was the most abundant invertebrate in all the mackerel deployments. The two decapods, *cf Hymenopenaeus* and *Plesiopenaeus armatus*, were

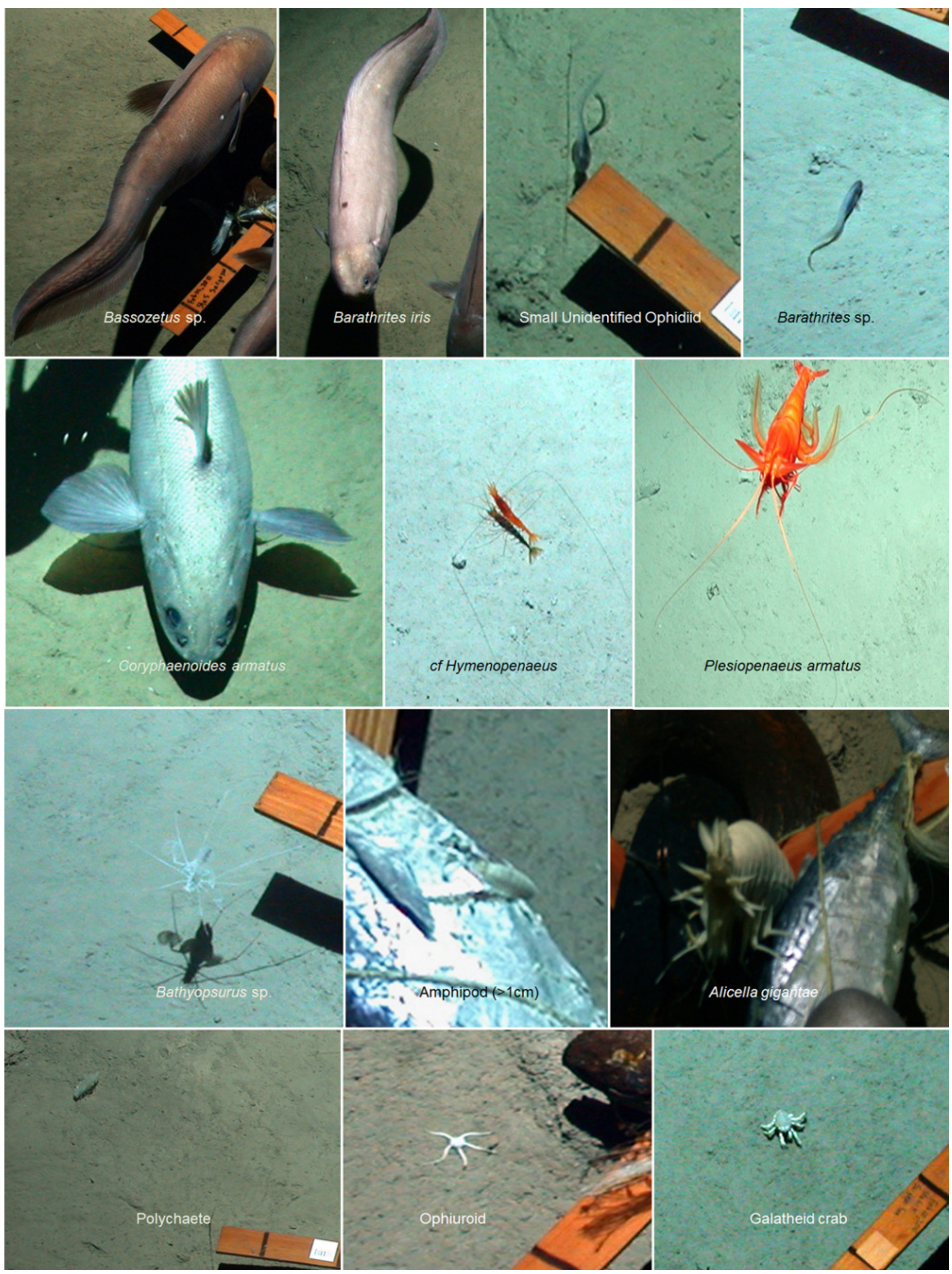

Fig. 2. Scavenging species observed in the Sargasso Sea.

always the first species to arrive after small amphipods. An unidentified polychaete arrived >900 min in each deployment and was observed crawling on the bait, but it is uncertain if it was scavenging or not. The giant amphipod, *Alicella gigantea*, appeared 730 min into deployment S3-07 and was observed feeding on the bait for approximately 90 min. Two species, the ophiuroid and the asellote isopod *Bathyopsurus* sp. (Family Munnopsidae), were only observed passing through the field of view.

The community attracted to the *Sargassum* bait differed from that attracted to the mackerel bait. A total of eight different species (Fig. 2), six of which were invertebrates, were observed which contrasts to the dominance by fish at the mackerel bait (Fig. 3). The isopod *Bathyopsurus* sp. was the primary species attracted to the *Sargassum* reaching a peak abundance of six and arriving within 220 min to 300 min for both deployments. Between the two *Sargassum* deployments, S6-01 and S6-06, it was observed five times that a *Bathyopsurus* sp. left the bait station with a piece of *Sargassum* (Fig. 1(B)–(F)). The second most abundant species was an ophiuroid. On one occasion an ophiuroid was observed handling a small piece of *Sargassum* for 30 min. Due to the time the ophiuroid handled the *Sargassum*, it is reasonable to assume that the ophiuroid was feeding on the small piece. Fewer small amphipods were seen on the clump of *Sargassum* bait than the mackerel bait; however, no amphipods (>1 cm) were attracted to the *Sargassum* bait. Polychaetes were seen crawling on the *Sargassum*, but it is uncertain if they were scavenging or not. The two decapods, *cf Hymenopenaeus* and *P. armatus*, were also observed around the bait. A galatheid crab was also observed in S6-06, but remained at the edge of the field of view and was never observed approaching the bait.

The two smaller fish, *Barathrites* sp. and the Small Unidentified Ophidiid in S6-01, were not observed feeding on the *Sargassum* bait. *Barathrites* sp. arrived early into the *Sargassum* deployment and was observed intermittently in photos for the next five hours. At one point it was observed swimming underneath the thinly veiled outcrops of the *Sargassum* sticking out over the anchor. The Small Unidentified Ophidiid, one-tenth the size of the larger, ~60 cm, *Bassozetus* sp., arrived towards the end of the *Sargassum* deployment and was seen only a few times never approaching the *Sargassum*. The larger fish *Bassozetus* sp., *Barathrites iris*, and *C. armatus* did not appear in any of the *Sargassum* deployments.

The differences described above were reflected in a cluster analysis of scavenger communities. The analysis clearly separated the deployments by bait type (Fig. 4; simprof test, $p<0.05$). Between bait types there was about 40% similarity whereas within bait type the deployments were >75% similar.

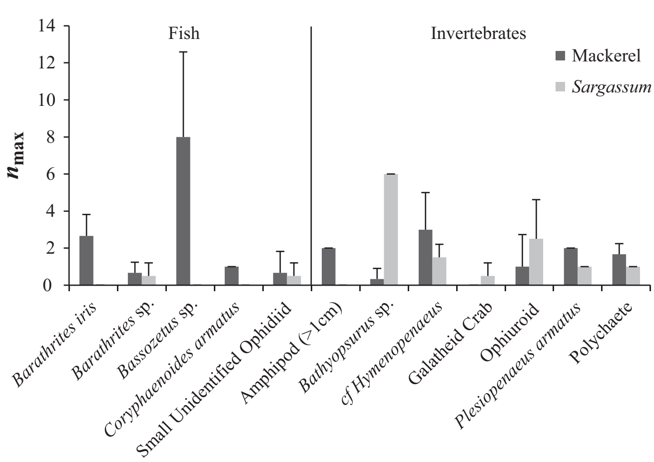

Fig. 3. Mean scavenger abundance (n_{max}) for mackerel and *Sargassum* baited stations. Error bars are standard deviation.

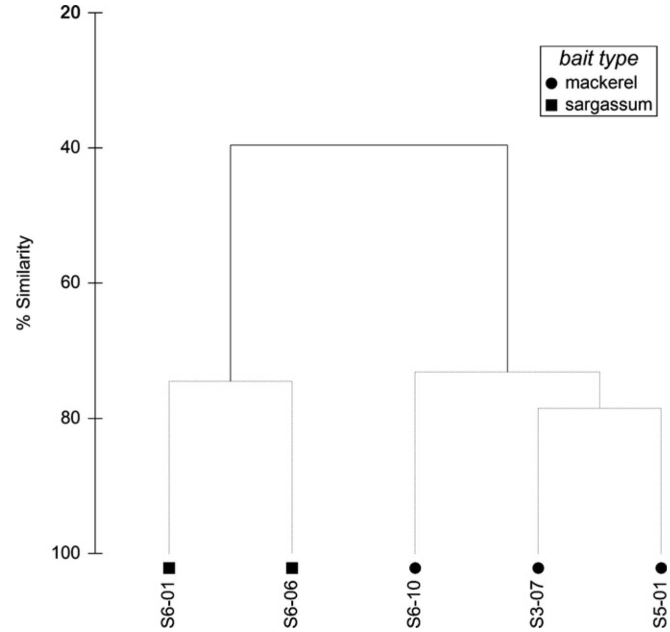

Fig. 4. Cluster analysis of n_{max} data for each species across deployments. Data was square root transformed and used to construct a Bray–Curtis similarity matrix for the analysis (see methods). Solid lines separate clusters which are significantly different (simprof test, $p>0.05$).

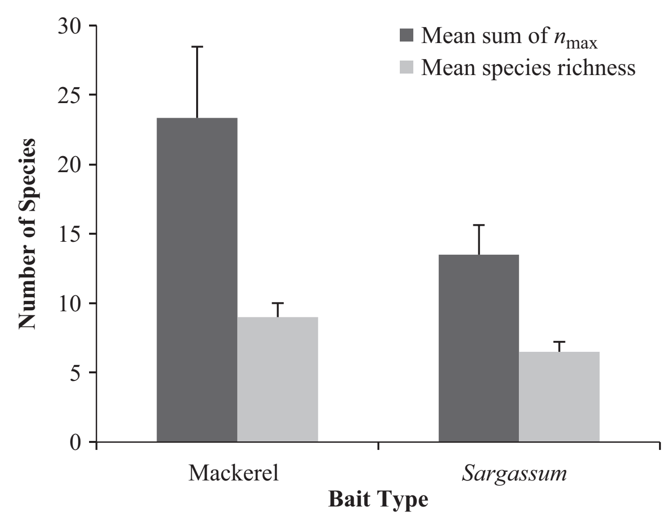

Fig. 5. Mean sum of n_{max} and species richness for mackerel and *Sargassum* baited deployments. Error bars are standard deviation.

Relative abundance for all species, mean $\sum n_{max,}$ was higher for the mackerel deployments (23.3 ± 5.13) than for the *Sargassum* deployments (13.5 ± 2.12) (Fig. 5). The mean species richness was also higher for the mackerel deployments (9.0 ± 1.0) than for the *Sargassum* deployments (6.5 ± 0.71). The invertebrate fauna comprised 58.3% of the mackerel baited species richness while comprising 75% of the *Sargassum* baited species richness. Of the 58.3% of invertebrate fauna only 28.6% was found scavenging on the mackerel bait. Of the 75% of invertebrate fauna attracted to the *Sargassum* 33.3% was observed scavenging on the bait.

4. Discussion

The community of scavengers attracted to the mackerel bait was different than that found in other regions of the North

Atlantic. In the oligotrophic Sargasso Sea (annual chlorophyll biomass <0.25 mg/m^3; Longhurst, 2007) ophidiids, particularly *Bassozetus* sp., were the primary scavengers. On the Porcupine Abyssal Plain (PAP), Madeira Abyssal Plain (MAP), and off Cape Verde, Africa other baited camera studies documented abundant macrourids, mostly *C. armatus* (Nielsen, 1986; Armstrong et al., 1992; Thurston et al., 1995; Priede and Merrett, 1998; Henriques et al., 2002). These study sites are slightly shallower (PAP 4800m, MAP 4900m, Cape Verde 4000 m) than ours which might explain the difference. However, a more likely explanation is the overlying surface productivity. More ophidiids were observed at the more oligotrophic MAP (annual chlorophyll biomass <0.50 mg/m^3; Longhurst, 2007) compared to the more eutrophic PAP (annual chlorophyll biomass <1.5 mg/m^3; Longhurst, 2007). This difference in abundance is attributed to productivity differences (Armstrong et al., 1992; Thurston et al., 1995) and trawl studies which suggest a zone of ichthyofaunal change in this region of the abyss in relation to differences in seasonality of surface production (Merrett, 1987). Furthermore observations elsewhere in the world suggest that macrourids are more common in eutrophic regions. Scavenging communities in the eutrophic California Current in the North Pacific (Priede et al., 1994) are known to be dominated by macrourids while oligotrophic regions such as the North Pacific subtropical gyre are dominated by ophidiids (Yeh and Drazen, 2009). While surface production clearly affects community composition its effects on any particular group may not be straightforward. For instance, in the Arabian Sea, both seasonally high productivity sites and more oligotrophic sites had scavenging fish communities of zoarcids and ophidiids, though ophidiids were more abundant at the more oligotrophic site (Janssen et al., 2000).

Contrary to Jeffreys et al. (2010, 2011) results of fish scavenging on simulated plant food falls, this study found no fish regularly attracted to *Sargassum*, a natural and commonly occurring plant fall material in the Sargasso Sea. We observed two smaller ophidiid taxa appearing sporadically in 7.4% of the photographs around the *Sargassum* in one deployment. They did not appear to be scavenging directly on it. The fish may have been attracted to the epifaunal organisms that were attached to the *Sargassum* instead of the macroalgae. The Small Unidentified Ophidiid appeared to be floating around the *Sargassum* like its larger counterparts around the mackerel bait and perhaps was attracted to the amphipods on the *Sargassum* as snailfish are known to consume the amphipods attracted to carrion falls (Thurston, 1990; Jamieson et al., 2009).

In contrast to the results for the fish carrion, a community of invertebrates was found directly interacting with the *Sargassum* within hours of its arrival to the seafloor. The isopod *Bathyopsurus* sp. most likely fed on the *Sargassum* and was observed removing pieces of *Sargassum* from the central clump (Fig. 1(B)–(F)). It is unusual for isopods to be attracted to baited cameras, but in previous studies isopods have also been observed removing and walking away with pieces of mackerel bait (Svavarsson et al., 1993; Brandt et al., 2004; Jamieson et al., 2012). Previous stomach analyses of the isopods *Bathyopsurus nybeleni* and *Paropsurus giganteus* captured in the Puerto Rico Trench were found filled with *Sargassum* and fucalean algae (Wolff, 1962). It is highly likely that *Bathyopsurus* sp. either fed on the *Sargassum* or redistributed the algae across the abyssal plain. *Bathyopsurus* sp. was the most prominent species in each of the *Sargassum* deployments and appears to be directly attracted to it. This may indicate that the macroalgae or attached organisms creates an odor plume attracting these invertebrates.

Previous studies have suggested that ophiuroids scavenge on *Sargassum* food falls (Schoener and Rowe, 1970), which our study supports. However, considering the *Sargassum* was not cleaned of invertebrates it is possible that the ophiuroid was actually feeding on the epifauna on the algae instead of solely the algae. Polychaetes and amphipods were also attracted to the *Sargassum*, which has been observed in *Sargassum* baited traps in shallower locations (Wolff, 1979b; Lawson et al., 1993). Oceanic *Sargassum* has a C:N ratio of 49.4, similar to other macroalgal detritus and considerably higher than that found in fish carcasses ($\sim$3–6), suggesting it is a relatively poor nutritional source (LaPointe, 1995). This probably explains why there were fewer species observed and lower maximum numbers compared to mackerel baits. However, the large production of *Sargassum* in surface waters and its common occurrence on the seafloor may be the reason that at least some animals such as the isopods appear to be adapted to rapidly find and possibly consume it. A similar community might rapidly respond to turtle grass, *Thalassia* spp., as well. Sediment samples with clumps of *Thalassia* have been collected with a similar community of isopods, polychaetes, and amphipods (Wolff, 1979b; Lawson et al., 1993). *Thalassia* has a C:N ratio of $\sim$18.3 (Rowes and Dawes, 1999), suggesting it is a more labile nutritional source than *Sargassum* but probably not a viable food source for deep-sea fish (Crabtree, 1995).

It is possible the fauna was attracted to the wooden scale bars; however, fauna attracted to wood would likely colonize the wood over long periods of time and not arrive within the short period of the deployment (Grassle and Morse-Porteous, 1987; Bernardino et al., 2010; Kobayashi et al., 2012). There were also no amphipods observed directly on the wooden scale bars, but instead only on the *Sargassum* (Kobayashi et al., 2012). Thus the wooden scale bars, though made of vegetable matter, did not appear to attract a faunal community over the short term.

In summary, our results show that a community of benthic fauna is attracted to, most likely consumes, and in the case of an isopod, disperses falls of *Sargassum* on the abyssal seafloor in the Sargasso Sea. Though two fishes were observed they were most likely individuals which encountered the *Sargassum* and were feeding on attached animals or amphipods. In contrast, the scavenging community attracted to mackerel bait was dominated by fishes as in most other baited camera studies in the North Atlantic (Nielsen, 1986; Armstrong et al., 1992; Thurston et al., 1995; Priede and Merrett, 1998; Henriques et al., 2002). However, in this case the fishes were dominated by ophidiids, and macrourids were rare, probably as the result of the oligotrophic nature of the Sargasso Sea. Further studies should be conducted comparing the scavenging fishes observed in other abyssal regions across a range of surface productivity to reach clearer conclusions.

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