Key taxa in food web responses to stressors: the *Deepwater Horizon* oil spill

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Identifying key taxa in the response of ecosystems to perturbations relies on quantifying both their sensitivity to stressors and their importance in the overall web of interactions. If sensitive taxa occupy key network positions, then they may decrease the capacity of ecosystems to resist perturbations. Despite widespread concern for coastal marshes after the 2010 *Deepwater Horizon* oil spill in the Gulf of Mexico, impacts on individual taxa were variable, and the effects on the overall marsh food web have not been assessed. Here, we synthesize published studies on trophic relationships and oil sensitivity to identify critical taxa in the response of marsh food webs to the oil spill. Taxa such as carnivorous marsh fishes are expected to enhance resilience, while gulls, terns, and omnivorous snails may destabilize the food web. Our framework for identifying key taxa can be applied to other environmental stressors or ecosystems if both the sensitivity of individual taxa to a stressor and the food web structure are known.

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At a time when ecosystems face multiple threats, predicting the future of biodiversity is an essential task for ecologists (Mouquet *et al*. 2015). Identifying critical taxa for ecosystem responses to environmental stressors relies on quantifying both the sensitivity of individual taxa and their importance in the overall web of interactions. The occurrence of especially sensitive taxa in important network positions could decrease the capacity of ecosystems to resist perturbations (Mills *et al*. 1993; Ellison *et al*. 2005). The role of an individual taxon in the response of a food web to a stressor will depend on both its sensitivity to that stressor and its importance to food web structure and dynamics (by "importance" we mean that it is highly connected and topologically unique [occupies a unique position in the food web]). For example, if a taxon is sensitive and topologically important in the food web, then negative effects on this taxon (eg reduced abundance) may have cascading consequences throughout the food web (such taxa are characterized as "critically sensitive"; Figure 1). These are the taxa of greatest concern, because they have the potential to alter or destabilize the food web. On the other hand, key taxa for providing resilience might be those that play a vital role within the food web and are relatively insensitive to perturbations ("critically resilient"; Figure 1). These taxa should buffer the food web against the effects of the perturbation. On the other hand, one might expect few indirect effects on the food web from taxa that are highly sensitive, but are not topologically important ("Sensitive, but few food web effects"; Figure 1). We use this framework to assess the role of individual taxa in the responses of coastal marsh food webs to the *Deepwater Horizon* oil spill, one of the most serious environmental stressors in recent history.

In a nutshell:

- We present an approach for predicting the role of individual taxa in the response of food webs to perturbations, and use this framework to quantify the relative trophic importance and oil sensitivity of salt marsh organisms to the 2010 *Deepwater Horizon* spill
- Our synthesis identified taxa that are expected to enhance the resilience of or to destabilize the food web in response to an oil spill
- This work highlights research priorities to improve current understanding of marsh food webs and taxa whose sensitivity to oil is unknown

The 2010 *Deepwater Horizon* (DWH) oil spill released nearly 5 million barrels of crude oil into the Gulf of Mexico (GOM) and over 1000 km of shoreline were oiled. Louisiana marshes were the most affected (BPOSC 2011). Despite expectations of catastrophic effects for the economically and ecologically important coastal environments of the Gulf Coast, impacts on these habitats have been variable and are still being evaluated. Most research on the DWH effects on coastal environments has focused

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on particular species or assemblages (eg marsh vegetation, Lin and Mendelssohn 2012; marsh fishes, Able *et al.* 2015; bottlenose dolphins [*Tursiops truncatus*], Lane *et al.* 2015). For some marsh taxa, severe negative impacts were observed at the organismal level (eg genomic, physiological, and developmental impacts; Garcia *et al.* 2012; Whitehead *et al.* 2012; Dubansky *et al.* 2013), but only moderate negative effects or rapid recovery occurred at the population level (McCall and Pennings 2012; Moody *et al.* 2013; Fodrie *et al.* 2014). Like other environmental stressors, the impacts of oil spills on individual species can lead to indirect effects that affect other portions of the food web (Fleeger *et al.* 2003). Nevertheless, there have been few attempts to understand the effects of the DWH spill on the structure or dynamics of coastal food webs. A holistic understanding of the effects of the DWH spill is essential because the delivery of valuable ecosystem services (including coastal protection, nurseries for fisheries, and nutrient cycling; Barbier *et al.* 2011) by coastal environments such as salt marshes is linked to the overall functioning of the food web. A food web perspective may also explain how apparently positive effects of oil on some taxa can occur via indirect effects (Fleeger *et al.* 2003).

Here, we classify salt marsh taxa based on their topological importance in the food web and their sensitivity to oil to understand the response of marsh food webs to the DWH oil spill and to inform predictions about potential effects of future oil spills on this coastal Louisiana ecosystem. Quantitative field sampling of the complete marsh food web before and after the DWH spill would have been one means for understanding the holistic effects of oil, but to our knowledge, no such study was completed. However, we constructed a food web network model from published studies and our field experience (eg Fodrie *et al.* 2014; Able *et al.* 2015) to synthesize the current understanding of marsh food webs.

First, a model of the marsh food web was needed to quantify the importance of individual taxa to the marsh food web. While published food webs exist for nearby habitats (eg Lake Pontchartrain [Davis 2009], Breton Sound [de Mutsert *et al.* 2012], or open-water areas [de Lewis *et al.* 2016; Mutsert *et al.* 2016]), none explicitly include the marsh platform (intertidal vegetated areas) and its associated organisms. Therefore, we assembled a food web that represents a complete Louisiana salt marsh, including aquatic and terrestrial organisms in multiple sub-habitats, such as the marsh platform, creeks, ponds, and subtidal edges. We built the food web to represent marshes in the Barataria Bay region of Louisiana, where some of the heaviest shoreline oiling occurred (Michel *et al.* 2013) and where many of the authors are currently conducting field studies (eg Able *et al.* 2015); however, the model can also serve as a starting point for studies on other marsh habitats. The oil sensitivity of marsh taxa was also evaluated from a synthesis of research, including the growing number of studies conducted in the aftermath of the DWH spill and published as of March 2016.

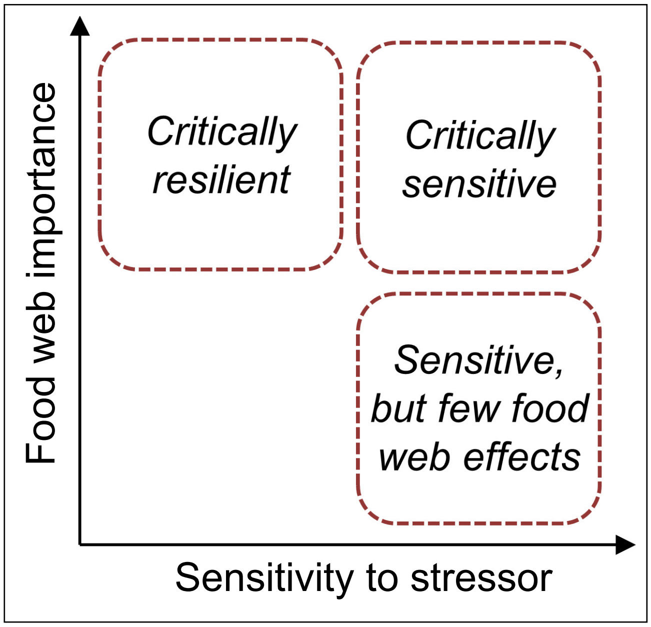


Figure 1. *Schematic of identifying key taxa in the response of food webs to environmental stressors using food web importance and sensitivity to a stressor.*

In addition to identifying key indicator taxa in marshes affected by oil spills, we highlight important information gaps in the current understanding of both the food web ecology of Louisiana marshes and the sensitivity of marsh taxa to oil. This work will therefore help identify future research needs in both areas. Furthermore, our approach allows for an assessment of future environmental disturbances and can be applied to other natural or anthropogenic stressors that act in a variety of ecosystems, including marshes.

■ Building the food web

To construct a food web of a Louisiana salt marsh, we conducted a literature review of studies documenting feeding interactions between marsh-associated consumers and resources. We developed a list of potential taxa in the food web based on field sampling efforts in the Barataria Bay region (McCall and Pennings 2012; Bergeon Burns *et al.* 2014; Able *et al.* 2015) and from published food webs from the nearby region (Davis 2009; de Mutsert *et al.* 2012, 2016; Lewis *et al.* 2016). The list of taxa in the food web was expanded when additional species were identified as either consumers or resources during the course of the literature search.

We included a feeding link between a consumer–resource pair when a study reported direct observations of feeding (ie visually in the field, experimentally, or via analysis of gut contents or scat). In some cases, studies of closely related species, studies from outside of GOM salt marshes, expert opinion of the authors, or stable isotope studies were used to further refine or identify feeding links. To exclude taxa that are consumed rarely or are transient in the marsh, we included a feeding link only if the gut content consisted of greater than 5% of that item (by volume or mass). If a study reported an unweighted list of diet items, we assumed that all items represented common dietary resources and feeding connections were included. Due to differences in diet resolution between studies, we combined several species or life stages into aggregated nodes in the food web on many occasions (see Panel 1 for definitions of "nodes" and other special terms associated with food web networks). For example, if some studies reported a diet item as "bivalves" while others reported a particular species (eg eastern oyster [*Crassostrea virginica*]), an aggregated node for all bivalves was included in the food web. In other cases, we used expert opinion and assumed that a consumer feeds on all species within a taxon (eg if many studies listed "insects" as a diet item, all appropriate insect nodes were connected to that consumer). Although aggregation of species into nodes will have some effect on the results of this analysis, there is no clear pattern of directional bias regarding our interpretation of food web importance. For instance, if a number of primary producer species were aggregated into a single node (eg "phytoplankton"), this would affect food web indices of the resources and their consumers differently. The single phytoplankton node might have a higher out-degree since the total number of consumers of the aggregated node could be greater than any single phytoplankton species. On the other hand, the in-degree of a consumer that eats five phytoplankton species would be one, rather than five if all phytoplankton species received their own nodes.

We synthesized data from 124 studies to develop our food web. A full list of feeding links and the sources used for their justification, as well as the complete diet matrix, are available (McCann *et al.* 2016). A list of taxa included in each node of the food web is provided in WebTable 1. The final version of the food web contains 52 nodes (including a non-living detritus node) and 376 links (Figure 2). Our index of food web importance quantifies the topological position of taxa by combining several network indices measuring the connectedness and unique-

Panel 1. Using ecological network analysis to define food web importance

Network terminology

- ***Nodes:*** The entities of a network that interact; also known as vertices. In the case of a food web, these are species, life stages of species, or assemblages, and are collectively called taxa here. In this study, we aggregated multiple species or life stages into nodes based on available data and their trophic similarity.
- ***Edges:*** The interactions or connections between nodes; also known as links. In the case of a food web, these are the consumer–resource interactions between nodes.
- ***Directed* versus *undirected edges:*** Directed edges specify a direction of the interaction; undirected edges do not. In the case of a food web, edges are directed and typically point from the resource to the consumer (ie in the direction of energy flow).
- ***Weighted* versus *unweighted edges:*** Edges can have a strength of interaction (weighted) or simply indicate the presence or absence of an interaction (unweighted). In the case of this study, our food web has unweighted edges. Food webs can have weighted edges that represent carbon flow, per capita interaction strengths, or other measures of interaction intensity.

Network indices

The tools of network analysis offer several measures that can describe the position of a taxon within a food web (Borrett *et al.* 2013). A number of centrality indices exist, including those used here on our directed, unweighted network:

- ***In-Degree:*** The number of edges going into a node. Equal to the number of prey items that a node feeds on. Generalist consumers will have a higher in-degree than specialists. For the lowest trophic levels in our food web, in-degree will be 0, since they have no resources.
- ***Out-Degree:*** The number of edges going out of a node. Equal to the number of predators that feed on a node. Nodes at higher trophic levels may be expected to have a lower out-degree, since they have fewer predators. Higher out-degree suggests that more consumers use that taxon as a resource.
- ***Betweenness:*** The number of shortest paths from all nodes to all others that pass through a node. Betweenness will typically be higher for nodes at intermediate trophic levels.

Other network indices can quantify a node's importance by its uniqueness in the network, including:

- ***Regular equivalence:*** Two nodes are regularly equivalent if they interact with nodes with similar network positions (but not necessarily the same nodes). The sum of all regular equivalence values between a focal node and all other nodes in the network quantifies the uniqueness of that node in the network (Lai *et al.* 2012).

Defining food web importance

We developed a food web importance score that combines network indices capturing several aspects of topological connectedness and uniqueness, and avoids highly correlated indices (Scotti and Jordán 2010). Taxa that are both highly connected (ie central) and topologically unique were considered the most important according to our index. We calculated the in-degree, out-degree, and betweenness for all nodes (excluding the non-living node, detritus) using the R package igraph and calculated the regular equivalence values using the R package blockmodeling (Ziberna 2015). The four network indices (ie in-degree, out-degree, betweenness, and sum of regular equivalences) were then scaled as a z-score (by subtracting the mean and dividing by the standard deviation). To combine the four indices into one, the scaled values were averaged to determine a single food web importance score for each node. This definition of food web importance could also be used in weighted networks, where link strengths would weight each of the network indices. The values of each network index and the overall food web importance score for each node are presented in WebTable 2.

ness of the taxa in the food web. Taxa that are both highly connected (ie central) and topologically unique were considered to be the most important. Details of quantifying food web importance are described in Panel 1.

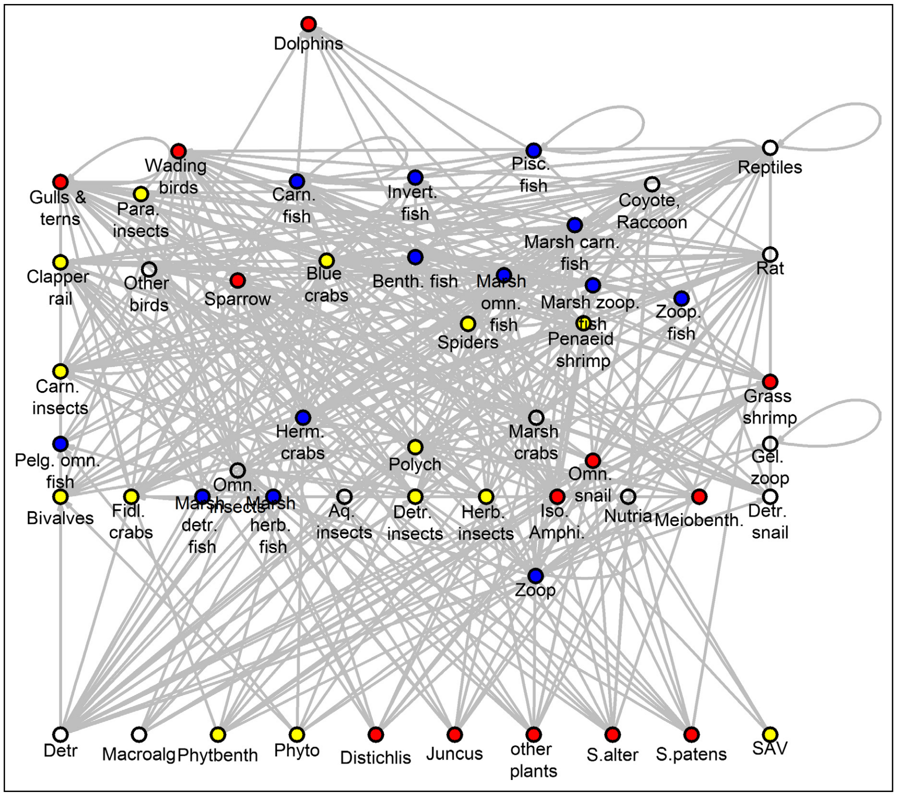


Figure 2. *The salt marsh food web with oil sensitivity ratings for each node. Clear circles indicate no data available, whereas blue, yellow, and red circles depict sensitivity scores of 0, 1, and 2, respectively. Nodes are arranged so that trophic level increases vertically. A list of taxa aggregated in each node and complete node labels are provided in WebTable 1.*

Determining sensitivity

The relative sensitivity of salt marsh taxa to oil was determined by a literature review of studies documenting population-level impacts of the DWH oil spill on marsh organisms (ie effects on densities or abundances in the field). We used the references cited in each study we found, our knowledge of the literature, and data available from the Natural Resource Damage Assessment up to February 2016 (DHNRDAT 2016) to identify additional studies that were not discovered in the initial search. If studies on DWH impacts were unavailable for a particular taxon, we expanded the search to include other oil spills inside the GOM, spills outside of the GOM, or laboratory experiments. In some cases, if physiological impacts in the field were well documented and widespread, population-level impacts were inferred. We opted not to weight studies based on their experimental design (ie laboratory versus field), since there is no clear consensus whether a controlled but highly simplified laboratory study or an uncontrolled but realistically complex field study should be given greater weight. We excluded assessments of the effects of chemical dispersants (artificial compounds used in spill mitigation efforts, to break up oil in aquatic settings) on marsh organisms, because >98% of dispersants were applied >18 km offshore (DHNRDAT 2016) and high concentrations of dispersants were found only in the immediate vicinity of the wellhead (Gray *et al.* 2014).

On the basis of this literature, we developed an oil sensitivity index to score each node of our diet matrix. Each unique taxon in a study was scored as a 0 for no response observed at any level of oiling (including differences that were not statistically significant); 1 for a weak but statistically significant population response (including taxa that had rapid recovery); or 2 for a strong and statistically significant population response, especially those taxa that showed slow or no recovery. Taxa that exhibited a positive response to oil (ie increased biomass or density) received a 0, since this outcome was likely a result of indirect effects (eg predators or competitors were negatively impacted or the large-scale closure of fisheries in the northern GOM in 2010 [Fodrie and Heck 2011]). If multiple studies evaluated oil sensitivity in the same taxon, then the sensitivity scores were combined. Subsequently, taxa with oil sensitivity scores were matched to the nodes named in our food web. Similarly, if there were multiple taxa in a node with individual oil sensitivity scores, then an overall score for the node was determined by combining the individual scores.

Our scoring of oil sensitivity was based on 37 studies. Oil sensitivity scores and data sources for all food web nodes are available in McCann *et al.* (2016). Of the 51 nodes in the food web (detritus excluded), 11 did not have any data on oil sensitivity. Thirteen, fourteen, and thirteen nodes received oil sensitivity scores of 0, 1, and 2, respectively (Figures 2 and 3). Potential direct and indirect consequences of oiling on the food web through the most sensitive taxa are explored in WebPanel 1.

Identifying critical food web components

Critically sensitive

Negative impacts on critically sensitive marsh taxa can lead to a destabilization of the overall food web. Gulls

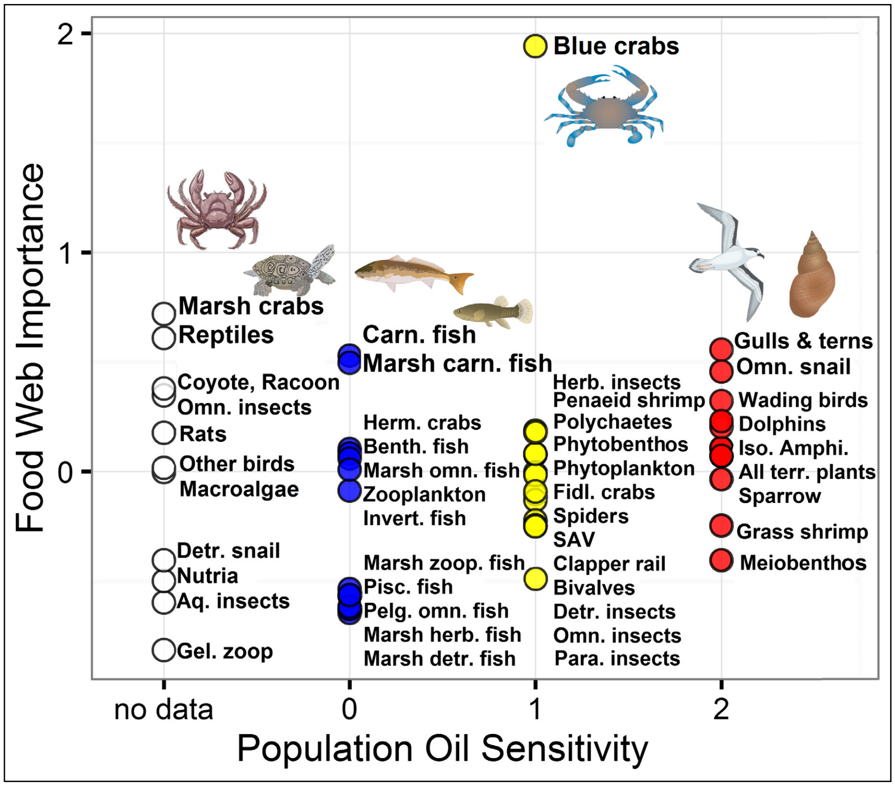


Figure 3. *Food web importance and oil sensitivity ratings of salt marsh taxa. Food web importance values were scaled and standardized (ie z-scores), so a score of 0 is the average food web importance value. A list of taxa aggregated in each node and complete node labels are provided in WebTable 1. Source of organism images: http://ian.umces.edu/imagelibrary.*

and terns, omnivorous snails, and wading birds had high oil sensitivity and high food web importance (ie such taxa were designated as highly connected and topologically unique) and can be considered critically sensitive in the response of the marsh food web to oil (Figure 3; Figure 4, a and b). Gulls and terns had the fourth highest food web importance score (out of 51 nodes) and are highly sensitive to oil, with a 12–32% population mortality in the aftermath of the DWH based on surveys of carcasses (Haney *et al.* 2014). The omnivorous snail *Littoraria irrorata*, an intermediate consumer in the food web (effective trophic level: 2.15), had high food web importance (rank 7 of 51). Despite evidence showing equivocal effects of oil (McCall and Pennings 2012), this group was rated as highly sensitive given that numerous studies documented 50–100% reduction of snails after the DWH spill (Silliman *et al.* 2012; Zengel *et al.* 2015, 2016). Wading birds – including herons, egrets, and ibises – should also be categorized as a potentially destabilizing node in the food web because of their high topological importance (rank 10 of 51) and high sensitivity to oil (DHNRDAT 2016). Other taxa that may be critically sensitive include bottlenose dolphins, isopods and amphipods, and terrestrial plants, because of their above-average food web importance scores and high sensitivity (Figure 3).

Critically resilient

Carnivorous fish living on the marsh platform, creeks, and ponds ("Marsh carn fish") and those living primarily in the open water off of the marsh complex ("Carn fish") should enhance the resilience of the food web in the aftermath of an oil spill, given their high food web importance and low oil sensitivity (Figure 3). Carnivorous fishes living in marsh habitats – such as Gulf killifish (*Fundulus grandis*), bayou killifish (*Fundulus pulvereus*), and rainwater killifish (*Lucania parva*) – are highly important to the food web (rank 6 of 51). In comparisons of unoiled and oiled sites and Before-After-Control-Impact (BACI) designs, carnivorous marsh fishes were considerably resilient to the toxic effects of oil at the population level (Rozas *et al.* 2000; Roth and Baltz 2009; Able *et al.* 2015), despite showing strong negative physiological and developmental impacts at the individual level (reviewed by Fodrie *et al.* [2014]). Carnivorous fishes living off the marsh platform include gafftopsail catfish (*Bagre marinus*), spotted gar (*Lepisosteus oculatus*), black drum (*Pogonias cromis*), spotted seatrout (*Cynoscion nebulosus*), and red drum (*Sciaenops ocellatus*) (rank 5 of 51). These fishes were also highly important to the food web and insensitive to oil, and should therefore enhance the resilience of the ecosystem. Other taxa that may be critically resilient include hermit crabs and large fish species feeding on the benthos of the marsh edge (eg croaker [*Micropogonias undulatus*], hardhead catfish [*Arius felis*], and spot [*Leiostomus xanthurus*]) (Figure 3 and Figure 4c).

Sensitive, but few food web effects

Although some nodes with high oil sensitivity, such as meiobenthos and grass shrimp (*Palaemonetes pugio* and *P anternnarius*), may experience severe oil-related impacts, due to their low food web importance the negative effects of oil on these taxa are less likely to have indirect effects for the rest of the food web (Figure 3). Because grass shrimp are less important in the food web (rank 38 of 51), strong negative effects of oil on this group (Rozas *et al.* 2000; Moody *et al.*

2013) should have few consequences for the rest of the ecosystem. Meiobenthos – including nematodes, ostracods, and harpacticoid copepods – experienced high mortality due to oil contamination of sediments and in some cases had yet to recover after more than 4 years since the DWH spill (Carman *et al.* 2000; Fleeger *et al.* 2015). Nevertheless, negative effects of oil on the meiobenthos node may not propagate throughout the food web due to a relatively low food web importance compared to other nodes (rank 40 of 51).

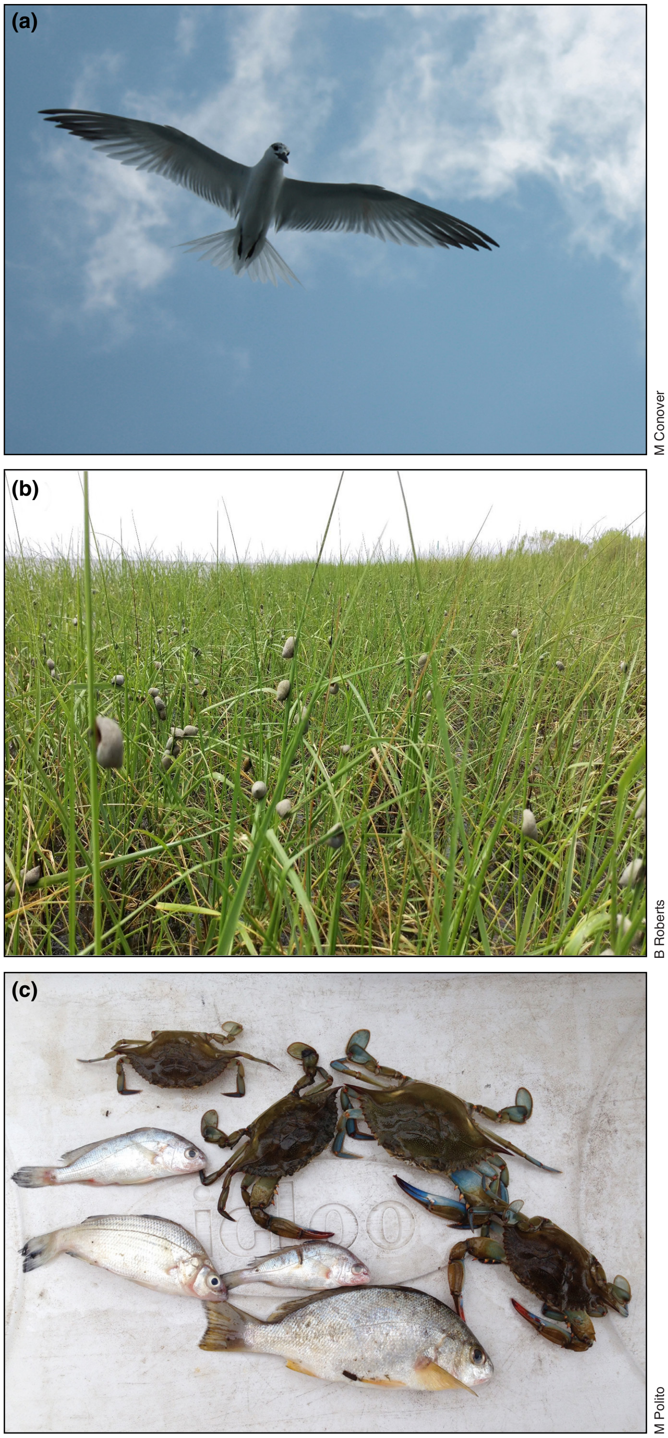
Uncertain consequences for the food web

Blue crabs were the most important node to food web structure (rank 1 of 51), but were only moderately sensitive to oil. It is unclear what role they will play in the food web response to oil (Figure 3 and Figure 4c). We cannot say definitively whether a highly important node with a moderate oil sensitivity score of 1 will be stabilizing or destabilizing for the food web after an oil spill. Abundances of adult blue crabs were unchanged in the field following the DWH event, but early life stages (ie larvae and megalopae) were less abundant (Moody *et al.* 2013; Grey *et al.* 2015). Future work is needed to clarify the indirect effects of oil mediated through this critical species throughout its life stages.

■ Research needs

For 11 of the 51 nodes in the food web (excluding detritus), there were no published studies examining their sensitivity to oil. Some of the nodes without sensitivity data are topologically important in the food web, including marsh crabs (eg *Armases cinereum*; rank 2), reptiles (eg snakes, terrapins, and alligators; rank 3), omnivorous terrestrial mammals (ie coyotes and raccoons; rank 7), and omnivorous insects (some species of katydids and the non-insect, hexapod springtails; rank 9). Determining the sensitivity to oil spills of these structurally important nodes should be prioritized.

While this work represents substantial progress by synthesizing a large amount of information on marsh food webs, many trophic interactions, particularly at lower trophic levels, remain only coarsely resolved. Improving the taxonomic resolution of groups such as primary producers is limited by the fact that most studies reporting a consumer's diet do not identify the actual species consumed. For example, a study may simply list "marsh grass", "algae", or "phytoplankton" as components of a consumer's diet. So although we may be able to identify the individual species that make up a node in this food web, increasing their taxonomic resolution and reducing the degree of aggregation are not possible because of the nature of most published studies of primary consumers' diets. Furthermore, a food web model with weighted links (eg carbon flow, per capita interaction strengths) should be developed in the future. Data on weighted interactions will provide additional insight into the food web importance of nodes (Borrett *et al.* 2013) and may be used to generate a different assessment of food web importance. For instance, the importance of foundation species (ie terrestrial marsh plants) or keystone species may be greater in a network that is based on weighted



M Conover

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Figure 4. *(a) Laughing gull (*Larus atricilla*); (b) the omnivorous snail* Littoraria irrorata *on* Spartina alterniflora*; and (c) blue crabs (*Callinectes sapidus*) and assorted fish, including spot (*Leiostomus xanthurus*).*

links such as carbon flow than in an unweighted network. Future investigations should also consider nontrophic interactions – for instance, creation of habitat refugia – when quantifying importance to the ecosystem, as well as focus on the sublethal effects of oil (those without direct mortality, such as changes to foraging, predator recognition, behavior, and fecundity) that may have food web consequences.

Our salt marsh food web model focused on the Barataria Bay region and incorporated multiple marsh sub-habitats therein. By adjusting for spatiotemporal variation in the structure of the food web observed within the greater GOM region and at different times of the year, this model could be adapted to predict responses to oil spills at particular sites or under specific conditions of interest.

■ Conclusions

This work introduces a general framework for assessing the role of individual taxa in food web responses to environmental stressors. By synthesizing results from the published literature (including field-based studies), we have introduced a general framework for identifying key taxa in the Louisiana salt marsh food web and assessing their roles in response to the DWH oil spill; our framework can also be used to make predictions about future spills in marsh ecosystems. While some organisms are expected to enhance food web resilience (such as the "critically resilient" carnivorous marsh fishes and carnivorous off-marsh fishes), others may make the overall food web more sensitive to oil (including "critically sensitive" taxa, such as gulls and terns, omnivorous snails, and wading birds). Negative effects of oil on taxa with low food web importance should not propagate throughout the food web (taxa like meiobenthos and grass shrimp, which were designated as "sensitive, but [with] few food web effects").

This effort has also helped identify information gaps – in particular, recognizing taxa that play important roles in the marsh food web but that currently lack data regarding their relative sensitivity to oil (eg marsh crabs; reptiles such as snakes, terrapins, and alligators; and omnivorous insects). Understanding the impacts of oil on these organisms is essential. Finally, in addition to oil spills, there are other environmental threats to coastal GOM ecosystems, including eutrophication, fisheries overharvest, sea-level rise, and an altered hydroperiod [time spent inundated]). This work is relevant to those environmental stressors as well. For example, a synthesis of published studies on salinity tolerances of marsh taxa could be conducted to predict taxa that are key to a marsh food web's response to freshwater diversions, an emerging environmental risk throughout the coastal Louisiana region (eg Kearney *et al.* 2011; de Mutsert *et al.* 2012). Regardless of the threat, organisms with high food web importance should be a conservation priority because of the potential for negative effects cascading throughout the rest of the food web (Mills *et al.* 2013).

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1474/suppinfo