frontiers in Marine Science

EDITORIAL
published: 09 March 2021
doi: 10.3389/fmars.2021.653074

Editorial: Deep Pelagic Ecosystem Dynamics in a Highly Impacted Water Column: The Gulf of Mexico After *Deepwater Horizon*

Tracey T. Sutton[1], Kevin M. Boswell[2], Heather D. Bracken-Grissom[2], Jose V. Lopez[1], Michael Vecchione[3] and Marsh Youngbluth[4]*

[1] Guy Harvey Oceanographic Center, Halmos College of Arts and Sciences, Nova Southeastern University, Dania Beach, FL, United States, [2] Department of Biological Sciences, Institute of Environment, Florida International University, North Miami, FL, United States, [3] NMFS National Systematics Laboratory, National Museum of Natural History, Washington, DC, United States, [4] Harbor Branch Oceanographic Institution at Florida Atlantic University, Fort Pierce, FL, United States

Keywords: epipelagic, mesopelagic, bathypelagic, ecology, biodiversity, connectivity, biophysical coupling

Editorial on the Research Topic

Deep Pelagic Ecosystem Dynamics in a Highly Impacted Water Column: The Gulf of Mexico After Deepwater Horizon

OPEN ACCESS

Edited and reviewed by:
Eva Ramirez-Llodra,
REV Ocean, Norway

****Correspondence:***
Tracey T. Sutton
tsutton1@nova.edu

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

Received: *13 January 2021*
Accepted: *12 February 2021*
Published: *09 March 2021*

Citation:
Sutton TT, Boswell KM, Bracken-Grissom HD, Lopez JV, Vecchione M and Youngbluth M (2021) Editorial: Deep Pelagic Ecosystem Dynamics in a Highly Impacted Water Column: The Gulf of Mexico After Deepwater Horizon. Front. Mar. Sci. 8:653074. doi: 10.3389/fmars.2021.653074

AIMS AND OBJECTIVES OF RESEARCH TOPIC

The intermediate-sized midwater fauna (fishes, shrimps, and cephalopods; "micronekton" collectively) are dominant components of the pelagic ocean, which is by far the largest ecosystem type on Earth by several metrics (volume, organismal numbers, biomass, and productivity). Deep-pelagic micronekton, those animals residing in the water column below 200 m depth during the day, are the direct link between plankton and oceanic top predators, and through the linked processes of feeding and daily vertical migration facilitate one of Earth's most important ecosystem services to humans, carbon sequestration. Despite increasing recognition of this importance, a disconnect exists between stewardship and human impact; only a miniscule fraction of the deep-pelagic ocean has been studied in detail, while anthropogenic threats to that system are increasing rapidly. Perhaps nowhere on Earth is that dichotomy more demonstrable than the Gulf of Mexico (Gulf hereafter), a complex, high-diversity ecosystem under intense human usage and subjected to arguably the worst marine pollution event in human history.

Assessment of the impacts of the *Deepwater Horizon* disaster to the deep-pelagic biota was impeded from the start by the lack of pre-event information, both in terms of baselines (faunal composition, abundance, and distribution) and in terms of understanding natural variability, against which impacts of anthropogenic disturbance could be detected and quantified. In this Research Topic, we present a description of three interlinked research programs (ONSAP, DEEPEND, and DEEPEND|RESTORE, described below) that began in 2010 and continue as of this writing. These programs were designed to investigate key aspects of the Gulf pelagic ecosystem, including its faunal structure, biophysical drivers of that structure, organismal and community ecology, natural variability, and potential resilience to disturbance. The contributed papers are grouped below by major themes, indicated in the conceptual model (**Figure 1**) of DEEPEND (Deep Pelagic Nekton Dynamics; www.deependconsortium.org), the largest of the three aforementioned research programs.

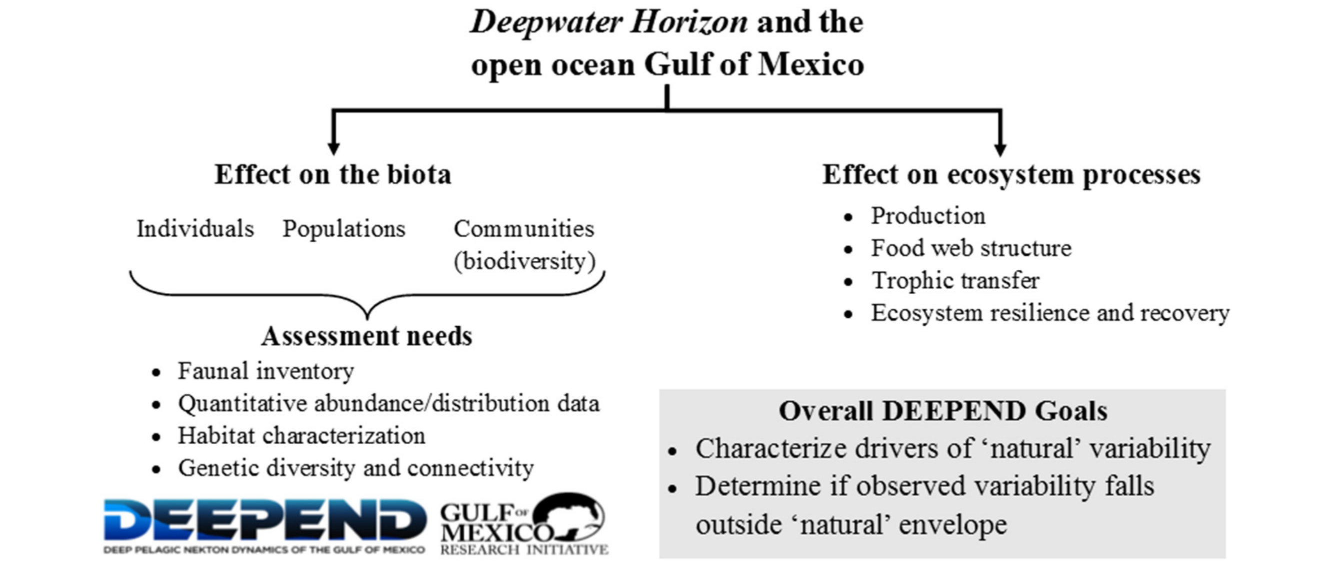

FIGURE 1 | The conceptual framework of the DEEPEND research consortium.

INTEGRATED, MULTIDISCIPLINARY RESEARCH TO TACKLE A COMPLEX TOPIC

The pelagic Gulf is characterized by dynamic physical oceanography, high species richness (as determined by the research programs described herein), and complex faunal distributions resulting from the interplay between daily vertical animal movement and current-mediated horizontal transport. Thus, assessment of the system and the potential effects of the *Deepwater Horizon* disaster (DWH hereafter) on that system required a multidisciplinary approach, as described in Cook et al., Boswell et al., Easson et al., and Timm et al. The full suite of integrated approaches included *in situ* sampling, water column profiling, acoustic sensing, satellite remote sensing, microbial and metazoan genetic analysis, trophic analysis using traditional and biochemical methodologies, petrogenic contamination analysis, imaging, AUV sensing, and numerical modeling.

The primary focus of research devoted to this Research Topic issue was research conducted by DEEPEND, a 5-year (2015–2020), 102-member, 19-organization research consortium supported by The Gulf of Mexico Research Initiative (GoMRI; https://gulfresearchinitiative.org). DEEPEND was an expanded successor of the NOAA-supported Offshore Nekton Sampling and Analysis Program (ONSAP; 2010–2015), whose explicit mission was to provide faunal composition and abundance information for NOAA's DWH natural resource damage assessment (Sutton et al., 2020). DEEPEND's approaches included: (1) a direct assessment of Gulf deep-pelagic community structure, from the surface to 1,500 m, with simultaneous investigation of the physical and biological (including microbial; Easson and Lopez, 2019) drivers of this structure; (2) quantification of 'natural' variability against which longer-term disturbance and recovery trends could be detected; (3) a time-series biophysical modeling approach comparing data collected shortly after DWH (2010–2011; ONSAP sampling) to 2015–2018 (DEEPEND sampling); and (4) an assessment of the extant and potential future consequences of DWH on the pelagic biota of the Gulf. At the culmination of the 10-year tenure of GoMRI in 2020, DEEPEND was funded to continue time-series analysis and to translate information gained into resource management products via the NOAA RESTORE Science Program.

COMMUNITY ECOLOGY: DIVERSITY, POPULATION DYNAMICS, AND REPRODUCTION

Several papers provided corroboration for the classification of the Gulf as one of the global ocean's most speciose mesopelagic ecosystems (Sutton et al., 2017). A highly resolved inventory of biological diversity is critical in systems exposed to intense natural and anthropogenic perturbations (such as the Gulf), as diversity is a fundamental emergent property of ecosystems, reflecting complexity and resilience, as well as indicating regime shifts and alternate stable states. Moore et al. highlighted the dominant contribution of a chronically overlooked pelagic faunal group, eels (specifically, leptocephalus larvae), including numerous new records for the Gulf, while Frank et al., Judkins and Vecchione, Meinert et al., and Milligan and Sutton provided detailed quantitative faunal inventories of euphausiids ("krill"), cephalopods, ichthyoplankton, and lanternfishes, respectively.

Other papers examined aspects of the abundance, distribution, and reproduction of foundational oceanic taxa of the Gulf. These papers relate to the spatial and temporal attributes of the pelagic fauna as a function of DWH exposure. Were some fauna more prevalent in the DWH footprint, and did key ecological processes, such as reproduction, coincide with the DWH? Frank et al. examined the euphausiid assemblage of the Gulf and its relationship to the "oceanic rim," reporting higher abundances but lower diversity over the continental slope (200–1,000 m bottom depth) compared to open water (>1,000 m bottom depth). These authors also noted evidence for seasonal spawning in the Gulf, a critical element of vulnerability to, and recovery from, point-source disturbances. Marks et al. highlighted the dearth of information about the organismal biology of deep-pelagic species in general and provided the first reproductive information about the dominant mesopelagic fish predators of the Gulf (dragonfishes, Family Stomiidae). They found that dragonfishes are gonochoristic (separate sexes and not hermaphroditic), iteroparous, batch spawners with protracted reproductive capacity throughout the year. Such data are crucial for understanding what may be the largest data gap in deep-pelagic ecology, the reproductive timing and rates of its constituents.

VERTICAL MIGRATION DYNAMICS

The largest coordinated animal movement on Earth happens every day in the pelagic ocean in the form of diel (daily) vertical migration (DVM), with meso- and sometimes bathypelagic animals ascending from deep daytime residence depths to shallower nighttime depths to feed, then descending again at daybreak. DVM is one of the primary elements of the "biological pump," whose value to humans in sequestering carbon has been estimated in the 100's of billions to trillions of dollars (USD; Hoagland et al., 2019). Boswell et al. used integrated acoustical, remote sensing and net-sampling data to illustrate relationships of depth and intensity of "deep scattering layers" (i.e., layers of maximal faunal abundance, inferred from acoustic backscatter) with oceanographic conditions and light intensity. This was particularly evident within the Gulf's major oceanographic feature, the Loop Current, where they acoustically estimated that biomass was two to four times lower than residual Gulf waters. Easson et al. found shifting environmental DNA (eDNA) profiles tied to DVM, providing another tool with which to study DVM dynamics. Judkins and Vecchione found that a very large percentage (95%) of the Gulf's cephalopod assemblage is distributed at the deep-meso/bathypelagic interface (1,000–1,400 m depth), coincident with a large subsurface hydrocarbon/dispersant plume that developed after DWH (Camilli et al., 2010). Milligan and Sutton reported that the strong DVM habits of lanternfishes (Family Myctophidae) paired with depth-specific, multidirectional current shear resulted in the broad distribution of the assemblage as a whole. In essence, the entire lanternfish assemblage of the northern Gulf can be treated and managed as one contiguous stock.

MESOSCALE BIOPHYSICAL COUPLING

Assessment of pelagic community structure, and its variation, in a given area is complicated by the effect of constant water movement and water mass replacement, akin to the adage "you never put your foot in the same river twice." In both the Gulf and pelagic regions worldwide, depth is the primary determinant of community structure, with the proviso that depth is a multivariate factor; light, heat, pressure, water density, sound transmission, and food availability all vary directly with depth. In the horizontal/geographical context of the Gulf, mesoscale oceanographic features are the primary components of habitat variability (see Johnston et al., 2019), and thus putative drivers of community structure. In addition to findings of Boswell et al. mentioned previously, Meinert et al. reported in this Research Topic that cyclonic eddies, frontal features, and areas of upwelling are areas of higher biodiversity of fish larvae, and that the mixed layer is an essential habitat for deep-pelagic fishes during early-life stages. In a study of larval and juvenile tunas of the Gulf, Pruzinsky et al. reported that over large spatial scales, early-life-history stages of commercially important species partition habitat on the mesoscale in addition to the temporal scale tied to adult spawning. These factors are important for spatially and temporally explicit modeling developed to predict stock sizes of higher trophic levels in oceanic ecosystems. Timm et al. investigated comparative population genomics and biophysical oceanography, which suggested that vertical migration habits (or lack thereof) have important implications for horizontal transport between the Gulf and adjacent waters via the fast moving waters of the Loop Current. Studies such as these are essential to establish an envelope of natural variability against which variability caused by a pollution event can be compared.

PELAGIC ECOSYSTEM CONNECTIVITY

The pelagic ocean has been historically delineated into depth strata based on light penetration (epipelagic, mesopelagic, and bathypelagic domains, representing the photic, disphotic, and aphotic layers of the water column, respectively). Research has often been stratified in this manner as well, with little or no integration across depths and oceanographic subdisciplines. Thus, the connectivity between these depth zones is poorly documented (Sutton, 2013). Likewise, connectivity between ocean basins and sub-basins, and connectivity between the neritic and pelagic domains, are understudied. Several DEEPEND publications have examined vertical distribution patterns within and between pelagic populations, including Boswell et al., Easson et al., Judkins and Vecchione, Milligan and Sutton, and Timm et al. from this Research Topic (please see D'Elia et al., 2016; Sutton et al., 2020 for references of previous works). Milligan and Sutton and Timm et al. also added a horizontal connectivity component, both within the Gulf basin proper and the adjacent seas, respectively. Frank et al. reported increased euphausiid abundances over the continental slope compared to open water, emphasizing the important connectivity of oceanic and coastal ecosystems through "boundary communities" of putatively enhanced trophic interaction. In terms of ecological connectivity, the study of Richards et al. determined that isotopic values of particulate organic matter can vary significantly over relatively small horizontal and vertical scales, and that baseline variation can be conserved in the signatures of higher-order consumers. In terms of DWH, one of the primary attributes of this disaster compared to those that preceded it was the wide range of habitats effected, in other words the high connectivity of the disaster. Research on connectivity of the biota affected must be conducted on a similar scale for this and future large-scale pollution events.

IMPLICATIONS FOR RESOURCE MANAGEMENT

One of the grand challenges of deep-sea research is convincing the public, stake holders, resource managers and even other scientists that the deep sea really matters (Jamieson et al., 2020). The need for such awareness is manifest in the summary findings of DEEPEND and its associated programs, namely that the Gulf is a highly integrated unit that should be managed holistically rather than in parts. The current efforts of the DEEPEND consortium, and future work funded by the NOAA RESTORE Science Program (www.restoreactscienceprogram.noaa.gov), are focused on that theme. For example, Romero et al. in this and previous works (e.g., Romero et al., 2018) emphasized the need for long-term monitoring of petrogenic contamination in the deep-pelagic fauna to ascertain the persistence of oil spill effects and reverberate after the source has been contained. With the steadily increasing depths of oil production in the Gulf (Gulf "ultra-deep" wells now provide the majority of US oil production; Murawski et al., 2019) and the likelihood of accidents increasing with platform depth (Muehlenbachs et al., 2013), deep oils spills are not just possible, they are likely. Resource management efforts such as NOAA's Natural Resource Damage Assessments require such information now and in response to future spills. Multiple authors in this Research Topic have also shown that the northern Gulf is a critical habitat for the juveniles of commercially important fish and invertebrate species, as well as other coastal, demersal, and benthic species (Pruzinsky et al.; Meinert et al.; Moore et al.). The deep-pelagic micronekton are vital components of oceanic food webs (Frank et al.; Judkins and Vecchione; Milligan and Sutton,; Richards et al.), the trophodynamics of which represent one of the major data gaps with respect to the stewardship of apex predatory fishes, cetaceans, and seabirds (including endangered species).

The DWH disaster emphasized the lack of faunal inventories and baselines for deep-sea pelagic ecosystems being exposed to industrial disturbance. In creating quantitative and genetic inventories for the pelagic Gulf (e.g., Frank et al.; Moore et al.), the DEEPEND group had to sequentially decipher information written in English, French, Russian, Spanish, and Italian. These data are now accessible in a collated form for use in resource management. We anticipate that this Research Topic will serve to advance deep-sea research beyond the strictly "*Challenger*-era" domain of descriptive science. Although description is an absolutely essential first step and one from which we are still very far away for much of the global ocean, the next-level analyses presented here of emergent properties, ecosystem functioning, and ecosystem resilience are necessary for understanding the ecosystem as well as results of human impacts on it.

AUTHOR CONTRIBUTIONS

TS, KB, HB-G, JL, MV, and MY conceived the Research Topic and wrote the manuscript. All authors approved the submitted version.

ACKNOWLEDGMENTS

We would like to thank the collaboration of 36 reviewers for making this collection of papers possible. We thank the 42 authors for their tireless pursuits during the DEEPEND program, and for sharing the products of their research for this issue. Last but not least, we thank The Gulf of Mexico Research Initiative, the NOAA Office of Response and Restoration, and the NOAA RESTORE Science Program for funding the research encompassed herein.

REFERENCES

Camilli, R., Reddy, C. M., Yoerger, D. R., Van Mooy, B. A. S., Jakuba, M. V., Kinsey, J. C., et al. (2010). Tracking hydrocarbon plume transport and biodegradation at Deepwater Horizon. *Science* 330, 201–204. doi: 10.1126/science.1195223

D'Elia, M., Warren, J. D., Rodriguez-Pinto, I., Sutton, T. T., and Cook, A. B. (2016). Diel variation in the vertical distribution of deep-water scattering layers in the Gulf of Mexico. *Deep-Sea Res. I* 115, 91–102. doi: 10.1016/j.dsr.2016.05.014

Easson, C. G., and Lopez, J. V. (2019). Environmental drivers of bacterioplankton community structure in the northern Gulf of Mexico. *Front. Microbiol.* 9:3175. doi: 10.3389/fmicb.2018.03175

Hoagland, P., Jin, D., Holland, M., Kostel, K., Taylor, E., Renier, N., et al. (2019). Ecosystem services of the mesopelagic. *Woods Hole Oceanographic Inst.* 2019:35. doi: 10.1575/1912/25013

Jamieson, A. J., Singleman, G., Linley, T. D., and Casey, S. (2020). Fear and loathing of the deep ocean: why don't people care about the deep sea? *ICES J. Mar. Sci.* fsaa234. doi: 10.1093/icesjms/fsaa234

Johnston, M., Milligan, R., Easson, C., DeRada, S., Penta, B., and Sutton, T. (2019). An empirically-validated method for characterizing pelagic habitats in the Gulf of Mexico using ocean model data. *Limnol. Oceanogr. Meth.* 17, 362–375. doi: 10.1002/lom3.10319

Muehlenbachs, L., Cohen, M. A., and Gerarden, T. (2013). The impact of water depth on safety and environmental performance in offshore oil and gas production. *Energy Policy* 55, 699–705. doi: 10.1016/j.enpol.2012.12.074

Murawski, S., Ainsworth, C., Gilbert, S., Hollander, D., Paris, C., Schlüter, M., et al. (2019). *Scenarios and Responses to Future Deep Oil Spills: Fighting the Next War.* Springer. doi: 10.1007/978-3-030-12963-7

Romero, I. C., Sutton, T. T., Carr, B., Quintana-Rizzo, E., Ross, S. W., Hollander, D. J., et al. (2018). Decadal assessment of polycyclic aromatic hydrocarbons in mesopelagic fishes from the Gulf of Mexico reveals exposure to oil-derived sources. *Envir. Sci. Tech.* 52, 10985–10996. doi: 10.1021/acs.est.8b02243

Sutton, T. T. (2013). Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *J. Fish Biol.* 83, 1508–1527. doi: 10.1111/jfb.12263

Sutton, T. T., Clark, M. R., Dunn, D. C., Halpin, P. N., Rogers, A. D., et al. (2017). A global biogeographic classification of the mesopelagic zone. *Deep Sea Res. I* 126, 85–102. doi: 10.1016/j.dsr.2017.05.006

Sutton, T. T., Frank, T. M., Romero, I. C., and Judkins, H. (2020). "As Gulf oil extraction goes deeper, who is at risk? Community structure, distribution, and connectivity of the deep-pelagic fauna," in *Scenarios and Responses to Future Deep Oil Spills – Fighting the Next War*, eds S. A. Murawski, C. Ainsworth, S. Gilbert, D. Hollander, C.B. Paris, M. Schlüter, and D. Wetzel (Cham: Springer), 403–418. doi: 10.1007/978-3-030-12963-7_24

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