









## Complexities of disturbance response in a marine food web

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### ABSTRACT

A primary aspect of applied marine ecology assesses how food webs change in response to ecosystem disturbances. In 2010, the drilling rig *Deepwater Horizon* (DWH) discharged ~3.19 million barrels of crude oil into the northern Gulf of Mexico. The spill, followed by widespread dispersant application to enhance oil degradation, represented a significant anthropogenic disturbance in the region. We created network models of four multi-year periods, to represent the acute and chronic food web responses to the DWH spill. Using ecological network analysis (ENA) and information theory, we compared multiple food web metrics among these periods in the context of food web resilience theory. This analysis was conducted at three levels of hierarchical organization: whole ecosystem, nekton community, and individual nekton taxa. We analyzed how individual taxa contribute to resilience of the food web with a novel informational index: Redundancy/Ascendency. Apparent responses to the disturbance differed across hierarchical levels. Some metrics dependent on biomass change and flow distribution temporarily increased during the years immediately following the discharge and subsequently returned to pre-DWH levels. Metrics of energy flow linked to primary production rose in the last two periods, perhaps reflecting eutrophication. Other metrics changed little or had no obviously explainable patterns. Overall, our results indicate the nektonic food web in this region is flexible to disturbance and likely has redundant energy pathways explaining the reported ecosystem resilience to the DWH spill. We show that an ENA, when applied to multiple levels of ecosystem hierarchy, may aid understanding of marine food web resilience.

A primary focus of applied marine ecology is to assess how food webs change following major natural and anthropogenic disturbances (and associated management actions). Stability in community structure is a potentially useful yet debated indicator of food web resilience in marine ecosystems (Oliver et al. 2015). Community stability may be represented as resilience or resistance in the face of perturbation (see Table 1 for definitions used in this study), but the mechanisms by which stability is linked to community structure continues to be deliberated (Rooney et al. 2006; Loreau and De Mazancourt 2013; Oliver et al. 2015; Ulanowicz 2018). Species diversity

may affect resilience mechanistically via attributes of the species and their interactions. For instance, flexibility in trophic interactions among species within a food web may help promote resilience via high degree of omnivory (Dunne et al. 2004; Thompson et al. 2007; Valentine et al. 2008), the spatial and temporal variation in the distribution of prey or predators, and the Redundancy of energy flows (i.e., evenness of alternative and parallel pathways of energy flow, Ulanowicz 1986, 1997). Interactions between community diversity, productivity, and resilience might indicate that changes in stability can be either a cause or effect of changes in productivity and resilience (Worm and Duffy 2003). There is also the potential for community diversity to be less important for short-term food web resilience but play a larger role in long-term recovery (Oliver et al. 2015).

Some propose that functional diversity, which considers trait differences among species (e.g., variations in behavior, trophic interactions, and phenology), is a better indicator of food web resilience than species diversity or changes in community structure in the face of disturbances (Peterson et al. 1998; Dunne et al. 2002; Lefcheck and Duffy 2015; Oliver et al. 2015;

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**Table 1.** Ecological network and information metrics. We provide network and information theory definitions recognizing multiple definitions in the literature and the obscure use of some of these terms.

Network metric	Definition
Ascendency	The product of informational constraint placed upon the flow of energy/material within a food web and the Total Systems Throughput. A system with fewer parallel or redundant flows is less likely to remain stable in light of a disturbance (Ulanowicz 2018). Traditionally, the higher this value the less resilient the system.
Ascendency/capacity (A/C)	Ascendency as a proportion of developmental capacity (relative ascendency). Allows for the comparison of multiple energy pathways supporting a compartment between food webs
Connectance index	The number of interactions in a network divided by the total interactions.
Developmental capacity	Flow diversity as indicated by the Shannon's Index for the distribution of flows times the Total System Throughput. Capacity is the theoretical maximum of Ascendency (Ulanowicz 2004).
Finn's cycling index	The percentage of total flow that cycles among compartments between entering and exiting a system. Increases in this value suggest that energy remains in the system for longer periods of time (Finn 1980, Fath et al. 2019).
Finn's mean path length	The mean number of paths material (energy) travels before it leaves the system (Finn 1976). Mean path length is higher in ecosystems with a more diverse set of flows and will decrease with perturbations (Christensen 1995, Tecchio et al. 2015).
Flexibility	The potential to contribute to unconstrained, internal flows. Flexibility is the informational component of redundancy (bits). A system or taxon that exhibits high flexibility, is said to contribute more to a resilient system—able to maintain stability through a disturbance.
Indeterminacy	The uncertainty related to the flows within a system
Omnivory index	Quantifies the distribution of feeding interactions among trophic levels of the food web through the weighted average of omnivory of the consumers (Heymans et al. 2014).
Overhead	The product of the unconstrained component of Shannon's flow diversity of energy/material within a food web and the Total System Throughput. Can be explained as the functional Redundancy in a system (Ulanowicz 2018).
Redundancy	The evenness and richness of internal energy flows in the food web. The flexibility of energy or material flows and the Total System Throughput. Represents the multiple energy pathways between species groups (Ulanowicz 2018).
Resilience	The ability of an ecosystem to return to its previous equilibrium after a disturbance.
Resistance	The ability of an ecosystem to maintain its current state in the face of a disturbance.
Shannon's diversity index	The common ecological index used to characterize species diversity in a system and accounts for both abundance (or biomass) and evenness of the species present in the system.
Stability	Persistence of an ecosystem to maintain current state (Ulanowicz 2018). Stability here, is defined as having multiple components: resilience and resistance (Canning and Death 2019).
Structure	The configuration of compartments and flows within a system
Taxon-specific redundancy/ascendency (R/A)	A dimensionless index of the redundancy (flexibility) of a taxon divided by the ascendency of a taxon. The relative contribution of that taxon to the flexibility of energy flow vs the organization of energy flow.
Throughput	The sum of flows of each compartment.
Total system throughput (TST)	Total activity in a system as the sum of all flows (Ulanowicz 2018).

Ulanowicz 2018). That is, stability in species composition does not necessarily beget resilience of that system (Oliver et al. 2015). High diversity as resilience supposes that species contributions to ecosystem functioning are equal (Mouchet et al. 2010). A focus on functional diversity by considering energy flow in various subcomponents (specific taxa or taxa groups) of the ecosystem is thought to provide new insights beyond changes in community structure (Mills and Doak 1993; Ellision et al. 2005; Angeler and Allen 2016). This approach intends to capture the differential effects of various species on ecosystem structure and function (Mouchet et al. 2010). Here, we present results of a study evaluating the acute and chronic impacts of a major disturbance in the northern Gulf of Mexico on the marine food web over two

decades. Considering the previously documented in community stability detailed in Martin et al. (2020), we extend this work to assess food web energy flow and functional diversity using ecological network analysis and information theory.

In the northern Gulf of Mexico, community stability has been widely documented after the drilling rig Deepwater Horizon (DWH) exploded in 2010 (Fodrie and Heck 2011; Moody et al. 2013; Able et al. 2015; Schaefer et al. 2016; Martin et al. 2020). This disaster discharged ~3.19 million barrels (~0.5 million m<sup>3</sup>) of crude oil over 180,000 km<sup>2</sup>. The spill, which was followed by the widespread application of dispersants to enhance oil degradation, represented a significant disturbance to northern Gulf of Mexico waters from Louisiana to

the panhandle of Florida (Mitra et al. 2012; Michel et al. 2013; Nixon et al. 2016). In the wake of this disaster, concerns for public health led to the closure of recreational and commercial fisheries across the northern Gulf of Mexico. At the closure, approximately 88,500 km<sup>2</sup> were closed to fishing of all kinds, accounting for 35% of all federal waters in the northern Gulf of Mexico and 40% of state waters in Alabama (Upton 2011). After initial impacts of the spill, marine communities in the northern Gulf showed little subsequent disruptions of species' abundance, composition, or size (Rozas et al. 2000; Fodrie and Heck 2011; Moody et al. 2013; Able et al. 2014; Van Der Ham and De Mutsert 2014; Schaefer et al. 2016; Martin et al. 2020). Roth and Baltz (2009) noted similar community stability following a smaller oil spill in Barataria Bay, Louisiana, in 2005 (~600 barrels). The authors observed a significant decrease in overall species abundance and a shift in community structure immediately after the spill, which they attribute to behavioral avoidance to the oil (*sensu* Martin 2017). A year later, community structure appeared to return to pre-spill conditions. Likewise, in studies published to date, marine nekton subjected to the DWH oil spill appear to have either demonstrated little impact or recovered to pre-spill community structure within a few years (Fodrie et al. 2014). These previous studies, however, have yet to sufficiently address the role that functional diversity played in determining the documented stability and if those findings are indicative of a resilient or resistant food web in the northern Gulf of Mexico (McCann et al. 2017).

Of particular importance here, Martin et al. (2020) analyzed the impacts of the DWH spill on the nekton community structure within two decades inclusive of multiple natural disturbances (e.g., hurricanes). Using fishery-independent data, the researchers observed increases in abundance of several key species, which drove a decrease in overall diversity during and just after the DWH oil spill: Atlantic Bumper (*Chloroscombrus chrysurus*), Atlantic Croaker (*Micropogonias undulatus*), Gulf Butterfish (*Peprilus burti*), and Longspine Porgy (*Stenotomus caprinus*). The largest changes in abundance and diversity appeared to return to pre-spill conditions by 2017, exhibiting a pulse-like response. The authors suggested that the structure of the community was likely altered in the weeks following the spill. Proposed mechanisms that might explain the pulse response in abundance and changes in community structure included behavioral avoidance of oil, death, or emigration of higher-level consumers from the impacted area, fisheries closures, and documented changes in freshwater inflow. To garner more insight into how functional diversity may have contributed to food web resilience observed after the DWH accident (Oliver et al. 2015), we now expand on the Martin et al. (2020) analyses. To go beyond community stability and diversity as indicators of system resilience, here we evaluate the impacts of the DWH spill on food web metrics and consider nekton- and taxon-specific carbon flows.

Ecological network analyses (ENA) can address functional diversity beyond simple taxonomic diversity (Ulanowicz 2018). These analyses have been broadly used to assess the resilience of ecosystems to disturbances but can be laborious given data

needs and ecosystem process information. The ENA used here provides a quantitative, holistic estimate of how a food web in the northern Gulf of Mexico responds to perturbations such as the DWH spill (Borrett et al. 2018). One important benefit of using ENA, in comparison to traditional measures of biological diversity (e.g., species richness and diversity), is that trophic interactions between taxa are weighted by their relative importance in the food web (i.e., numbers, positions, and flow rates of connections). Using the same dataset as Martin et al. (2020), we evaluated mechanisms of resilience at the ecosystem level and then further investigated contributions of the nekton community and individual nekton taxa. We developed four networks to account for multi-year variability in the northern Gulf of Mexico in the absence of major hurricanes: Time Period 1 (1997–2001) precedes major hurricane events Ivan and Katrina; Time Period 2 (2007–2009) follows these hurricanes and precedes DWH; Time Period 3 (2010–2012) shortly follows DWH and includes the period of management responses; and Time Period 4 (2014–2017) represents the ecosystem several years after DWH. Our objectives were to: (1) Determine patterns in disturbance response across multiple levels of food web hierarchy; (2) Determine the taxon-level flexibility (functional diversity) in each period to identify its potential role in ecosystem resilience; and (3) Consider how findings of this ENA align with a previously conducted community analysis using the same data sets (Martin et al. 2020).

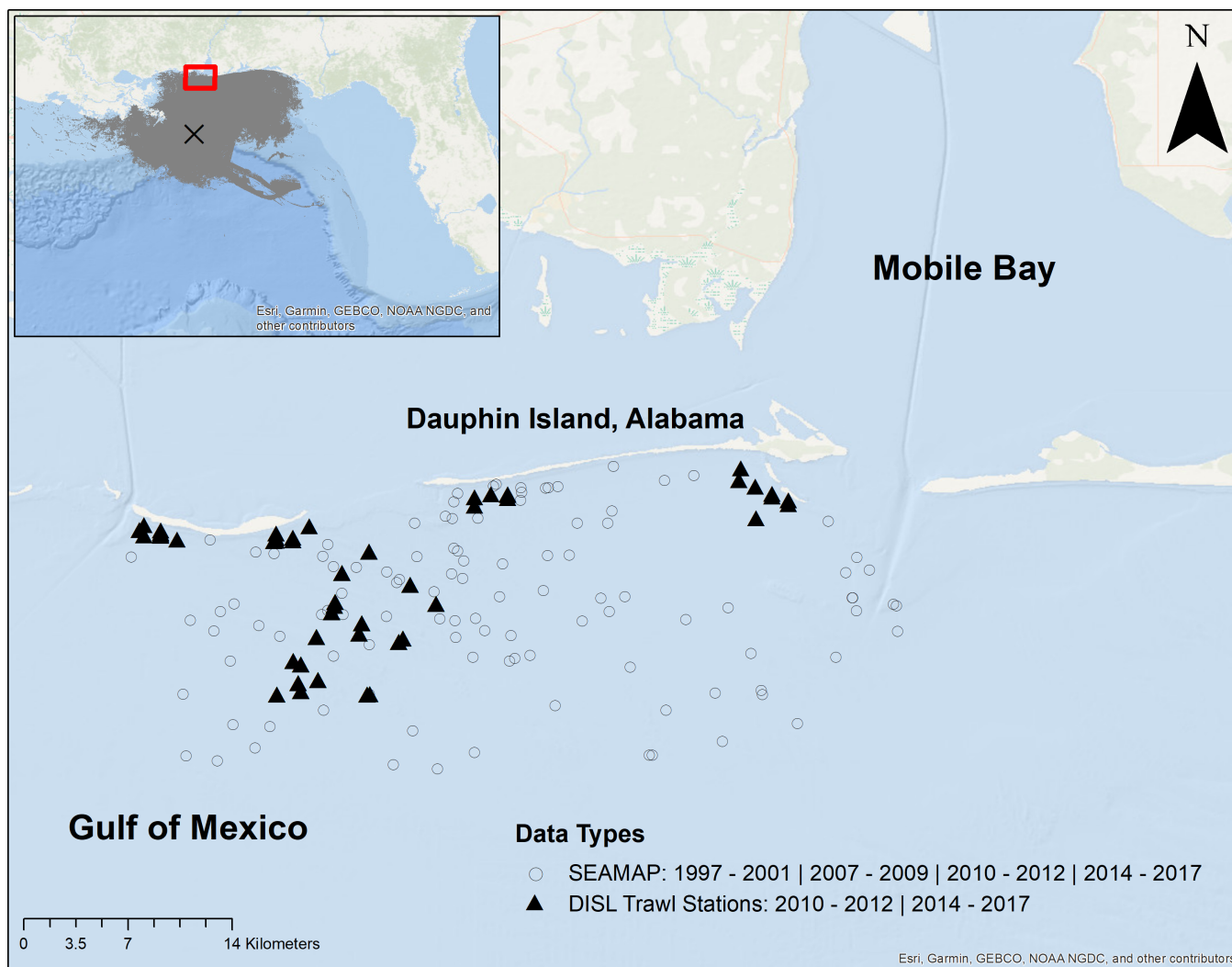
## Methods

### Study site

This study was conducted using data collected from the waters of coastal Alabama and Mississippi (south of the region's barrier islands), where oil (and dispersant) heterogeneously covered the area following the onset of the DWH spill (Fig. 1). This biodiverse region is centrally located in the northern Gulf of Mexico and features unvegetated sandy bottom along the southern shores of barrier islands and submersed vegetation, saltmarshes, and oyster reefs in protected nearshore areas (Valentine et al. 2004). These structurally complex habitats serve as nurseries for many nearshore and offshore species (Fodrie et al. 2014). The barrier islands were impacted by oil, ranging from light to heavy maximum oiling conditions (Michel et al. 2013). Moreover, significant management efforts occurred in this area, with fishing closures during the spill, stationed cleanup crews, riprap breakwaters placed to protect inshore waters (personal observation), and significant freshwater influx from Mississippi River diversions and Mobile Bay.

### Sample collection

We used the same datasets included in the Martin et al. (2020) study, which selected four distinct periods to build representative food web models before and after the DWH accident, accounting for major hurricanes. The biomass



**Fig. 1.** Trawl sample locations for this study in coastal Alabama and Mississippi, with years of sample collection included. Triangles indicate DISL (2010–2012, 2014–2017) trawl sampling, while circles indicate routine SEAMAP trawl sampling (1997–2001, 2007–2009, 2010–2012, 2014–2017). The inset shows an X indicating the location of the DWH platform, surrounded by gray regions marking the oil spill coverage.

values for the nekton compartments were derived from fisheries independent trawl samples in the study area. Time Periods 1 and 2 represent the years prior to the DWH spill (1997–2001 and 2007–2009), which precede and follow, respectively, hurricanes Katrina and Ivan. Time Period 3 was shortly after DWH oil leaked into the northern Gulf of Mexico (2010–2012), and during Time Period 4 (2014–2017), the surface oil had dissipated in the coastal waters of the northern Gulf of Mexico. Bottom trawls for Time Periods 1 and 2 were conducted through Southeast Area Monitoring and Assessment Program (SEAMAP) only. Trawls for Time Periods 3 and 4 were conducted through SEAMAP surveys (SEAMAP, Eldridge 1988) and Dauphin Island Sea Lab (DISL) surveys. The two surveys (SEAMAP and DISL) were conducted using the same methodologies and gear. For more information about the sources and handling of the data used in this study, please see Martin et al. (2020).

### Network model development

Four food web models representative of the study area over two decades were constructed using the Ecopath with Ecosim (v. 6.6.1; www.ecopath.org; EwE) modeling software. Model compartments represent individual species or species guilds (multiple species whose function within the food web is similar). All compartments were mass balanced. The development of a mass balanced Ecopath model relies on parameterizing the model using three of four initial conditions pertaining to each species or guild to solve two governing equations in the model. These parameters are initial biomass (B), production to biomass ratio (P/B), consumption to biomass ratio (Q/B), and ecotrophic efficiency (EE; Christensen and Walters 2004, Christensen 2013). A diet matrix representing the relative proportions of prey items in the diet of each species or species group was constructed (see below for further details).

Two master equations form the foundation of Ecopath and are used to determine the production of each functional group in the model, as well as the energy balance within a group (Eqs. 1 and 2). The first master equation in Ecopath pertains to the production of each functional group in the model:

$$\left(\frac{P_i}{B_i}\right) \times B_i \times EE_i - \sum_{j=1}^n B_j \times \left(\frac{Q_j}{B_j}\right) \times DC_{ji} - Y_i - E_i - BA_i = 0 \quad (1)$$

$\left(\frac{P_i}{B_i}\right)$  is the production to biomass ratio for group  $i$ ,  $EE_i$  is the ecotrophic efficiency,  $B_i$  and  $B_j$  are the biomasses of prey  $i$  and predators  $j$ ,  $\left(\frac{Q_j}{B_j}\right)$  is the consumption to biomass ratio,  $DC_{ji}$  is the fraction of prey  $i$  in predator  $j$ 's diet,  $Y_i$  is the catch rate for the fishery for group  $i$ ,  $E_i$  is the net migration rate, and  $BA_i$  is the biomass accumulation for group  $i$  (Christensen and Walters 2004).

The second master equation in Ecopath pertains to energy balance within a group (Christensen and Walters 2004):

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated energy} \quad (2)$$

where production is described as

Production = predation mortality + catches + net migration + biomass accumulation + other mortality.

### Biomass determination

As seen in Eq. 1, EwE requires biomass values that describe initial conditions in the Ecopath base model. For most of the species in the model, we used the trawl monitoring data collected from the SEAMAP and DISL datasets to determine biomass values. These values were calculated using the estimated tow distance (m) of each trawl which was calculated as the product of vessel speed ( $\text{m s}^{-1}$ ) and fishing time (s). Tow distance was then multiplied by the open trawl width of 12.95 m to obtain area swept ( $\text{m}^2$ ). Biomass measurements for individual species from each trawl were then divided by area swept to obtain species-specific estimates of biomass per area sampled ( $\text{g m}^{-2}$  or  $\text{t km}^{-2}$ ). The selection of nekton species used in the models were based on the top 90% of biomass in each of the two datasets (SEAMAP, DISL; Martin et al. 2020). Several species were split into adult and juvenile categories (multi-stanza groups) to better represent ontogenetic diet shifts that can occur in a species' life history. For organisms and groups with insufficient survey data, biomass values were sourced from previously published studies in the region (Supporting Information, Table S1). These literature values were applied to Large Coastal Sharks, Small Coastal Sharks, Dolphins, Birds of Prey, Seabirds, Pelecaniformes, Sea Turtles, Zoobenthos, Macrozooplankton, Microzooplankton, Benthic Algae, and Detritus. Some species, such as Red Drum (*Sciaenops ocellatus*) and Spotted Seatrout (*Cynoscion nebulosus*), are commonly found in the northern Gulf of Mexico but were omitted due to their lack of occurrence in the trawl datasets. This approach permitted species compartments to be consistent across

models for all Time Periods. In a few instances, species were caught in two or three Time Periods and were not caught in another period. In these cases, a value of  $0.0001 \text{ t km}^{-2}$  was entered as the biomass value (basically equating it to zero), and the species were omitted from trophic interactions for that Time Period (setting the diet matrix to blank for these species). In this way, we maintained identical potential compartments across all Time Periods.

Customarily, phytoplankton biomass in Gulf of Mexico EwE models is given a baseline value of  $25 \text{ t km}^{-2}$  in the absence of locally available phytoplankton or chlorophyll-*a* data (Okey and Mahmoudi 2002; Walters et al. 2006; De Mutsert et al. 2016; Sagarese et al. 2017), which was drawn from Steidinger's (1973) estimate. To reflect more precise estimates of changes in phytoplankton biomass over time in our study area, we used data from National Estuarine Research Reserve System-Wide Monitoring Program stations in Grand Bay, MS to calculate proportional changes in chlorophyll-*a* in each period relative to Time Period 1. Proportional changes in chlorophyll were then applied to the baseline value of  $25 \text{ t km}^{-2}$  assigned to Time Period 1 (e.g., if chlorophyll increased by 14% between Time Periods 1 and 2, then phytoplankton biomass was increased by 14%).

### Diet matrices

A baseline diet matrix was constructed using species diets reported by FishBase (www.fishbase.in), published studies, and researcher knowledge (Supporting Information, S3). The relative proportion of each prey item in a predator's diet was determined first by the proportion of the group in the trawl survey data and then by occurrence frequency in predator stomachs in literature sources and expert opinion. The baseline diet matrix was applied to each model, with several subsequent adjustments made to ensure mass-balance (Christensen 2013). The original diet matrix applied across models resulted in massive over-consumption in some functional groups. For these species, we iteratively reduced the proportional amount of consumption by predators for each prey within the diet matrix, re-balancing the model after each adjustment (see Supporting Information, S3 for more details on how each model was balanced).

### PREBAL plug-in

We acknowledge that food web models represent one potential snapshot of the system. To evaluate whether certain input parameters in our models were biologically realistic, we used the PREBAL plug-in developed specifically for Ecopath (Link 2010), as recommended in Heymans et al. (2016). For all Time Periods, estimates of biomass decreased with increasing trophic level, indicative of normal biomass decomposition patterns (Link 2010). The same pattern was true for P/B and Q/B parameters, indicating these values were acceptable model inputs since the relationship between vital rates and trophic level generally follow the same trends as body size and biomass (Link 2010). Some of the lower trophic level species (and species guilds), such as Zoobenthos and Microzooplankton,

had values that deviated from the expected pattern. We concluded these deviations were acceptable as these compartments were estimated from other similar models and are used primarily as a food source for higher trophic level species. The P/Q ratios for trophic levels in each period were also scrutinized. Acceptable P/Q ratios are expected to fall reasonably below 1.0, since a taxon cannot produce more than what is eaten (Link 2010), and the P/Q values for all functional groups across Time Periods met this criterion (Supporting Information, Fig. S1).

### Ecological network analysis

Ecological network analysis is a method of examining ecosystem structure and function (Ulanowicz 1986) and allows for comparisons among ecosystems (or the same ecosystems from different time intervals in this study). Part of this approach measures the efficiency by which energy is used, transferred, and assimilated within the system (Baird and Ulanowicz 1993). To complete this analysis, we organized canonical trophic levels, *sensu* Lindeman (1942), to allow calculation of numerous statistics (see below). Basic summary statistics calculated for the system and included in this analysis were the sum of all production, net system production, and total biomass (excluding detritus). We specifically focused on several indices that may be germane to resiliency, which included average Omnivory Index, Total System Throughput (TST), Ascendency, Overhead, and Developmental Capacity (Ulanowicz 2018; Canning and Death 2019). The Omnivory Index is more commonly used to evaluate community processes, while the metrics derived from ENA and information theory are less used in resilience studies (see Table 1 for expanded definitions of these network and information metrics). Ecopath has a built-in capability to generate ENA and information theory metrics based on Ulanowicz (1986) and are described as follows: Ulanowicz (1986, 2004) divided the indeterminacy (uncertainty) of flows in an ecosystem (network) into three information metrics (1) Developmental Capacity—the overall indeterminacy of flows; (2) Ascendency—how much of the flows are explained through structure or organization, and (3) Overhead—the remaining indeterminacy of the system. In addition, the Redundancy of the system represents the portion of the Overhead associated with the compartmental interactions, such as feeding and detrital production. It should be noted that Overhead can also be subdivided into components for imports, exports, and respiration, but these were not included here. We also considered other metrics in our analysis that included Ascendency/Capacity, Finn's Cycling Index, Finn's Mean Path Length, and mean trophic level (Table 1).

We first used the ecosystem-level metrics generated by EwE, and described above, to evaluate how flexible the model ecosystems have been through decades of large-scale disturbances. Then, in a novel application of ENA drawn from the insights of Ulanowicz and Baird (1999), Heymans

et al. (2002), Loreau and De Mazancourt (2013), and Angeler and Allen (2016), we deconstructed the ecosystem-level metrics (Table 2) and considered nekton community (Table 3) and individual taxa metrics (Fig. 2) to evaluate functional diversity in each Time Period and to identify its potential role in resilience. In other words, after evaluating the network characteristics of the entire food web, we then used subsets of these outcomes to evaluate only the nekton species whose modeled biomass was derived from the fisheries-independent surveys.

The units of the information metrics are tracked as *flow* × *bits*. These metrics can be parsed into Throughput, their flow component ( $\text{t km}^{-2} \text{ yr}^{-1}$ ) and their information component denoted in bits, derived from Shannon's equation for flow and derivatives (Ulanowicz 1986). The ecosystem-level versions of the metrics (e.g., Ascendency, Developmental Capacity, Overhead, and Redundancy) are the sums of indeterminacy associated with each compartment and its associated flow × Total System Throughput. Thus, each individual compartment or taxon can be represented as part of the sum (Heymans et al. 2002). We also created dimensionless metrics for each compartment caught in the fishery independent trawls, Redundancy/Ascendency (R/A). This index provides the flexibility of internal interactions per unit of flow relative to the amount of constraint on complexity (i.e., mutual information). That is, if a taxon has a high R/A, it should provide high potential contribution to resilience through the relative indeterminacy of its flows. That potential is realized by the amount of Throughput of the taxon.

Taxon-specific R/A was calculated for each individual nekton species or species guild and stanza (i.e., age group). Ecopath calculates taxon-specific Ascendency, Developmental Capacity, Overhead, Throughput, and respiration, but not Redundancy. We determined the taxon-specific Redundancy in two steps. First, we calculated the Overhead attributed to respiration ( $O_{res}$ ) from Eq. 3, where *Resp* is species/guild respiration and *T* represents Throughput as the sum of flows out of each compartment, not TST. Second, we calculated *Redundancy* as the difference between the taxon's total Overhead (*O*) and  $O_{res}$  (Eq. 4). This process was carried out for nekton as these species had no imports to or exports from the system.

$$O_{res} = Resp \times \log_2 \frac{Resp^2}{Resp \times T} \quad (3)$$

$$Redundancy = O - O_{res} \quad (4)$$

We then divided the flexibility component by the metric that contributes to the structure (i.e., taxon-specific Ascendency) to normalize the taxon-specific Redundancy: (R/A). Redundancy/Ascendency indexes the flexibility per unit flow relative to the taxon's contribution to organization and structure. This dimensionless metric was then scaled by the Throughput of each taxon to evaluate the potential importance to resiliency of both the informational ( $R_i/A_i$ ) and flow ( $T_i$ ) characteristics of

**Table 2.** Ecosystem level network metrics across all Time Periods. In the pattern column, NC indicates little or no change across Time Periods (TPs), P indicates a pulse response at TP 3, S indicates a step increase after TPs 1 and 2 that remains similar between TPs 3 and 4, and O indicates other patterns.

Pattern	Metric	1997–2001 (TP 1)	2007–2009 (TP 2)	2010–2012 (TP 3)	2014–2017 (TP 4)
P	Total biomass (excluding detritus, t/km <sup>2</sup> )	90	101	143	115
	Shannon's diversity index	1.6	1.72	2.10	1.52
	Overhead (flowbits)	15,484	20,270	23,618	16,444
S	Total system throughput (t/km <sup>2</sup> /year)	7252	8493	12,265	12,276
	Ascendency (flowbits)	8377	8641	15,164	14,361
	Calculated total net primary production (t/km <sup>2</sup> /year)	3008	3386	5025	5531
	Sum of all production (t/km <sup>2</sup> /year)	3498	4001	5705	6001
NC	System Omnivory index	0.15	0.14	0.18	0.16
	Mean trophic level	2.90	2.85	2.90	2.90
	Connectance index	0.12	0.12	0.11	0.12
O	Ascendency/capacity %	35.11	29.89	39.1	46.62
	Finn's cycling index (% TST)	3.08	3.86	2.08	1.72
	Finn's mean path length	2.41	2.39	2.31	2.22

**Table 3.** Summed nekton species metrics (i.e., trawl survey species for which biomass was derived from fishery independent samples). In the pattern column, NC indicates little or no change across Time Periods (TPs) and P indicates a pulse at TP 3. The step and other patterns were not observed in the nekton metrics.

Pattern	Metric	1997–2001 (TP 1)	2007–2009 (TP 2)	2010–2012 (TP 3)	2014–2017 (TP 4)
P	Total nekton biomass (t/km <sup>2</sup> )	2.45	4.95	30.71	3.22
	Nekton TST	86.68	45.43	269.54	28.61
	Nekton ascendency (flowbits)	130	79	508	69
	Nekton overhead (flowbits)	615	424	2379	320
NC	Nekton mean trophic level	2.77	2.72	2.77	2.77
	Nekton Shannon's diversity index	2.16	1.93	2.10	2.55
	Nekton ascendency/capacity %	17.4	15.6	17.6	17.7

each nekton species. The results were plotted by Time Period; the vertical axis (R/A) provides information on how each compartment partitions its contribution to flow indeterminacy but does not provide information on how much flow is going through the compartment (Fig. 2). The *x*-axis is the taxon's Throughput, and the higher this value, the more energetically important it is in the system.

## Results

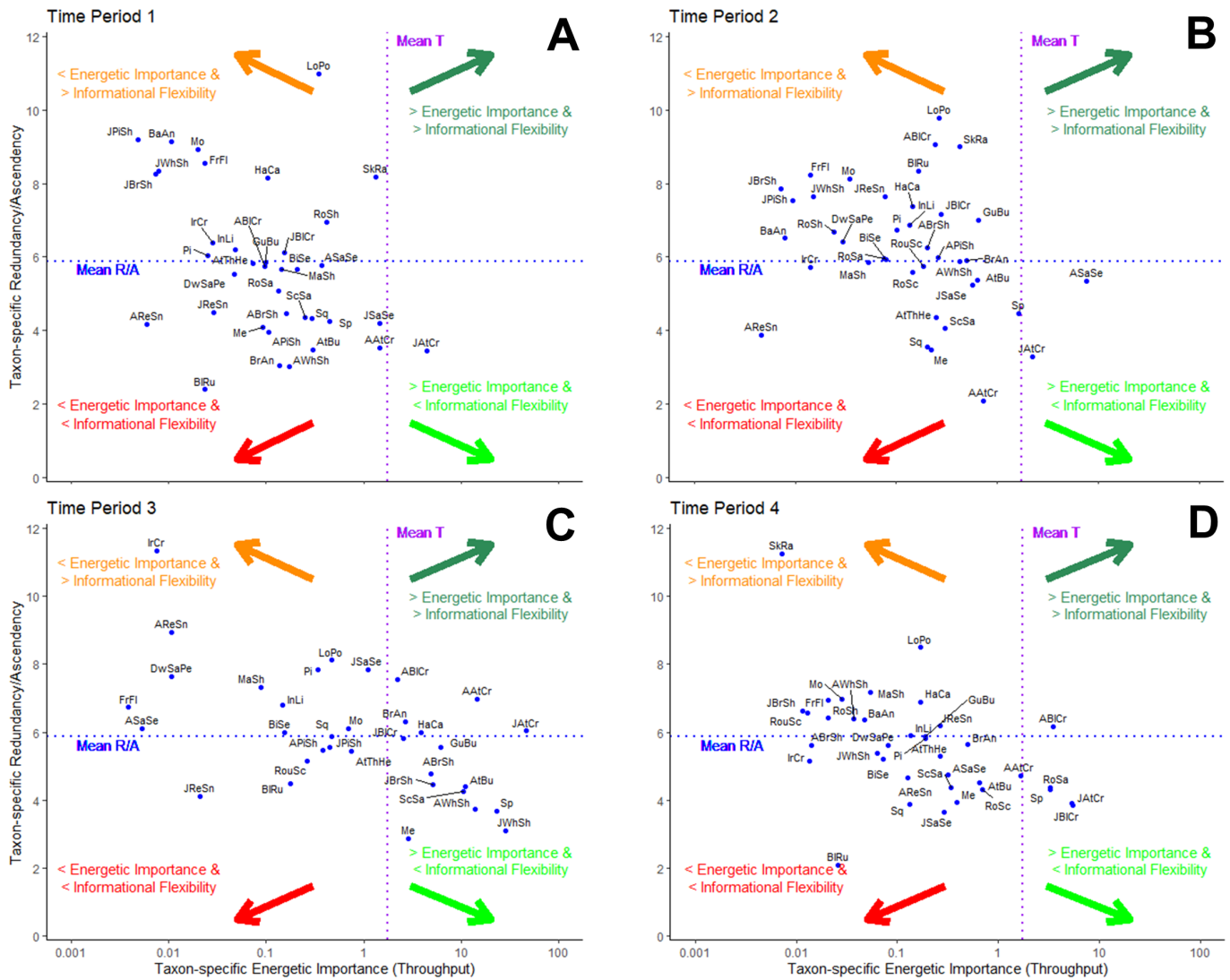
Two important points need to be made before interpreting the results. First, the patterns described below refer to a response outcome, not a type of disturbance. There is a rich body of literature that categorizes disturbances as being either pulse or press and how those types of perturbations differentially impact organisms and trophic guilds, but we make the distinction here that we are describing responses to disturbances in general, not the types of disturbances themselves.

Second, while our results make it unfeasible to use inferential statistics due to lack of samples within groups, comparisons involving large differences (generally more than a 30%–50% change in a period relative to the previous period) allowed for the interpretation of more descriptive changes in the same system over time.

### Ecosystem-level attributes

The ENA demonstrated multiple patterns of responses to the DWH disaster across Time Periods and levels of modeled food web organization. We therefore categorized the metrics by response pattern to establish shared attributes for metrics within each response type. Three patterns were prominent. First, outputs for some metrics suggest that trophic structure and energy flow did not vary greatly among the selected Time Periods (NC: little or No Change), indicating resistance. The metrics with No Change are System Omnivory





**Taxon Legend**

Common Name	Sp. Code	Common Name	Sp. Code	Common Name	Sp. Code	Common Name	Sp. Code
Juvenile Red Snapper	JReSn	Juvenile Atlantic Croaker	JAtCr	Moonfish	Mo	Juvenile Brown Shrimp	JBrSh
Adult Red Snapper	AReSn	Adult Atlantic Croaker	AAtCr	Atlantic Thread Herring	AtThHe	Adult Brown Shrimp	ABrSh
Juvenile Sand Seatrout	JSaSe	Pinfish	Pi	Dwarf Sand Perch	DwSaPe	Juvenile Pink Shrimp	JPiSh
Adult Sand Seatrout	ASaSe	Hardhead Catfish	HaCa	Squid	Sq	Adult Pink Shrimp	APiSh
Blue Runner	BIRu	Gulf Butterfish	GuBu	Bay Anchovy	BaAn	Juvenile White Shrimp	JWhSh
Bigeye Seabrobin	BiSe	Atlantic Bumper	AtBu	Broad-striped Anchovy	BrAn	Adult White Shrimp	AWhSh
Inshore Lizardfish	InLi	Longspine Porgy	LoPo	Round Sardine	RoSa	Iridescent Crab	IrCr
Skates and Rays	SkRa	Menhaden	Me	Scaled Sardine	ScSa	Juvenile Blue Crab	JBICr
Fringed Flounder	FrFl	Round Scad	RoSc	Mantis Shrimp	MaSh	Adult Blue Crab	ABICr
Spot	Sp	Rough Scad	RouSc	Roughback Shrimp	RoSh		

**Fig. 2.** Taxon-specific relative flexibility for Time Period 1 (panel **A**), Time Period 2 (panel **B**), Time Period 3 (panel **C**), and Time Period 4 (panel **D**). The dotted blue line indicates the mean R/a value across all Time Periods (5.87). Taxon-specific energetic importance (flow) is represented as taxon-specific throughput on a log<sub>10</sub> scale.



Index, mean trophic level, and Connectance Index (Table 2). Second, some metrics increased in Time Period 3 and then returned to levels similar to Time Periods 1 and 2 in Time Period 4 (P: Pulse response). Pulse responses included biomass, biomass-based diversity (Shannon's index), and Overhead (Table 2). Third, other metrics indicate that Time Periods 3 and 4 were similar to each other, but dissimilar to Time Periods 1 and 2 (S: Step response). The Step response metrics include Total System Throughput, Ascendency, total net primary production, and the sum of all production. Those metrics that do not fit into one of the above three categories, were placed into an Other (O) category: Ascendency/Capacity, Finn's Cycling Index, and Mean Path Length.

### Nekton community attributes

Several nekton community metrics had a pulse response with a transient change in Time Period 3: nekton biomass, nekton TST, Ascendency, and Overhead. The nekton-level metrics that include biomass were at times up to 90% lower compared to the totals for the entire food web (Table 3 compared to Table 2, total biomass, TST, Ascendency and Overhead). The nekton-level metrics that exhibited No Change across Time Periods were Ascendency/Capacity %, Shannon's diversity index, and mean trophic level. Results indicate that the Step and Other response patterns were not apparent in the metrics considered.

### Individual taxon attributes

We used a novel, taxon-specific ratio, Redundancy/Ascendency (R/A), to index relative informational flexibility of taxa and thereby its potential to contribute to resilience. The ratio is not directly dependent on taxon-specific Throughput. Therefore, ratios for each nekton species and species-specific age-class (where applicable) were plotted against the taxon-specific Throughput (T not TST) as a measure of the taxon's energetic importance during each period (Fig. 2). Redundancy/Ascendency values ranged from 2 to 12, with higher values indicating a greater contribution of the taxon to system flexibility than organization.

We examined the species that exceeded the mean R/A value of 5.87 (nondimensional) across all periods and/or exceeded the grand mean taxon-specific Throughput value of  $1.75 \text{ t km}^{-2}$  across all periods. There was a trend during each period for species with higher potential flexibility (i.e., higher R/A) to be among those with the least energetic importance (i.e., lower Throughput), and more energetically important species to be among those with less potential flexibility (Fig. 2). This trend eased during Time Period 3 when higher ratio species became more energetically important (i.e., moving to the right on the  $x$ -axis; Fig. 2C). Time Period 2 had the greatest number of species with R/A values that exceeded the grand mean (23 total), indicating that this period had the most species with potential to contribute to resilience. The majority of the species with greater than

average R/A values were not common across all four Time Periods, with Fringed Flounder (*Etropus crossotus*) and Longspine Porgy being the only species with consistently high R/A values ( $R/A > 6$  and  $R/A > 8$  respectively over all periods). Time Period 3 had 15 species with greater than average Throughput, compared with one taxon in Time Period 1 (juvenile Atlantic Croaker), two taxa in Time Period 2 (adult Sand Seatrout, juvenile Atlantic Croaker), and five taxa in Time Period 4 (Spot, juvenile Atlantic Croaker, Round Sardine, juvenile blue crab [*Callinectes sapidus*], adult blue crab). There were five species that showed higher than grand mean energetic importance and higher than grand mean informational flexibility in Time Period 3: adult blue crab, adult Atlantic Croaker, Broad-striped Anchovy, juvenile Atlantic Croaker, and Hardhead Catfish (Fig. 2C, upper right quadrant).

### Discussion

Developing a better understanding of how an ecosystem functionally responds following a major disturbance remains a primary goal of applied ecology (Canning and Death 2019). An equally challenging endeavor is improving how we quantitatively measure ecosystem resilience in the face of perturbations (Mouchet et al. 2010, Angeler and Allen 2016). One of the critical gaps identified in Angeler and Allen (2016); among others) is the lack of studies evaluating multiple resilience metrics and functional Redundancy across organismal guilds (Mills and Doak 1993; Heymans et al. 2002; Ellision et al. 2005). In addition, Ulanowicz (2018) described the limitations of using a single metric to characterize system resilience. We used multiple static food web models to conduct a hierarchical ENA that addresses these gaps and provides a better understanding of ecosystem resilience beyond community-level analyses by exploring resilience characteristics of the nekton community and individual taxa. Building off the previous assessment of community impacts from the DWH spill conducted by Martin et al. (2020), we extended this initial assessment to include an evaluation of impacts of the DWH disturbance on energy flow at various levels of organization in the context of resilience mechanisms. The hierarchical nature of this study confirms that ecosystem responses to disturbances are complex, given the differential results observed among ecosystem, nekton community and individual taxonomic levels. Scaffolding the ENA begins to provide some clarity to those responses.

Patterns of taxon-specific R/A emerged that were largely compatible with the hypothesis of Ulanowicz (1986, 1997, 2018), that system resiliency derives from the internal functional Redundancy of traits within a system. Redundancy/Ascendency values ranged from 2 to 12, indicating a greater contribution by all species to system flexibility rather than organization (i.e., more organization is thought to make a system more efficient, but less resilient). There was a general trend that less energetically important species (low Throughput) were

more potentially resilient (higher R/A; upper left quadrant in Fig. 2 panels). Thus, potential resilience may be reserved in numerous and relatively low-biomass species. The only high-biomass species with R/A and Throughput values above the grand means were adult Atlantic Croaker, juvenile Atlantic Croaker, and adult blue crab (Time 3 only; Fig. 2C), indicating they may be most important in actively contributing to resilience in the system. These results agree with previous studies in the region that suggest that blue crab and Atlantic Croaker have multiple redundant energy pathways and were topologically unique (McCann et al. 2017). It appears that during the period just after the DWH disturbance, species with greater capacity to contribute to resilience became more dominant in the food web (high R/A and high Throughput). We hypothesize that two major factors may have contributed, perhaps collectively, to these results. First, Atlantic Croaker are a well-known and significant proportion of commercial shrimp trawl bycatch, suggesting a decrease in fishing effort from the NOAA imposed moratorium may have played a factor here (Martin et al. 2020; Tables 2 and 3). Since the fishing moratorium likely increased the flow through Atlantic Croaker (both age groups), the management action (likely unknowingly) enhanced the resilient properties of the ecosystem, since Atlantic Croaker exhibit both high R/A and high Throughput in Time Period 3. Second, it is suspected that emigration of mobile species from the west, nearer to the site of the spill, had an influence in the increasing abundances in the period short after the spill (Time Period 3; Martin et al. 2020). We can infer that the disturbances of the DWH spill and potentially subsequent management actions resulted in an increase in biomass of species that had the most flexibility in their food web interactions and that they had enough biomass to realize the amount of Throughput needed to effect resilience or resistance.

The R/A analysis is unique and represents an extension of this idea used by Christian et al. (2010). In that study, the authors separated Throughput from the nondimensional Ascendency/Overhead (A/O) to track the effects of eutrophication on nitrogen cycles among multiple lagoonal ecosystems. This approach, in turn, was an application of the use of information theory to assess ecosystem health (Mageau 1995). Christian et al. (2010) found that eutrophic lagoons had lower A/O values with high TST (i.e., eutrophic systems). Here, we use R/A, which accentuates relative indeterminacy (uncertainty of flows), flexibility, and thereby potential resilience. The advantage of using Redundancy instead of Overhead is that Redundancy captures more directly the indeterminacy of compartment interactions. The potential resilience of a nekton species is represented by R/A but must be put into context with the species' Throughput to assess its broader contribution to resilience (Fig. 2). Contributions to resilience increase as both R/A and Throughput increase.

The Pulse and No Change responses illustrate characteristics of resilience in the system. The pulse in the Overhead metric implies an increase in functional Redundancy in the

system during Time Period 3. Overhead, a product of the indeterminate component of Shannon's diversity index  $n$  and TST (which both increased at the ecosystem and nekton levels in Time Period 3) indicates that flow among compartments increased the flexibility of the system in the months following the spill, allowing for the system to return to its previous state by Time Period 4. The increase in system Overhead also proposes a link to the increase in the size of the flows driven by nekton biomass increases during the fishing moratorium or temporary shifts of biomass from west to east. Metrics of No Change also suggest resistance to disturbance for some aspects of the food web. Results at both the ecosystem (Table 2) and nekton level (Table 3) show that while biomass increased dramatically during Time Period 3 (41% and 520% change respectively), mean trophic levels, Omnivory Index, and Connectance Index remain relatively stable over all Time Periods. Taken together, these measures of the food web suggest that the general food web structure in the face of DWH remained relatively constant (Fath et al. 2019). That is, the general interrelationships of groups and position within the model food webs are indexed by these metrics. Thus, while the overall flow of energy increased and changes in importance of groups shifted with Pulse or Step responses, the general structure of the food web remained similar over the Time Periods, which suggests resistance.

Metrics that exhibit a Step response at the ecosystem level suggest that some aspects of the food web display a decreased ability to return to predisturbance conditions; however, this conclusion is complicated. The Step responses of TST, Ascendency, and productivity metrics (at the ecosystem level) show dominant flow increases that ranged from 55% to 73% change between Time Periods 1 and 2 and Time Periods 3 and 4. Changes in total primary production, multi-species lower trophic level compartments and detrital activities appear to be driving this pattern. Total net primary production increased from 3000 to 3400  $\text{t km}^{-2} \text{ yr}^{-1}$  during Periods 1 and 2 to over 5000  $\text{t km}^{-2} \text{ yr}^{-1}$  during and post DWH Time Periods. These flows represent >85% of total production and contribute significantly to the TST. Ascendency, the product of TST and average mutual information (i.e., a metric of constraint on flow), shows a clear increase in the latter two Time Periods as well. Total System Throughput drove the change in Ascendency with the latter two periods averaging 56% increase over the former because the average mutual information in the latter periods increased on average only 11%. We then conclude that most of the food web organization represented by increased Ascendency is linked to the amplified processing of carbon (high primary productivity) and energy rather than shifts in flow distribution to greater constraint. Given this conclusion, the interpretation that increased Ascendency reduces resilience of the entire system may be overstated in this case given the strong influence of primary production (Ulanowicz 1997; Christian et al. 2010).

Given the nonuniform but explainable responses, we make the case for evaluating resilience metrics at multiple levels of organization using an ENA. Our results support the hypothesis that the informational relationship between community stability and disturbance can be considered as a function of species position and connections in the food web. That is, a species' position in the food web may be a determinant of response to disturbance and therefore provide mechanistic insight for how resilient the system may be to disturbance. For instance, if Ascendency were only evaluated at the ecosystem level, the interaction effect between increased productivity and the increased biomass could be overlooked. In other words, productivity and Throughput dominate any changes in the topology of the food web. Identifying synergistic effects of the production metrics and the increases in nekton biomass gives a unique perspective in understanding the stability of the system and the complexities of describing an ecosystem as stable or otherwise.

To our knowledge, no other investigation has continued a community-level analysis (i.e., Martin et al. 2020) with an investigation of system energy flow and functional diversity in the context of resilience. This scaffolded approach to research gave us the ability to test one of the primary conclusions in Martin et al. (2020) - a "short-term ecosystem-wide restructuring occurred in the food web after the spill and that there may be alterations to energy flow within the system." Here, we can confirm that the hypothesized short-term changes in energy flow did occur through several specific compartments (e.g., Atlantic Bumper, Atlantic Croaker, Gulf Butterfish, Longspine Porgy, blue crab) and these changes allow for both the flexibility and enough energy flow to provide resilience properties to the system. These same species (with the exception of blue crab) exhibit a Pulse response in abundance in Time Period 3 in Martin et al. (2020), but without an understanding of their potential network flexibility, we could not verify that a pulse in abundance helped to create resilient properties.

## Conclusion

All modeling studies have limitations. As previously mentioned, given the limits in power, we could not use inferential statistics to compare metrics across Time Periods and thus had to consider qualitative trends over time. While fishery independent data were used to develop the food web models herein, certain decisions on grouping species were made to invoke parsimony, which thus deviates the modeled system from reality and limits the interpretation of results. A shortcoming of modeling studies globally is the dearth of diet data from any particular system, collected consistently over time. The ability to create models using trophic data specific to both time and space would provide a more realistic understanding of system dynamics. Thus, we urge fishery management agencies to allocate funds for

spatial-temporal diet monitoring programs, which would give managers more confidence in the interpretation of modeled outcomes. As the use of food web models as part of ecosystem-based fisheries management and environmental impact studies continue to expand, the need for more refined data will increase as well.

Hindsight also showed us that primary production and potentially the eutrophication of the system drove many of the ecosystem level metrics. To obtain a deeper understanding of energy flow through these lower trophic levels, we suggest future food web models used for ENAs consider more compartments for primary consumers and small consumers. These data are known to be challenging to obtain, so we again call for the expansion of monitoring programs in the northern Gulf of Mexico and in all our global coastal systems to address these limitations.

One final note about the functional groups chosen for the four models constructed in comparison with similar models in the region (e.g., Walters et al. 2008; De Mutsert et al. 2016). We chose to omit two recreationally important fishery species, Red Drum and Spotted Seatrout from our species list, given that we did not catch any of those organisms in the fish surveys. We do acknowledge these two species are found in the study area, but given historical sampling experience using various gear types, they are more ubiquitous inshore, rather on the seaward side of Dauphin Island, Alabama. The distribution for Seatrout is driven mostly by the availability of their preferred inshore marsh habitat, and our model area is mostly unvegetated sandy bottom. In the case of Red Drum, we incorporated other Sciaenids in the model, such as Atlantic Croaker and Spot that are closely related and fill similar trophic niches. Given that these two species were not caught in the our survey gear and that other species with higher biomasses filled a similar niche, we moved forward without these two species in the model.

These nuanced results using energy flow beyond biomass or abundance metrics, revealed some of the mechanisms that drive system stability and suggest this region of the northern Gulf of Mexico has exhibited characteristics of a resilient system to disturbances like the DWH spill. But if the eutrophication we modeled is occurring, this resilience may be compromised. Moreover, we provided quantitative data that aligned with conclusions in Martin et al. (2020), that suggested a short-term change in energy flow occurred through several specific nekton species. This change allowed the food web enough energy and flexibility to promote resilience properties system wide. Applying this methodology to other systems will help determine if these outcomes can be replicated, and if similar examples can be generated, natural resource managers will develop a deeper understanding of which species and/or processes are driving resilience in their systems. Still left to debate, and outside of the scope of this paper, is if the baseline the system returned to in Time Periods 1 and 2, are indicative of a thriving system.

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### Conflict of interest

None declared.

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