Science of the Total Environment 859 (2023) 160245

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Review

Contaminants disrupt aquatic food webs via decreased consumer efficiency

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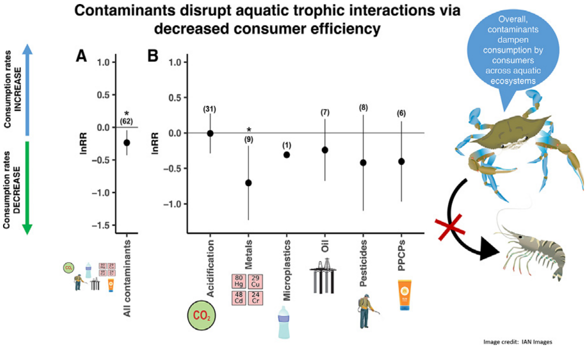
HIGHLIGHTS

- Overall, contaminants reduce consumption rates across aquatic ecosystems.
- Contaminants disproportionately impact consumers relative to resource taxa.
- Contaminants have greater negative effects on primary consumers with sedentary resources.
- Metal contaminants have relatively strong dampening effects on consumption.
- 33 % of studies expose contaminants to only consumer or resource, not both.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Daniel A. Wunderlin

Keywords:
Consumer-resource interactions
Meta-analysis
Acidification
Heavy metals
Oil
Pesticides

ABSTRACT

Changes in consumer-resource dynamics due to environmental stressors can alter energy flows or key interactions within food webs, with potential for cascading effects at population, community, and ecosystem levels. We conducted a meta-analysis to quantify the direction and magnitude of changes in consumption rates following exposure of consumer-resource pairs within freshwater-brackish and marine systems to anthropogenic CO_2, heavy metals, microplastics, oil, pesticides, or pharmaceuticals. Across all contaminants, exposure generally decreased consumption rates, likely due to reduced consumer mobility or search efficiency. These negative effects on consumers appeared to outweigh co-occurring reductions in prey vigilance or antipredator behaviors following contaminant exposure. Consumption was particularly dampened in freshwater-brackish systems, for consumers with sedentary prey, and for lower-trophic-level consumers. This synthesis indicates that energy flow up the food web, toward larger – often ecologically and economically prized – taxa may be dampened as aquatic contaminant loads increase.

Contents

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http://dx.doi.org/10.1016/j.scitotenv.2022.160245
Received 7 October 2022; Received in revised form 9 November 2022; Accepted 13 November 2022
Available online 17 November 2022

1. Introduction

Consumer-resource interactions are key ecological processes that dictate the flow of nutrients or energy through ecosystems and across trophic levels, and also shape community structure (DeAngelis, 1992; van der Putten et al., 2004). For instance, Peruvian anchoveta (*Engraulis ringens*) represent the largest single-species wild-harvest fishery on Earth (Carlson et al., 2018). These extraordinary fishing yields are possible because of very high anchoveta biomass, which is supported by the abundance of large phytoplankton (diatoms) that small fish can forage on directly and without trophic intermediaries (Barber and Chávez, 1986). Notably, interannual fluctuations in anchoveta biomass are large and tightly correlated with El Niño-Southern Oscillation patterns and upwelling dynamics that regulate phytoplankton productivity, highlighting the significance of these consumer-resource dynamics in a "bottom-up" context (but see also: Micheli, 1999). Reciprocally, "top-down" dynamics also demonstrate the fundamental ecological importance of consumer-resource relationships in structuring ecosystems; for example, predator-prey interactions involving great sharks hunting herbivorous sea turtles can ultimately regulate standing-stock plant biomass in tropical seagrass meadows (Heithaus et al., 2014). This control on seagrass biomass has cascading effects on ecosystem services such as nursery provision and carbon capture (Orth et al., 2006).

Across diverse ecosystems, consumer-resource interactions are mediated by a suite of abiotic and biotic factors such as temperature (Carr et al., 2018), light (Ringelberg, 1995), habitat structural complexity (Heck and Crowder, 1991), parasitism (Ives and Murray, 1997), and indirect effects within food webs (Fodrie et al., 2008). Many human activities are changing the nature of these synecological conditions that are likely to impact consumer-resource dynamics in complex ways, with potential to either increase or decrease consumption/predation rates. Consider, global warming (O'Connor et al., 2009), light pollution (Minnaar et al., 2015), and habitat fragmentation (Yarnall et al., 2022) may generally shift systems toward higher consumption rates via increases in consumer metabolic demands and search efficiency, while stressors such as noise pollution may decrease consumption via diminished foraging success (Siemers and Schaub, 2011).

Aquatic ecosystems are also increasingly impacted by a complex suite of chemical and physical contaminants (e.g., endocrine disruptors) that can have ecosystem-level effects (Clements et al., 2012). Many of these effects are acute, generally depressing organismal vital rates such as survival, growth, and reproductive fitness (Birge et al., 1981). The impacts of aquatic contaminants, however, may also manifest via indirect pathways related to animal movement or behavior (Giattina and Garton, 1983), and as chronic stressors that interact with other burdens to disrupt ecosystem dynamics (e.g., warming; DeCourten et al., 2019). In this context, contaminants may also impinge on food-web integrity via altered consumer-resource interactions.

There is little theoretical guidance regarding the likely direction or magnitude of effects of chemical contaminant cocktails on consumer-resource dynamics, primarily because both higher- and lower-trophic level species may suffer injuries and exhibit reduced performance following exposure. Among predatory fishes, for example, neurotoxins can lower serotonin and dopamine levels that reduce motor control and swimming functions (i.e., induce narcosis; Tsai et al., 1995, Panula et al., 2006). Concurrently, aquatic prey exposed to contaminants often express reduced vigilance (individually or via loss of social behaviors such as schooling), lower fleeing performance, decreased production of chemical defenses, and altered activity patterns resulting in elevated conspicuousness (Mesa et al., 1994; Scott and Sloman, 2004). Both predators and prey exhibit reduced abilities to interpret external stimuli (e.g., visual and olfactory cues), leading to delayed or altered reactions to foraging opportunities or threats (Little and Finger, 1990). Given this potential for injuries to both members of predator-prey pairs, as well as shifts in palatability, the net effects of contaminant exposure on consumer-resource may be highly context and system specific – a function of baseline species behaviors or trophic level, pollution sensitivity, and exposure intensity (sensu Relyea et al., 2005). In the absence of easily applied predictive theory, it is critical to consider the empirical evidence regarding trends and variability in contaminant effects on consumer-resource dynamics.

We conducted a meta-analysis to investigate the effects of distinct contaminant types on consumer-resource interactions in freshwater-brackish and marine ecosystems, including: (1) anthropogenic CO_2 (i.e., ocean acidification; OA), (2) heavy metals (and ionic liquids), (3) microplastics, (4) oil (and related hydrocarbons), (5) pesticides, and (6) pharmaceuticals and personal care products (PPCPs). We were primarily focused on the net effects of contaminants for consumer-resource pairs: specifically, whether net consumption rates increased or decreased following exposure. We also assessed whether responses across aquatic systems varied as a function of salinity regime (freshwater-brackish vs marine systems), consumer trophic level (primary consumer, secondary consumer, or tertiary consumer) and resource mobility (sedentary, mobile). We anticipated these environmental/ecological contexts to be important windows through which we consider contaminant effects given evidence that: (1) contaminant toxicity can vary across salinity regimes (Kuhl et al., 2013); (2) body size – generally positively correlated with trophic level – can modulate contaminant effects (Peng et al., 2018); and (3) resource mobility may control the nature/magnitude of reduced avoidance behaviors following contaminant exposure (e.g., fleeing abilities not as impacted for sedentary prey relative to mobile prey; Weis et al., 2001).

2. Materials and methods

2.1. Literature search and data extraction

We conducted a literature search using Google Scholar and ISI Web of Science through May 2021 using keywords such as "consumer", "predator", "prey", and "contaminants." We also searched for literature using specific contaminants such as "No.2 fuel oil," "mercury," or "Pentachlorophenol (PCP)." Contaminants were grouped into six categories: (1) OA (2) metals, (3) microplastics, (4) oil, (5) pesticides, and (6) PPCPs. Twenty-nine studies met the following criteria: (1) was peer-reviewed, (2) used contaminants that were grouped into one of our six target categories (note: interactions among contaminants are not explored), (3) detailed experiments measuring direct consumer-resource interactions (i.e, consumption) and (4) exposed both consumers and resources to a contaminant. We initially flagged, but ultimately did not use, an additional 12 papers that only exposed the consumer or resource (not both) to a contaminant prior to documenting consumer-resource interactions. Six categories of response variable were designated as consumption in our analysis: capture rate or consumption efficiency, consumption rate, number of consumption events, percent of animals feeding, number of resources consumed, and resource survival (SM Table 1).

For each experiment we included, we collected metadata such as contaminant type, experimental setting (in situ vs. ex situ), consumer and resource taxa, exposure duration, and contaminant concentration. We also recorded the number of trials conducted for each experiment. We then extracted the response of consumer-resource pairs to each contaminant and control treatment directly from tables or figures using the software Datathief III (Tummers et al., 2006).

Salinity regime (freshwater vs marine) was designated by the salinity (ppt) regime for each experiment. Salinities <6 ppt were designated as freshwater-brackish while any salinity value >15 ppt was designated as marine. There were no studies with salinity values between 6 and 15 ppt. Consumer trophic level was designated as primary consumer, secondary consumer, or tertiary consumer based on trophic level data from FishBase (Froese and Pauly, 2010) if available, or the type of resource that was consumed in the trial. For instance, primary consumers fed solely on primary producers such as plants and algae, while secondary consumers fed on herbivorous species or a combination of primary producers and primary consumers, and tertiary consumers fed partially or solely on secondary consumers. Lastly, resource items were designated as mobile or sedentary based on the taxa's ability to actively move to a new location to escape consumers in response to threat stimuli. All data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org/data/R6.x808.000:0064 (Fodrie et al., 2021).

2.2. Statistical analysis

To quantify the effect of contaminants on consumer-resource interactions we calculated effect sizes as log response ratios (lnRR). The experimental log response ratios were

$$\ln\left(\frac{\overline{X}_e}{\overline{X}_c}\right)$$

the ratio of the mean response of consumer-resource interactions in experimental treatments (i.e., contaminant exposure) over the mean response in control treatments (i.e., no contaminant exposure). On the log scale, an effect size of zero indicates that contaminants had no effect on consumer-resource interactions. A positive lnRR indicates that consumption (e.g., foraging success, predation rate, proportion eaten, etc.) increased with contaminant exposure. Conversely, a negative lnRR indicates that the consumer had a relative decrease in consumption following contaminant exposure.

Utilizing the calculated lnRRs, we investigated the effects of each contaminant type on consumer-resource interactions across a broad range of taxa. As not all experiments in our study reported sampling error or sample size, we were unable to assess our dataset with more complex analyses using the 'metafor' package in R (Viechtbauer, 2010). Therefore, we employed a series of parametric tests to draw inferences regarding statistical patterns in the data, as lnRRs passed exploratory tests gauging data normality (Shapiro-Wilk test) and homoscedasticity (Levene's test). While we readily acknowledge advantages of the 'metafor' tool (e.g., assessing within-study effects), previous synthesis analyses that have compared results using these alternative statistical approaches have come to overwhelmingly similar ecological conclusions (e.g., Heck et al., 2003 compared to McDevitt-Irwin et al., 2016; both approaches leveraged in Yarnall et al., 2022). To test for statistical clarity regarding the effects of contaminant exposure on consumer-resource interactions, we serially employed one-sample *t*-tests to determine if the lnRRs were different than 0 (sensu Micheli, 1999).

We also investigated the effect of contaminants on consumer-resource interactions in relation to multiple ecological contexts: salinity regime (fresh/brackish or marine), consumer trophic level (primary consumer, secondary consumer, tertiary consumer), and prey mobility (mobile or sedentary). For each ecological factor and separately among levels within each factor, we conducted serial one-sample t-tests to determine if contaminants increased or decreased consumption. Low sample sizes prevented direct comparisons among different contaminant groups across these ecological factors with statistical analyses such as Analysis of Variance (ANOVA). Therefore, all inferences about differences among contaminant types were drawn from overall effect sizes and individual t-tests. All analyses were carried out in R 4.0.5 (R Development Core Team, 2021).

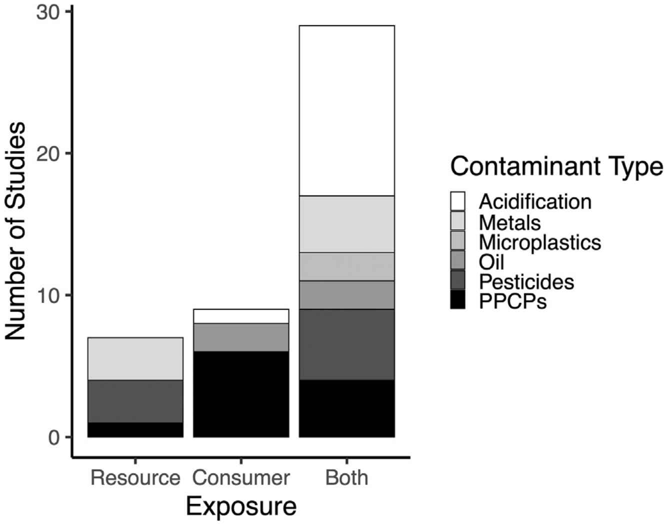

Fig. 1. The number of studies found for each contaminant that exposed only the resource, only the consumer or both.

3. Results

Twenty-nine papers with 62 individual experiments exposed both consumer and resource to a contaminant, examined consumption, and therefore were included in our analyses (Fig. 1). Among the 62 experiments, 50.0 % focused on OA, 14.5 % on metals, 1.6 % on microplastics, 11.3 % on oil, 12.9 % on pesticides, and 9.7 % on PPCPs (SM Table 1). The majority of studies focused on species found in marine ($n = 43$) habitats compared to predominantly freshwater and brackish systems ($n = 19$). Forty-three experiments used mobile prey and nineteen studies utilized sedentary fauna, plant, or algal resources for consumption experiments. Our analysis included 28 resource species spanning 8 distinct phyla (ranging from algae to amphibians; SM Table 1). Across the 62 experiments, there were 40 different consumer species from 7 distinct phyla (SM Table 1), of which fourteen were primary consumers, eight were secondary consumers, and forty were tertiary consumers. All studies were published after 1995 with one exception (pesticide; Tagatz, 1976). Furthermore, all OA, microplastic, and PPCPs studies were published after 2010.

When all contaminants were assessed together, the mean lnRR was −0.24 (95 % CI = −0.43, −0.04) indicating a statistically clear negative effect of contaminants, broadly defined, on consumption (i.e., a dampening effect on consumption; $t = -2.46$, $p = 0.016$; Fig. 2). When each contaminant was examined separately, metals were the only contaminant with a lnRR statistically distinct from zero indicating a clear decrease in consumption rates relative to across-study variability (lnRR = −0.7, 95 % CI = −1.23, −0.18; $t = -3.101$, $p = 0.014$). We do note that consumption rates trended lower following exposure to all of the other contaminants we considered (Fig. 2), but were not statistically different than zero due to high variability among trials relative to mean effect sizes, and in the case of OA, small mean effect size (OA: lnRR = −0.007, CIs = −0.28, 0.27, $t = -0.05$, $p = 0.96$; Oil: lnRR = −0.31, CIs = −0.68, 0.20, $t = -1.01$, $p = 0.35$; Pesticides: lnRR = −0.42, CIs = −1.09, 0.26, $t = -1.50$, $p = 0.18$; PPCPs: lnRR = −0.40, CIs = −0.97, 0.16, $t = -1.83$, $p = 0.13$). Microplastics had a lnRR of −0.31; however, due to low sample size ($n = 1$) the statistical clarity of microplastics effects on consumer-resource interactions could not be evaluated.

Contaminant exposure had differing effects on consumer-resource interactions among salinity regimes (Fig. 3A). In freshwater-brackish systems, there were strong effects of contaminant exposure on consumer-resource interactions that resulted in dampened consumption (lnRR = −0.44, CIs = −0.77, −0.12, $t = -2.86$, $p = 0.01$). In contrast, contaminant exposure in marine systems did not clearly influence consumer-resource interactions (lnRR = −0.14, CIs = −0.38, 0.09, $t = -1.22$, $p = 0.23$). The

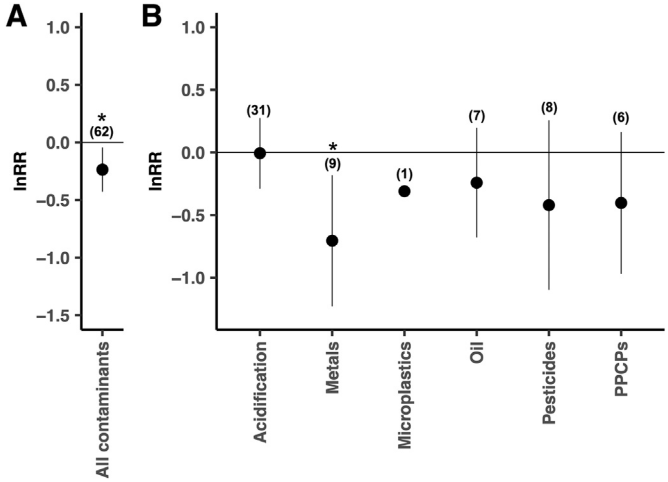

Fig. 2. The effect of all contaminants (A), as well as acidification, metals, microplastics, oil, pesticides, and pharmaceuticals and personal care products (PPCPs) (B; each separately) on direct consumer-resource interactions. Values are mean lnRR ± 95 % confidence intervals. Parentheticals indicate number of studies (n). Asterisks indicate $p < 0.05$.

effect of contaminants on consumer-resource interactions varied across consumer trophic levels (Fig. 3B). Specifically, lower trophic-level consumers (i.e., primary consumers) were most affected by contaminant exposure, significantly dampening consumption rates (lnRR $= -0.59$, CIs $= -0.96, -0.21$, $t = -3.39$, $p = 0.005$). Consumption by secondary consumers (lnRR $= -0.28$, CIs $= -0.93, 0.36$, $t = -1.04$, $p = 0.33$) or tertiary consumers (lnRR $= -0.11$, CIs $= -0.34, 0.14$, $t = -0.86$, $p = 0.39$) on their resource items trended negative, but were not statistically distinct from zero. For these higher-order consumers, mean contaminant effects appear weak relative to among-study variability. Contaminant exposure significantly dampened the consumption of sedentary or immobile prey resources by consumers (lnRR $= -0.55$, CIs $= -0.89, -0.21$, $t = -3.36$, $p = 0.004$), but had no detectable influence on species interactions among consumers with mobile prey (lnRR $= -0.09$, CIs $= -0.32, 0.13$, $t = -0.86$, $p = 0.39$; Fig. 3C).

4. Discussion

As ecosystems continue to be modified by myriad human activities, it is essential to understand how anthropogenic stressors alter ecological interactions and food-web dynamics. We synthesized the literature reporting effects of contaminant exposure on trophic interactions within aquatic ecosystems and found that contaminants appear to reduce consumption rates. This key summary finding should broaden our understanding of how contaminants may affect aquatic communities, and in particular adds to the body of work that has more regularly focused on impacts to individual organisms or single species (Fleeger et al., 2003). Integrated across larger spatial, temporal, and population scales, our results vis-à-vis consumer-resource dynamics suggest that increased aquatic contaminant loads may disrupt existing top-down (Heithaus et al., 2014; Orth et al., 2006) and bottom-up (Barber and Chávez, 1986) processes. In addition, the dampening of consumption rates may reduce biomass accumulation at higher trophic levels within the food web, with potential for socioeconomic effects related to economically and ecologically prized species. Notably, these consequences may manifest most noticeably in freshwater-brackish systems, or in food-web modules comprised of herbivories and/or sedentary prey.

This synthesis also highlights a number of ancillary – but important – findings related to the investigation of contaminant effects within aquatic food webs. We acknowledge that our meta-analysis was built upon 29 published studies and 62 distinct experiments that directly measured how contaminant exposure affected consumption rates in consumer-resource pairs. These are modest sample sizes, although in line with similar ecological syntheses (Fodrie et al., 2014; Gittman et al., 2016; Yarnall et al., 2022). These sample sizes suggests that this topic remains an emerging area of focus, and while our findings appear meaningful, they merit revisiting across the next 10–20 years as more studies emerge. In particular, we were unable to apply inferential statistics to directly compare the effects of individual contaminants to each other or explore potential interactive

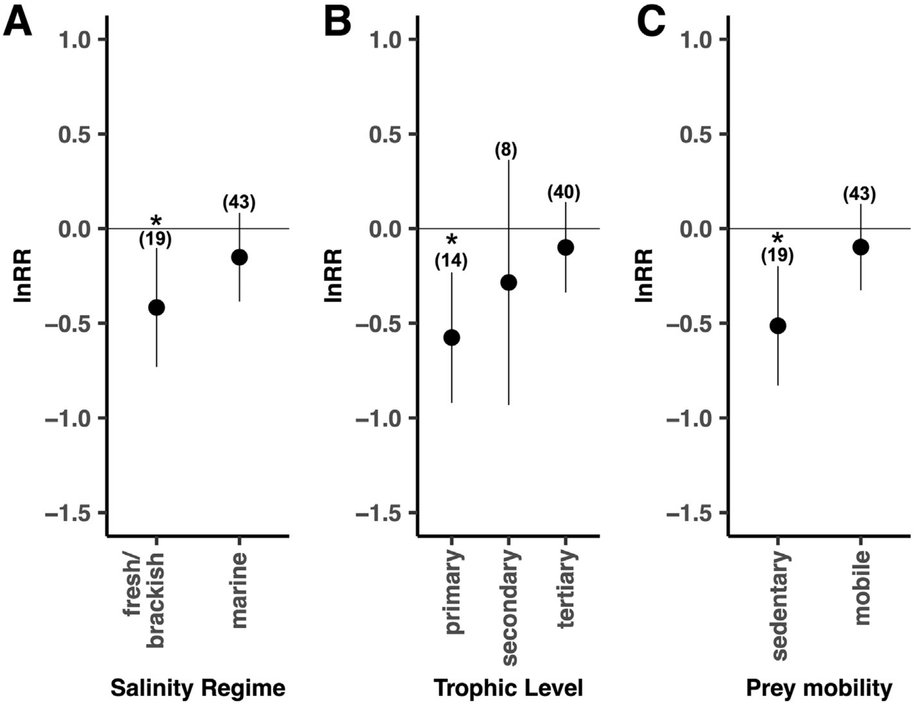

Fig. 3. The effect of contaminants (i.e., acidification, metals, microplastics, oil, pesticides, and pharmaceuticals and personal care products considered collectively) on consumer-resource interactions in relation to: (A) salinity regime; (B) trophic level of consumers; and (C) prey mobility. Values are mean lnRR ± 95 % confidence intervals. Parentheticals indicate number of studies (n). Asterisks indicate $p < 0.05$.

effects between specific contaminants and environmental/ecological contexts. This is highlighted by only a single existing study documented in our search that evaluated how microplastics affect consumption rates for consumer-resource pairs. However, our sample sizes were sufficient to demonstrate statistically significant and ecologically meaningful reductions in consumption following contaminant exposure (viewed collectively). Furthermore, even in the absence of statistically clear evidence, we note that contaminant effects consistently trended toward reduced consumption rates across all contaminant types, salinity regimes, trophic levels, and prey mobility contexts. This pattern furthers our confidence that aquatic contaminants disproportionately impact consumers' ability to capture resources relative to the ability of resource taxa to evade capture/consumption. Surprisingly, this result is in contrast to our hypothesis that body size may mediate the effects of contaminants for larger bodied organisms. Our literature search also highlighted that approximately 33 % of studies exploring the consequences of aquatic contaminants on consumer-resource dynamics exposed only the consumer or resource (not both). We encourage future studies employing this approach to provide mechanistic explanations for the ecological relevance of exposing only consumers or resources (e.g., perhaps one member occupies a spatial refuge from exposure, while the other transits between contaminated and uncontaminated areas), or fully discuss potential experimental biases of exposing a single member within consumer-resource pairs in the context of trophic dynamics.

There are a number of factors that could contribute to consumers being disproportionately impacted by contaminants, relative to resources, to explain decreased consumption rates following exposures. Contaminants may disrupt sensory abilities of both consumers and resources (Lürling and Scheffer, 2007), as well as the motor functions of consumers to capture prey (Scott and Sloman, 2004) or resources to evade predators (Lefcort et al., 1998; Rodríguez et al., 2017). In many cases, however, resources may be sedentary, and therefore while contaminants may decrease the physiological performance (Saaristo et al., 2018) or palatability (Sotka et al., 2009) of resource taxa, those injuries have relatively little effect on the nature in which those organisms can evade consumption (while consumer abilities may be impacted broadly). Indeed, our chief result of decreased consumption following contaminant exposure of consumer-resource pairs was strongly supported by scenarios in which the resource taxa were sedentary (also note, most small-bodied herbivorous consumers were foraging on sedentary resources). Additionally, consumers searching for sedentary or cryptic resources can rely heavily on chemical cues that are strongly modified by chemical contaminants. For instance, certain fish species rely heavily on olfactory cues to find suitable prey in areas of high turbidity (Johannesen et al., 2012). Contaminants such as metals have been shown to directly affect sense organs resulting in larger negative consequences for species that rely on those chemical cues for foraging (Baatrup, 1991). We also suspect that contaminant exposures that equally impact the sensory and motor abilities of consumers and mobile resources would still have a dampening effect on consumption (i.e., the trend we observed in our analysis). Mechanistically, consumers experiencing some form of narcosis may not be capable of the precise directed motions or dexterity required to acquire resources, while impaired resources may continue to avoid capture despite erratic or altered behaviors. Furthermore, decreased swimming/movement of consumers (and potentially resource taxa) is likely to decrease encounter rates of consumer/resource pairs leading to dampened consumption rates (Brewer et al., 2001; Lefcort et al., 1998; Makaras et al., 2020; Painter et al., 2009).

While future synthesis efforts that leverage additional studies may revise our initial conclusions regarding differences in effect sizes across contaminant types, we were struck that metal contaminants, in particular, appeared to have relatively strong dampening effects on consumption. Although defined by high variability, oil, pesticides, and PPCPs also trended toward notable dampening on consumption. In contrast, OA had very weak if any effects on consumption. There are a number of causal mechanisms and correlative factors that could have contributed to these patterns. In the studies examined, metals tended to affect locomotion (Bernot et al., 2005) and trigger neurotransmitters that depress motivation to forage (Smith and Weis, 1997), reducing both foraging attempts and success by consumers. In contrast, OA decreases the amount of available carbonate ions in the ecosystem that organisms use in the formation of shells, potentially affecting shell forming consumers more so than species with internal skeletal structures. As there was a balanced number of studies that examined shell forming taxa versus those with internal skeletons, the observed net effects of this contaminant on trophic interactions were potentially counterbalancing.

It is also important to note that all OA studies were conducted in marine systems, while metals were predominantly conducted in freshwater-brackish systems. Regardless of salinity regime, metal exposure was consistently negative. The large negative effects of metal exposure on consumers in freshwater/brackish systems may account for the overall variation in contaminant effects among salinity regimes. In addition, brackish systems are inherently stressful for aquatic organisms and increased salinity stress in freshwater systems has been shown to negatively affect communities (Lind et al., 2018). The addition of contaminants into freshwater/brackish systems may function as an additional stressor rather than one in singularity.

None of the studies we examined exposed consumer-resource pairs to multiple contaminant types in a crossed design. Polluted environments can have several different contaminants that may have interactive, synergistic or antagonistic effects on organisms and species interactions (Cabral et al., 2019). Microplastics can absorb other chemicals or contaminants (Rios et al., 2007), making them a potential vector for chemicals and other harmful substances (Andrady, 2011; Brennecke et al., 2016) in the environment. While some contaminants may not be as harmful individually, the combined effects of contaminant cocktails or with changing environmental conditions (e.g., temperature) can disrupt consumer-resource interactions across all levels of the food chain. Studies indicate the combination of multiple anthropogenic stressors (e.g., excess CO_2 and increased temperature) act synergistically to greatly reduce survival or physiological processes (Munday et al., 2009; Nowicki et al., 2012; Sokolova and Lannig, 2008). However, we argue that without a clear understanding of the baseline effects of single contaminant exposure on direct species interactions it will be difficult to predict the combined influence of multiple stressors on food web dynamics with continued climatic change.

As contaminant loads in aquatic systems continue to increase, the major focus of ecotoxicology research must be to understand the integrated ecological impacts of these environmental stressors (independently and interactively) to guide management strategies to preserve and restore the integrity of natural habitats (Fleeger et al., 2003). In this context, our synthesis highlights important ecosystem-relevant effects and remaining data imperatives of contaminant exposure that researchers, managers, and public stakeholders should be aware of: (1) as aquatic contaminant loads increase, energy flows up food webs toward larger – often ecologically and economically prized – taxa may already be compromised due to weakening trophic transfers at low trophic levels; and (2) further research regarding impacts of diverse, potentially interacting contaminants on consumer-resource dynamics, as well as the implications for ecosystem function and productivity, are severely needed.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.160245.

Data availability

Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https:// data.gulfresearchinitiative.org (doi: 10.7266/1WXDC382).

Declaration of competing interest

The authors declare no financial interests/personal relationships which may be considered as potential competing interests.

Acknowledgements

We thank A. McMains and M. McMains for assistance with data extraction. Thanks to the Byers Ecology Lab at UGA for constructive comments on this manuscript. Financial support was provided by the National Science Foundation (1926395) and the Gulf of Mexico Research Initiative via the Coastal Waters Consortium. Data are publicly available through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at https://data.gulfresearchinitiative.org (doi: https://doi.org/10.7266/1WXDC382). Financial sources played no role in the design or interpretation of this synthesis.

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