8-12-2022

Effects of Net Type on the Quantification of Pelagic Shrimp and Krill in the Gulf of Mexico

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NSUWorks Citation
Eric J. Lee. 2022. *Effects of Net Type on the Quantification of Pelagic Shrimp and Krill in the Gulf of Mexico.* Master's thesis. Nova Southeastern University. Retrieved from NSUWorks, . (97) https://nsuworks.nova.edu/hcas_etd_all/97.

Thesis of
Eric J. Lee

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

August 2022

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NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

Effects of net type on the quantification of pelagic shrimp and krill in the Gulf of Mexico

By

Eric Lee

Submitted to the Faculty of
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ABSTRACT

Trawls are an effective and widely used method for collecting micronekton because they can sample large volumes of sparsely distributed organisms, as well as allow for direct species identification of collected samples. However, net sampling methods are known to be highly variable in terms of design and catchability, and comparisons of deep-sea trawl data from two different types of nets over the same spatial and temporal scale are relatively rare. The current study is unique because it provides such an analysis for micronektonic crustaceans in the Gulf of Mexico (GOM) by comparing the trawling efficacy of a smaller 10 m^2 Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) and an Irish Herring Trawl (165.47 $m^{2)}$) over the same time period and region. This was done by comparing parameters of the crustacean assemblage from samples collected by both nets from December 2010 – September 2011 in region surrounding the *Deepwater Horizon* oil spill in the GOM. This study demonstrated that net type significantly affects the characterization of the standardized abundances (n/m^3), biomass (g/m^3), and carapace/body lengths (mm) of crustacean species from the five dominant taxa analyzed in this study (i.e. Superfamily Oplophoroidea and families Sergestidae, Benthesicymidae, Euphausiidae, and Eucopiidae): the MOCNESS had higher abundances and biomass per trawl, and the IHT had larger specimen sizes and trawled volumes. Overall, this study demonstrates that net type significantly affects our description of the GOM pelagic shrimp and krill assemblage, indicating that generalizability of data from a single net type is limited.

Keywords: Sampling gear comparison, Deep sea, Gulf of Mexico, Micronekton, Euphausiacea, Decapoda, Lophogastrida, *Deepwater Horizon* Oil Spill

INTRODUCTION

The Gulf of Mexico

Our oceans cover about 72% of the Earth's surface and contain approximately 97% of the planet's water (NOAA, 2014). Together, they comprise a vast and diverse habitat, and are vital to all known life forms (Drogin, 2009). Despite the size of this habitat, it is estimated that only about 5% of the Earth's oceans have been explored (NOAA, 2014). The deep sea, which includes depths below 200 m, contains some of the least explored ocean regions (Herring, 2002). In addition to the sea floor, the deep sea is made up of four distinct pelagic (water column) zones: the mesopelagic zone (200-1000 m), the bathypelagic zone (1000-4000 m), the abyssopelagic zone (4000-6000 m), and the hadalpelagic zone, which includes all depths deeper than 6000 m (Fujikura *et al.,* 1999).

The Gulf of Mexico (GOM) includes the epipelagic (0-200 m), mesopelagic, bathypelagic, and abyssopelagic zones, extending to a maximum depth of 4383 m (Turner, 1999; Nipper *et al.*, 2004). It is the world's 9th largest body of water and holds approximately 2,500,000 km^3 of water at any given time (Nipper *et al.*, 2004). The GOM is characterized as being a low latitude oligotrophic environment with high species richness, home to large assemblages of micronektonic organisms, including over 100 known species of pelagic decapod crustaceans (Hopkins and Sutton, 1998; Burghart *et al.*, 2010). Micronekton is a collective term given to pelagic animals with body sizes ranging from 2-20 cm, that can actively swim as opposed to drifting in currents (Sutton, 2013). During the 1980s and early 1990s, studies describing the micronektonic crustaceans in the GOM were conducted, but were relatively limited in spatial variability, as all collections were from a "Standard Station" with an 18 km radius (Hopkins, 1982; Hopkins *et al.*, 1989; Hopkins *et al.*, 1994) using a smaller net called a Tucker Trawl. Further studies describing the crustacean micronekton assemblage in the northeastern GOM were conducted 20 years later at a number of stations in the vicinity of the *Deepwater Horizon* Oil Spill (DWHOS) on micronektonic crustaceans (Burdett *et al.* 2017; Nichols, 2018; Frank *et al.*, 2020; LaSpina, 2021; Hine, 2022) using a 10-m^2 Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) (Burdett *et al.*, 2017; Nichols, 2018 ; Frank *et al.*, 2020; LaSpina, 2021; Hine, 2022). As such, much remains unknown about the GOM micronektonic crustacean assemblages with respect to larger taxa that may be sampled with larger nets.

On the 20th of April 2010, the *Deepwater Horizon* mobile drilling platform exploded and sank in the GOM and was considered the largest marine oil spill in U.S. history (McNutt *et al.*, 2012). A total of 3.19 million barrels of oil spilled into the northeastern GOM over 87 days until the well was capped on July 15, 2010 (Reddy *et al.*, 2011; U.S. District Court, 2015). Even though oil spills only represent a small fraction of total crude oil discharge into the ocean, they can have strong acute and long-term impacts on marine ecosystems depending on their magnitude and environmental context, including effects from the toxicity of their chemical compounds and physical damage (i.e. physical contamination and smothering) (Almeda *et al.*, 2013; Vikebo *et al.*, 2014). In addition, both crude oil and dispersants (e.g. the polycyclic aromatic hydrocarbon 1-methylnaphthalene) can have lethal and sub-lethal impacts on invertebrates, including altered reproduction, feeding, growth, locomotion, and respiration rates (Almeda *et al.*, 2013; Peiffer and Cohen, 2015; Knap *et al.*, 2017). Since no pre-spill data exists for the pelagic GOM assemblage, the new data from this study provided by a large midwater trawl (LMT) will add to the "impacted" dataset provided by MOCNESS studies, against which the post-DWHOS recovery, or lack thereof, of the GOM micronektonic crustacean assemblage can be monitored.

The micronektonic crustacean assemblage in the GOM

Micronektonic crustacean assemblages (defined as a group of species co-occurring in a given area) are major components of pelagic ecosystems (Hopkins *et al*., 1994). They include many pelagic euphausiid and decapod shrimp species, which play important roles in the trophic dynamics of the food web and contribute greatly to the biomass of micronekton in deep-sea communities worldwide (Pearcy and Forss, 1966; Hopkins *et al.*, 1994; Atkinson *et al.*, 2009). Both euphausiid and decapod crustaceans are primarily planktivores, feeding on ichthyoplankton, chaetognaths, copepods, and other smaller crustaceans in the water column (Foxton and Roe, 1974; Omori, 1974; Hopkins, 1982; Roe, 1984; Jayalakshmi *et al.*, 2011). They are in turn preyed upon by cetaceans, cephalopods, and many species of commercially important pelagic fishes (Borodulina, 1972; Hopkins *et al.*, 1994; Jayalakshmi *et al.*, 2011). In addition, many of these pelagic euphausiid and decapod species undertake diel vertical migrations (i.e. nocturnal foraging migrations to the surface from deeper daytime depths), making them important to food webs in multiple pelagic depth zones (e.g. epipelagic and mesopelagic) and over day-night cycles (Foxton, 1972; Chace, 1986).

Based on previous studies, five families of micronektonic crustaceans are particularly abundant and diverse in the GOM: Euphausiidae, Oplophoridae (now split into Acanthephyridae and Oplophoridae), Pandalidae, Sergestidae, and Benthesicymidae (Hopkins *et al.*, 1994; Burghart *et al.*, 2007; Atkinson *et al.*, 2009; Fine, 2016; Burdett *et al.*, 2017). These families contain species that undergo diel vertical migrations and are ecologically important for the reasons stated earlier (Hopkins *et al.*, 1989; Andersen and Sardou, 1992; Burdett *et al.*, 2017, Fine 2016). Burghart *et al.* (2007) used a Tucker Trawl to collect samples of Decapoda, Lophogastrida, and Mysida from the bathypelagic zone in the eastern GOM. They found that the bathypelagic zone was dominated by different species than those found in the mesopelagic zone by Hopkins *et al.* (1989); in the bathypelagic zone, the dominant species from family Oplophoridae were *Acanthephyra stylorostratis* and *Hymenodora glacialis,* while *Acanthephyra purpurea* and *Systellaspis debilis* dominated in the mesopelagic zone, with *A. stylorostratis* thought to be relatively rare prior to that study. These results showed the abundance of micronektonic crustaceans can vary drastically with depth.

Net types and study significance

Trawls are an effective and widely used method for collecting and studying micronekton because they can sample large volumes of water containing sparsely distributed organisms, enable direct species identification of collected samples, and come in a large variety of mouth, mesh, and codend sizes (Heino *et al*, 2011). However, the design and deployment methods of trawl nets vary widely and can affect selectivity, catch efficiency, and quantitative sampling performance (Reeves *et al.*, 1992; Gjøsæter *et al.*, 2000; Ordines *et al.*, 2006; Itaya *et al.*, 2007; Tsai *et al.*, 2009). Pelagic micronektonic organisms that range in size from 2-20 cm are highly diverse, and a single trawl type or mesh size does not collect all types of micronekton equally well (Sutton, 2013). Generally, a trawl's mouth size, which determines the net's ability to cover larger areas and capture fast-swimming organisms, must be traded off against mesh size, which determines the retention of small organisms (Heino *et al.*, 2011), due to the much greater resistance to flow of the smaller mesh sizes.

Heino *et al.* (2011) explored net performance variability by comparing the catchability of three different sized trawls for deep-living nekton in the mid-North Atlantic, and found significant variations in efficiency of these trawls in catching organisms from different taxa (i.e. fishes, cephalopods, decapod crustaceans, and large medusae). They found that a macrozooplankton trawl with a 36 m^2 opening and a 6 mm uniform mesh tended to capture more organisms per towed distance than an "Åkra" medium-sized fish trawl (660 m^2 opening, 22 mm graded mesh) and an "Egersund" large fish trawl (5000 m^2 opening, 50 mm graded mesh), but also that the two larger nets tended to collect much larger individuals. A study by Potter *et al.* (1990) compared the Atlantic cod (*Gadus morhua*) catching efficacy of 10 m^2 MOCNESS against a 51 m^2 International Young Gadoid Pelagic Trawl (IYGPT) with a 150 mm graded mesh, a type of LMT. They found that the IYGPT caught significantly larger individuals than the smaller MOCNESS, both during day and night deployments. Lastly, Judkins *et al.* (2016) found that an LMT collected significantly more cephalopods than a MOCNESS, when both nets were deployed at the same stations.

The 10 m^2 MOCNESS has been used to collect data for several recent studies on GOM crustacean assemblages (Burdett *et al.*, 2017; Fine, 2016; Hine, 2022), and has a uniform 3 mm mesh (Wiebe *et al.*, 1976; Wiebe *et al.*, 1985; Hopkins *et al.*, 1996). Another net used to study pelagic crustaceans in the GOM was a Tucker Trawl (Burghart 2007, 2010), an opening/closing rectangular mid-water trawl with a 9 m^2 opening and a 4 mm mesh. While these two nets have been instrumental in providing data on the GOM crustacean assemblages, they both have relatively small mouth areas and mesh sizes compared to the larger trawls used by Potter (1990) and Heino (2011). Use of these smaller nets could have precluded the capture of rarer, larger, and potentially faster swimming organisms, which the larger LMTs (like the IYGPT mentioned above) are better suited for since their larger mouth and mesh sizes allow for faster towing and filtering larger volumes of water (Potter, 1990).

Study aims

This study aims to broaden our quantitative understanding of the GOM crustacean assemblage by evaluating how using differently sized nets can affect our perception of the assemblage. This study will be the first comparison of the trawling efficacy for crustaceans between two pelagic trawl nets of different size classes (MOCNESS and an LMT) over the same time frame and region in the GOM. To date no studies on the GOM crustacean assemblage have been conducted using an LMT, let alone alongside the more widely used MOCNESS system. As such, the data from this study will provide new information on the abundance and diversity of deep-sea micronektonic crustaceans in the GOM, as well as a rigorous comparative analysis of two different net sampling methods.

METHODS

Sample acquisition

Seven survey cruises were conducted in the northern GOM from December 2010 through September 2011 as part of the NOAA-supported Natural Resource Damage Assessment (NRDA) following the DWHOS. To determine the abundance, composition, and distribution of the offshore micronektonic fauna that were potentially affected by the DWHOS, the Offshore Nekton Sampling and Analysis Program (ONSAP) was established. The ONSAP utilized two research vessels to conduct sampling: the M/V *Meg Skansi* and the NOAA FRV *Pisces*. The current project incorporates specimens collected from both vessels using a 10 m^2 MOCNESS and an IHT, respectively. A summary of the sampling dates and net types utilized by the cruise series for both vessels is in Table 1, with all sampled stations for each net shown in Figures 1 (FRV *Pisces*, IHT) and 2 (M/V *Meg Skansi*, MOCNESS). From these stations, the ones analyzed for the purposes of this study are listed in Table 2.

Table 1. FRV *Pisces* and M/V *Meg Skansi* cruises conducted in the GOM as part of the 2010-2011 ONSAP.

Vessel	Cruise Number	Dates	Net Type*
NOAA FRV *Pisces*	PC8	12/1/10 – 12/20/10	IHT
NOAA FRV *Pisces*	PC9	3/22/11 – 4/11/11	IHT
NOAA FRV *Pisces*	PC10	6/23/11 – 7/13/11	IHT
NOAA FRV *Pisces*	PC12	9/8/11 – 9/27/11	IHT
M/V *Meg Skansi*	MS6	1/25/11 – 4/1/11	MOCNESS
M/V *Meg Skansi*	MS7	4/20/11 – 6/29/11	MOCNESS
M/V *Meg Skansi*	MS8	7/20/11 – 9/29/11	MOCNESS

*IHT = Irish Herring Trawl (type of large midwater trawl), MOCNESS = Multiple Opening and Closing Net and Environmental Sensing System

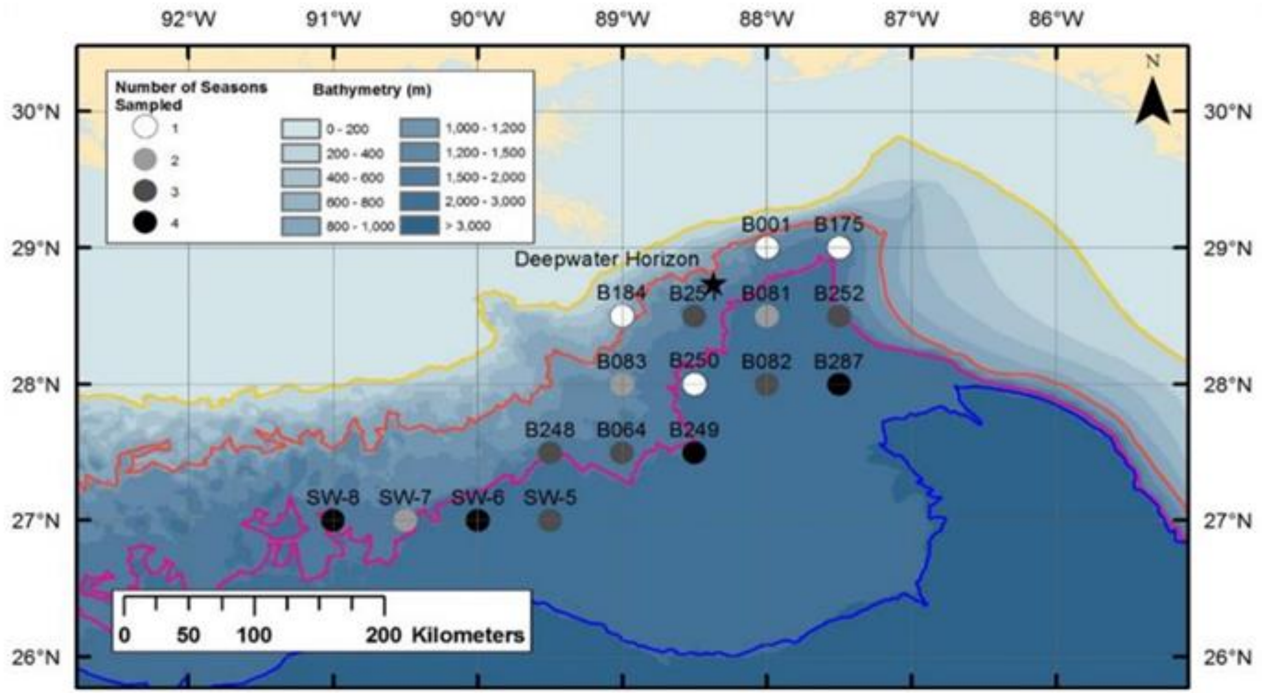


Figure 1. Stations sampled by the NOAA FRV *Pisces* as part of the 2010-2011 ONSAP in the GOM. Stations are colored based on the number of times they were sampled. The orange line indicates the 1000m isobath (adapted from French-McCay *et al.*, 2011).

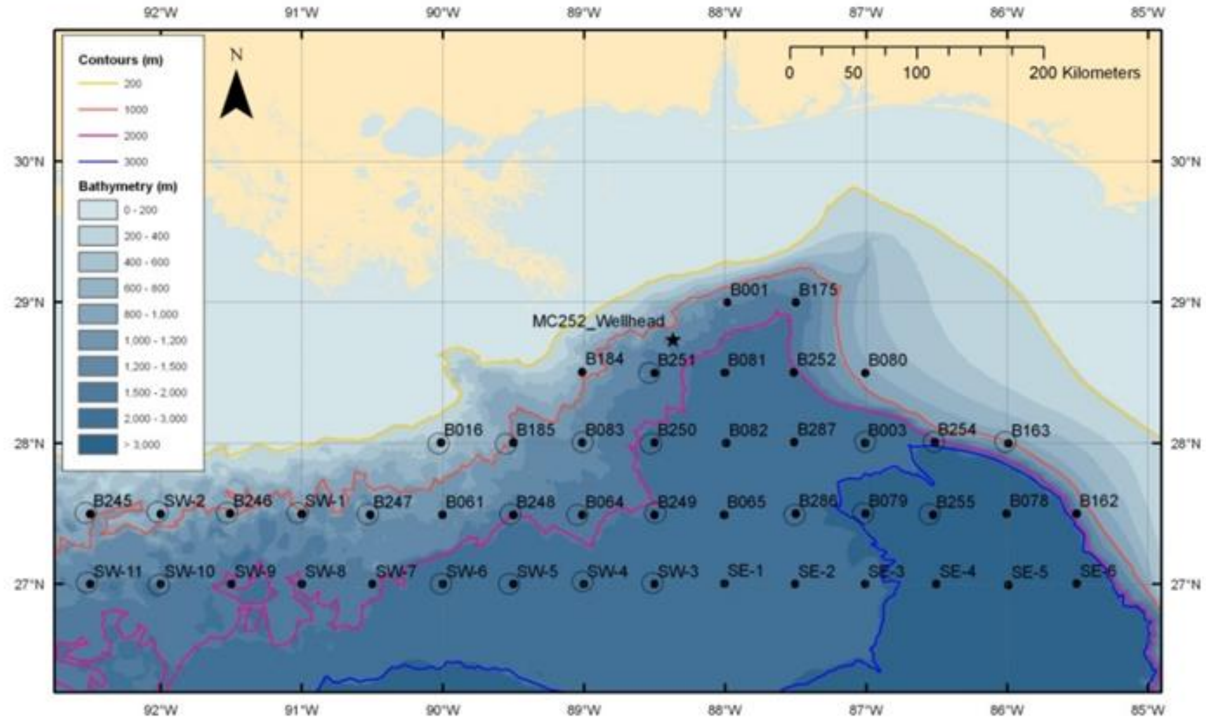


Figure 2. Stations sampled by M/V *Meg Skansi* as part of the 2010-2011 ONSAP in the GOM (adapted from French-McCay *et al.*, 2011).

Table 2. Stations that contributed data for this study from crustaceans collected by MOCNESS and IHT deployments as part of the 2010-2011 ONSAP in the GOM.

MOCNESS	B003	B061	B065	B078	B079	B081	B082	B248	B249
	B255	B286	B287	SE1	SE2	SE3	SE4	SE5	SE6
	SW10	SW11	SW3	SW5	SW6	SW7	SW8	SW9	
IHT	B064	B081	B082	B083	B248	B248			
	B249	B287	SW5	SW6	SW7	SW8			

Sampling conducted aboard the FRV *Pisces* utilized a modified Irish herring trawl (IHT), a type of large midwater trawl (LMT), which has an effective mouth area (EMA) of 165.47 m^2, and a 3.2 m mesh at the mouth which tapered to a 50 mm mesh at the cod end (Novotny, 2018). Since this LMT was a non-closing net that was towed obliquely through the water column, discrete-depth intervals could not be sampled. Samples were collected from December 2010 to September 2011, with each survey lasting approximately three weeks. Each of the 17 stations were sampled obliquely, with "shallow" and "deep" trawls conducted during both day and night (i.e. four trawls per station within 24 h). The "shallow" trawls sampled from the surface to less than 800 m, generally targeting a depth of approximately 700 m. The "deep" trawls exceeded 800 m depth and generally sampled from the surface to 1300 – 1500 m depth. All trawl deployments began at least one hour after sunrise and one hour after sunset to avoid periods of active ascents and descents during vertical migrations. Trawl samples were stored in a 10% formalin solution until they could be analyzed in the Deep-Sea Biology Lab at NSU.

Sampling was also conducted in aboard the M/V *Meg Skansi* using a 10 m^2 MOCNESS with a uniform 3 mm mesh (Burdett *et al.*, 2017). The MOCNESS had six nets and was deployed twice at each station for a duration of 4 – 6 hours per trawl, resulting in one day trawl and one night trawl. Like the FRV *Pisces* deployments, the trawls were timed to avoid periods of active ascent/descent during vertical migrations and were centered around noon and midnight for the day and night trawls respectively. Each net was opened at discrete intervals from 0 – 1500 m according to pelagic depth zones (i.e. epipelagic, mesopelagic, and bathypelagic), as shown in Table 3. Collected specimens were fixed in 10% formalin and also analyzed in the Deep-Sea Biology Lab.

Table 3. Depth intervals sampled by the MOCNESS on the M/V *Meg Skansi*

Net Number	Depth Codes
0	0 – 1500 m
1	1200 – 1500 m
2	1000 – 1200 m
3	600 – 1000 m
4	200 – 600 m
5	0 – 200 m

Sample processing

Individual specimens from each sample were identified to the lowest possible taxonomic level (genera or species) using taxonomic keys and descriptions from Abele and Kim (1986), Baker *et al.*, (1990), Chace (1940), Crosnier & Forest (1973), Dall (2001), Holthius (1993), Kensley (1971), Lunina *et al*. (2019) and Vereshchaka (2009). Carapace length (mid-dorsal distance between the posterior end of the carapace and the posterior eye orbit – Figure 3) was measured for the decapod species and body length was measured for the euphausiid species (Figure 4). The post-formalin/pre-ethanol wet weight of all individuals identified to the same taxonomic level were measured together to the nearest 0.01g. Following analysis, specimens were stored in 50% ethanol.

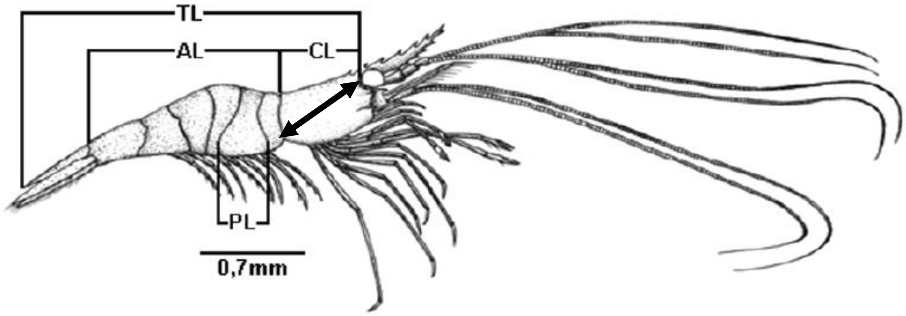


Figure 3. General scheme for shrimp size dimensions for orders Decapoda and Lophogastrida adapted from Paschoal *et al*. (2013); carapace length (CL) was the parameter used in this study.

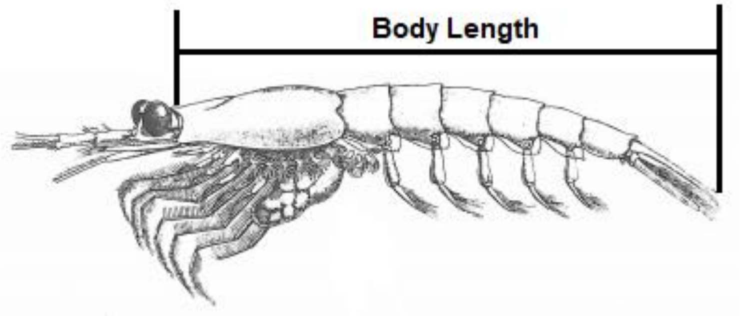


Figure 4. Diagram for shrimp size dimensions for order Euphausiacea, adapted from Baker *et al.* (1990); body length was the parameter used in this study for the Euphausiacea.

STATISTICAL ANALYSIS

Data organization

Cruises were divided into three groups and designated as winter, summer, or fall according to sampling dates (Table 3). This was done to account for any seasonal changes in crustacean abundance (Frank *et al.*, 2020). The absence of a spring category was due to equipment failure experienced on cruise PC9, which resulted in the lack of the filter volumes necessary to standardize sample data for comparison with the spring MS cruises (Table 1). These non-quantitative PC9 trawls along with all trawls from the other cruises that were also missing filter volumes were omitted from analysis. Only stations that were trawled from 0-1500 m (categorized as offshore as opposed to near-slope) were analyzed for both nets (Figure 5), as previous studies showed that the abundance and biomass of the near-slope crustacean assemblage differed significantly from that of offshore stations (Burdett *et al.*, 2017, Frank *et al.*, 2020).

Table 4. Analyzed FRV *Pisces* and M/V *Meg Skansi* cruises organized by season.

Cruise Number	Dates	Net Type	Season Designated
MS6	2/13/11 – 2/20/11	MOCNESS	Winter
PC8	12/1/10 – 12/20/10	IHT	
MS7	6/3/11 – 6/29/11	MOCNESS	Summer
MS8	7/20/11 – 7/31/11	MOCNESS	
PC10	6/23/11 – 7/13/11	IHT	
MS8	9/8/11 – 9/29/11	MOCNESS	Fall
PC12	9/8/11 – 9/27/11	IHT	

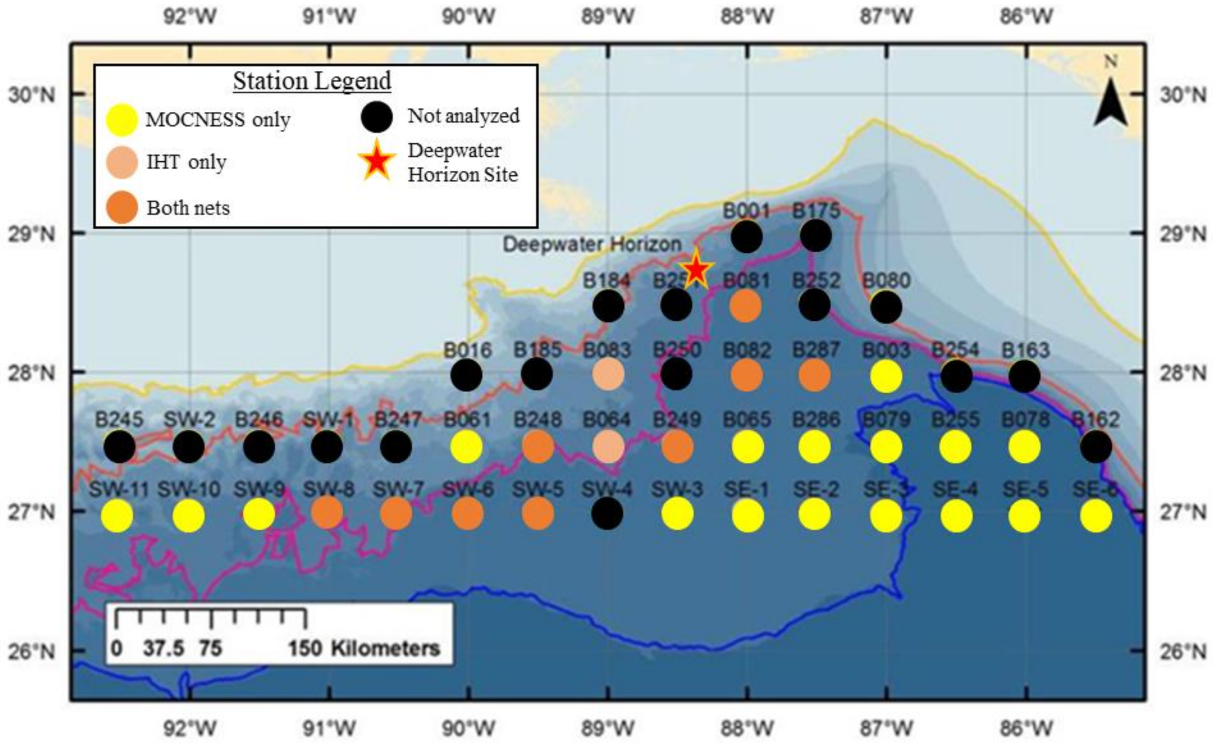


Figure 5. Analyzed offshore stations where specimens were captured by the NOAA FRV *Pisces* (IHT) and M/V *Meg Skansi* (MOCNESS) between December 2010 and September 2011 (adapted from French-McCay *et al.*, 2011). Dot colors indicate which net was deployed at each station. Orange line represents the 1000m isobath.

To compare the abundance, biomass, and length of specimens from MOCNESS samples vs. IHT samples, the data from all trawls at each station sampled by the MOCNESS or IHT during each season were summed and averaged, to compare with similarly combined stations that were sampled by the other net during the same season. As both day and night trawls were conducted during all cruises, combining the data in this manner not only allowed for uniform statistical analysis, but also accounted for potential variations in species data from diel vertical migrations (Burdett *et al.,* 2017; Frank *et al.* 2020; Hine, 2022). For each species (or lowest taxonomic level identified) at a given station, the counts (n) and biomass (g) from all trawls were summed and divided by the total volume filtered (m^3) for those trawls. The mean carapace length (all families except Euphausiidae) or body length (Euphausiidae) was calculated for each species in those trawls.

Data analysis

As the goal of this study was to determine how the type of sampling gear used affects the perception of the overall crustacean assemblage, the combined species data were organized into their respective families before being compared across the two net types. In previous studies, genera now considered to be a part of family Acanthephyridae (i.e. *Acanthephyra, Ephyrina, Hymenodora, Meningodora*, and *Notostomus*) were treated as members of family Oplophoridae along with the genera *Janicella, Oplophorus,* and *Systellaspis* (following Burdett *et al.,* 2017). As such, for this study the superfamily Oplophoroidea was used instead of the family Oplophoridae to keep in line with the latest accepted taxa, while remaining consistent with previous studies. To reflect this, the term "family" and its variants will be italicized from this point on to indicate the inclusion of a superfamily. Rare species, defined as those with n < 10 across all cruises, were omitted from analysis. All statistical analyses were performed using R software (R Core Team, 2017)

To compare captured abundances between the two net types, a GLM was constructed to analyze the data after a Shapiro-Wilk test showed that the data were not normally distributed and remained non-normal after log transformations. *Family* abundances (n) for each station at every season were standardized by using the total volume filtered (m^3) as an offset term in the GLM model. If this analysis determined that net type had a significant effect on abundance, Mann-Whitney Wilcoxon tests were applied to determine if abundance by *family* differed significantly between the two nets and between seasons.

Biomass for each *family* per cubic meter of seawater filtered from each station (g/m^3) was analyzed with respect to the net type and season. The Shapiro-Wilk test indicated that the data were not normally distributed, therefore Mann-Whitney Wilcoxon tests were utilized to determine if there were significant differences between captured biomass for MOCNESS vs. IHT for each season.

To determine if there was a significant difference in specimen sizes captured by MOCNESS vs. IHT, the combined average carapace and body lengths for the species captured at each station were organized into their respective *families* and compared at each season, using net type as a categorical independent variable. Mann-Whitney Wilcoxon tests were applied to determine significance once a

Shapiro-Wilk test showed that the data were not normally distributed. These differences were then further explored by comparing the mean carapace and body lengths of the most abundant (nm^{-3}) species captured by each net.

To compare how net type affects conclusions about the relative abundance and biomass of crustacean *families* in the Gulf of Mexico assemblage, the percentage contributed by each *family* to the total standardized abundance (nm^{-3}) and biomass (gm^{-3}) of crustaceans from the five most abundant *families* (i.e. Oplophoroidea, Sergestidae, Benthesicymidae, Euphausiidae, and Eucopiidae) was calculated for each net type.

RESULTS

Abundance

A total of 64,277 specimens belonging to the *families* Benthesicymidae, Eucopiidae, Euphausiidae, Oplophoroidea, and Sergestidae were collected by the MOCNESS, and 12,414 were collected by the IHT (Table 5). Only the five most abundant *families* captured by each net and season were used for comparison as they made up 94.97% of the total specimens analyzed in this study (Figure 6). After these data were standardized by trawl volume (m^3) and organized into the three seasons (i.e. Winter 2010, Summer 2011, and Fall 2011), a negative-binomial GLM showed that net type was a significant factor related to the differences in crustacean abundance ($P < 0.001$). MOCNESS collected significantly more crustaceans per volume filtered (nm^{-3}) than the IHT for each of the five *families* across all three seasons (Mann-Whitney Wilcoxon, $P < 0.001$) (Figure 7). In terms of each *family*'s contribution to the total abundance (nm^{-3}) of collected specimens, in the IHT Oplophoroidea (29.47%) was the most abundant, followed by Sergestidae (24.86%), Benthesicymidae (27.51%), Eucopiidae (14.36%), and Euphausiidae (3.80%) being the least abundant by far. In contrast, in the MOCNESS samples, the Euphausiidae were most abundant (61.49%), with Benthesicymidae (11.57%) being the next most abundant, followed by the Eucopiidae (9.57%), Sergestidae (9.06%), and Oplophoroidea being the least abundant (8.30%) (Figure 11).

Table 5. Total number of specimens (n) from the five most abundant crustacean *families* collected on FRV *Pisces* and M/V *Meg Skansi* cruises.

"Family"	MOCNESS	IHT
Benthesicymidae	7375	3169
Eucopiidae	6074	1859
Euphausiidae	39675	450
Oplophoroidea	5228	3543
Sergestidae	5925	3393
Total	64277	12414

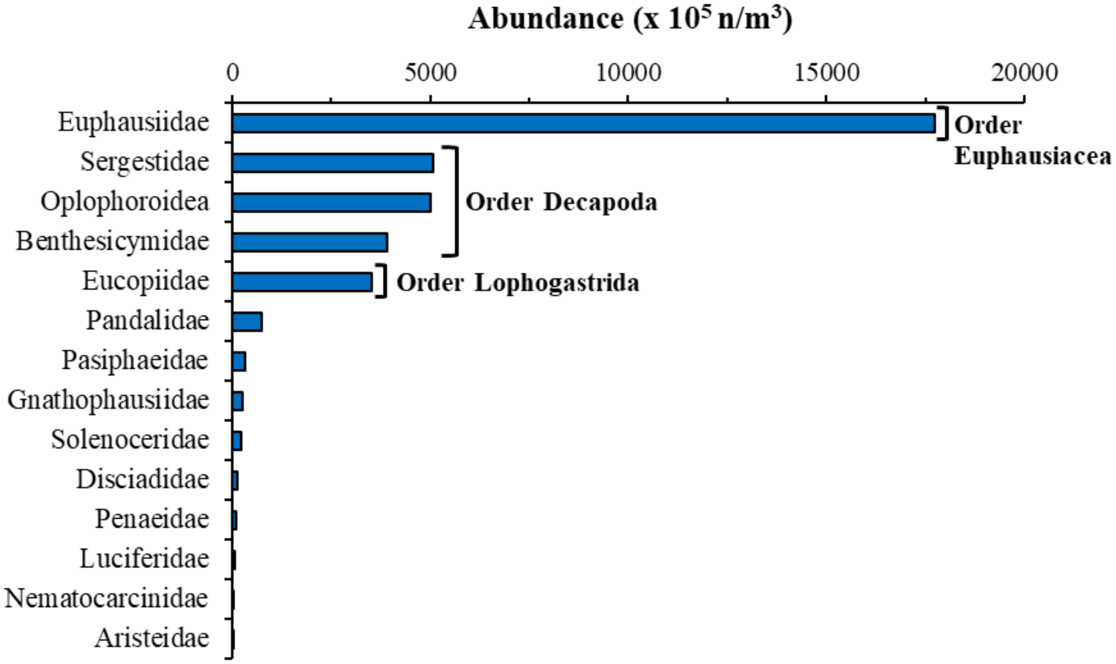


Figure 6. Total abundance (10^5 n/m^3) of crustacean *families* arranged from highest to lowest.

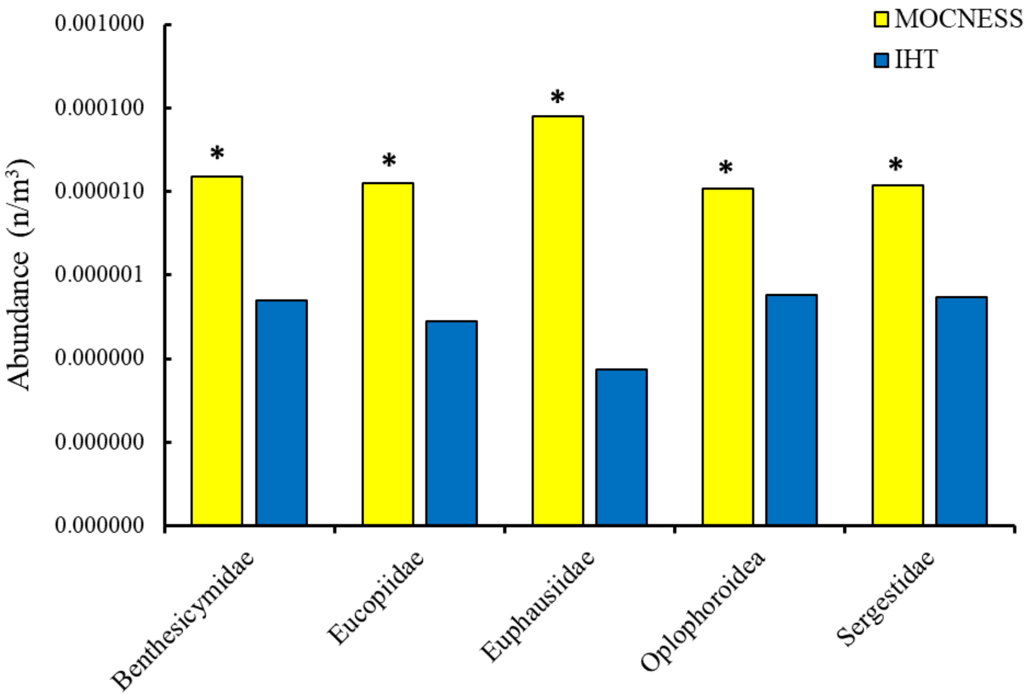


Figure 7. Sampling gear comparison of mean crustacean abundance across all three seasons for the five most abundant *families*. Axis log-transformed for presentability, error bars represent standard error, * represents a significantly higher abundance than the compared net.

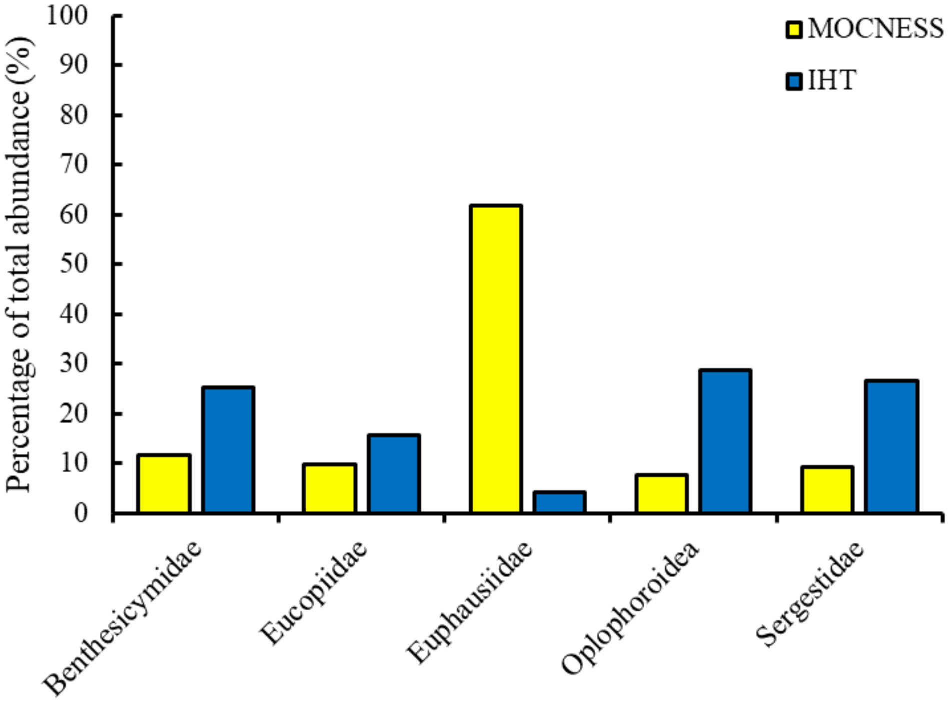


Figure 8. Percent contribution of each of the top five most abundant crustacean *families* to the total standardized abundance (n/m^3) of specimens from these five *families* collected by each net.

Biomass

Like abundance, the overall crustacean biomass collected per trawl and standardized by trawl volume (gm^{-3}) was significantly higher for the MOCNESS than it was for the IHT (Mann-Whitney Wilcoxon, $P < 0.001$), as was the biomass of each individual *family*. These data represent summed samples collected over three seasons (Figure 8). In terms of each *family*'s contribution to the total biomass (gm^{-3}) of collected specimens, the *family* Oplophoroidea had the greatest relative biomass in the IHT samples (69.73%), followed by Sergestidae (19.75%), Benthesicymidae (6.17%), Euphausiidae (2.23%) and Eucopiidae (2.12%) (Figure 12). For the MOCNESS, the order of *family* contribution was almost the same, with the Benthesicymidae coming in second and Sergestidae coming in third, but due to the substantially smaller size of the Oplophoroidea (see below), the percentages were more equal: Oplophoroidea (39.53%), Benthesicymidae (21.23%), Sergestidae (14.91%), Euphausiidae (13.56%), and Eucopiidae (10.77%).

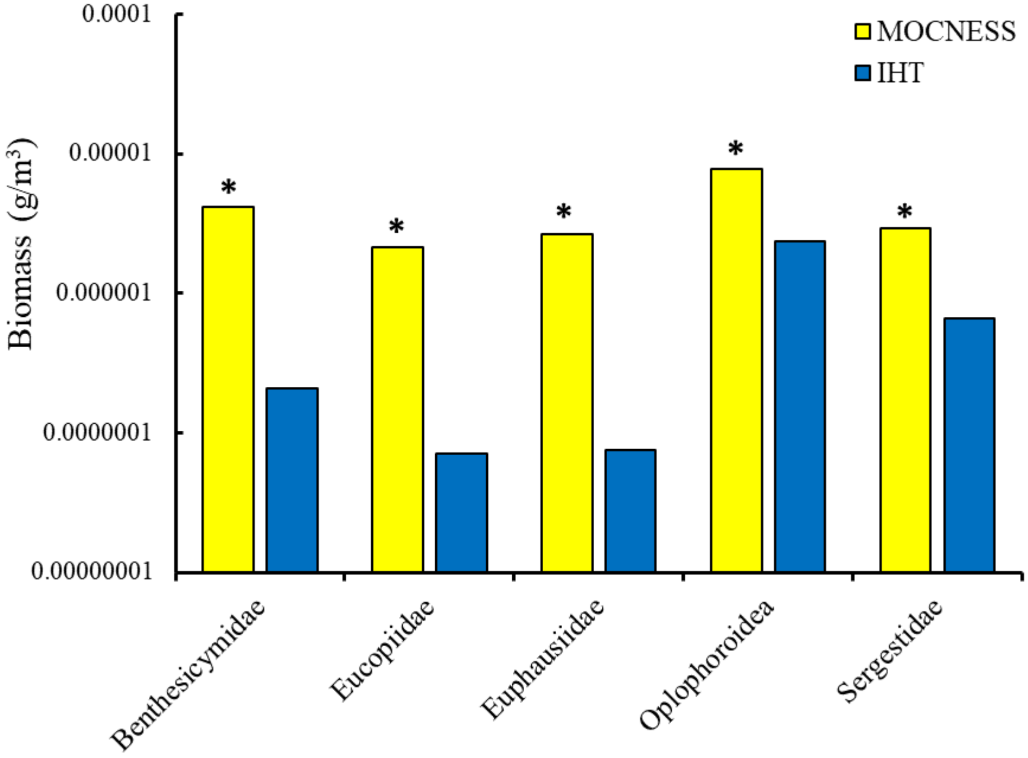


Figure 9. Sampling gear comparison of mean crustacean biomass across all three seasons, for the five most abundant families. Axis log-transformed for presentability, error bars represent standard error, * represents a significantly higher abundance than the compared net.

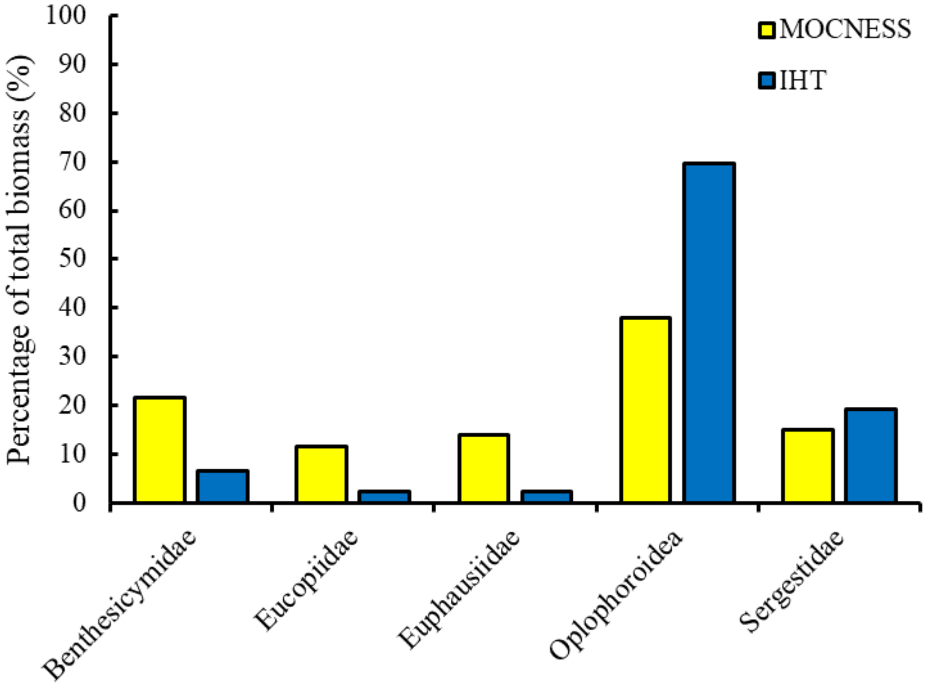


Figure 10. Percent contribution of each of the top five most abundant crustacean *families* to the total standardized biomass (g/m^3) of specimens from these five *families* collected by each net.

Body Size

For body size (mm), only four out of the five most abundant *families* (i.e. Benthesicymidae, Euphausiidae, Oplophoroidea, and Sergestidae) were analyzed, as many IHT specimens from family Eucopiidae were too damaged to measure and not enough data could be collected for a meaningful comparison with the Eucopiidae specimens collected by MOCNESS. Carapace and body lengths (mm) were significantly larger for specimens collected by the IHT compared to those collected by the MOCNESS (Mann-Whitney Wilcoxon, $P < 0.001$), both within each season and overall (Figure 9). A side-by-side comparison of the mean carapace and body lengths of the 10 most abundant euphausiid species and 15 decapod species (Tables 5 and 6) showed differences in abundance and body size between the two nets, with the most abundant IHT species having larger lengths overall than the most abundant MOCNESS species. One species from family Pasiphaeidae (*Parapasiphae sulcatifrons*) was included in Table 6, as it was amongst the most abundant decapods in the IHT, despite Pasiphaeidae not being among the five most abundant crustacean *families* overall.

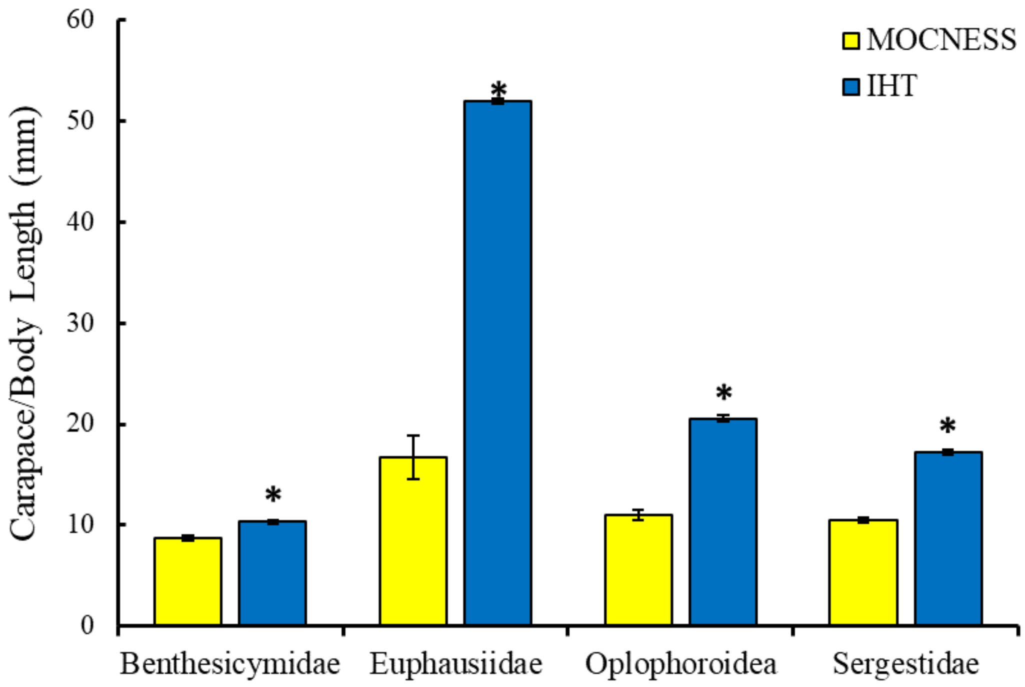


Figure 11. Sampling gear comparison of mean carapace (all *families* except Euphausiidae) and body lengths (Euphausiidae) across all 3 seasons, for the five most abundant *families*. Family Eucopiidae was omitted due to insufficient numbers of measurable specimens. Error bars represent standard error, * represents a significantly higher mean size than the compared net.

Table 6. Mean body lengths of the 10 most abundant euphausiid species/genera, ranked from most to least abundant.

MOCNESS	Family	Abundance ($10^{-3}m^{-3}$)	Mean Body Length (mm)
Nematoscelis atlantica/microps	Euphausiidae	1.53	15.79
Stylocheiron abbreviatum	Euphausiidae	0.60	14.18
Euphausia mutica	Euphausiidae	0.54	12.58
Thysanopoda monocantha	Euphausiidae	0.49	12.47
Thysanopoda obtusifrons/aequalis	Euphausiidae	0.35	15.70
Euphausia gibboides	Euphausiidae	0.33	15.57
Stylocheiron elongatum	Euphausiidae	0.26	13.02
Thysanopoda acutifrons/orientalis	Euphausiidae	0.24	22.24
Thysanopoda tricuspidata	Euphausiidae	0.17	18.06
Nematobrachion boopis	Euphausiidae	0.15	18.91
IHT	Family	Abundance ($10^{-6}m^{-3}$)	Mean Body Length (mm)
Thysanopoda acutifrons/orientalis	Euphausiidae	1.20	39.44
Thysanopoda egregia	Euphausiidae	0.98	55.43
Thysanopoda pectinata	Euphausiidae	0.94	42.73
Thysanopoda tricuspidata	Euphausiidae	0.90	27.09
Thysanopoda cristata	Euphausiidae	0.63	45.56
Thysanopoda cornuta	Euphausiidae	0.54	94.64
Bentheuphausia amblyops	Euphausiidae	0.44	48.82
Nematobrachion sexspinosum	Euphausiidae	0.36	31.15
Euphausia gibboides	Euphausiidae	0.34	17.82
Thysanopoda obtusifrons/aequalis	Euphausiidae	0.31	38.40

Table 7. Mean body lengths of the 15 most abundant decapod species/genera, ranked from most to least abundant.

MOCNESS	*Family*	Abundance ($10^{-4}m^{-3}$)	Mean Carapace Length (mm)
Gennadas valens	Benthesicymidae	3.54	9.53
Janicella spinicauda	Oplophoroidea	1.98	5.21
Sergestes pectinatus	Sergestidae	1.94	6.19
Acanthephyra stylorostratis	Oplophoroidea	1.94	8.59
Sergia splendens	Sergestidae	1.68	8.77
Acanthephyra purpurea	Oplophoroidea	1.52	11.44
Hymenodora gracilis	Oplophoroidea	1.48	7.55
Systellaspis debilis	Oplophoroidea	1.39	11.70
Acanthephyra brevirostris	Oplophoroidea	1.36	5.34
Sergestes edwardsii	Sergestidae	1.26	6.19
Plesionika richardi	Pandalidae	1.21	7.84
Sergestes sargassi	Sergestidae	1.02	6.99
Sergestes vigilax	Sergestidae	0.90	7.31
Sergia regalis	Sergestidae	0.82	14.40
Systellaspis cristata	Oplophoroidea	0.82	6.29

IHT	*Family*	Abundance ($10^{-6}m^{-3}$)	Mean Carapace Length (mm)
Gennadas valens	Benthesicymidae	7.90	10.93
Sergia tenuiremis	Sergestidae	5.44	19.76
Sergia robusta	Sergestidae	3.64	19.42
Oplophorus gracilirostris	Oplophoroidea	3.28	14.12
Bentheogennema intermedia	Benthesicymidae	3.27	13.20
Acanthephyra acutifrons	Oplophoroidea	2.74	34.91
Acanthephyra stylorostratis	Oplophoroidea	2.62	12.00
Sergia regalis	Sergestidae	2.24	19.29
Systellaspis debilis	Oplophoroidea	1.87	13.53
Acanthephyra curtirostris	Oplophoroidea	1.66	16.26
Notostomus gibbosus	Oplophoroidea	1.64	33.12
Parapasiphae sulcatifrons	Pasiphaeidae	1.60	26.69
Gennadas capensis	Benthesicymidae	1.25	10.22
Sergia splendens	Sergestidae	1.10	9.98
Challengerosergia challengeri	Sergestidae	1.09	19.36

Trawl volume

Volumes filtered by all net tows at each station (separated by season) were totaled and averaged across the total number of stations sampled by that net for that season, where it was found the mean trawl volume per station for the IHT was approximately 20-40 times that of the MOCNESS across all compared stations (Figure 10).

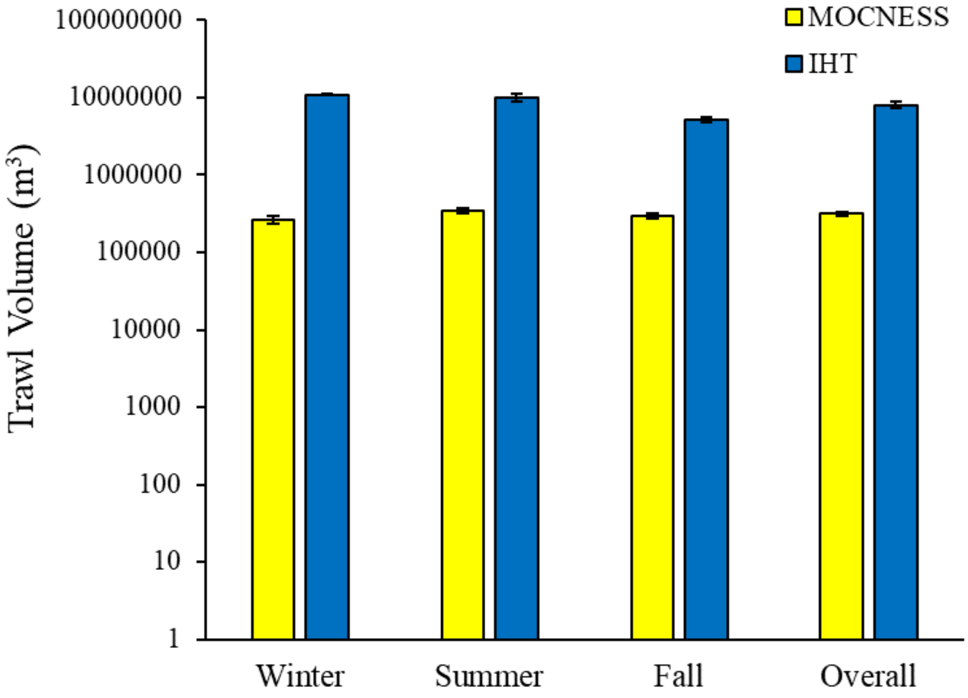


Figure 12. Mean trawl volumes for offshore stations sampled by both gear types from December 2010 to September 2011. Axis log-transformed for presentability, error bars represent standard error.

DISCUSSION

The data from this study build on the work of Heino *et al.* (2011), who observed significant variations in the efficiency of three different sized trawls in catching organisms from different taxa (i.e. fishes, cephalopods, decapods, and large medusae) in the mid-north Atlantic. The nets they used were analogous to the MOCNESS and IHT used in this study, and they found that the small net with a small uniform mesh was more efficient at capturing pelagic decapod crustaceans than the large net with a larger graded mesh. Our results support these findings and demonstrate that the type of net used can have a significant effect on the estimates of abundance, biomass, and size of collected specimens. When the species data from the top five most dominant crustacean *families* - Oplophoroidea, Sergestidae, Benthesicymidae, Euphausiidae, and Eucopiidae (which made up 94.97% of total abundance) was compared between the two gear types, the abundance and biomass of samples collected by the MOCNESS was significantly higher than samples collected by the IHT regardless of season, even though the volume trawled by the IHT was significantly greater. However, the specimens collected with the IHT were significantly larger than those collected by the MOCNESS. These differences in abundance, biomass, and body size may have been due to differences in net characteristics such as the greater retention provided by the 3 mm mesh of the MOCNESS compared to the graded 50 mm mesh of the IHT, as smaller micronektonic (i.e. free swimming from 2-20 cm) organisms would be missed by the larger mesh of the IHT, but the larger mouth of the IHT may have covered an area sufficient to reliably capture crustaceans that were large and strong enough swimmers to evade the MOCNESS, or rarer (e.g. large and/or sparsely distributed individuals) and thus more likely to be captured by a trawl with a larger mouth (i.e. more volume filtered).

Understanding the contributions of individual families to assemblages is important, as pelagic krill and decapod shrimp species play significant roles in pelagic food webs and make substantial contributions to the total biomass in all deep-sea pelagic communities studied so far (Pearcy and Forss 1966, Foxton and Roe, 1974; Roe, 1984; Hopkins et al. 1994). As a result of these significant catch and size differences between the MOCNESS and the IHT samples, the two nets provide different perceptions of the relative dominance (by percentage contribution) of each of the five crustacean *families* in terms of abundance and biomass. Regarding abundance, the biggest contrast between the two nets was observed in the percentage contribution of Euphausiidae (krill). This *family* was by far the most abundant in the MOCNESS, making up 61.49% of specimens and contributing almost 50% more to total abundance than the second most abundant *family* Benthesicymidae (11.57%). Conversely, Euphausiidae was the least abundant *family* in the IHT, making up only 3.80% of specimens and contributing >10% less than the second least abundant *family* Eucopiidae (14.36%).

The Oplophoroidea was the most abundant *family* in the IHT, making up 29.47% of captured specimens. Unlike Euphausiidae in the MOCNESS however, Oplophoroidea did not make up a large majority of IHT specimens, and there was a more even spread among the remaining *families* of: Sergestidae (27.51%), Benthesicymidae (24.86%), and Eucopiidae (14.36%), with the Euphausiidae being the least abundant (3.80%). Taking into account that a majority of euphausiid species have relatively small body sizes compared to the other four crustacean families, and that Oplophoroidea is known to contain relatively larger individuals (Fine, 2016), these results support the assertion that the MOCNESS tends to efficiently collect smaller crustaceans, while the IHT tends to collect larger crustaceans, albeit less efficiently.

Regarding differences in individual species abundance, the three most abundant euphausiid species in the MOCNESS were 1) *Nematoscelis atlantica/microps*, 2) *Stylocheiron abbreviatum*, and 3)

Euphausia mutica while in the IHT, the three most abundant euphausiid species were 1) *Thysanopoda acutifrons/orientalis*, 2) *Thysanopoda egregia*, and 3) *Thysanopoda pectinata*. These observations suggest that the euphausiids captured by both nets differ not only in terms of quantity and size, but also species composition.

As for the decapods/lophogastrids, in the MOCNESS the three most abundant oplophoroid species were 1) *Janicella spinicauda*, 2) *Acanthephyra stylorostratis*, and 3) *Acanthephyra purpurea* and 1) *Oplophorus gracilirostris*, 2) *Acanthephyra acutifrons*, and 3) *Acanthephyra stylorostratis* in the IHT. Similar differences were observed for Sergestidae, as in the MOCNESS the three most abundant species were 1) *Sergestes pectinatus,* 2) *Sergia splendens,* and 3) *Sergestes edwardsii,* while in the IHT the three most abundant species were 1) *Sergia tenuiremis,* 2) *Sergia robusta*, and 3) *Sergia regalis.* For Benthesicymidae, *Gennadas valens* was not only the most abundant benthesicymid in both nets, but also the most abundant decapod overall. However, in the MOCNESS no other Benthesicymidae species were present in the 15 most abundant decapods and lophogastrids, whereas in the IHT both *Bentheogennema intermedia* and *Gennadas capensis* were among the 15 most abundant decapods/lophogastrids.

Within each of the four *families* where carapace/body sizes were compared (i.e. Benthesicymidae, Euphausiidae, Oplophoroidea, and Sergestidae), the extent to which species abundances and rankings differed correlated with the extent of their disparity in average body sizes (i.e. the greater the difference in abundance and ranking, the greatest the difference in body size). For example, the greatest disparity in species abundances and body sizes were observed in *family* Euphausiidae, where only three out of the ten most abundant species were shared between the two nets. Notably, *Thysanopoda acutifrons/orientalis*, which was the most abundant IHT euphausiid by far, was only ranked the 8th most abundant euphausiid in the MOCNESS. Similarly for Sergestidae, where only one species was shared between the two nets, and Oplophoroidea, where only two species were shared, the most abundant IHT species from these *families* had much larger mean carapace lengths (9.98 – 19.76 mm) than those of the MOCNESS (6.19 – 14.40 mm), and the few shared species were ranked differently in each net. Interestingly and in contrast to the other three *families*, for Benthesicymidae both nets identified the same species (*Gennadas valens*) as the most abundant overall, and there was not a large disparity between the mean individual carapace lengths (10.93 mm in the IHT vs. 9.53 mm in the MOCNESS).

For biomass, Oplophoroidea and Benthesicymidae were the two *families* that made the greatest contribution to the assemblage biomass in the MOCNESS samples, contributing 39.53% and 21.23% respectively. For the IHT samples, Oplophoroidea and Sergestidae were the first and second largest contributors to both abundance and biomass. Together, they contributed 89.48% of total IHT biomass, with Oplophoroidea (69.73%) contributing a large majority of the total biomass and Sergestidae (19.75%) alone contributing more biomass than the remaining three *families* combined. These findings support the work of Heino *et al.* (2011), who found that two species of decapods from Sergestidae (*S. corniculum & S. henseni*) were more efficiently captured by the larger nets. The IHT data contributed by this study differ from the MOCNESS data (Burdett *et al.*, 2017; current study) in that Benthesicymidae is the second largest contributor to pelagic crustacean biomass in the GOM, as well as providing new insights into the extent of oplophorid biomass contribution. These findings are in line with the results of Potter *et al.*'s (1990) and Heino *et al.*'s (2011) studies, suggesting that crustacean families containing larger individuals would be more represented larger nets such as the IHT.

Despite the potential 'inefficiency' (i.e. catching fewer organisms per volume filtered) of LMTs, the significantly larger body sizes of crustaceans collected by the IHT in this study suggest that sampling with LMTs can yield valuable species data that would ordinarily be precluded by only using smaller nets such as the MOCNESS. For example, *Thysanopoda acutifrons/orientalis* was one of the most abundant euphausiids in both nets, but the largest specimen was 47.45 mm (body length) in the MOCNESS, and 64.98 mm in the IHT. These differences in maximum sizes between the two nets could influence our understanding of these crustaceans' life history since life histories are calculated based on maximum body size (Fenwick, 1984; King and Butler, 1985). These findings are in line with the work of Potter *et al.* (1990) which demonstrated that while larger trawls with large mesh sizes tended to miss smaller specimens, they also caught larger specimens than the smaller trawls. The absence of MOCNESS specimens of comparable size to the largest IHT specimens in this study indicate that mesh size alone is not enough to explain these differences (unlike for abundance and biomass discussed above), as the IHT would collect the same maximum sizes as the MOCNESS were net retention the only determining factor. Instead, based on the findings of similar studies (Barkley, 1964, 1972; Potter *et al.*, 1990; Bethke *et al.*, 1999; Heino *et al.*, 2011), a more plausible explanation is that the larger mouth opening of the IHT lowered the chance of net avoidance, substantially increasing its likelihood of capturing larger, more mobile organisms. This avoidance hypothesis is supported by the IHT being towed at approximately 5 knots compared to the ~1.5 knots the MOCNESS was towed. This, when combined with the much larger effective mouth area of the IHT could also explain why the volume filtered by the IHT was several orders of magnitude higher than the MOCNESS.

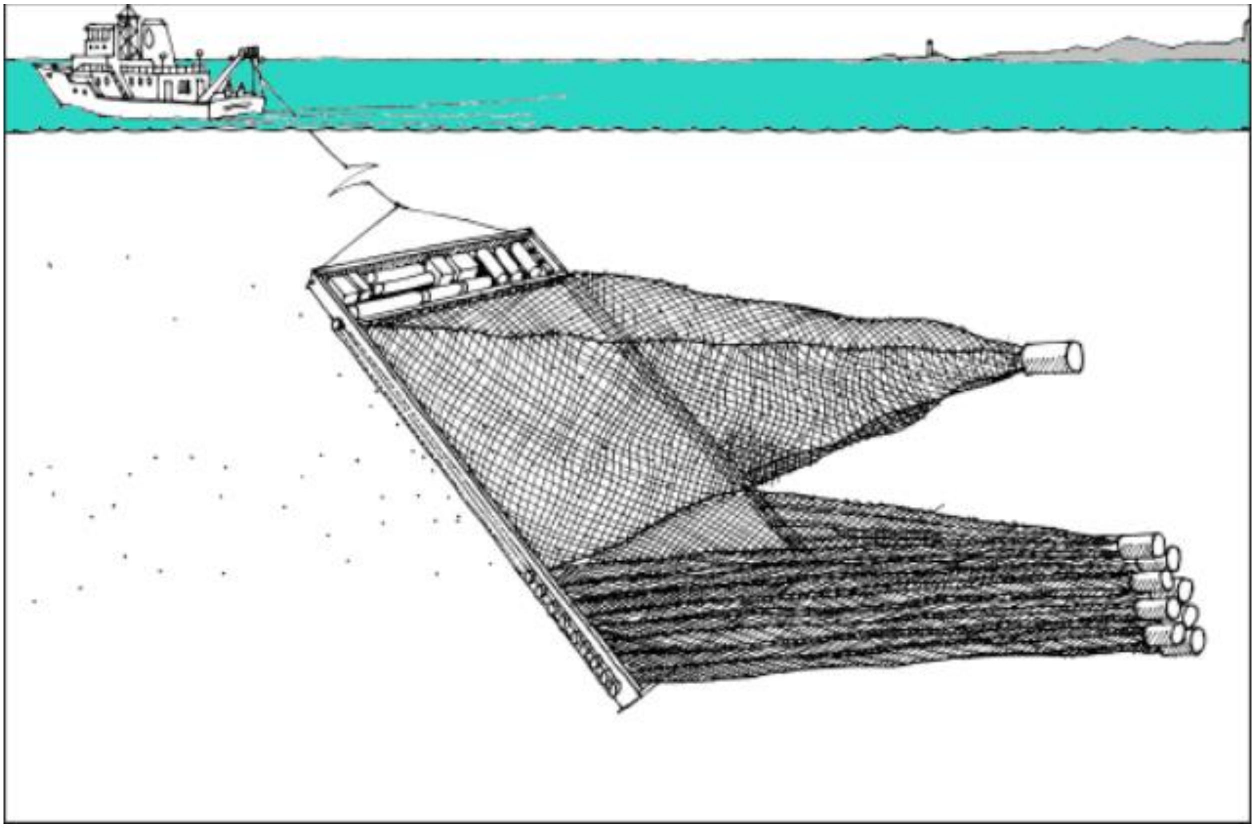
Net avoidance may not be the only explanation for the IHT collecting significantly larger specimens than the MOCNESS. In most population structures, individuals that have survived long enough in their respective environments to grow larger than their conspecifics tend to be relatively rare (Huete-Ortega *et al.*, 2010). Considering that many GOM crustacean species are known to be egg layers that utilize the r-reproductive strategy (i.e. larger litters but higher mortality) (Hopkins *et al.*, 1989; Fine, 2016; Nichols, 2018; La Spina, 2020), it can be reasonably assumed that these larger individuals would be rare and have larger nearest neighbor distances than smaller members of the same species. This assumption is supported by the data from this study, where the larger individuals captured by the IHT were significantly less abundant by trawl volume than the smaller MOCNESS individuals. As such, while net avoidance presents a well-supported hypothesis for the prevalence of larger crustaceans in the LMT, it is also plausible that these observations were simply due to the much larger filtered volumes in the LMT, which results in greater capture efficiency of rarer larger specimens.

The IHT data from this study are valuable contributions to the existing GOM assemblage data collected by the MOCNESS in previous studies (Fine, 2016; Burdett *et al.*, 2017; Nichols, 2018; Frank *et al*., 2020; Hine, 2022), and the comparative analysis conducted between the two net types demonstrates how the quantification of the pelagic crustacean assemblages ideally should be conducted with multiple gear types. Since LMTs tend to collect larger individuals, deploying them to study pelagic crustaceans could shed more light on the distribution and abundance of larger shrimp specimens that are not caught by a smaller net such as the MOCNESS. In addition, data on larger individuals from *families* such as Oplophoroidea and Sergestidae might improve our understanding of their reproductive cycle, as significant differences have been observed between the body sizes of sexually mature vs. immature individuals (Heino *et al.* 2011; Burdett *et al.,* 2017). Future LMT deployments may collect data that improve our understanding of the maximum sizes and life histories of pelagic euphausiid and decapod species in the GOM, both factors which are relevant to crustaceans, as they exhibit both indeterminant growth and deep-sea gigantism (Sebens, 1987; Wilson and Ahyong, 2015). These advantages of using LMTs complement those of the MOCNESS when studying deep sea crustaceans. The smaller net, in addition to being deployable from non-purpose-built vessels unlike most LMTs, has been shown in previous works to accurately sample discrete depth intervals and retain a high number of individuals per volume sampled. Overall, this study demonstrates that net type is a key factor in quantifying the GOM pelagic crustacean assemblage and recommends that future studies use several different net types in tandem where possible.

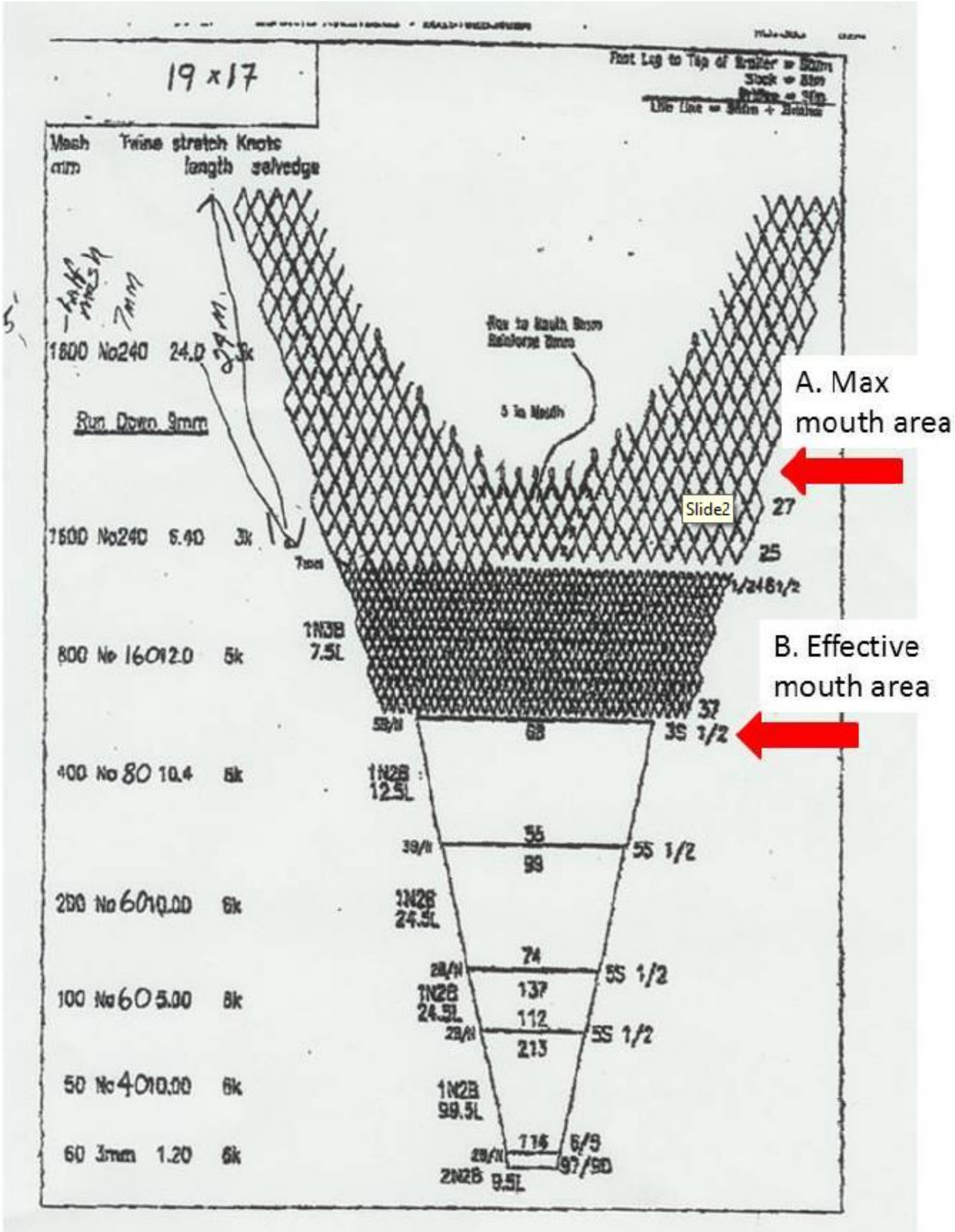
Notes on the Deepwater Horizon Oil Spill (DWHOS)

Accurate assemblage data is critically important when establishing baselines that allow us to evaluate the impacts of environment disasters, as our perceptions of assemblages directly influence decisions on how to take effective recovery action. When the largest oil spill in US history (i.e. DWHOS) happened back in 2010, crustacean populations were observed deteriorating in an unprecedented manner over the following years (Nichols, 2018; La Spina, 2020; Hine, 2022), but these changes in the GOM ecosystem could not be directly attributed to the oil spill due to the lack of a pre-spill baseline on the micronektonic crustacean assemblage. As suggested by Fine (2016), oil impacts on euphausiids could vary depending on their body sizes, as smaller individuals may be more susceptible to oil droplets due to their lower surface area to volume ratios: Fine speculated that the dominant Euphausiidae species in his study were larger than those analyzed in previous studies (Kinsey and Hopkins, 1994; Gasca *et al.*, 2001) because of the impact of oil on smaller species, though again these observations could not be supported due to the lack of a pre-spill baseline. With the additional species data collected by the LMT in this study to supplement the studies conducted with the MOCNESS following DWHOS, we now have the data to compile a more comprehensive ‘impacted dataset’ for the GOM crustacean assemblage with which we can monitor future changes to the GOM ecosystem. Future studies should carefully consider the shortcomings and advantages of each net demonstrated in this study, and more LMT crustacean data are needed to obtain a better understanding of the GOM micronektonic assemblage.

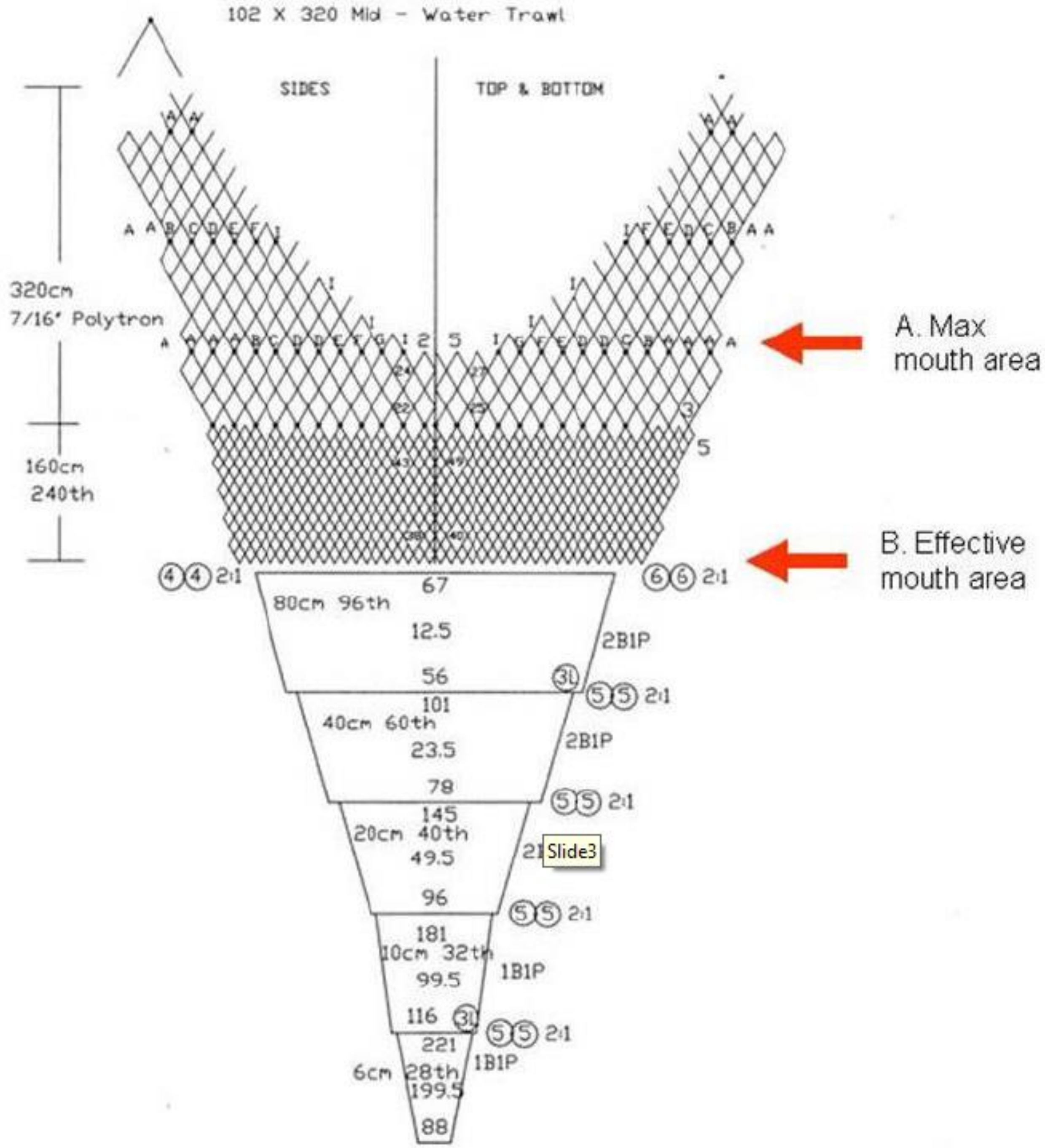
APPENDICES



Schematic showing general MOCNESS deployment, from NRDA Winter 2011 Cruise Plan, Meg Skansi



Schematic of the IHMT used during the December and Mar/Apr *Pisces* cruises. Net plan provided by NOAA NMFS Northeast Fisheries Science Center.



Schematic of the IHT used during the Jun/Jul and Sep 2011 *Pisces* cruises. Net plan provided by Superior Trawl, Wakefield, RI.

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