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The Association between Stomach Fullness and Vertical Migration Behavior in Deep-Pelagic Crustaceans and Fishes in the Gulf of Mexico, with Notes on Microplastic Ingestion

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Thesis of
Ryan P. Bos

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Environmental Sciences

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

April 2019

Approved:
Thesis Committee

Major Professor: Tamara M. Frank

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The Association between Stomach Fullness and Vertical Migration Behavior in
Deep-Pelagic Crustaceans and Fishes in the Gulf of Mexico, with Notes on
Microplastic Ingestion

By:

Ryan Piers Bos

Submitted to the Faculty of Nova Southeastern University

Halmos College of Natural Sciences and Oceanography in partial fulfillment of the
requirements for the degree of Master of Marine Science with a concentration in:

Marine Science

Nova Southeastern University

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ABSTRACT

This thesis presents: 1) the first statistically rigorous support for the longstanding hypothesis that state of satiation modifies diel vertical migration patterns of deep-sea micronektonic crustaceans and fishes; and, 2) the first assessment of microplastic ingestion by deep-pelagic micronekton in the Gulf of Mexico and Straits of Florida. Deep-sea pelagic crustaceans and fishes significantly contribute to abundance and biomass of pelagic ecosystems, are frequently consumed by commercially valuable fishery species, and serve to transport both nutrients and pollutants between shallow and deep waters. The results presented herein will be valuable for assessing risk associated with potential biomagnification of plastic through consumption or indirect consumption of deep-sea biota. Moreover, these data demonstrate that the extent of feeding at depth by non-migratory taxa as well as non-migrating individuals of migratory taxa is substantial. Feeding at depth is usually excluded from biogeochemical models, and these data demonstrate that this is an important factor that must be included to obtain more precise estimates of active nutrient flux by micronekton.

Keywords: Deep sea, Micronekton, Vertical migration, Stomach fullness, Microplastics

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Introduction

Deep-Pelagic Micronektonic Crustaceans and Fishes

While Earth's oceans cover 71% of its surface, humans have explored less than five percent of this huge habitat (NOAA, 2012). Of this uncharted territory, the deep sea is the largest, yet most unexplored environment. Exemplified by depths greater than 200 m, the deep-sea water column, known as the pelagic realm, envelops four depth divisions which each have their own trophic structure and ecosystem: the mesopelagic (200 m - 1000 m), bathypelagic (1000 m - 4000 m), abyssopelagic (4000 m - 6000 m), and hadalpelagic (>6000 m) zones. Of the aforementioned depth zones, only two, the meso- and bathypelagic, are pertinent to the Gulf of Mexico (hereafter referred to as GoM). These two environments are characterized by high faunal diversity, including more than 100 species of crustaceans and 700 species of fishes (Hopkins and Sutton, 1998; Sutton *et al.* 2017), the two groups of metazoan taxa that are the focus of this study.

The micronektonic crustaceans and fishes (2 - ≤20 cm) examined in this study are at the base of the food web for commercially important fisheries. These crustaceans and fishes make significant contributions to food webs and total biomass in all deep-sea assemblages (Gjosaeter and Kawaguchi 1980; Hopkins *et al.* 1994; Sutton *et al.* 2008; Kaartvedt *et al.* 2012; Irigoien *et al.* 2014). Moreover, these taxa significantly contribute to the biological carbon pump through foraging in the epipelagial and respiration and excretion in the meso- and bathypelagial (reviewed in Sutton, 2013) while also serving as crucial trophic intermediates to higher trophic levels. The deep-sea fishes in the current study are chiefly selective zooplanktivores and are consumed by a variety of seabirds, commercially important fishes, mammals, and cephalopods (Beamish *et al.* 1999). The deep-sea decapod crustaceans analyzed here are primarily planktivores and are consumed by cephalopods and commercially important fishes (Borodulina, 1972; Hopkins *et al.* 1994).

Diel Vertical Migration

Many meso- and bathypelagic crustaceans and fishes undergo diel vertical migrations into the epipelagic zone to forage at night (reviewed in Longhurst, 1976; Gjosaeter and Kawaguchi, 1980; Cohen and Forward, 2005). Diel vertical migration is the largest animal

migration (by abundance and biomass) on Earth and is undertaken by a variety of deep-sea fauna (reviewed in Maul *et al.* 2017) including a majority of the most abundant families of deep-pelagic micronektonic crustaceans and fishes in the GoM and Straits of Florida. Vertical migration is beneficial to deep-sea biota because animals ascending to forage in surface waters at night encounter a larger prey density and do so under the cover of darkness, thereby avoiding visual predators (Judkins and Fleminger, 1972; Foxton and Roe, 1974; Gliwicz, 1986; Clark and Levy, 1988; Bollens and Frost, 1989; Lampert, 1993). The most common migration pattern is an ascent to shallow-pelagic waters (<600 m) at sunset and descent to deep-pelagic waters (>600 m) before sunrise, and this phenomenon is controlled by a variety of exo- and endogenous factors. Light is generally regarded as the primary causal factor triggering and controlling the timing and extent of movement of these migrators (Ewald, 1910; Rose, 1925; Russel, 1926; Clarke, 1930; Ringelberg, 1964; reviewed in Cohen and Forward, 2005). These migrations can be staggered with respect to the influence of light, however, and this may be because of the varied ability (photosensitivity) of animals to respond to light cues (Frank and Widder, 1997; Myslinski *et al.* 2005).

In addition to light and predator avoidance, vertical migration behavior can also be affected by a variety of other external factors such as currents (Bennett *et al.* 2002), tidal cycle (Hill, 1991), lunar cycle (Alldredge and King, 1980), and food availability (Huntley and Brooks, 1982), and internal factors such as feeding periodicity (Mullin, 1963), circadian rhythms (Haney, 1993), and state of satiation (Waterman *et al.* 1939; reviewed in Cohen and Forward, 2005b). Importantly, these factors may influence micronektonic taxa differently and alter migration patterns between species and amongst individuals of the same species. However, the observed lack of synchrony between adult migrators of the same species cannot solely be attributed to light, as light levels change in a consistent fashion (Forward, 1988).

After feeding in shallow-pelagic waters, these animals sink back to cold, deep-pelagic waters while digesting and defecating. In doing so, micronekton contribute to active-nutrient flux by expediting the flux of essential nutrients like carbon, nitrogen, and phosphorus to deeper waters (Pearre, 2003), and are therefore important for the biogeochemical cycling of nutrients. This active-nutrient flux is invaluable to the deeper layers of the oceanic realm because gravitational flux, or passive sinking of organic matter, decreases exponentially with depth (Vinogradov, 1968). In some cases, the biogeochemical impact of diel vertical migration is

extreme, as consumption of oxygen in shallower waters by deep-pelagic organisms may intensify oxygen depletion in oxygen minimum zones (Bianchi *et al.* 2013).

Cessation of migration in some individuals during nocturnal feeding periods has been documented in chaetognaths (Pearre 1973, 1979), copepods (Mackas and Bohrer, 1976; Hays *et al.* 2001), and during periods of high food availability in shallow-pelagic waters (Geller, 1986). Furthermore, ocean acoustics data and trawl data have shown that while a portion of any given species-assemblage vertically migrates, another portion remains at depth and does not migrate (Sutton *et al.* 1996; Onsrud and Kaartvedt, 1998; Hays *et al.* 2001; Kaartvedt *et al.* 2009; Dypvik *et al.* 2012; Brierley, 2014). Refraining from migrating into more productive waters during periods of decreased predation pressure is counterintuitive. One explanation for this phenomenon is the longstanding Hunger-Satiation Hypothesis, which suggests that the non-migrating portion of a migrating assemblage refrains from migrating if they have full or partially full stomachs from diurnal or nocturnal feeding (Simrad *et al.* 1985; reviewed in Forward, 1988; reviewed in Pearre 1973, 1979, 2003). However, stomach fullness data are sparse and conflicting for micronektonic crustaceans and fishes (Donaldson, 1975; Hu, 1978; Roe, 1984; Podeswa, 2012), with some crustaceans and fishes feeding throughout their entire depth distribution and some apparently feeding only in surface waters during their nocturnal migrations. While feeding in the deep-scattering layer both during night and day has been reported to occur in micronektonic crustaceans (Roe 1984, Podeswa 2012) and macro- and mesozooplankton (Hu, 1978; Baars & Oostherhuis, 1984), this factor is not included in current biogeochemical flux models.

Given that these animals comprise one of the largest migrations on Earth, substantially contribute to nutrient flux, and the extent at which they feed at depth is unknown, studying the stomach fullness of these animals is important for providing more precise estimates of their contribution to the biogeochemical cycling of nutrients. Likewise, decoupling preferential feeding at the surface from feeding at depth will also provide more precise estimates of active-flux. Thus, estimating stomach fullness of non-migratory taxa as well as migrating and non-migrating individuals of migratory taxa was one of the goals of this study.

Microplastics

Since excised stomachs remained after estimations of stomach fullness, the other goal of this study was to examine this stomach tissue and determine the extent of microplastic ingestion

by deep-pelagic crustaceans and fishes. Microplastics are known to be ingested by migratory and non-migratory taxa of deep-pelagic fishes (Boerger *et al.* 2010; Davison and Asch, 2011; Choy and Drazen, 2013; Lusher *et al.* 2016; Wieczorek *et al.* 2018), with migrators consuming more microplastics than non-migratory taxa (Davison and Asch, 2011; Lusher *et al.* 2016), although no statistical significance was observed. However, only one study documented microplastics in deep-pelagic crustaceans (Bordbar *et al.* 2018), whereas four studies documented microplastics in deep-sea benthic crustaceans (Taylor *et al.* 2016; Courtene-Jones *et al.* 2017; Carreras-Colom *et al.* 2018; Jamieson *et al.* 2019). Comparing these four studies, the non-migratory deep-sea benthic crustacean species ingested significantly more microplastics than the migratory species *Plesionika narval* that was studied in Bordbar *et al.* (2018). The deep-pelagic crustaceans and fishes in the current study are exemplary targets for comparative studies on microplastic ingestion because various taxa with variable feeding modalities occupy different niches in deep-pelagic systems, residing or co-occurring at different depths in the water column. Furthermore, these taxa preferentially feed on specific prey species, and some exhibit ontogenetic shifts in feeding. Consequently, comparing the stomach contents of these animals may reveal the potential role that feeding strategy and depth may play on microplastic ingestion.

The term 'microplastics' has been used extensively since the year 2004 to describe an eclectic mixture of synthetics (polymers) ranging from a few microns to five millimeters in diameter. The definition of the microplastics category has changed over the years, however, with the term's first appearance in a 1968 U.S. Airforce Materials Laboratory publication, although this document was not part of scientific literature (reviewed in Crawford and Quinn, 2017). At that time, the term 'microplastics' was used to describe the deformation of plastic material resulting from increased flexural stress. This definition is no longer used, as all extant definitions of microplastics refer to the physical size of particles rather than the physical load required to deform them. When this term first appeared in scientific literature in 2004, the category of 'microplastics' was defined as being of 1 µm - <1 mm in diameter (Thompson *et al.* 2004). Since then, an updated definition of microplastics was proposed in hopes of serving as a standard of what constitutes as a microplastic, and this definition divided microplastics into a mini-microplastics (1 µm - <1 mm along its longest dimension) and microplastics (1 mm - <5 mm along its longest dimension) categories (Crawford and Quinn, 2017). Nevertheless, the definition that has been predominantly used in scientific literature is that of microplastics being

classified as 1 um to <5 mm along its longest dimension, and this is the definition that is used in the present study.

The collective category of 'microplastics' is divided into two additional categories based on their origin: primary and secondary. Primary microplastics are manufactured at sizes of 1 um to <5 mm along their longest dimensions. Examples of primary microplastics include, but are not limited to, beads and fibers used in cosmetics and textiles, respectively, and resin pellets for plastic manufacturing and industrial scrubbers (NOAA, 2010; Wright *et al.* 2013). Secondary microplastics arise from the fragmentation of larger pieces of plastic (Moore 2008; Andrady, 2011; Wright *et al.* 2013). Despite microplastics fragmenting into smaller particles from mechanical weathering (Eriksen *et al.* 2014), they possess physiochemical properties that enable them to persist for hundreds to thousands of years (reviewed in Barnes *et al.* 2009). Positive buoyancy notwithstanding, mechanical weathering causes sinking of microplastics, and turbulent mixing via currents and wave driven processes circulates debris and organics throughout the ocean, rendering them accessible at nearly all depths. Moreover, turbulent downward fluxes facilitate microplastic transfer at night during periods of sea-surface cooling, whereas fluxes of debris are suppressed during periods of sea-surface heating when solar radiation is at its peak (Kukulka *et al.* 2016). Turbulent fluxes and the differences in density between seawater and plastic particles may be a major contributor to sinking of plastics and the large portion of plastic that is unaccounted for at an estimated five trillion pieces weighing 250,000 tons (Gregory, 2009; Thompson *et al.* 2009) in the World Oceans. The presence of both primary and secondary microplastics have been documented in high concentrations on marine shorelines (Carpenter *et al.* 1972; Santos *et al.* 2009; Browne *et al.* 2011), surface ocean waters (Law *et al.* 2010; Collignon *et al.* 2012) and deep-sea marine sediments (Van Cauwenberge *et al.* 2013; Woodall *et al.* 2014). Furthermore, plastic production has increased dramatically worldwide over the last sixty years (Avio *et al.* 2016) and it is estimated that the number of fishes and plastic particles in the ocean will be equal by the year 2050 (reviewed in Crawford and Quinn, 2017*)*. As such, there has been a surge of scientific publications on sources, occurrence, abundance, distribution, ingestion and associated consequences by and for biota (reviewed in Thompson, 2015), but thus far there have been no studies examining microplastic consumption by deep-sea fauna in the GoM or the Straits of Florida.

The fate and long-term environmental impacts of microplastics are not clear (Avio *et al.* 2016), but it is known that microplastic particles can exert physiological duress in the forms of pseudosatiation, obstruction of feeding appendages, decreased reproductive fitness, physical translocation to tissues, the inability to egest or regurgitate the plastic, and death. These effects of microplastic ingestion are of growing concern and observations of frequent plastic ingestion have been documented in commercially valuable benthopelagic crustaceans (Devriese *et al.* 2015), shore crabs (Watts *et al.* 2016), zooplankton (Cole *et al.* 2013; Desforges *et al.* 2015), larval forms of animals (Torre *et al.* 2014; Cole and Galloway, 2015; Lonnstedt and Eklov, 2016), and deep-sea crustaceans and fishes (Boerger *et al.* 2010; Davison and Asch, 2011; Choy and Drazen, 2013; Lusher *et al.* 2016; Taylor *et al.* 2016; Courtene-Jones *et al.* 2017; Bordbar *et al.* 2018; Carreras-Colom *et al.* 2018; Wieczorek *et al.* 2018; Jamieson *et al.* 2019). In the Northern Pacific Subtropical Gyre, species with the highest incidence of ingested plastic debris were thought to be primarily mesopelagic and unlikely to come in contact with surface waters, which suggests that a potential subsurface layer of plastic aggregation may exist (Choy and Drazen, 2013). Ingestion of microplastics by lower trophic orders, such as the micronekton in the current study, is especially problematic because historic appraisals of abundance and distribution of deep-sea animals have been underestimated by an order of a magnitude, demonstrating an even more vital role in the biological carbon pump than previously thought (reviewed in Sutton, 2013). This increased role in active nutrient flux by crustaceans and fishes by retaining and repackaging of organic matter (Hopkins *et al.* 1994) may facilitate the transfer of microplastics to depths previously thought to be unaffected.

Hydrographic Setting

Micronektonic fish samples were collected from two distinct hydrographic regions – the GoM and Straits of Florida, whereas micronektonic crustaceans were collected only from the GoM. These two regions are ideal locations for estimates of stomach fullness and microplastic ingestion by micronekton, because there is a diverse supply of micronekton collected on previous research cruises, and the natural diets of these taxa are known from previous studies.

Formed 300 million years ago, the GoM is a partially enclosed body of water that occupies an approximate geographic range between 30 and 20 $^{\circ}$ north and 80 to 97 $^{\circ}$ west. The coastal GoM is impacted by the West Florida Shelf current and the Louisiana-Texas shelf

current. These currents are maintained by internal waves driven by stratification from freshwater input from the Mississippi River (Sherman and Hempel, 2008) and the west coast of Florida. In addition, the Loop Current, coming in from the Caribbean, is the largest input of salt water into the GoM. This dynamic hydrological feature creates marked changes in temperature and salinity, and these incongruities can be extended to deep-pelagic waters. In fact, the GoM can be referred to as a two-layer system with respect to seawater dynamics, with the dynamics of the upper layer (0 – 1200 m) controlled by meso- and submesoscale features spinning off from the Loop Current, and the lower layer (>1200 m) being semi-isolated containing water with residence times of 250 years (Rivas *et al.* 2005). At the same time, cyclonic meso- and submesoscale eddies breaking free from the Loop Current may encourage upwelling of nutrients (Wiseman and Sturges, 1999). However, anticyclonic eddies (such as the Loop Current itself) promote downwelling and consistently contain low concentrations of nutrients. Thus, primary productivity in these mesoscale features is low and therefore these regions contain low abundance of zooplankton (Biggs, 1992). Mesoscale eddies are known to trap, concentrate, and transport microplastics to and from the surface ocean (Brach *et al.* 2018). Planktonic organisms may accumulate on the periphery of mesoscale eddies, which potentially brings animals closer to plastic pollution (Wieczorek *et al.* 2018).

Four submarine canyons are present in the northern GoM: Green, Keathley, Mississippi, and Veracruz Canyons. These canyons are close to massive freshwater inputs from the Mississippi River that is replete with nutrients, terrigenous sediments, and anthropogenic litter (Phillips and Bonner, 2015). Given that currents, internal waves, and bottom topography influence patterns of plastic distribution, the unique flow regime of currents, discontinuities of salinity causing stratification of freshwater from the Mississippi River, and bottom topography of the northern GoM makes it a unique area for study of plastic pollution and microplastic ingestion in marine animals. Areas characterized by upwelling, downwelling, and turbidity – like Mississippi Canyon – have the potential to transport microplastics vertically, horizontally, and to the open ocean from the coast (Avio *et al.* 2016; Sherman and Sebille, 2016). Furthermore, microplastics have been found in high concentrations in previous studies on continental shelves, slopes, seamounts, banks and mounds, and in deep basins and submarine canyons in other locations, which makes the northern GoM a potential area of concern for plastic aggregation (Pham *et al.* 2014).

There have been no studies on microplastic ingestion in the GoM by deep-pelagic micronekton. The only study on microplastic ingestion in the GoM is centered in the epipelagic realm and reported that 42.4% of fishes captured between Galveston Bay and Freeport, Texas contained microplastics in their digestive tracts (Peters *et al.* 2017). The only study to quantify microplastics concentrations in GoM seawater, which focused on coastal waters west of the Mississippi River Delta, reported concentrations of plastic that rivaled the largest globally reported values (Di Mauro *et al.* 2017). Lastly, there has been only one microplastics study in the deep-benthic realm of the GoM. There, the authors did not process biological samples for plastic ingestion. Instead they documented anthropogenic litter on sediments, with the focal point of litter being in Mississippi Canyon, proximal to the Mississippi River outflow (Wei *et al.* 2012).

Straits of Florida

The Straits of Florida, or Florida Strait, is located at 23.3875° N, 82.3886° W between the GoM and Sargasso Sea. The Straits' proximity to the North American coast and connectivity with the GoM make it a crucial location to survey for plastic ingestion. One of the pioneering surveys of plastic debris done by Colton *et al.* (1974) was conducted with plankton tows in the northwest Atlantic Ocean, with some sampling in the Straits of Florida. In that study, they documented a variety of plastic particles in this region, and those particles fell into the current microplastics size category, although this category definition didn't exist at that time.

The hydrodynamics of the Straits of Florida are largely influenced by the Loop Current. Large cyclonic mesoscale eddies breaking free from the Loop Current that can last up to 140 days propagate through the Straits (Fratantoni *et al.* 1998). Upon entry to the Straits, these eddies become deformed and shrink in size due to the narrowing topography, and therefore may concentrate nutrients, organisms, and plastics on their periphery. Furthermore, similar depths on opposite sides of the Loop Current in the Straits have substantially different temperatures, with the average temperature at 200 m on the western side of the straits being 10° C, while it is 10° C at 600 m on the eastern side. The difference in flow, turbidity, and temperature creates a large biophysical and biogeographic boundary for deep-sea animals, and these former environmental conditions are known to concentrate plastic as well.

Materials and Methods

Sample Collection and Processing

Samples were collected in the GoM on cruises onboard the M/V *Meg Skansi* (as part of the Offshore Nekton Sampling and Analysis program) and R/V *Point Sur* (as part of the Deep Pelagic Nekton Dynamics of the Gulf of Mexico Consortium research). The sampled stations from the GoM selected for this study by Dr. Tracey Sutton coincide with pre-established locations and nomenclature of the Southeast Area Monitoring and Assessment Program (SEAMAP) sampling grid (French-McCay *et al.* 2011, Figure 1).
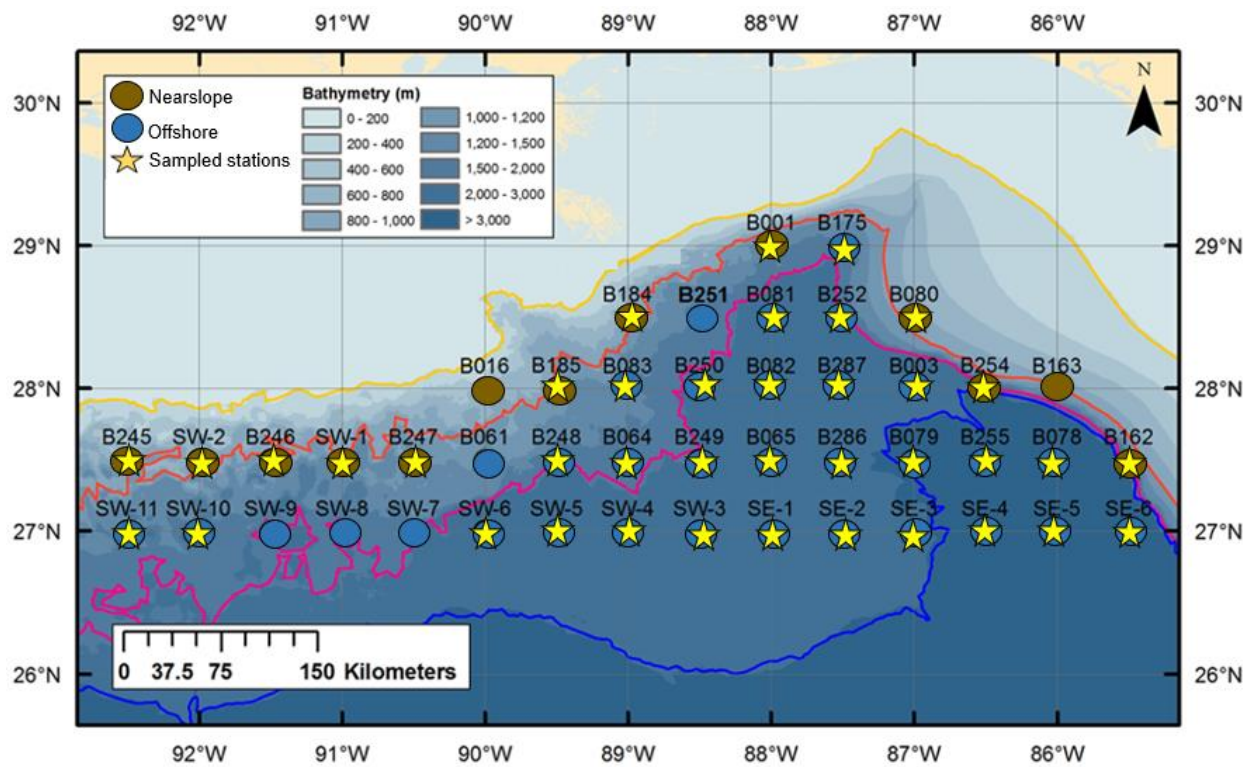
Figure 1. The locations (SEAMAP Codes) of the 10-m² MOCNESS trawl deployments during M/V *Meg Skansi* and/or R/V *Point Sur* cruises in near-slope (brown circles) and offshore environments (blue circles). Yellow stars indicate stations where samples used for stomach fullness estimates and microplastics analyses were collected (Adapted from French McCay *et al.* 2011).

The selected SEAMAP stations were classified as being 'near-slope' or 'offshore,' with near-slope stations located landward of the 1000 m isobath, and offshore stations located on the ocean side of the 1000 m isobath (Burdett *et al.* 2017). In addition, using CTD and MOCNESS

sensor data, SEAMAP stations were classified as containing Common Water or Loop Current Origin Water during the time of sampling (Johnston *et al.* in press).

Animals used for analyses in this study came from samples that were collected in the GoM over a span of six years starting with *Meg Skansi* cruises in 2011 and ending with the DEEPEND cruises from 2015-2017 (Table 1). Samples were collected using a 10-m^2 Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) equipped with 3-mm nylon mesh (Wiebe *et al.* 1976).

Table 1. Cruise dates of samples that were collected in the GoM.

Cruise Name	Sample Dates
MS6	January 25th - April 1st, 2011
MS7	April 20th - June 29th, 2011
MS8	July 20th - September 29th, 2011
DP01	May 1st - May 8th, 2015
DP02	August 8th - August 21st, 2015
DP03	April 30th - May 14th, 2016
DP04	August 5th - August 18th, 2016
DP05	May 1st - May 11th, 2017

The MOCNESS collected samples from five discrete depth bins by opening and closing at the depths defined in Table 2, and each station was sampled twice during a 24-hour period, once during the day (deployed between 1000 h - 1600 h) and once at night (deployed between 2200 h - 0400 h). These samples were fixed in 10% formalin and sent to the Oceanic Ecology Laboratory (fishes) and the Deep-Sea Biology Laboratory (crustaceans) at Nova Southeastern University for identification and analysis. Samples used for the current study came from all five depth bins (Table 2) during both day and night

Table 2. 10-m^2 MOCNESS depth codes.

Net Number	Depth Bin (m)
5	0-200 m
4	200-600 m
3	600-1000 m
2	1000-1200 m

| 1 | 1200-1500 m |
| 0 | 0-1500 m |

Samples were also collected in the Straits of Florida aboard the R/V *Walton Smith*, on a one-week long NSF- funded cruise in July 2016. Fish samples from the Straits of Florida were collected from three stations (Figure 2) during both the day and at night using a 9-m^2 opening/closing Tucker Trawl. Daytime collections were between 600 – 800 m, while nighttime collections were between 100 – 300 m. As no samples were collected from deep-pelagic waters at night in the Straits, and all the crustaceans were being used for other studies, only fishes were processed for presence or absence of microplastics. These samples were also fixed in 10% formalin/seawater at sea and returned to the Deep-Sea Biology Laboratory at NSU for processing.
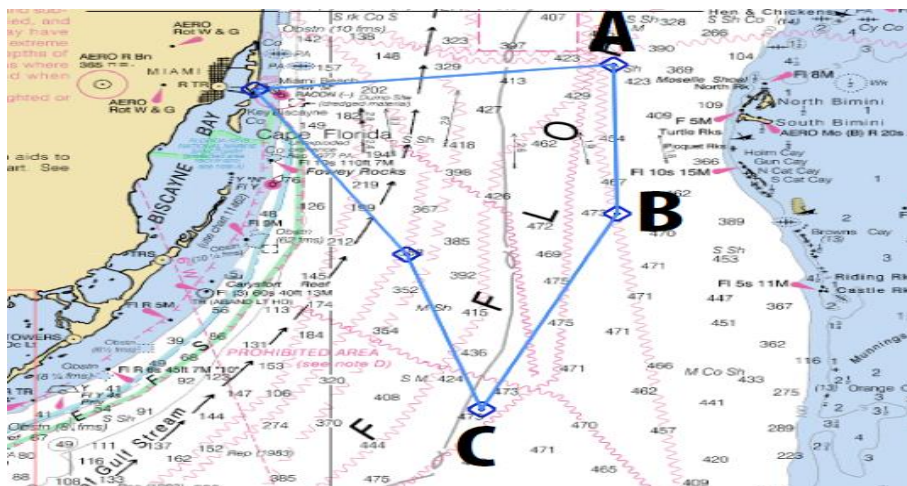
Figure 2. Map of sampling stations in the Straits of Florida aboard the R/V *Walton Smith* in 2016.

The crustacean and fish species included in the stomach fullness portion of this thesis are displayed in Tables 3 and 4 (see Results section). Of the crustacean species included in stomach fullness analyses, seven are known vertical migrators while five are non-migratory. For the fishes, seven species are known vertical migrators while five exhibit non-migratory behavior.

The crustacean and fish species included in the microplastic ingestion portion of this thesis are displayed in Tables 13, 14, and 15 (see results section). Of the crustacean species

appraised for microplastic ingestion, 12 species are vertical migrators while five are non-migrators whereas for the fishes, 27 species exhibit migratory behavior while five species do not.

Sample Processing

After species identification of fishes (in the Oceanic Ecology Lab), and crustaceans (in the Deep-Sea Biological Laboratory, wet masses of crustaceans and fishes were measured with a P114 balance (Denver Instruments) to the nearest 0.01 g. Standard length (fishes) and carapace length (decapod crustaceans) were measured to the nearest 0.1 mm using a carbon fiber composite digital caliper (CO030150 electronic digital caliper, Marathon Management®). Standard lengths of fishes were measured as the distance from the tip of the rostrum to the end of the hypural plate (Royce, 1942) and carapace lengths of crustaceans were measured as the distance between the posterior end of the carapace and the insertion of the eyestalk (Hanamura and Evans, 1996).

Estimation of Stomach Fullness

The workstation was thoroughly cleaned three times with 70% ethanol to remove any residual microplastics that could contaminate samples. Each animal was rinsed thoroughly with type I ultrapure water, dipped into an acetone rinse, and stored in an acetone-sterilized petri dish covered with acetone-sterilized convex clock glass until ready for dissection. This ensured that there was no contamination by airborne microplastics (Crawford and Quinn, 2017) to safeguard the validity of results for the second goal of this study. Further rigorous precautions were made to avoid microplastic contamination such as wearing non-plastic clothing coupled with a 100% cotton laboratory coat as suggested by Enders *et al.* (2015) and Lusher *et al.* (2015). Sterilized forceps were used to handle all samples and for each series of dissections, two moistened Whatman GF/F 0.7 - µm filters were placed next to the workstation as a measure of potential contamination. At the end of the dissection series, these 'control' filters were examined under a dissecting microscope (Crawford and Quinn, 2017).

After the workstation was sterilized, the digestive tract of each animal was excised, and stomach fullness was quantitatively estimated using a scale of 0 – 5 (Carmo *et al.* 2015, adapted from Sutton *et al.* 1996). This scale was used for both crustaceans and fishes, such that: 0 = completely empty; 1 = 1% - <20% of the total capacity of the stomach was filled with prey; 2 = 20% - 50% of the total capacity of the stomach was filled with prey; 3 = 50% - 70% of the total capacity of the stomach was filled with prey; 4 = 70% - 95% of the total capacity of the stomach

was filled with prey; 5 = >95% of the total capacity of the stomach was filled with prey with readily visible prey items seen through the stomach wall, or prey bulging out of the recently severed connection of the buccal cavity and esophagus.

Extraction and Analysis of Microplastics

After estimates of stomach fullness, the extracted digestive tracts, as well as the additional tracts excised from individuals collected from the Straits of Florida that were not used in the stomach fullness studies, were placed individually into labeled 11-mL borosilicate glass vials and digested using one of two digestive solutions. Fish and some crustacean (see below) digestive tracts were dissolved via a 1:1 potassium hydroxide-sodium hypochlorite (15% active chlorine) solution following protocols described in Enders *et al.* (2017). After one hour of digestion at room temperature, the glass vials were loaded onto a shaker table (VWR DS-500 Digital Orbital Shaker) in the Ecotoxicology laboratory at Nova Southeastern University and shaken for two hours. The glass vials were removed from the shaker table, heated (>80 C) for 10 minutes, diluted with 5 mL of heated (>50 C) type I ultrapure water, and heated a second time to >80 C to ensure total digestion of tissue. To our knowledge, this was the first study to test the efficacy of basic digestion proposed by Enders *et al.* (2017) on crustacean stomachs. While Enders *et al.* (2017) speculated that the proposed basic digestion could be effective in digesting flocculent, biogenic materials, results from the present study demonstrated that this basic digestion was inefficient for digesting crustacean stomach contents. The products of this digestion were a greasy slurry, which made it challenging to sort through for microplastics. For this reason, crustacean digestive tracts were instead digested with a 4:1 nitric (70%)-perchloric acid (70%) solution in individual 11-mL borosilicate vials following protocols described in DeWitte *et al.* (2014), who suggested that use of perchloric acid helped remove the greasy tissue fraction during digestion. The vials were covered with convex clock glass dishes, and tissues were left to digest overnight. The digestive solution inside the glass vials was then diluted with type I ultrapure water, and heated (>80 C) for 10 minutes. The digestive solution was diluted a second time with type I ultrapure water and heated to the same temperature for the same duration. While acid digestion is reported to tarnish common polymers, which can warp their chemical signature (Devriese *et al.* 2015; Enders *et al.* 2017), chemical identification of

polymers was not a goal of this project. Therefore, acid digestion was used to ensure complete dissolution of crustacean stomach contents.

After cooling for thirty minutes, the products of basic and acid digestion were filtered with type I ultrapure water through a 0.7- µm Whatman GF/F glass microfiber filter in a clean air flow hood (model 36204/36205 type A/B3). Particles that withstood acid and basic digestion were photographed using a camera (Canon DS126571) mounted on a stereomicroscope (Meiji Techno) under various magnifications (12 x to 50 x). These particles were then subjected to the 'hot-needle', or 'burn' test to determine if they were plastic. Upon being probed with a hot needle, plastic fragments, films, and beads stick to the needle, and the needle leaves a burn mark or slight charring on the plastic. In the case of fibers, these plastics are repelled by the needle, begin to curl up, and in some cases melt (Devriese *et al.* 2015; Karlsson *et al.* 2017; Lusher *et al.* 2017). In contrast, chitinous material, which can be visually confused with plastic, did not exhibit any sign of charring or melting when probed with a hot needle. Images of particles that were proven to be plastic particles were uploaded into the free software *ImageJ* (Schneider *et al.* 2012) for analysis of dimensions.

Microplastics removed from the digestive tracts of crustaceans and fishes were categorized with a modified version of the Standardized Size and Color Sorting (SCS) System to provide a breakdown of microplastics based on their size, color, appearance, and quanitity (Crawford and Quinn, 2017). The modified version of the SCS was different from the standard SCS because polymer codes and the mini-microplastics category were excluded. The SCS effectively categorizes plastic based on size and appearance in a stepwise approach. Step 1 categorizes plastic particles based on size. Macroplastics are particles greater than 25 mm along their longest dimensions, mesoplastics are particles between 5 mm and 25 mm along their longest dimensions, and microplastics are particles ranging in size from 1 µm to less than 5 mm along their longest dimension. Step 2 categorizes plastic morphologically, as a bead, fiber, film, foam, or fragment. Step 3 and 4 categorizes plastic by color and quantity respectively.

Data Analysis

Vertical migration

Due to substantial differences between Common Water and Loop Current Origin Water (Johnston *et al.* in press), only samples collected from Common Water stations were analyzed

because temperature is thought to be an important environmental stimulus for feeding and may impact migration patterns. Data from the ONSAP and DEEPEND sampling (Burdett *et al.* 2017; R. Milligan, Pers. Comm.) as well as published data on nocturnal and diurnal distributions of micronektonic crustaceans and fishes were used (Donaldson 1975; Roe, 1984; Hopkins *et al.* 1994) to classify taxa as migrators or non-migrators. Individuals from migratory taxa were classified as having migrated if caught between depths of 0-600 m at night or as having refrained from migrating if caught at depths greater than 600 m at night (with some exceptions described in Results).

Stomach Fullness and Percentages of Empty Stomachs

After classifiying individuals from migratory taxa as migrators or non migrators, stomach fullness levels (0-5) of migrating and non-migrating individuals were compared using a Chi-square frequency analysis, Fisher's exact test, or an extension of Fisher's exact test known as the Freeman-Halton exact test based on the data meeting the assumptions of each test (Freeman and Halton, 1951). The key assumption that must be met to use chi-square analysis is that no more than 20% of the count data to be analyzed can be less than 5. If the sample size was less than 5, Fisher's exact test (2 x 2 contingency table) or Freeman-Halton's exact test (any contingency table larger than 2 x 2) was used to get an exact p-value rather than an approximation given by the standard chi-square test. Only an approximation of significance can be generated using a chi-square test because the sampling distribution is calculated using a theoretical chi-square distribution. Therefore, an 'exact' test was used if more than 20% of the count data had less than 5 replicates.

Intraspecific (e.g. *Acanthephyra purpurea*, *Systellaspis debilis*) and intrafamily (Benthesicymidae vs. Oplophoridae) comparisons were made for crustaceans and fishes. However, the only time that fishes were compared with crustaceans was at the assemblage level. An additional comparison of stomach fullness of non-migrating individuals of migratory taxa and non-migratory taxa was conducted using a Freeman-Halton exact test. The percentage of empty stomachs was compared between depths of 600-1500 m was statistically compared with Chi-square analysis.

Microplastics

Percentage of Microplastic Ingestion

The percentage of plastic ingestion for each species was calculated as the number of individuals containing plastic/total number of individuals of that species – this calculation was done separately for Common Water and Loop Current Origin Water. In addition, plastic ingestion was quantified separately for crustaceans and fishes for each depth range and station. The percentage of plastic ingestion between water classifications and depth bins and number of individuals that ingested plastic based on their type of migration pattern (migratory or non-migratory taxa) was compared using Chi-square frequency analysis or Fisher's exact test, and the average number of plastics ingested at each sampled station was mapped using ArcMap 10.3 (ESRI, 2015) to serve as a descriptive aid for occurrences of ingestion.

Body Size

To assess the impact or lack thereof of body size on microplastic ingestion, empirical cumulative distribution functions (ecdf) of standard (fishes) and carapace (crustaceans) length for individuals that did and did not ingest plastic were plotted using the statistical software R. These one-dimensional distributions were compared using a non-parametric two-sample Kolmogorov-Smirnov test because a Shapiro-Wilk normality test demonstrated that length data for crustaceans and fishes were not normally distributed. The ecdf is a step function that increases by 1/n at each of the n data points. At any value of the ecdf, a specified experimentally measured standard or carapace length is the fraction of observations of the experimentally measured lengths that are less than or equal to the specified value, with a total probability of '1'.

Results

Stomach Fullness and Vertical Migrations

Most micronektonic crustacean and fish stomach tissues were used for both studies - estimates of stomach fullness and presence or absence of microplastics. However, the euphausiids *Nematobrachion boopis* and *Thysanopoda acutifrons* were excluded from these analyses because they were not dissected individually before inclusion in bulk digestion for the microplastics portion of this thesis. Furthermore, several species of crustaceans and fishes did not have sufficient numbers of migrating and non-migrating individuals for intraspecific

comparisons of stomach fullness. Thus, for the crustaceans, only individuals of *Acanthephyra purpurea, Gennadas capensis, Gennadas valens, Sergia splendens, Stylopandalus richardi, and Systellaspis* debilis were used for intraspecific stomach fullness comparisons between migrators and non-migrators and for the fishes, only individuals of *Benthosema suborbitale* and *Lampanyctus alatus* were used for intraspecific stomach fullness comparisons between migrators and non-migrators. In addition, no stomach fullness estimates were made on crustaceans or fishes collected from the Straits of Florida because the low number of individuals in each species precluded their inclusion in the stomach fullness studies.

The stomach fullness values of 823 individuals from 24 species and seven families of crustaceans and fishes were analyzed. Out of all samples processed, no individuals qualified as a '5' (full) on the stomach fullness scale, and a majority of individuals had partially full stomachs (1-3). Of the 12-crustacean species processed, seven taxa were vertical migrators, whereas five were non-migrators (Table 3); seven of the 12-fish species were vertical migrators while the other five were not (Table 4) (Donaldson, 1975; Roe, 1984; Hopkins *et al.* 1989; Hopkins *et al.* 1994; Burdett *et al.* 2017). The migratory species assemblage migrates into the epipelagic and must pass through the upper mesopelagial (200-600 m) to forage nocturnally. Therefore, individuals of known migratory taxa that were captured between 0-600 m depth at night were animals that underwent a nocturnal ascent, whereas individuals of known migratory taxa that were netted between depths 600-1500 m at night refrained from migrating. However, a substantial portion of the *Benthosema suborbitale* population was captured between depths of 200-600 m during the day (R. Milligan, pers. comm.), and approximately 30% of the *Stylopandalus richardi* assemblage was found at depths of 500 m during the day (Hopkins *et al.* 1994). Therefore, for both of these species, only individuals caught between depths 0-200 m at night were classified as having undergone a nocturnal ascent. Lastly, while there are some *Systellaspis debilis* individuals found at shallower depths during the day, the bulk of the population (~90%) was found at depths greater than 600 m during the day (Hopkins *et al.* 1994; Burdett *et al.* 2017), so individuals of this species that were caught between depths of 0-600 m at night were considered migrators. Animals were classified as being strong-, weak-, or non-migrators based on the rationale provided by Burdett *et al.* (2017). Strong migratory species were those that had greater than 50% of the individuals migrating, weak migratory species 15-50%, or non-migrators <15%.

Table 3. Crustacean species utilized for estimates of stomach fullness.   NVM = non-vertical migrators. SVM = strong vertical migrator.

Species	Migratory Behavior	# of Individuals	Average Carapace Length ± SD (mm)
Benthesicymidae			
Bentheogennema intermedia	NVM	38	10.2 ± 2.81
Gennadas capensis	SVM	60	8.10 ± 1.55
Gennadas valens	SVM	65	8.47 ± 2.60
Oplophoridae			
Acanthephyra acutifrons	NVM	36	9.61 ± 7.66
Acanthephyra curtirostris	NVM	40	11.6 ± 4.00
Acanthephyra purpurea	SVM	62	8.42 ± 3.69
Acanthephyra stylorostratis	NVM	44	8.02 ± 2.56
Notostomus gibbosus	NVM	18	16.7 ± 13.49
Systellaspis debilis	SVM	72	8.34 ± 3.59
Pandalidae			
Stylopandalus richardi	SVM	49	7.5 ± 1.53
Sergestidae			
Sergia splendens	SVM	57	7.8 ± 2.10
Sergia tenuiremis	SVM	15	17.2 ± 2.8
Total		**556**	

Table 4. Fish species utilized for estimates of stomach fullness. NVM = non-vertical migrators. SVM = strong vertical migrator.

Species	Migratory Behavior	# of Individuals	Average Standard Length ± SD (mm)
Gonastomatidae			
Cyclothone acclinidens	NVM	15	27.7 ± 1.44
Cyclothone obscura	NVM	15	39.1 ± 5.01
Cyclothone pallida	SVM	15	35 ± 5.90
Myctophidae			
Benthosema suborbitale	SVM	57	19 ± 5.56
Ceratoscopelus warmingii	SVM	16	56.1 ± 5.76
Lampanyctus alatus	SVM	64	36.4 ± 6.39
Lampanyctus lineatus	SVM	7	61.2 ± 15.8
Lepidophanes guentheri	SVM	18	35.3 ± 9.60
Notolychnus valdiviae	SVM	22	16.8 ± 1.27

Sternoptychidae

Argyropelecus hemigymnus	SVM	8	13.5 ± 2.4
Sternoptyx diaphana	NVM	27	11.7 ± 3.51
Sternoptyx pseudobscura	NVM	3	14.1 ± 1.38
	Total	**267**	

Stomach Fullness Analyses

When grouping all migratory crustacean species together (*Acanthephyra purpurea, Gennadas capensis, G. valens, Sergia splendens, Sergia tenuiremis, Stylopandalus richardi, Systellaspsis debilis*), individuals that undertook the nocturnal ascent had a higher percentage of empty stomachs than individuals that refrained from migrating, but this difference was not statistically significant (p = 0.0017, Chi-square, Table 5A). When grouping all migratory fish species (*Argyropelecus hemigymnus, Benthosema suborbitale, Ceratoscopelus warmingii, Lampanyctus alatus, L. lineatus, Lepidophanes guentheri, Notolychnus valdiviae*) together, individuals that underwent the nocturnal ascent had a higher percentage of empty stomachs than individuals that refrained from migrating and stayed at depth, although these differences were not statistically significant (p = 0.0174, Fisher's Exact, Table 5B).

Table 5. Percentages of crustaceans (A) and fishes (B) at each level of stomach fullness for migrating and non-migrating individuals of migratory taxa.

A

	Crustaceans	
GFI	**Migrators (n = 247)**	**Non-Migrator (n = 154)**
0	23.08%	12.34%
1	54.25%	56.49%
2	15.38%	20.78%
3	6.07%	8.50%
4	1.21%	1.95%
5	0.00%	0.00%

B

	Fishes	
GFI	**Migrators (n = 87)**	**Non-Migrator (n = 95)**

0	10.26%	4.21%
1	38.46%	50.53%
2	19.23%	30.53%
3	3.85%	9.47%
4	7.69%	5.26%
5	0.00%	0.00%

When examining trends within individual species, species-specific differences were apparent. Amongst the migrating benthesicymid crustaceans, higher percentages of empty stomachs were present in the non-migrating individuals of *Gennadas capensis* and *Gennadas valens*, although these differences were not statistically significant for *G. capensis* or *G. valens* (Fisher's Exact, $p = 0.4921$ and Fisher's exact, $p = 0.0566$, respectively – Table 6). Furthermore, no migrators of either species were found to have empty stomachs. In contrast, vertically migrating caridean *Acanthephyra purpurea* and *Stylopandalus richardi* individuals had significantly more empty stomachs than non-migrators (Fisher's Exact, $p = 0.0012$ and Fisher's Exact, $p = 0.0083$ respectively – Table 6). The same trend was observed for *Systellaspis debilis* and *Sergia splendens* individuals, although these differences were not statistically significant (Table 6).

Table 6. The percentage of migrating and non-migrating crustaceans at each level of the stomach fullness (0 – 5). ** indicates statistical significance.

Species	Stomach Fullness Index (0 – 5)	Migrators	Non-Migrators
Acanthephyra purpurea (Oplophoridae)	0	50.0%**	10.0%
	1	36.4%	57.5%
	2	9.1%	17.5%
	3	4.5%	10.0%
	4	0.0%	5.0%
	5	NA	NA
Gennadas capensis (Benthesicymidae)	0	0 %	6.5%
	1	69.0%	51.6%
	2	27.6%	29.0%
	3	3.5%	9.7%
	4	0.0%	3.2%

	5	NA	NA
Gennadas valens **(Benthesicymidae)**	0	0.0%	14.3%
	1	50.0%	62.9%
	2	20.0%	14.3%
	3	23.3%	8.6%
	4	6.7%	0.0%
	5	NA	NA
Sergia splendens **(Sergestidae)**	0	27.8%	19.0%
	1	63.9%	61.9%
	2	8.3%	19.0%
	3	0.0%	0.0%
	4	0.0%	0.0%
	5	NA	NA
Stylopandalus richardi **(Pandalidae)**	0	45.45%**	6.3%
	1	45.45%	56.3%
	2	9.09%	31.3%
	3	0.0%	6.3%
	4	0%	0.0%
	5	NA	NA
Systellaspis debilis **(Oplophoridae)**	0	23.8%	14.3%
	1	55.6%	42.9%
	2	15.9%	21.4%
	3	4.8%	21.4%
	4	0.0%	0.0%
	5	NA	NA

Amongst the myctophid fishes, vertically migrating Lampanyctus alatus individuals exhibited a significantly higher percentage of empty stomachs relative to non-migrating conspecifics (Fisher's exact, p = 0.0013, Table 7). Conversely, for Benthosema suborbitale, more empty stomachs were observed in non-migrators, although this difference was not statistically significant (Fisher's exact, p = 1, Table 7).

Table 7. The percentages of migrating and non-migrating fishes at each level of stomach fullness (0-5). ** indicates statistical significance.

Species	Stomach Fullness Index (0 – 5)	Migrator	Non-Migrator
Benthosema suborbitale	0	0.0%	2.4%
	1	66.7%	61.9%
	2	20.0%	28.6%
	3	6.7%	4.8%
	4	6.7%	2.4%
	5	NA	NA
Lampanyctus alatus	0	27.00%**	0.00%
	1	57.70%	56.00%
	2	15.30%	31.00%
	3	0.00%	11.00%
	4	0.00%	2.00%
	5	NA	NA

Percentages of Non-Migrators for Meg Skansi and DEEPEND

Due to the four-to-six-year gap between the *Meg Skansi* and DEEPEND cruises, data from the *Meg Skansi* (2011) cruises (Table 8) were analyzed with respect to the DEEPEND (2015-2017) cruises (Table 9). Of the six crustacean species for which there were enough data to make this comparison, four of these species (*Gennadas valens, Sergia splendens, Stylopandalus richardi, Systellaspis debilis*) had a significantly higher percentage of non-migrating individuals during *Meg Skansi* cruises relative to DEEPEND (Chi-Square, p = 0.0053, p = 0.0007, p = 0.0225, p = 0.0009, respectively, Tables 8 and 9). Intraspecific comparisons were not made for migratory fish species between cruises because the Oceanic Ecology Lab is analyzing those data.

Table 8. Percentage of non-migrating individuals of migratory crustacean taxa (MS7-MS8).

Species	Total Individuals	Non-Migrators	Percentage of Non-Migrators
Acanthephyra purpurea	963	226	23.5%
Gennadas capensis	328	133	40.5%
Gennadas valens	3420	1111	32.5%
Sergia splendens	1300	297	22.8%
Stylopandalus richardi	1066	160	15.0%
Systellaspis debilis	579	80	13.8%

Table 9. Percentage of non-migrating individuals of migratory crustacean taxa (DP01-DP05).

Species	Total Individuals	Non-Migrators	Percentage of Non-Migrators
Acanthephyra purpurea	123	32	26.0%
Gennadas capensis	184	74	40.2%
Gennadas valens	891	246	27.6%
Sergia splendens	362	53	14.6%
Stylopandalus richardi	140	11	7.9%
Systellaspis debilis	196	10	5.1%

In addition to comparing crustacean stomach fullness levels between migrating and non-migrating individuals of migratory taxa, stomach fullness levels of non-migratory taxa were compared with non-migrating individuals of migratory taxa by combining all cruises. Both non-migrating individuals of migratory taxa and non-migratory taxa exhibited similar percentages at each level of stomach fullness, and no statistical difference was observed (Freeman-Halton, $p = 0.783$, Table 10). The same comparisons were made for fishes, except *Cyclothone* spp. and *Sternoptyx* spp. were compared separately with migratory taxa, as differences in feeding periodicity were apparent between these genera. Non-migrating individuals of migratory fish taxa had significantly fuller stomachs than *Cyclothone* spp. (Freeman-Halton, $p = 0.00001$). However, there was no difference in the percentage of empty stomachs between non-migrating individuals of migratory taxa and *Sternoptyx* spp. (Fisher's Exact, $p = 0.571$), although *Sternoptyx* individuals had no empty stomachs and increasingly fuller stomachs, with most possessing stomach fullness levels of '4'.

Table 10. Percentages of crustacean stomach fullness levels in non-migrating individuals of migratory taxa and non-migratory taxa.

Non-Migrating Individuals of Migratory Taxa (n = 154)	Non-Migratory Taxa (n = 115)	SFI
12.34%	14.78%	0
56.49%	51.30%	1
20.78%	21.74%	2
8.50%	7.83%	3
1.95%	4.35%	4
NA	NA	5

Table 11. Percentages of fish stomach fullness levels in non-migrating individuals of migratory taxa and non-migratory taxa.

Non-Migrating Individuals of Migratory Taxa (n = 95)	Non-Migratory *Cyclothone* spp. (n = 45)	Non-Migratory *Sternoptyx* spp. (n = 30)	SFI
4.21%	60.0%	0.00%	0
50.53%	33.3%	3.33%	1
30.53%	6.7%	16.67%	2
9.47%	0.00%	26.67%	3
5.26%	0.00%	53.33%	4
NA	NA	NA	5

Comparisons of Empty Stomachs with Depth with Notes on Temporal Influences

To assess the extent of feeding at depth, the percentage of empty stomachs was quantified for all non-migratory crustacean and fish taxa. For both crustaceans (*Meg Skansi* and DEEPEND samples) and fishes (*Meg Skansi*), there was an increasing percentage of empty stomachs with depth below 600 m, with a 14.6% and 12% increase in empty stomachs for crustaceans and fishes, respectively, between the meso- (600-1000 m) and bathypelagial (1000 - 1200 m), and these differences were statistically significant (Chi-square, p = 0.004, p = 0.00001).

Temporal comparisons for fish species between *Meg Skansi* and DEEPEND cruises with depth were not possible due to the limited sample size of fishes available from DEEPEND trawls for the present study. For mesopelagic non-migratory crustacean taxa (*Acanthephyra curtirostris*, *Acanthephyra stylorostratis, Bentheogennema intermedia*), there were no

differences between the percentages of empty stomachs between *Meg Skansi* and DEEPEND cruises, although percentages were higher for *A. curtirostris* and *B. intermedia* for DEEPEND (Chi-square, p = 0.678, Fisher's Exact, p = 1, Chi-square, p = 0.937, respectively) (Table 12). Further comparison of empty stomachs was done strictly using MS7 bathypelagic crustacean samples relative to DEEPEND bathypelagic samples (Table 12). The abundance and biomass of samples collected on *Meg Skansi* 7 (2011) were higher relative to all DEEPEND cruises analyzed in the present study (Sutton *et al.* in prep.; Nichols, 2018). There was a significantly higher percentage of empty stomachs for both *A. curtirostris* and *A. stylorostratis* in the DEEPEND samples compared to the *Meg Skansi 7* samples (Fisher's Exact, p = 0.00001; Chi-square, p = 0.00001, Table 12). The same comparisons made for *B. intermedia* individuals showed there was no statistical difference in the percentage of empty stomachs between sampling schema (Chi-square, p = 0.6654, Table 12).

 Table 12. Temporal comparisons of empty stomachs between *Meg Skansi* and DEEPEND cruises at mesopelagic (600-1000 m) and bathypelagic (1000-15000 m) depths. ** indicates statistical significance.

Species	Mesopelagic (MS7-MS8)	Mesopelagic (DP01-DP05)	Bathypelagic (MS7)	Bathypelagic (DP01-DP05)
Acanthephyra curtirostris	11.70%	16.66%	0.00%	15.80%**
Acanthephyra stylorostratis	0.00%	0.00%	5.88%	44.40%**
Bentheogennema intermedia	6.67%	10.00%	8.70%	9.50%

Microplastic Ingestion Analyses

Contamination Prevention

Visual inspection of the 'control' Whatman GF/F filters placed around the workstation showed only three clear microplastic fibers on a total of 38 control filters. Thus, airborne microplastic contamination was considered to be negligible.

Appraisal of Microplastic Ingestion

Of the crustacean species appraised for microplastic ingestion, 12 species are vertical migrators while five species are non-migrators, whereas for the fishes, 27 species are vertical migrators while five species are not. A total of 637 individuals (315 fishes and 322 crustaceans)

from a combined 44 species and 11 families were assessed for the presence or absence of microplastics (Tables 13-15). In addition, 96 *Thysanopoda acutifrons* individuals were bulk processed but excluded from Table 13 because they were not individually dissected. While both *T. acutifrons* and *Nematobrachion boopis* were not individually dissected, a percentage of individuals containing microplastics was calculated for *N. boopis* because zero microplastics were found after digestion. At least one microplastic particle was found in the digestive tract of 27% and 29% of crustaceans and fishes collected from the GoM respectively, whereas 22% of fishes collected from the Straits of Florida contained microplastics.

Table 13. Crustacean species from the Gulf of Mexico that were analyzed for plastic ingestion. SVM = strong vertical migrator; WVM = weak vertical migrator; NVM = non-vertical migrator.

Species	Migratory Behavior	# of Individuals	Average Carapace Length ± SD (mm)	# of Microplastics Ingested [% individuals]	Feeding Guild
Benthesicymidae					
Bentheogennema intermedia	NVM	15	13.2 ± 2.19	11 [40 %]	Generalist, detritivore
Gennadas capensis	SVM	15	8.6 ± 1.5	13 [47 %]	Generalist, detritivore
Gennadas valens	SVM	21	9.2 ± 2.2	13 [33 %]	Generalist, detritivore
Euphausiidae					
Nematobrachion boopis	WVM	22	NA	0 [0 %]	Omnivore
Oplophoridae					
Acanthephyra acanthitelsonis	WVM	2	18.2 ± 1.13	1 [50 %]	Piscivore
Acanthephyra acutifrons	NVM	15	25.1 ± 11	9 [53 %]	Piscivore
Acanthephyra curtirostris	NVM	16	14.1 ± 4.34	14 [50 %]	Piscivore
Acanthephyra purpurea	SVM	43	10.7 ± 4.71	11 [28 %]	Mixed Zooplanktivore
Acanthephyra stylorostratis	NVM	28	9.3 ± 2.33	11 [21 %]	Piscivore

Notostomus elegans	SVM	7	18.3 ± 6.33	7 [57 %]	Piscivore
Notostomus gibbosus	NVM	15	34.3 ± 10	8 [33 %]	Mixed Zooplanktivore
Systellaspis debilis	SVM	46	9.96 ± 3.34	12 [20 %]	Mixed Zooplanktivore
Pandalidae					
Stylopandalus richardi	SVM	46	7.6 ± 1.9	15 [24 %]	Piscivore
Pasiphaeidae					
Pasiphaea merriami	SVM	4	18.0 ± 3.76	0 [0 %]	Mixed Zooplanktivore
Sergestidae					
Sergia splendens	SVM	12	9.7 ± 2.1	1 [8 %]	Mixed Zooplanktivore
Sergia tenuiremis	SVM	15	17.2 ± 2.8	2 [13 %]	Mixed Zooplanktivore
Total		**322**		**128**	

Table 14. Fish species from the Gulf of Mexico that were analyzed for microplastic ingestion. SVM = strong vertical migrator. NVM = non-vertical migrator.

Species	Migratory Behavior	# of Individuals	Average Standard Length ± SD (mm)	# of Microplastics Ingested [% individuals]	Feeding Guild
Gonastomatidae					
Cyclothone acclinidens	NVM	15	27.7 ± 1.5	2 [13 %]	Mesozooplanktivore
Cyclothone obscura	NVM	15	39.1 ± 5.2	7 [33 %]	Mixed Zooplanktivore
Cyclothone pallida	NVM	15	35.0 ± 6.1	1 [7 %]	Mesozooplanktivore
Sigmops elongatus	SVM	6	39.0 ± 5.2	2 [17 %]	Mixed Zooplanktivore
Myctophidae					
Benthosema suborbitale	SVM	17	24.1 ± 3.4	9 [53 %]	Mixed Zooplanktivore
Ceratoscopelus warmingii	SVM	18	53.8 ± 9.1	7 [19 %]	Generalist

Species					
Diaphus dumerilii	SVM	1	52.9 [NA]	0 [0 %]	Mixed Zooplanktivore
Diaphus lucidus	SVM	5	66.4 ± 13.6	0 [0 %]	Mixed Zooplanktivore
Lampanyctus alatus	SVM	57	37.4 ± 3.7	32 [39 %]	Mixed Zooplanktivore
Lampanyctus lineatus	SVM	18	61.6 ±15.8	6 [18 %]	Mixed Zooplanktivore
Lepidophanes guentheri	SVM	11	35.3 ± 9.9	5[28 %]	Mixed Zooplanktivore
Notolychnus valdiviae	SVM	25	16.8 ± 1.3	5 [12 %]	Mixed Zooplanktivore
Notoscopelus resplendens	SVM	14	35.4 ± 7.3	1 [7 %]	Mixed Zooplanktivore
Sternoptychidae					
Argyropelecus aculeatus	SVM	2	30.5 ± 15.5	0 [0 %]	Generalist
Argyropelecus hemigymnus	SVM	8	13.5 ± 2.4	4 [50 %]	Mixed Zooplanktivore
Sternoptyx diaphana	NVM	27	11.7 ± 3.6	14 [33 %]	Generalist
Sternoptyx pseudobscura	NVM	3	14.1 ± 1.7	0 [0 %]	Generalist
Stomiidae					
Chauliodus sloani	SVM	1	129.0 [NA]	0 [0 %]	Piscivore
Total		**257**		**95**	

Table 15. Fish species from the Straits of Florida that were analyzed for microplastic ingestion. SVM = strong vertical migrator. NVM = non-vertical migrator.

Species	Migratory Behavior	# of Individuals	Average Standard Length ± SD (mm)	# of Microplastics Ingested [% individuals]	Feeding Guild
Gonastomatidae					
Cyclothone pallida	NVM	3	38.3 ± 0.88	0 [0 %]	Mesozooplanktivore
Sigmops elongatus	SVM	13	76.1 ± 29.7	10 [54 %]	Mixed Zooplanktivore
Myctophidae					

Bolinichthys photothorax	SVM	2	25.8 ± 0.63	2 [100 %]	Mixed Zooplanktivore
Ceratoscopelus warmingii	SVM	8	21.5 ± 3.2	1 [13 %]	Generalist
Diaphus brachycephalus	SVM	1	27.2 [NA]	0 [0 %]	Mixed Zooplanktivore
Diaphus dumerili	SVM	2	23.4 ± 3.0	0 [0 %]	Mixed Zooplanktivore
Diaphus spp.	SVM	1	25.3 [NA]	0 [0 %]	NA
Diaphus taaningi	SVM	1	55.1 [NA]	0 [0 %]	Mixed Zooplanktivore
Hygophum taaningi	SVM	3	28.2 ± 6.3	2 [67 %]	Mixed Zooplanktivore
Lampanyctus alatus	SVM	2	34.3 ± 4.1	0 [0 %]	Mixed Zooplanktivore
Lampanyctus lineatus	SVM	2	31.6 ± 13.6	0 [0 %]	Mixed Zooplanktivore
Lampanyctus spp.	SVM	1	37.5 [NA]	2 [100 %]	NA
Lepidophanes guentheri	SVM	10	36.5 ± 4.7	0 [0 %]	Mixed Zooplanktivore
Opisthoproctidae					
Opisthoproctus soleatus	NVM	1	24.6 [NA]	0 [0 %]	Gelatinovore
Sternoptychidae					
Argyropelecus aculeatus	SVM	1	60.2 [NA]	0 [0 %]	Generalist
Argyropelecus hemigymnus	SVM	1	17.8 [NA]	1 [100 %]	Mixed Zooplanktivore
Stomiidae					
Borostomias elucens	NVM	1	132.1 [NA]	0 [0 %]	Piscivore
Chauliodus sloani	SVM	2	65.0 ± 52.6	0 [0 %]	Piscivore
Eustomias brevibarbatus	SVM	1	51.0 [NA]	0 [0 %]	Piscivore
Eustomias richardsoni	SVM	1	34.1 [NA]	0 [0 %]	Piscivore
Leptostomias gladiator	SVM	1	185.1 [NA]	1 [100 %]	Piscivore
Total		**58**		**19**	

Micronekton crustaceans contained a total of 143 plastic particles, whereas 114 plastic particles were found in fishes. All pieces and categories of plastic (beads, fibers, films, fragments – no foams were found) fell into the microplastic category. The composition of ingested microplastics was 59.9% fibers (n = 154), 29.5% fragments (n = 76), 5.8% beads (n = 15), and 4.6% films (n = 12). Crustaceans consumed predominantly fibers (78% fiber; 16% frag; 4% film; 2% bead) while fishes ingested approximately equal percentages of fragments and fibers (46% fiber; 41% frag; 7% film; 6% bead). Examples of some of the different microplastics categories found in the present study are shown in Figure 3. Microplastic particles ranged in size from 0.27 mm to 3.97 mm with an average size of 0.5 mm ± 0.2 mm.
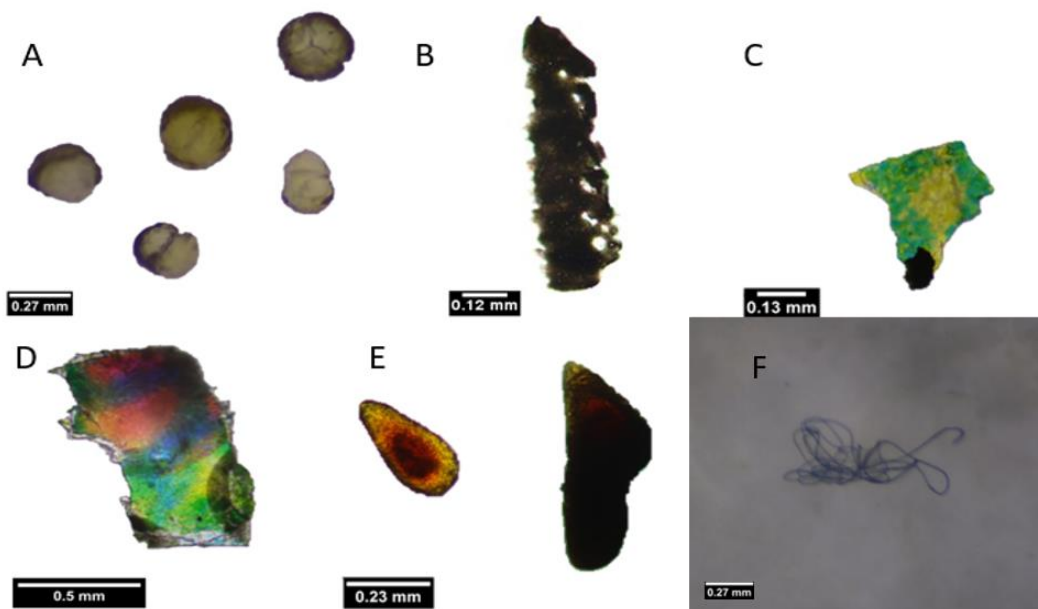
Figure 3. Examples of beads (A), fragments (B, C, D, E), and a ball of fibers (F) ingested by deep-pelagic crustaceans and fishes.

In terms of length, 67.7% of microplastics were less than 1 mm along their longest dimension, and this category was chiefly comprised of fibers. The 1.01-2.00 mm category encompassed 26.8% of microplastics found and was composed mainly of fragments (73.9%). The 2.01-3.00 mm category was comprised of an even split of beads and films, and the least prevalent size classes of microplastics were the larger size classes (3.01- 4.00 mm and 4.01-5.00 mm). The 3.01- 4.00 mm length category was composed of three fragments and one film, and of

the 257 microplastics found in the present study, none fell into the 4.01-5.00 length category (Figure 4).
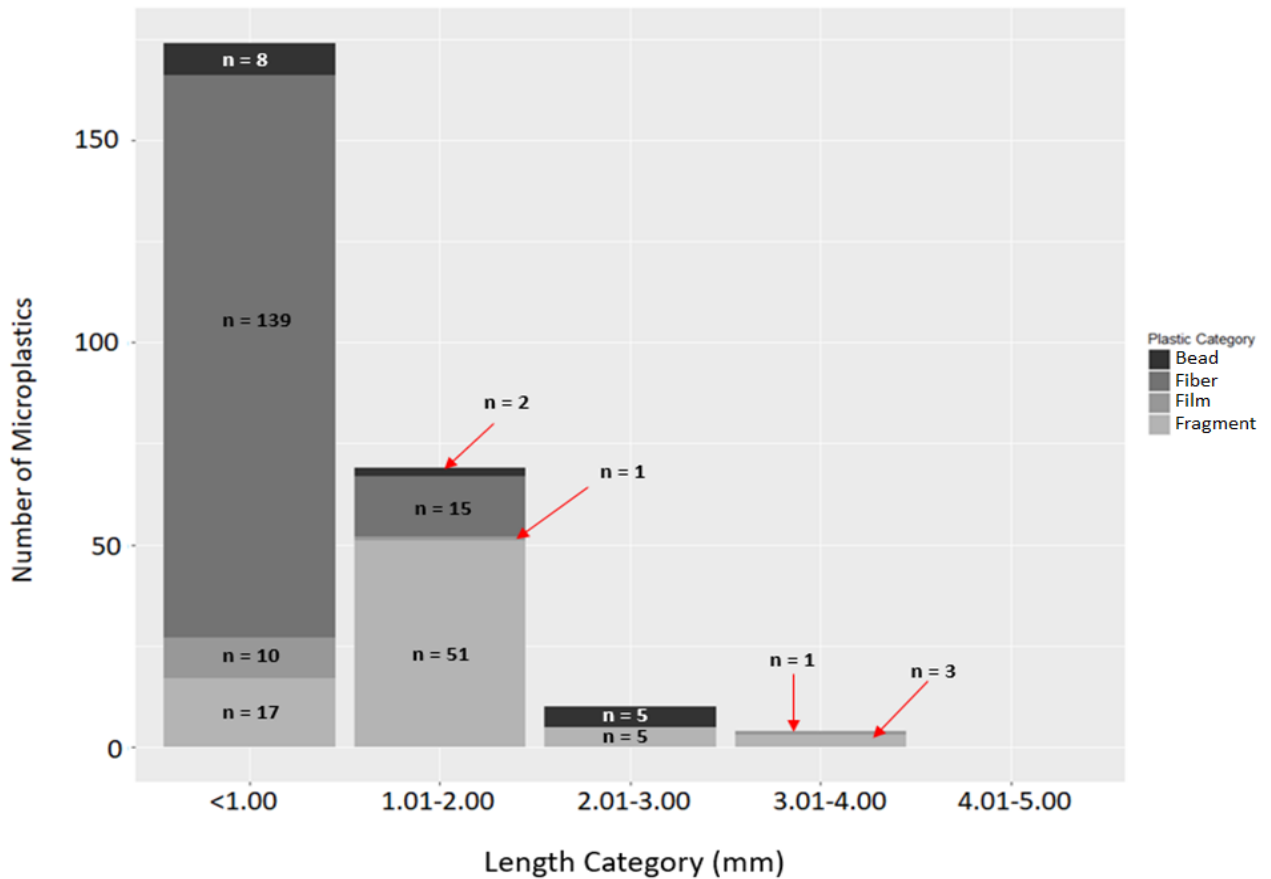
Figure 4. Breakdown of size classes and plastic categories of microplastics removed from digestive tracts of deep-pelagic crustaceans and fishes from the GoM and Straits of Florida.

Color of Microplastics

Microplastics were split into four distinct color categories (Figure 5): blue (37%), red (17%), clear (12%), and black (9%). A fifth category, 'other' (23%) included any color not encompassed by the former four categories, and a sixth category, 'multicolored' was for particles that consisted of two or more colors (5%) (per Crawford and Quinn, 2017). Microfibers were primarily blue, red, or black while fragments exhibited a larger diversity of colors.
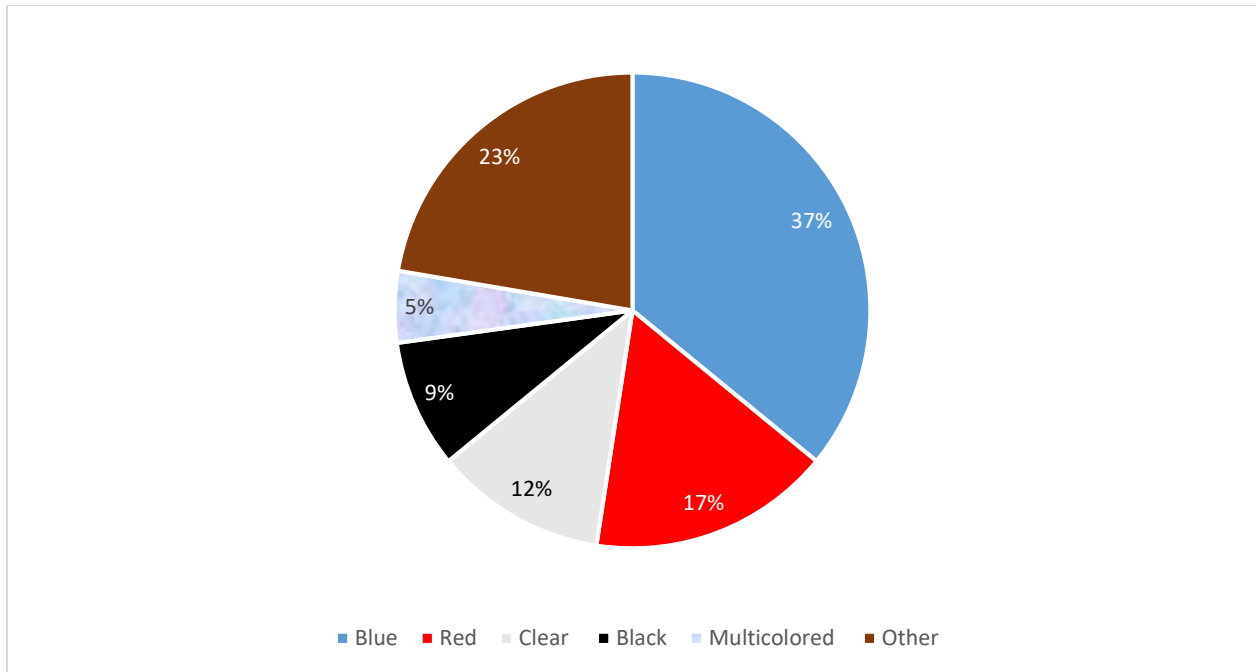
Figure 5. Breakdown of color of microplastics removed from digestive tracts of deep-pelagic crustaceans and fishes from the GoM and Straits of Florida.

Solar Cycle and Plastic Ingestion

When combining all crustacean and fish samples, there was no observed difference between the percentage of crustaceans and fishes collected during the day that had plastic in their digestive tracts (28.9%) and those collected at night (27.5%). When analyzing the crustacean taxa separately from the fishes, the percentage of crustaceans that ingested microplastics was higher during the day (32%) than at night (26%), but this difference was not statistically significant (Chi-square, $p = 0.320$, Figure 6). The opposite was true for the fish – a higher percentage of individuals ingested plastic at night (29%) than during the day (24%), but again, this difference was not statistically significant (Chi-square, $p = 0.235$, Figure 6).
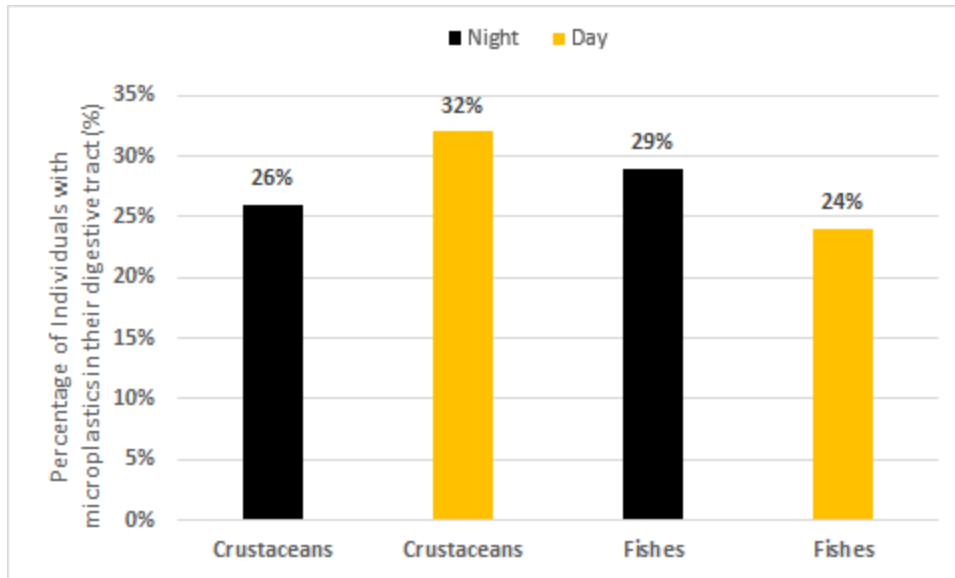
Figure 6. Percentage of crustaceans and fishes that ingested microplastics collected during the day (yellow) and night (black).

Vertical Migration and Plastic Ingestion

Of the 16 crustacean species analyzed (Table 13), nine are vertical migrators while seven are non-vertical migrators. For the fishes (Table 14-15), 22 species are vertical migrators while seven species are non-migrators. Non-migratory taxa in this study mostly dwelled in either the lower meso- or upper bathypelagial or overlapped both zones. Vertically migrating taxa of fishes ingested more microplastics (28%) than non-migratory taxa (23%), but these differences were not statistically significant (Chi-square, p = 0.270, Figure 7). The opposite was true for crustaceans - non-migratory taxa ingested significantly more plastics (37%) than migratory taxa (23%) (Chi-square, p = 0.0120, Figure 7).
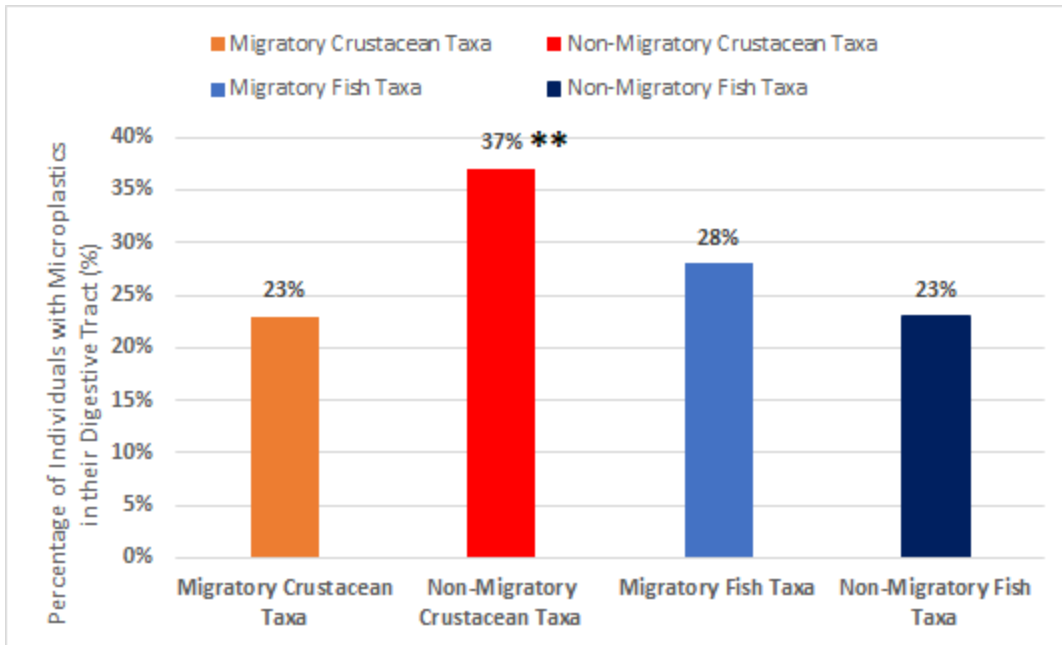
Figure 7. Percentage of migratory and non-migratory crustacean and fish taxa that ingested at least one piece of plastic. (**) denotes statistical significance between crustacean groups.

Microplastic Ingestion by Depth

Grouping crustaceans and fishes together, the highest percentage of individuals containing plastic in their digestive tract was found at depths of 600-1000 m, both during the day and at night. The percentage decreased between depths of 1000-1200 m, then increased again between depths of 1200-1500 m (Figure 8).
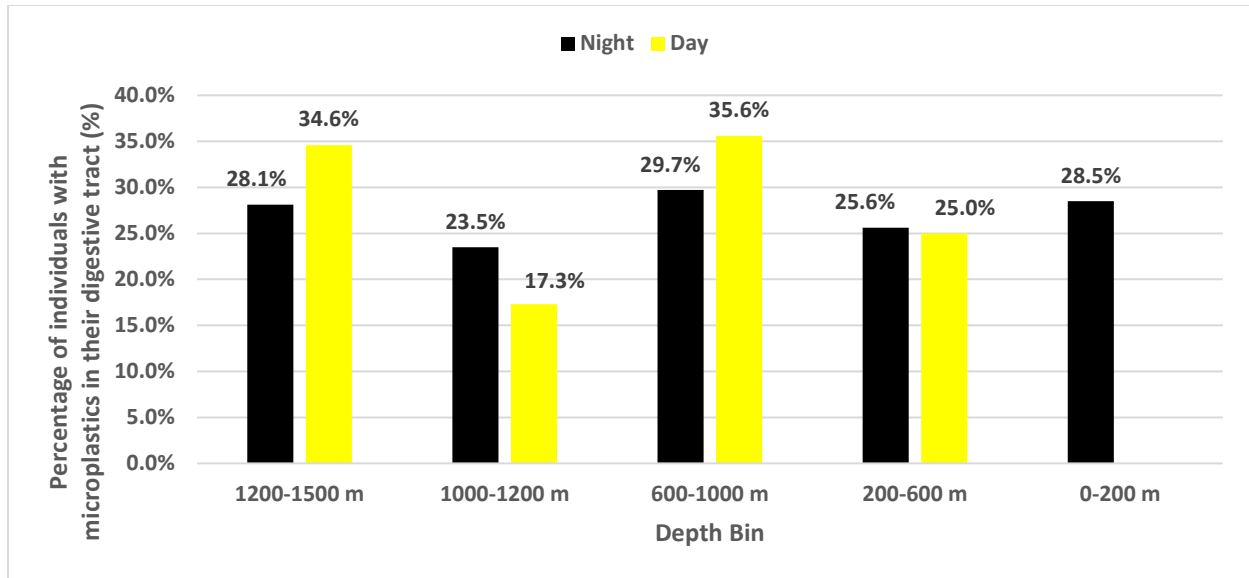
Figure 8. Percentage of individuals (crustaceans + fishes) ingesting microplastics vs. depth.

The percentage of individuals of migratory crustacean taxa that ingested plastic was relatively consistent across all depths (± 5.0% difference), except for depths of 1000-1200 m where migrators had the lowest percentage (8.0%) of individuals containing plastic (Figure 9). The percentage of non-migratory crustacean taxa containing microplastics in their digestive tract was also consistent across all depths (± 2.0% difference), except for depths of 600-1000 m where the non-migratory taxa category had the highest percentage of individuals ingesting microplastics (44.0%). When comparing migratory and non-migratory crustacean taxa, however, there were significant differences in the percentage of individuals containing microplastics for each depth range comparison, with non-migrators consuming more microplastics at all depths where comparisons were possible. The largest difference between migratory and non-migratory taxa was observed at depths of 1000-1200 m, and this depth range had the lowest percentage of individuals ingesting microplastics for both taxa groupings (Figure 9).
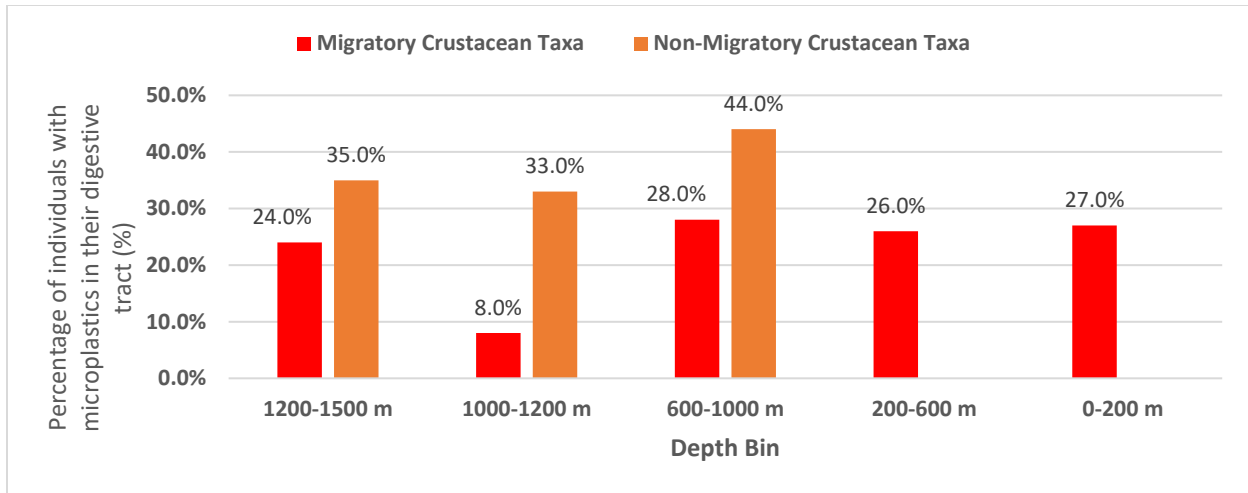
Figure 9. Percentages of individuals from migratory and non-migratory crustacean taxa containing microplastics in their digestive tract by depth.

Unlike the crustaceans, the percentage of individuals of migratory fish taxa that ingested microplastics was inconsistent across depths, with no trend visible (Figure 10). Similar to the migratory crustaceans, migratory fish taxa had the highest percentage of individuals with microplastics in their digestive tract at depths of 600-1000 m and the lowest percentage at depths of 1000-1200 m, while the percentage of non-migratory fish taxa that ingested microplastics did show a trend of increasing plastic ingestion with depth. Like migratory and non-migratory crustacean taxa, collectively, fish taxa exhibited the highest percentages of individuals containing microplastics at depths of 600-1000 m and 1200-1500 m (Figure 10).
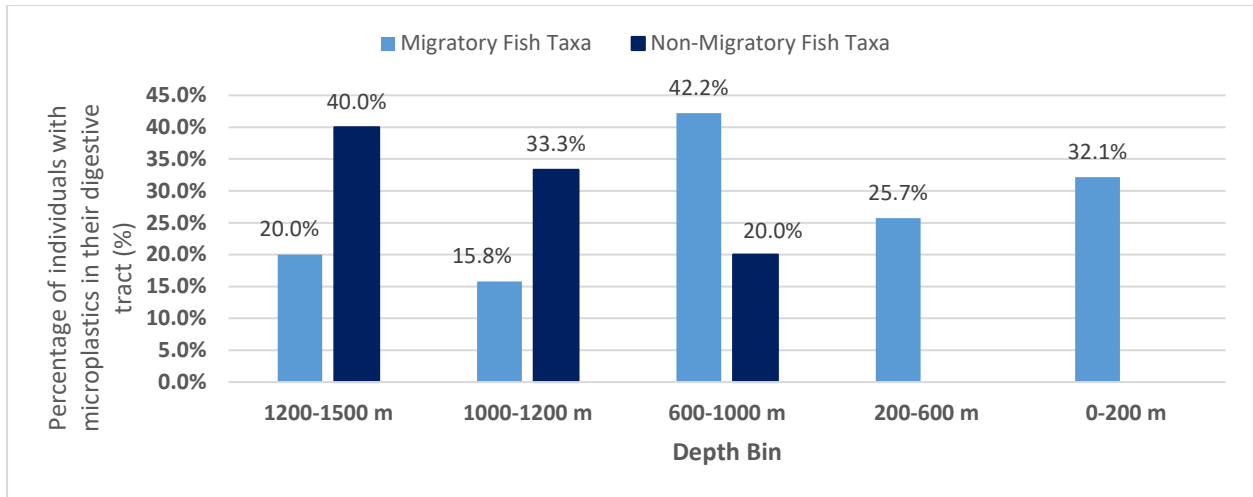
Figure 10. Percentages of individuals from migratory and non-migratory fish taxa containing microplastics in their digestive tract by depth.

Microplastic Ingestion by Location

Higher percentages of individuals containing microplastics were present in the western (30%) portion of our GoM sampling schema relative to the eastern (27%) (Figure 11). Samples from stations at which Loop Current Origin Water was present exhibited a significantly higher (Chi-square, p = 0.001) percentage of individuals (52%) containing microplastics than those collected from Common Water stations (21%). The 'hot spots' for plastic ingestion in Common Water stations were B001, B064, B245, SW1, and SW4 while areas with little to no plastic ingestion were found at B078, B082, and SW10. Notably, the percentage of individuals that ingested at least one of piece of plastic was significantly higher at near-slope stations versus offshore stations (Chi-square, p = 0.023, Figure 11).
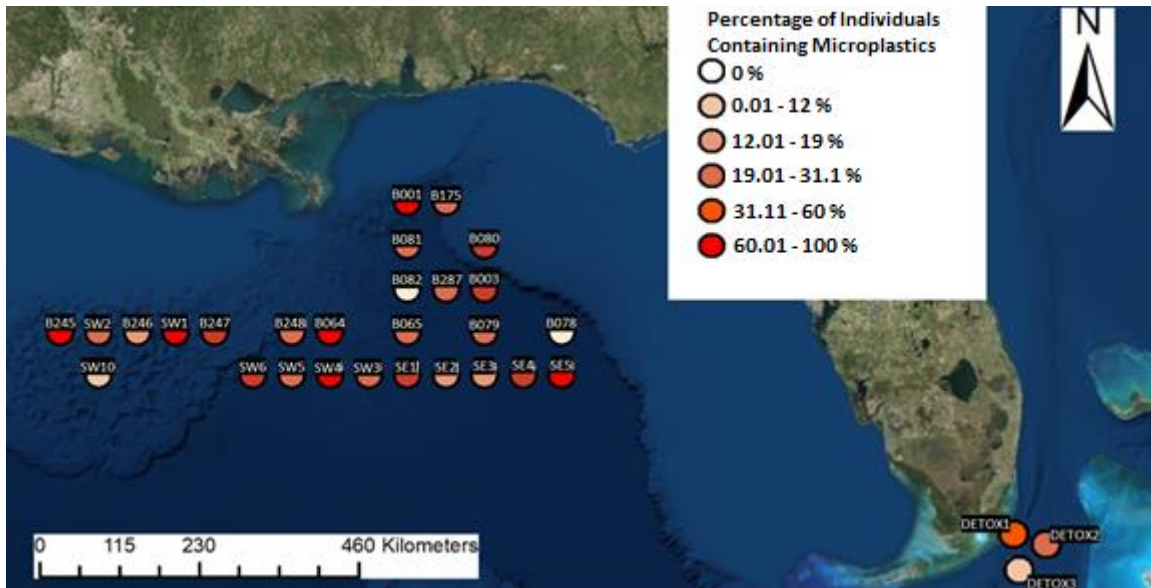
Figure 11. Percentages of crustaceans and fishes containing microplastics in their digestive tract at GoM and Straits of Florida sampling stations.

The Effect of Animal Size on Microplastic Ingestion

Empirical cumulative distribution functions of carapace and standard lengths of crustaceans and fishes that did and did not ingest plastic were compared with one another using a Kolmolgorov-Smirnov test (Figure 12). Two separate Kolmolgorov-Smirnov tests generated p-values of 0.09 and 0.924 for crustaceans and fishes, respectively, which indicated that carapace and standard length were not correlated with microplastic ingestion.

A Distribution Functions of Crustacean Plastic Ingestion

B Distribution Functions of Fish Plastic Ingestion
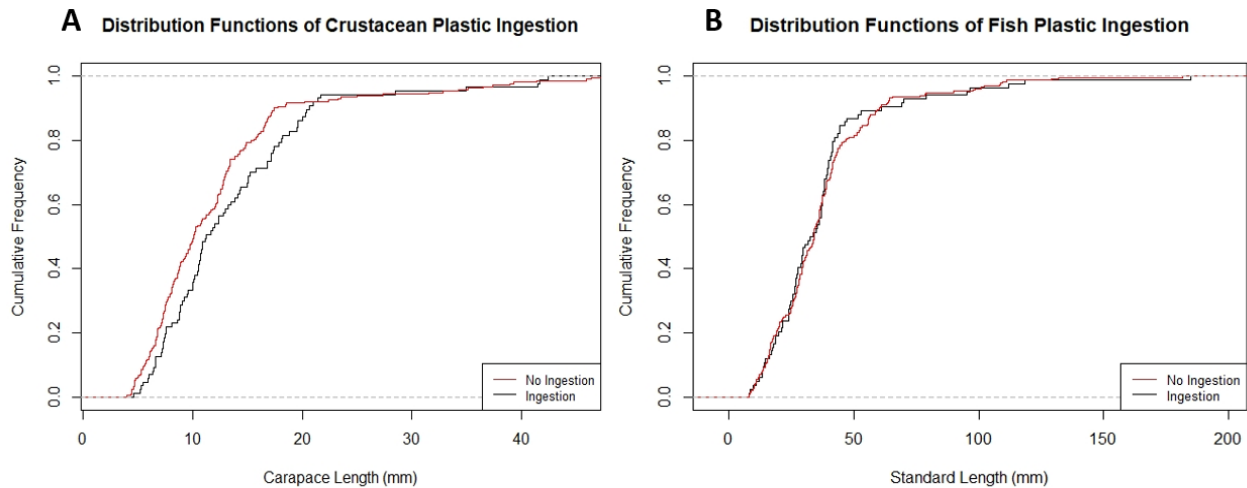
Figure 12. Empirical cumulative distribution functions of carapace length of crustaceans (A) and standard length of fishes (B) that did and did not ingest microplastics.

Discussion

Trawl data from *Meg Skansi* 6-8 and DP01-DP05 support findings from previous acoustics and trawl studies (Sutton *et al.* 1996; Onsrud and Kaartvedt, 1998; Kaartvedt *et al.* 2009; Dypvik *et al.* 2012; Brierley, 2014) that a portion of the migrating-species assemblage refrains from undergoing nocturnal ascents to shallower waters (Tables 8 and 9). Results from this study are the first statistically rigorous verification that state of satiation is correlated with vertical migration patterns, and stomach fullness analysis of several migrating and non-migrating individuals of migratory micronektonic crustacean and fish taxa provide evidence for the longstanding Hunger-Satiation Hypothesis. However, these results would only apply if stomachs take more than one day to completely clear. If prey contents take less than one day to digest completely, then what is in the stomach would have to have been acquired at depth, or during the descent back to deep waters.

Stomach Fullness Analyses

The species whose migration behavior appeared to be associated with their state of satiation were the crustaceans *Acanthephyra purpurea, Sergia splendens, Stylopandalus richardi, Systellaspis debilis*, and one species of fish, *Lampanyctus alatus* (Tables 6 and 7). This supposition is based on the results that there were higher percentages of empty stomachs in

migrating individuals of *A. purpurea, S. richardi, L. alatus, S. splendens,* and *S. debilis* compared to individuals of the same species that remained at depth at night, with the differences being statistically significant for the first three species. The data regarding *S. richardi* support the suggestion by Podeswa (2012) that individuals of this species preferentially feed at night based on data that the stomach fullness index was significantly higher between 12:00 am – 5:30 am than 12:30 pm – 5:30 pm. Similarly, *S. splendens* individuals are known to contain less food in their foreguts during the day than at night, and extensively migrate to shallow-pelagic waters to forage at night (Donaldson, 1975; Flock and Hopkins, 1992). The significantly higher percentage of empty stomachs in *S. splendens* that migrated at night compared to those that stayed at depth supports previous findings of preferential/intensive feeding at night (Foxton and Roe, 1974; Hopkins *et al.* 1989).

The observation that there were significantly fewer empty stomachs in those that stayed at depth suggests that they had partially full stomachs from feeding during the previous night's migration or from feeding at depth during the day. The data presented here cannot be used to determine whether food found in the stomachs during the day results from daytime feeding or was left over from feeding on the previous night's migration, and there is a lack of information about the rate at which these taxa evacuate their digestive tracts, which should be a topic of future studies.

In contrast, the migration behavior of *Gennadas capensis* and *Gennadas valens* individuals was not associated with their state of satiation (Table 6). In these two species, a substantially greater percentage of the assemblage refrained from migrating than all other species analyzed in this study (Tables 8 and 9), with the exception of *Acanthephyra purpurea* during DEEPEND sampling, where equal percentages of *G. valens* (27.6%) and *A. purpurea* (26%) refrained from migrating. Past studies on *Gennadas* suggest that a larger portion of individuals may refrain from undertaking the nocturnal ascent because their preferred prey (consisting largely of metazoans and marine snow) is plentiful, and that individuals are not forced to selectively forage in shallow-pelagic waters (Donaldson, 1975; Heffernan and Hopkins, 1981; Hopkins *et al.* 1994). While a large portion of the assemblage refrained from migrating for both species of *Gennadas* in the present study, similar to what was reported by Heffernan and Hopkins (1981) and Hopkins *et al.* (1994), the stomachs of these non-migrating individuals were

less full compared with the migrating conspecifics (Table 6). If *Gennadas* individuals were refraining from migrating to preferentially feed on marine snow or another prey item at depth to conserve energy, it would be expected that non-migrators would have more full stomachs relative to migrators. However, nothing is known about when these species start their migrations. It is possible that they may start their migrations earlier than other species in this study, given their smaller body size, which is a factor that has been shown to influence crustacean species' migrations in the Gulf of Maine (Frank and Widder, 1997).

Amongst the fish species, the migration pattern of *Benthosema suborbitale* individuals did not appear to be associated with state of satiation as it was for *Lampanyctus alatus* individuals (Table 7). Individuals of *B. suborbitale* and *L. alatus* are both strong vertical migrators and consume the same preferred copepod prey (Genus: *Pleuromamma*) in nearly identical numbers (Hopkins and Baird, 1985), and it is not clear why the migratory behavior of *B. suborbitale* was not correlated with state of satiation. However, *B. suborbitale* may have a faster metabolism than *L. alatus* and an increasing need to migrate because of its active lifestyle, despite having partially full stomachs. Indeed, firm bodied myctophids like *B. suborbitale* with large eyes and silvery scales are thought to be strong vertical migrators that follow isolumes (Barham, 1971), as opposed to less-active myctophids like *L. alatus* with relatively small eyes and less muscular, all black bodies. Thus, non-migrating *L. alatus* may be more ecomorphologically and physiologically suited to refrain from migrating relative to *B. suborbitale* individuals. The daily ration for *L. alatus* individuals has been estimated to be 2 - 4 % of its body weight, and the energy expenditure for vertical migration in this species is estimated to be equal to the energy stored in one 1-mm long adult copepod (Genus: *Pleuromamma*) (Hopkins and Baird, 1985). Moreover, *L. alatus* individuals selectively target copepods with large wax ester reserves (Hopkins and Baird, 1985), perhaps to assist with conservation of energy in colder, deeper waters, and achieving neutral buoyancy at depth. The higher energy expenditure in the more muscular *B. suborbitale* suggests that the daily ration would be higher, although this has not been studied. Another reason for the lack of effect of state of satiation on *B. suborbitale* may be that *B. suborbitale* has a shallower core daytime range (200-600 m) than *L. alatus* (200-1000 m) (R. Milligan, pers. comm.). Therefore, it has to migrate shorter distances to get to shallower waters. For energy conservation purposes, there is likely a desired state of satiation that outweighs the need to invest energy in vertically

migrations, and this is likely related to the distance that must be traveled to reach desired prey, which may explain why a greater percentage of *L. alatus* individuals refrain from migrating.

Crustacean gut fullness comparisons between non-migrating individuals of migratory taxa and individuals of non-migratory taxa were statistically similar (Table 10). This result may be attributed to varied food availability with depth and different metabolic rates between migratory and non-migratory taxa. Migratory crustacean taxa that refrained from undergoing the nocturnal ascent may have been previously exposed to higher food concentrations in shallower waters during the previous night's migration, whereas non-migratory crustacean taxa that generally dwell deeper than migratory taxa are exposed to lower concentrations of food. In addition, non-migratory taxa spend a relatively large amount of time quiescent in cold water with reduced visual predation risk to conserve energy (Childress *et al.* 1980; Seibel and Drazen, 2007), which contrasts with migratory taxa that have higher rates of energy usage and therefore may have higher gut clearance rates (Childress *et al.* 1980). When comparing migratory with non-migratory taxa, even though non-migrating individuals of migratory taxa are exposed to higher food concentrations, the faster gut clearance rate of migratory taxa likely balances with the slow gut clearance rate of non-migratory taxa and therefore may explain the similar amounts of food stored in the gut at the time of sampling.

Non-migratory fish genera (*Cyclothone, Sternoptyx*) were analyzed separately and compared with non-migrating individuals of migratory fish taxa because they potentially have differences in feeding periodicity. In the present study, non-migrating individuals of migratory taxa had a significantly lower percentage of empty stomachs relative to *Cyclothone* individuals (Table 11). This observation likely results from the fact that *Cyclothone* individuals feed aperiodically, as they are known to possess high percentages of empty stomachs and digested prey material exclusively in their intestines 80% of the time (Burghart *et al.* 2010). Our observation of empty *Cyclothone* stomachs supports Burghart *et al.* (2010), as 60% of *Cyclothone* individuals processed during both the day and night in the present study possessed empty stomachs.

Sternoptyx individuals are voracious predators reported to have fresh prey in their stomach and high stomach fullness levels throughout their diel cycle (Carmo *et al.* 2015). This observation also corroborates data from Hopkins and Baird (1985) that *Sternoptyx* is an

opportunistic feeder that may eat large volumes of prey at a time. Data from the present study support the conclusions from the previous studies in that the stomach fullness level with the highest percentage of occurrence was '4', and no *Sternoptyx* individuals possessed empty stomachs (Table 11). In addition, non-migrating individuals of migratory taxa had a higher percentage of empty stomachs relative to *Sternoptyx* individuals, although this difference was not statistically significant. Previous evidence that *Sternoptyx* individuals have three times the daily ration of other species (Carmo *et al.* 2015), coupled with the observation of no individuals possessing empty stomachs in the present study suggests that non-migratory midwater fishes like *Sternoptyx* are important for nutrient flux and should be incorporated into biogeochemical models for more precise estimates.

Non-migratory crustacean taxa from the mesopelagic zone had a significantly lower percentage of empty stomachs relative to those collected in the bathypelagial (Table 12). This observation is likely directly related to the decreasing supply of nutrients and lower biomass with increasing depth, and therefore decreasing abundance of food availability with depth (Vinogradov, 1968). Comparisons of empty stomachs in non-migratory crustacean taxa sampled from the mesopelagial were statistically similar between *Meg Skansi* and DEEPEND samples, although the percentage of empty stomachs was higher during DEEPEND for *Acanthephyra curtirostris* and *Bentheogennema intermedia* (Table 12). Similarly, the three species of bathypelagic crustaceans in the DEEPEND samples (2015-2017) had higher percentages of empty stomachs than the *Meg Skansi* samples (2011), and for two of these, *A. curtirostris and A. stylorostratis,* the differences were statistically significant, while for *B. intermedia*, they were not (Table 12). The MS7 stomach fullness data for *A. curtirostris, A. stylorostratis,* and *B. intermedia* are comparable to data reported by Burghart *et al.* (2010). Interestingly, *B. intermedia,* which did not show a significant decrease in the percentage of empty stomachs between cruises, is also one of the species that appears to specialize in the consumption of marine snow and therefore may not be as impacted by changes in abundance and biomass as the rest of the assemblage, which may rely on other prey items for nutrition.

Microplastic Ingestion Analysis

Microplastic Ingestion by Crustaceans and Fishes

This is the first appraisal of microplastic ingestion for deep-pelagic micronektonic crustaceans and fishes in the GoM and Straits of Florida. Several studies have investigated deep-pelagic microplastic ingestion by fishes (Boerger *et al.* 2010; Davison and Asch, 2011; Choy and Drazen, 2013; Lusher *et al.* 2016; Wieczorek *et al.* 2018) and crustacean species (Taylor *et al.* 2016; Courtene-Jones *et al.* 2017; Bordbar *et al.* 2018; Carreras-Colom *et al.* 2018; Jamieson *et al.* 2019). Data collected in this study demonstrate the presence of microplastics in both crustaceans and fishes. Microplastics were isolated from digestive tracts by use of two digestive protocols; 1) basic digestion of fish stomachs proposed by Enders *et al.* (2017) and 2) acid digestion of crustacean stomachs proposed by (Claessens *et al.* 2013; reviewed by DeWitte *et al.* 2014). Acid digestion is reported to warp the appearance of or destroy common fibers such as polyamide and polyurethane and cause researchers to underestimate the number of plastics being ingested by animals. Given that crustaceans ingested a significantly higher percentage of fibers relative to fishes that were processed via basic digestion, which does not destroy any polymers, the differences of plastic ingestion between crustaceans and fishes may relate to feeding mechanisms. Similarly, the type and number of microplastics ingested by these taxa was impacted by migratory behavior and depth ranges.

Vertical Migration

Vertically migrating taxa of fishes had a higher (although not statistically significant) percentage of individuals ingesting microplastics than non-migratory taxa of fishes, which is consistent with findings from Davison and Asch, (2011) and Lusher *et al.* (2016). In contrast, crustaceans exhibited the opposite behavior, with non-migratory taxa (37%) ingesting significantly more microplastics than vertically-migrating taxa (23%) (Figure 7). This observation supports results from Courtene-Jones *et al.* (2017), Carreras-Colom *et al.* (2018), and Jamieson *et al.* (2019) in that 48%, 39%, and 72% of the non-migratory crustacean species contained microplastics respectively, as opposed to 6% of the migratory species *Plesionika narval* from Bordbar *et al.* (2018). This was unexpected, as plastic concentrations have been modelled to decrease exponentially within the first five meters of water-column depth (Reisser *et al.* 2015), and one would expect that migratory taxa have more access to plastic contamination when foraging in shallower waters. This result is probably linked to the preferred prey of non-migratory taxa (see below).

Microplastic Ingestion by Depth

Previous microplastic ingestion studies have rarely included comparison between migratory and non-migratory crustacean and fish taxa, and those that did include non-migrators were characterized by small sample sizes insufficient for analyses with depth. Therefore, this is the first instance of pelagic non-migratory taxa, that consistently dwell deeper than 600 m, being represented in high volume. The percentage of non-migratory fish taxa containing microplastics in their stomach increased from depths of 600-1500 m (Figure 10), whereas no trend was apparent for non-migratory crustaceans (Figure 9), although non-migratory crustaceans ingested more microplastics at each depth bin relative to migratory species. Furthermore, the percentage of individuals from non-migratory crustacean taxa ingesting microplastics was significantly higher than all other taxa (Figure 7). The difference in levels of microplastic ingestion observed between crustaceans and fishes with depth may indicate that niche portioning, resource competition, vertical migration behavior, and feeding strategy play a role in microplastic ingestion.

Discrete sampling of depth bins yielded two maxima for the percentage of individuals containing microplastics in their digestive tract, at depths of 600-1000 m and 1200-1500 m (Figure 8). This observation may be attributed to seawater density differences and the GoM being a two-layer system, with the upper layer (0-1200 m) of seawater dynamics being controlled by the Loop Current and associated eddies, and the lower layer (>1200 m) being semi-isolated, containing water with residence times of 250 years (Rivas *et al.* 2005). Findings of high percentages of individuals ingesting microplastics at depths of 600-1000 m leads to the possibility that a subsurface plume of plastic may be present at lower thermocline depths (600-1000 m), as suggested by Davison and Asch (2011) and Choy and Drazen (2013) for the North Pacific Gyre. Stratification of microplastic debris likely results from increases in microplastic density from water-logging due to prolonged submergence (Ye and Andrady, 1991), the incorporation of microplastics into marine aggregates (Zhao *et al.* 2017), and biotransformation from bacterioplankton and marine organisms (Zettler *et al.* 2013).

No previous analysis in the GoM has incorporated bathypelagic samples from depths of 1000-1500 m for study of microplastic ingestion, so it is not known if the lower percentage of plastic ingestion at depths of 1000-1200 m vs. depths of 1200-1500 m is specific to some

anomaly in the GoM or is a global phenomenon. The overall decrease in microplastic ingestion at depths of 1000-1200 m (Figure 8) may be attributed to the proximity to the transition depths between the waters of the GoM. Consequently, the seawater density at depths of 1000-1200 m may not be conducive for stratifying microplastics debris that has been biotransformed, as opposed to depths of 1200-1500 m, which contains seawater that is denser, as microplastics are thought to become stratified due to changes in seawater density with depth (T. Mincer, pers. comm.). However, data from the present study do not include depths greater than 1500 m, so it is unclear what rates of microplastic ingestion occur here. Nevertheless, it could be expected that microplastic concentrations are higher below depths of 1500 m, as the only exchange of deep-waters in the GoM occur at the Yucatan Sill (Rivas *et al.* 2005). Therefore, once microplastics enter the semi-isolated layer of the GoM, they could have exceptionally long residence times, and remain bioavailable to non-migratory animals until becoming buried in benthic sediments.

Only one previous study, conducted by Peters *et al.* (2017), quantified microplastic ingestion in coastal GoM fishes. In that study, 42% of coastal fishes ingested at least one microplastic, which is greater than the 27% of GoM fishes that ingested microplastics in the present study. This observation may result from higher microplastics concentrations in coastal GoM waters. While Di Mauro *et al.* (2017) estimated microplastic concentrations in shallow coastal GoM waters, there are no data on concentrations of microplastics in deeper waters of the GoM. The data on the percentage of non-migratory crustacean and fish taxa that ingested microplastics in the present study does not necessarily mean that background microplastic levels may be higher at these depths, as many of these species feed on vertically migrating species that are at depth during the day that may have ingested microplastics during their nocturnal migration. This information is only indicative that microplastic ingestion occurred at each depth range from which non-migratory taxa were sampled. Future studies in the GoM should include analysis of microplastics in seawaters collected from depths of 0-1500 m.

Crustacean Feeding Strategies and Microplastic Ingestion

The data in the current study support previous observations that the type and amount of microplastics ingested is related to feeding strategy and prey preference (Setälä *et al.* 2014; Cole *et al.* 2016; Taylor *et al.* 2016; Digka *et al.* 2018; Renzi *et al.* 2018). The crustaceans analyzed in the present study can be broken down into five feeding guilds: generalists/detritivore,

herbivores, mixed zooplanktivores, omnivores, and piscivores (Foxton and Roe, 1974; Donaldson 1975; Heffernan and Hopkins, 1981; Roe, 1984; Hopkins *et al.* 1994; Burghart *et al.* 2010 (Table 13). *Acanthephyra acanthitelsonis* (piscivore) and *Pasiphaea merriami* (mixed zooplanktivore) are not included due to insufficient sample sizes.

Generalists, Detritivores - Crustaceans

All three species of Benthesicymidae (*Bentheogennema intermedia, Gennadas capensis, G. valens*) had the highest percentage of individuals containing microplastics in their digestive tract (39%) as well as the highest average number of microplastics (1.85 microplastics per animal that ingested plastic) relative to all other taxa and are thought to be habitual consumers of marine snow (Heffernan and Hopkins, 1981; Hopkins, 1994; Burghart *et al.* 2010). These observations support findings of Carreras-Colom *et al.* (2018), who reported that 39% of *Aristeus antennatus* individuals contained microplastics in their digestive tract, as *Aristeus* feed on endobenthic prey. Thus, they are potentially more likely to be exposed to microplastics due to their prey preference and higher concentrations of plastic in sediments resultant from sinking marine snow aggregates. Thus, it is possible that there is an association between the consumption of marine snow and increased microplastic ingestion.

The observation that only 6% of detrivorous *Plesionika narval* individuals ingested microplastics (Bordbar *et al.* 2018) seems to contradict the conclusion that detritivore crustaceans are more prone to microplastic ingestion. However, these *P. narval* samples were collected from the eastern portion of the Mediterranean Sea, whereas *Aristeus antennatus* individuals were collected from the western fraction (Carreras-Colom *et al.* 2018). Therefore, *A. antennatus* and *P. narval* individuals should be collected from the same sampling locale for appropriate comparisons between species, as microplastic concentrations can vary between sampled locations. As feeding mechanisms and prey preference are known to change with locality and food availability (Vinogradov, 1968; Burghart *et al.* 2010), the correlation between detritivory and enhanced microplastics ingestion deserves further study.

Piscivores – Crustaceans

The piscivore feeding guild comprises crustacean species *Acanthephyra acanthitelsonis*, *A. acutifrons, A. curtirostris*, *A. stylorostratis, Notostomus elegans*, and *Stylopandalus richardi.*

Three of these species (*A. acanthitelsonis, N. elegans, S. richardi*) are vertical migrators, and three species are non-migratory (*A. acutifrons, A. curtirostris, A. stylorostratis*) (Hopkins *et al.* 1994; Burdett *et al.* 2017; Nichols, 2018). It should be noted that the non-migratory species are also consumers of marine snow (Hopkins *et al.* 1994). The piscivore feeding guild had the second highest percentage of individuals ingesting microplastics (Table 13), with nearly a third of all individuals containing microplastics. There are no existing data on piscivorous crustaceans and microplastic ingestion for comparison with results in the present study. However, one interesting observation is that the non-migratory piscivorous crustaceans that also incorporate marine snow into their diets, had a higher percentage of individuals containing microplastics as opposed to the migratory piscivore crustaceans that consume marine snow to a lesser extent, or not at all (Hopkins *et al.* 1994; Podeswa, 2012). This supports the data from the generalist crustacean feeding guild that there is an association between consumption of marine snow and microplastic ingestion.

Mixed Zooplanktivores – Crustaceans

The mixed zooplanktivore feeding guild comprised the crustacean species *Acanthephyra purpurea, Notostomus gibbosus, Pasiphaea merriami, Sergia splendens, Sergia tenuiremis,* and *Systellaspis debilis* (Table 13). The only non-migratory species in this feeding guild was *N. gibbosus.* Four of the zooplanktivorous crustacean species (*P. merriami, S. splendens, S. tenuiremis, S. debilis*) had the lowest percentages of individuals containing microplastics in their digestive tract. Two zooplanktivores, *A. purpurea*, which is also a consumer of fishes, and *N. gibbosus*, which is also a consumer of fishes and marine snow (Hopkins *et al.* 1994), had higher percentages of individuals containing microplastics relative to the rest of the mixed zooplanktivore feeding guild. This supports the pattern from the generalist and piscivorous crustaceans that incorporation of detrital matter and fish, respectively, is associated with a higher level of microplastic ingestion.

Herbivory and Omnivory - Crustaceans

Nematobrachion boopis and *Thysanopoda acutifrons* individuals were not dissected individually like the other micronekton in this study, but batch processed due to their small size, to quantify microplastics in the euphausiids. The percentage of *N. boopis* individuals (n = 22) that ingested microplastics was determined to be 0%, as no microplastics were found on the filter

after bulk digestion (Table 13), whereas a percentage of *T. acutifrons* individuals (n = 96) that ingested microplastics could not be determined because 15 microplastics were found on the filter after digestion. Although the data presented in this study are not for individual euphausiids, and the difference in number of microplastics left on the filter after bulk digestion may be due to having approximately four times as many *T. acutifrons* individuals relative to *N. boopis,* it is interesting that zero microplastics were found from bulk digestion of 22 *N. boopis* individuals. In all other crustacean species processed, those with sample sizes greater than seven had ingested at least one microplastic, and the same was true for fish species, with the exception of *Lepidophanes guentheri* sampled from the Straits of Florida. Therefore, the difference in microplastic ingestion between *T. acutifrons,* a known herbivorous species that filters seawater with a basketlike apparatus and *N. boopis*, an actively hunting, omnivorous species with morphological adaptations for capturing prey in the water column, is likely real. This evidence suggests that filter-feeding species may be at increased risk for microplastic ingestion.

Fish Feeding Strategies

In the current study, the deep-sea fishes analyzed could be broken down into five feeding guilds: generalists, mesozooplanktivores, mixed zooplanktivores, piscivores, and gelatinovores (Robison, 1984; Gordon *et al.* 1985; Hopkins and Baird, 1985; Hopkins *et al.* 1996; Sutton *et al.* 1996b; McClain-Counts *et al.* 2017; Sutton *et al.* in prep.) (Table 14-15). There were only enough data to include the following mixed zooplanktivore species in the discussion below: *Argyropelecus hemigymnus*, *Benthosema suborbitale*, *Cyclothone obscura, Lampanyctus alatus*, *Lampanyctus lineatum, Lepidophanes guentheri, Notolychnus valdiviae, Notoscopelus resplendens,* and *Sigmops elongatus.*

Mixed Zooplanktivores - Fishes

The most speciose feeding guild for fishes in this study was the 'mixed mooplanktivores', or those that predominantly consumed copepods. This guild was comprised of fish taxa *Argyropelecus hemigymnus*, *Benthosema suborbitale*, *Cyclothone obscura, Lampanyctus alatus*, *Lampanyctus lineatum, Lepidophanes guentheri, Notolychnus valdiviae, Notoscopelus resplendens,* and *Sigmops elongatus* (<50 mm), with eight species being vertical migrators and one being non-migratory (*Cyclothone*).

In the case of the myctophids *Benthosema suborbitale* and *Lampanyctus alatus*, these fishes primarily consume copepods (Genus: *Pleuromamma*) in nearly identical amounts (Hopkins and Baird, 1985), and ascend to near-surface waters at night to do so. This potentially makes individuals of these two species exemplary vectors for transporting microplastics between shallow and deep-pelagic waters, as 53% of *B. suborbitale* individuals and 39% of *L. alatus* sampled from the GoM contained microplastics (Table 14). The same is likely true for GoM sampled *Lampanyctus lineatus, Lampanyctus guentheri,* and *Notolychnus valdiviae,* as 18%, 28%, and 12% of individuals respectively, ingested microplastics. Given that myctophid fishes make significant contributions to abundance and biomass in pelagic assemblages, serve to transport both nutrients and potentially plastic marine debris, and are crucial trophic intermediates, further study is needed on the rates of microplastic ingestion and egestion in myctophid fishes.

Cyclothone obscura's diet is chiefly comprised of calanoid copepods and ostracods (DeWitt and Cailliett, 1972b; Burghart *et al.* 2010), although *C. obscura* is thought to eat infrequently, as many processed individuals contain empty stomachs (Burghart *et al.* 2010). Similarly, 53.3% of *C. obscura* individuals possessed empty stomachs in the present study. Nevertheless, 33% of these non-migratory fish contained microplastics in their stomach. As stomach contents were not analyzed for species composition in the present study, it is difficult to determine what mechanism contributes to these taxa ingesting microplastics. However, it is thought that *Cyclothone* may consume a large amount of gelatinous material and particulate organic matter (McClain-Counts *et al.* 2017), and the fact that 33% of *C. obscura* individuals ingested microplastics in the GoM may provide evidence for this playing a role in increased plastic ingestion. *C. obscura* is the deepest dwelling species of *Cyclothone* and organisms in the deep-pelagial are increasingly more reliant on marine snow for nutrition in the oligotrophic GoM. This observation coupled with the observation that habitual consumers of marine snow amongst the crustaceans (Benthesicymidae) had the highest percentage of individuals containing microplastics suggests that marine snow may be a vector for microplastic transport and amplification through food webs. Microplastics are known to interact with and become incorporated into marine aggregates. This has been shown to occur in *Mytilus edulis* individuals that selectively target microplastics (<1 mm) but have the ability to egest these particles via faeces, or pseudofaces, which are made bioavailable to coprophagous species. Therefore,

Mytilus edulis individuals in shallower coastal waters may facilitate the transfer of microplastics to deeper waters and into marine food webs. Consequently, that same process of marine snow formation and consumption may proliferate microplastics to previously unaffected depths in the pelagic realm and amplify through food webs.

Polymer Categories and Feeding Strategy

The apparent difference in microplastic categories ingested by crustaceans (78% fiber; 16% frag; 4% film; 2% bead) and fishes (46% fiber; 41% frag; 7% film; 6% bead) also suggests that feeding strategy impacts the type and number of microplastics ingested, as crustaceans consumed a significantly higher percentage of fibers (78%) than all other categories, and the difference between fibers (61 %) and fragments (31 %) ingested by fishes was not significantly different. The results concur with the five prior studies that documented microplastic ingestion by deep-pelagic and deep-sea benthic crustaceans where fibers were also the predominant microplastic category ingested (Taylor *et al.* 2016; Courtene-Jones *et al.* 2017; Bordbar *et al.* 2018; Carreras-Colom *et al.* 2018; Jamieson *et al.* 2019).

With respect to fishes, fibers (46%) and fragments (41%) were consumed in approximately equal numbers. This is in contrast to two previous studies that documented plastic categories in mesopelagic fishes, where fibers were the dominant category – 93% reported by Lusher *et al.* (2016) and 98% reported by Wieczorek *et al.* (2018). It is possible that the composition of plastics being ingested is different because of the different sampling location of the present study (GoM) and the other two studies (North Atlantic Gyre). Lusher *et al.* (2016) and Wieczorek *et al.* (2018) also sampled different target species and exclusively mesopelagic depths, while the current study included bathypelagic depths. Thus, the composition of microplastics ingested at meso- and bathypelagic depths may differ at a given area and between different bodies of water, and the same may be true for each species.

It is not clear why animals consume plastic, but ingestion is thought to occur in fish because they mistake plastic for prey due to the size and shape of a particle, or because of bioluminescent films adhering to plastic (Drazen and Sutton, 2017). Indeed, ingested particles found in planktivorous fishes were similar in size to their prey and were predominantly blue in color in the current study and in an earlier study (Boerger *et al.* 2010). Taylor *et al.* (2016) postulated that microfibers could emulate size classes of marine snow. Thus, it is possible that

the difference in percentages of crustacean and fish individuals containing a certain type and number of microplastics in their digestive tract is related to the prey they consume. For instance, individuals of copepodivorous fish species that were sampled from the GoM, such as *Argyropelecus hemigymnus, Benthosema suborbitale, Cyclothone obscura, Lampanyctus alatus,* and *Lepidophanes guentheri* all had more than 28% of individuals containing microplastics (Table 14), and most fragments consumed by fishes in this study were between 1.01-2.00 mm, which may emulate size classes of preferred adult copepod prey (Figure 4).

Impact of Body Size on Microplastic Ingestion

The accessibility of microplastics at the base of the food web is especially problematic because of the negative effects of plastic ingestion like pseudosatiation (Moore, 2008), decreased reproductive fitness (Cole *et al.* 2013; Sussarellu *et al.* 2016), and transfer of toxins (Mato *et al.* 2001; Teuten *et al.* 2009). Animals at the base of the food web, such as copepods and euphausiids in the epipelagic zone, are known to incorporate plastic in their diets (Cole *et al.* 2013), and are consumed by a diverse variety of metazoans, like the deep-pelagic crustaceans and fishes examined in this study. Results presented here suggest that within-species standard length (fishes) and carapace length (crustaceans) has no effect on microplastic ingestion (Figure 12, Tables 13-15), which is in accordance with findings reported by Davison and Asch (2011), but no previous data exist on what role size may play in microplastic ingestion in crustaceans. Microplastics were found in nearly all size classes of individuals processed, supporting the idea that microplastic ingestion is independent of animal size, at least for micronekton.

Conclusions on Vertical Migration

The trawl data analyzed in this study support previous findings from acoustics and trawl studies that a portion of the migrating-species assemblage refrains from undergoing nocturnal ascents to shallower, more productive waters. The results from stomach fullness analyses provide evidence for the longstanding Hunger-Satiation Hypothesis, as four crustacean and one fish species' migration behaviors were associated with their state of satiation, as indicated by frequency analyses. These results would only apply if stomachs take more than one day to completely clear. If prey contents take less than one day to digest completely, then what is in the stomach would have to have been acquired at depth, or during the descent back to deep waters. Species-specific differences were observed for crustaceans and fishes and for species whose

migration behavior was not associated with their state of satiation. Based on the current study and previous studies from other locales, the biogeochemical impact of vertical migration can be extreme. Therefore, the large portion of global biomass refraining from migrating at night can potentially have similar ecosystem effects, yet because the extent of feeding at depth by micronekton is not well-known, this factor is not included in biogeochemical flux models. Stomach fullness data such as these are critical for providing more precise estimates of nutrient-flux.

Conclusions on Microplastic Ingestion

This is the first study to determine the degree of microplastic ingestion by deep-pelagic biota in the Gulf of Mexico and Straits of Florida. Results from this study demonstrate the presence of microplastics in the digestive tract of deep-pelagic crustaceans and fishes from both regions. The type and number of microplastics ingested varied between crustaceans and fishes, and the extent of microplastic ingestion was impacted by vertical migration behavior, feeding mechanisms, and depth. Similar to previous studies on plastic ingestion, results from the current study suggest the potential for a subsurface plume of plastic at lower thermocline depths (600-1000 m). In contrast to previous investigation, data from the present study suggest there may be a subsurface plume in bathypelagic depths (1200-1500 m). A mechanism that may contribute to formation of these plastic plumes may be passive sinking of marine snow that is interspersed with microplastics. Marine snow also appears to contribute to increased levels of microplastic ingestion in animals that habitually consume it. Based on the previous rationale, it is likely that marine snow is important for the biogeochemical cycling of microplastics. Similarly, given that deep-pelagic micronekton serve as links between shallow and deeper waters and contribute substantially to nutrient flux, they are also likely important for the proliferation of microplastics in the deep sea.

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