Title: Water quality thresholds for coastal contaminant impacts on corals: A systematic review and meta-analysis

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ABSTRACT

Reduced water quality degrades coral reefs, resulting in compromised ecosystem function and services to coastal communities. Increasing management capacity on reefs requires prioritization of the development of data-based water-quality thresholds and tipping points. To meet this urgent need of marine resource managers, we conducted a systematic review and meta-analysis that quantified the effects on scleractinian corals of chemical pollutants from land-based and atmospheric sources. We compiled a global dataset addressing the effects of these pollutants on coral growth, mortality, reproduction, physiology, and behavior. The resulting quantitative review of 55 articles includes information about industrial sources, modes of action, experimentally tested concentrations, and previously identified tolerance thresholds of corals to 13 metals, 18 pesticides, 5 polycyclic aromatic hydrocarbons (PAHs), a polychlorinated biphenyl (PCB), and a pharmaceutical. For data-rich contaminants, we make more robust threshold estimates by adapting models for Bayesian hierarchical meta-analysis that were originally developed for biopharmaceutical application. These models use information from multiple studies to characterize the dose-response relationships (i.e., E_{max} curves) between a pollutant's concentration and various measures of coral health. Metals used in antifouling paints, especially copper, have received a great deal of attention to-date, thus enabling us to estimate the cumulative impact of copper across coral's early life-history. The effects of other land-based pollutants on corals are comparatively understudied, which precludes more quantitative analysis. We discuss opportunities to improve future research so that it can be better integrated into quantitative assessments of the effects of more pollutant types on sublethal coral stress-responses. We also recommend that managers use this information to establish more conservative water quality thresholds that account for the synergistic effects of multiple pollutants on coral reefs. Ultimately, active remediation of local stressors will improve the resistance, resilience, and recovery of individual reefs and reef ecosystems facing the global threat of climate change.

KEY WORDS

Pollutant, management, coral reef, Scleractinia, dose-response, Bayesian model, data synthesis

1. INTRODUCTION

Coral reefs are some of the most diverse and productive ecosystems on the planet (Reaka-Kudla, 1997). They provide coastal protection, tourism, and ecological benefits for communities in over 100 countries globally, but despite their importance, coral reefs are threatened by the compound effects of anthropogenic disturbances on global and local scales (Bishop et al., 2011; Bryant et al., 1998; Spalding et al., 2001). Over 60% of coral reefs are threatened by local stressors, which can include pollutants from terrestrial runoff (e.g., sedimentation, increased nutrients, pathogens, and toxins) and overfishing (Burke et al., 2011; Richmond and Wolanski, 2011). The impacts of local stressors can be exacerbated by global stressors such as ocean warming and acidification (Hughes et al., 2010). Though mitigating global stressors remains a priority for resource managers nationally and internationally, coral-reef managers often seek to control local stressors to increase reef resilience and recovery. Runoff and groundwater collectively transport nutrients, sediment, and pollutants onto reefs (Fabricius, 2005; Silbiger et al., 2020; Tuttle and Donahue, 2020; Zhao et al., 2021), but the impacts of pollutant transport have received less attention and are consequently less understood (van Dam et al., 2011). As such, we present a systematic, quantitative review and meta-analysis that addresses this knowledge gap and focuses on studies that have examined the physiological responses of scleractinian corals following direct exposure to chemical toxicants.

Coral reefs near the shoreline are more vulnerable to land-based runoff and submarine groundwater discharge, and they degrade faster than reefs farther offshore (Rodgers et al., 2015; Silbiger et al., 2020; Wenger et al., 2016). The persistence and dispersion of pollutants depend on their chemical composition and environmental conditions, such as water residence time and flushing rate, so corals downstream of watersheds in high retention bays are also more likely to be impacted by runoff from land-based activities (Wolanski et al., 2009). This gradient of decreasing water quality closer to land can lead to lasting changes at reefs closer to the shoreline, such as reduced coral genetic diversity (Tisthammer et al., 2020). Anthropogenic pollutants, such as pesticides, metals, pharmaceuticals, and sewage, can enter reef ecosystems through point sources (e.g., sewage outfall) or nonpoint sources. In many places, onsite waste disposal, leaking septic tanks, and other improper sewage disposal techniques also pose a risk to coastal reefs (Abaya et al., 2018). In areas with harbors, the surrounding reef may be additionally exposed to pollutants associated with boats, such as anti-fouling paints and polycyclic aromatic hydrocarbons (PAHs) (Sheikh et al., 2009).

In addition, pollutants of concern in developed industrial or residential areas and agricultural chemicals can enter marine ecosystems. Highly soluble contaminants have the potential to be carried far offshore, and some pollutants may also be transported through the atmosphere and redeposited, impacting areas far from the site of application (Nash and Hill, 1990). Because many of these compounds, especially herbicides, are designed to inhibit photosynthesis in plants, they can negatively impact the photosynthetic capacity of the algal symbionts in corals that provide up to 90% of coral energy (Muscatine, 1990). Glyphosate, atrazine, diuron, and other active ingredients in herbicides and insecticides have been found in water, sediment, and biological samples from streams that drain to the ocean in Hawai‘i and in the coastal coral reef ecosystems of the Great Barrier Reef, Hong Kong, and French Polynesia, indicating the widespread presence of these pesticides and their degradates in coral reef ecosystems (Roche et al., 2011; Shaw et al., 2008; Shaw et al., 2010; Hawai‘i State Dept. of Health & Ag., 2014; Spengler et al., 2019).

Sediment and freshwater directly and indirectly impact corals and other reef organisms while transporting chemical pollutants, which also affect corals (Table 1) (Tuttle and Donahue, 2020; Rodgers et al., 2018). Biological processes of early life stages of corals, including gamete fertilization, larval settlement, and recruit survival, are chemically mediated and therefore often more sensitive to xenobiotics, or chemicals that are not naturally found within the organism (Richmond et al., 1998; Richmond et al., 2018). Certain pollutants are also known to impact early life stages and processes more than others. For example, copper can reduce fertilization success at lower concentrations than zinc or cadmium and is likely more toxic than these other metals at early life stages (Reichelt-Brushett and Harrison, 1999).

Exposure to toxicants can also impact corals at later life stages, causing them to expel their algal symbionts, which are necessary for autotrophic feeding, and in some cases, the corals may also produce increased amounts of mucus, which can affect their ability to feed heterotrophically (Markey et al., 2007; Renegar et al., 2017). While hormone function in corals is still unclear, previous research has shown that corals contain many of the same steroidal hormones involved in reproduction as in other species such as estradiol, estrone, and testosterone (Tarrant et al., 2003). Herbicides that are designed to inhibit photosynthesis, such as atrazine and diuron (Table 1), will impact adult corals that rely on photosynthetic symbionts differently than earlier life stages that do not yet have symbionts. However, pesticides including atrazine and diuron have also been shown to be endocrine disruptors, which can have lasting impacts on organisms and their reproductive capacity (Boscolo et al., 2018; Hayes et al., 2003). Corals also show stress at the molecular level after exposure to chemicals. For example, *Pocillopora damicornis* exposed to insecticides and microplastics increased expression of detoxification enzymes and antioxidant enzymes, respectively (Tang et al., 2018; Wecker et al., 2018).

With this systematic, quantitative review and meta-analysis, we aimed to determine (1) the scope of existing research on the effects of chemical pollutants on scleractinian corals, (2) the concentrations at which marine pollutants elicit adverse physiological responses in corals, (3) the relative impact of different pollutants on coral health, and (4) the areas in need of additional study. Herein, we systematically review the effects on scleractinian corals of a comprehensive list of marine pollutants grouped into five categories: metals, pesticides (herbicide, insecticide, fungicide), polycyclic aromatic hydrocarbons (PAHs), polychlorinated biphenyls (PCBs), and other. This quantitative review and meta-analysis offers a detailed analytical assessment of stressor thresholds, when possible, and provides insight into the gaps that remain. We conclude with recommendations for future studies to address the current knowledge gaps, including critical data gaps in characterizing stressor-response relationships. This information is essential to managers as they aim to develop guidelines and policies to mitigate the impacts of pollutants on coral reef ecosystems.

2. METHODS

2.1 Systematic Literature Review

Article Searches: The systematic review began with previously published reviews on the effects of various pollutants on stony corals (Johnson and Roberts, 2009; Kroon et al., 2014; Mayer-Pinto et al., 2020; Pastorok and Bilyard, 1985; Richmond et al., 2018; van Dam et al., 2011), which were used to develop a list of benchmark studies to be included. The aim of the following literature search was to collect and synthesize all available evidence on the effects of select pollutant classes on hard corals. The search included peer-reviewed, public, and/or 'grey' literature to quantify pollutant-related stress responses in all life stages of all shallow (photic zone, ≤ 80 m depth), scleractinian corals in all warm-water ocean basins (20°–30°C).

The search engines and databases described and justified in Tuttle et al. (2020) were used in this study and can be found in the Supplementary Materials (Table S1). An exhaustive list of potential pollutants and additional characteristic terms was compiled through reference to existing reviews and consultation with experts. Search terms were refined by recording the number and accuracy of results produced in Web of Science searches of the format ([search term]* AND coral), where "*" is a wildcard and "AND" is a Boolean operator. Terms that resulted in double counting of results such as pesticid* and *icid* were refined to only include the term which produced the most results and was, therefore, more comprehensive. Focused searches were included for the following genera due to their listing as endangered or threatened under the U.S. Endangered Species Act (ESA): *Acropora, Anacropora, Cantharellus, Dendrogyra, Euphyllia, Isopora, Montastraea, Montipora, Mycetophyllia, Orbicella, Pavona, Porites, Seriatopora, Siderastrea,* and *Tubastraea*. The genera list was expanded to include those genera of particular importance to the Pacific Island Region: *Alveopora, Astreopora, Favia, Favites, Goniastrea, Goniopora, Leptastrea, Leptoria, Lobophyllia, Millepora, Platygyra, Pocillopora,* and *Turbinaria.* A full list of search terms can be found in Text S1. Possible limitations of this search include regional or language biases and the exclusion of some journals or conference proceedings from sampled database archives.

Article Screening and Eligibility Criteria: The search results were evaluated according to the methods and procedures described previously (Tuttle et al., 2020). After searches were completed, the resulting Bibtex and RIS files were imported to Mendeley, an open-source reference manager (Mendeley, 2020). Duplicate files were combined via Mendeley's duplicate merger tool. The unique citations (n = 9,332) were then imported into Abstrackr, a free web-based application for screening and organizing literature search results (Abstrackr, 2020), and abstracts were independently screened by at least two reviewers, with each classifying the titles as 'relevant' (n = 315), 'not-relevant' (n = 8,885), or 'maybe-relevant' (n = 132) to the research questions. Discrepancies in the classifications were addressed and resolved by a third reviewer.

The full texts for all 'relevant' sources were collected and screened by independent reviewers for each of the pollutant categories based upon the eligibility criteria from the PECO (Population, Exposure, Comparison, Outcome) framework (Morgan et al., 2018), which are described in the Supplementary Materials (Text S2). All sources that passed the full-text screening (n = 140) were appraised for internal and external validity following the detailed criteria within Tuttle et al. (2020). Articles that did not include coral responses that could be compared across studies were omitted at this step, leaving 127 studies that were considered for the quantitative review and meta-analysis. Studies focusing on oil and oil dispersants were excluded because several recent reviews and meta-analyses provide a thorough summary of the effects of oil and dispersants on corals and other marine organisms (Bejarano, 2018; Bejarano et al., 2016; NAS, 2020; Turner and Renegar, 2017). Microplastics were also excluded as a pollutant from this quantitative review because the described response to microplastics was typically related to a reduced capacity for heterotrophic feeding rather than an adverse physiological response to the stressor. A recent review (Huang et al., 2021) describes the impacts of microplastics on corals and notes that associations between microplastics and other toxins may increase the susceptibility of corals to disease, which is a response with physiological complexity that is beyond the scope of this study.

Data Extraction: Each article remaining in the "relevant" category that passed the study validity assessment (n = 55) had data extracted by a single reviewer. A complete list of studies can be found in the Supplementary Materials (Text S3). All methodology-related information on the study species, location and collection site, pollutant and concentration levels, and additional factors were recorded for each article (Table S2). Coral response data found in article figures (most commonly as treatment means +/- error) were extracted using tools such as Web Plot Digitizer (Rohatgi, 2020). When possible, reported no- and lowest-observed adverse effect levels (NOAEL, LOAEL) and half maximal effective concentrations (EC_{50}) were also extracted from the papers (Table S3). Many pollutant-response combinations did not have sufficient replication to be included in the meta-analysis (at least 3 independent, comparable articles), so they were assessed in the quantitative review only. We define an 'article' as a unique publication, and an 'experiment' as a unique set of related treatments, including both control and exposure conditions. Thus, an article could contain the results of multiple experiments.

In the extraction of data for meta-analysis of the effects of pollutants on photosynthetic efficiency, we focused on maximum quantum yield (MQY) instead of effective quantum yield (EQY). MQY is represented by F_v (= F_m - F_0) / F_m, where F_m is maximal fluorescence and F_0 is background fluorescence (Osinga et al., 2012). MQY is measured after the coral has been dark-adapted, meaning a complete relaxation of photochemical quenching activity (Osinga et al., 2012). EQY is measured under steady but illuminated conditions and can therefore be more variable (Enríquez and Borowitzka, 2010). Measurements can be affected by variable light intensity, driven in some cases by shading, which can be very important in measurements from corals where light is scattered throughout the skeletal matrix (Enríquez et al., 2017; Enríquez and Borowitzka, 2010). MQY was thus considered a more stable measurement of photosynthetic efficiency in response to stressors than EQY.

2.2 Meta-analysis

For each stressor-coral response combination that met the standards for inclusion in the meta-analysis, we fit a dose-response curve using a Bayesian, inhibitory log-logistic (E_{max}) model, adapted from models used in biopharmaceutical research (Thomas et al., 2014; Wu et al., 2018), with a Gaussian distribution using *brms*, v2.14.0 (Bürkner, 2017; Bürkner, 2018) and *rstan*, v2.21.2 (Stan Development Team, 2020) packages within the *R* statistical software, v4.0.1 (R Core Team, 2020). Data were fit to a four-parameter model (Equation 1), with parameters E_0, E_{max}, EC_{50} and the Hill coefficient (λ, curve steepness):

Equation 1.

$$(Response\ Level \mid Standard\ Error) \sim E_0 \times (1 - \frac{E_{max} \times Concentration^{\lambda}}{EC_{50}{}^{\lambda} + Concentration^{\lambda}})$$

Response level was conditioned on standard error because each datapoint represented the mean (+/- standard error) response of an experimental control/treatment group at a corresponding pollutant concentration. Within the hierarchical Bayesian model framework, we allowed random intercepts for the four parameters and compared model fits (using Bayesian R^2 and posterior distributions) with parameter slopes allowed to vary by experiment or experiment nested within article. The Bayesian priors for the four parameters were normally distributed, with E_{max} constrained between 0 and 1 and the Hill coefficient constrained as non-negative. The model specifications – including hierarchical structure, prior distributions, iterations, and convergence criteria – are described in Table S4.

To test specifically for the effect of Diuron exposure duration on adult corals, we conducted a multiple linear regression in the *R* statistical software, v4.0.1 for which we regressed MQY by duration (in days, $\log_{10}$-transformed; continuous variable) and concentration at three levels: 0, 1, and 10 µg L^{-1} (categorical variable). We used analysis of variance to choose the best-fit of three models: (1) equal slopes and intercepts (simple linear regression), (2) equal slopes and different intercepts, and (3) different slopes and intercepts. We visually inspected residuals of the best-fit model (2) to check that it met assumptions.

2.3 Quantitative Review

Stressor-response combinations that did not have sufficient data for meta-analysis were assessed in a quantitative review. For each stressor-coral response combination, we report the range of pollutant concentrations examined across all studies, the no- and lowest- observed adverse effect levels (NOAEL and LOAEL), and corresponding references were compiled and synthesized by coral life history stage. Further, we aggregated the most conservative thresholds reported for each stressor-response combination to inform management strategies in data limited scenarios.

3. RESULTS

3.1 Meta-analysis

Copper, nickel, and diuron were the only pollutants matched with coral responses that had sufficiently comparable data for inclusion in the meta-analysis. For copper, we examined four separate coral responses: gamete fertilization success (n = 9 articles with 17 experiments therein), larval settlement (n = 3 articles with 4 experiments therein), larval survival (n = 3 articles with 6 experiments therein), and adult photosynthetic efficiency (n = 4 articles with 11 experiments therein) (Table 2). Diuron had enough articles (n = 5 with 25 experiments therein) to assess its effect on adult photosynthetic efficiency. While there were at least three independent, comparable articles that examined the effects of nickel on fertilization success and copper on chlorophyll concentration, these stressor-response combinations did not exhibit a dose-response relationship that could be accurately modeled with an inhibitory log-logistic (E_{max}) model.

Coral gametes: Coral gametes are particularly vulnerable to copper exposure, with the rate of fertilization inhibited by 5% at 22.6 $\mu g\ L^{-1}$ and by 50% at 48.6 $\mu g\ L^{-1}$ (Table 2; Fig. 1A). Thresholds were estimated from inhibition curves for 9 articles that tested the effects of copper concentrations across 5 orders of magnitude (Fig. 1A) on corals from 12 species within 5 genera: *Acropora*, *Coelastrea*, *Goniastrea*, *Montipora*, and *Platygyra*. Coral gametes were less susceptible to exposure to other metals. We conducted a joint meta-analysis for the 10 metals for which there was an apparent log-linear decline in fertilization rate with increasing metal molar concentration (in $\mu mol\ L^{-1}$). Relative susceptibility to these metals, ranked from most to least susceptible in terms of estimated EC_{50} values, is as follows: copper, tin, zinc, lead, vanadium, gallium, nickel, aluminum, cadmium, and iron (Fig. 2). The posterior distributions of EC_{50} values are wide (Fig. 2B) indicating the relative paucity of data available to estimate the dose-response curves for most metals, with the notable exception of copper.

Coral larvae: Coral larvae were also relatively vulnerable to copper exposure. Settlement (i.e., metamorphosis) rates were inhibited by 5% at 27.7 $\mu g\ L^{-1}$ and by 50% at 44.8 $\mu g\ L^{-1}$ copper (Table 2; Fig. 1C). Thresholds were estimated from inhibition curves for 3 articles that tested the effects of copper concentrations across 5 orders of magnitude (Fig. 1C) on corals from 2 species: *Acropora millepora* and *Acropora tenuis*. Survival rates of pre-settlement coral larvae were inhibited by 5% at 44.7 µg L^{-1} and by 50% at 101.0 µg L^{-1} copper (Table 2; Fig. 1B). These thresholds were estimated from inhibition curves for 3 articles that tested the effects of copper concentrations across 3 orders of magnitude (Fig. 1B) on corals from 2 species: *Coelastrea aspera* and *Platygyra acuta*.

Coral adults: The only response of coral adults that was adequately comparable for meta-analysis across studies was photosynthetic efficiency measured as maximum quantum yield (MQY, F_v/F_m). Adult coral photosynthetic efficiency was relatively insensitive to copper exposure, with MQY inhibited by 5% at 285.5 µg L^{-1} and by 50% at 365.3 µg L^{-1} (Table 2; Fig. 1D). Thresholds were estimated from inhibition curves for 4 articles that tested the effects of copper concentrations across 3 orders of magnitude on corals from 2 species: *Mussismilia harttii* and *Pocillopora damicornis*.

Adult coral photosynthetic efficiency was much more sensitive to diuron exposure as compared to copper exposure, with MQY inhibited by 5% at just 2.5 µg L^{-1} and by 50% at 43.7 µg L^{-1} (Table 2; Fig. 3A). Thresholds were estimated from inhibition curves for 5 articles that tested the effects of diuron concentrations across 4 orders of magnitude (Fig. 3A) on corals from 5 species and genera: *A. millepora*, *Montipora digitata*, *P. damicornis*, *Porites cylindrica*, and *Seriatopora hystrix*. The effect of diuron exposure duration on MQY was slight but significant. A ten-fold increase in duration (in days) was associated with a decline in mean MQY of 0.03 (95% confidence interval: 0.01, 0.06; multiple linear regression $p = 0.019$; Fig. 3B).

3.2 Quantitative Review

Stressor-response combinations with fewer than three independent and comparable articles were excluded from the meta-analysis but were included in the quantitative review (Table 3; Table S3). Metals tended to affect coral responses at a range of concentrations that varied by metal, as seen with fertilization success (Fig. 2), which in general was more impacted by metals than by the pesticides examined. Considering all pollutants, larval survival and settlement were typically affected at low concentrations or were not affected at all until extremely high concentrations were applied. Juvenile survival was examined in response to a limited range of pollutants but appeared more affected by the metal examined than by the pesticides. In adult corals, the growth rate was impacted at lower pollutant concentrations than the mortality rate across a range of pollutants. Coral responses related to symbiotic zooxanthellae (e.g., bleaching, chlorophyll content, MQY) varied by pollutant.

Coral gametes: Fertilization success was examined in response to twelve metals and eight pesticides. The effect of metals on fertilization can be grouped into three broad categories: no impact at high concentrations, decreased fertilization at relatively high concentrations, and decreased fertilization at relatively low concentrations. Cobalt, iron, and manganese had no significant impact on fertilization at concentrations up to 2357 µg L^{-1}, 25,300 µg L^{-1}, and 71,200 µg L^{-1} respectively. Cadmium, gallium, vanadium, and aluminum impacted fertilization success at relatively high concentrations (5000 µg L^{-1}, 3230 µg L^{-1}, 2920 µg L^{-1}, and 2950 µg L^{-1} respectively). Tin, nickel, zinc, and copper had significant impacts on fertilization success at the comparatively low concentrations of 318 µg L^{-1}, 100 µg L^{-1}, 10 µg L^{-1}, and 6 µg L^{-1}, respectively. Of the eight pesticides examined, only the fungicide MEMC (2-methoxyethylmercuric chloride) had an impact on fertilization at 1 µg L^{-1}. The insecticides carbaryl, chlorpyrifos, chlorpyrifos-oxon, endosulfan, permethrin, and profenofos had no significant effect on fertilization success at concentrations up to 30 µg L^{-1}, and the herbicide diuron had no significant effect at concentrations up to 1000 µg L^{-1}.

Coral larvae: Survival rates of pre-settlement coral larvae were examined in response to exposure to five metals, five pesticides (all insecticides), and three PAHs. The impacts of metals on larval survival were variable by metal. Mercury had no impact on larval survival at concentrations up to 10 µg L^{-1}, though higher concentrations were not examined. Iron and manganese had significant negative effects at concentrations of 27,200 µg L^{-1} and 17,000 µg L^{-1}, respectively. Lead had a significant negative impact at 640 µg L^{-1}, and copper had a significant negative impact at concentrations as low as 10 µg L^{-1}. Copper also affected larval development and swimming velocity at 50 µg L^{-1}, and lead impacted swimming velocity at concentrations of 1,000 µg L^{-1}.

Among pesticides, the insecticides naled (0.56 µg L^{-1}) and permethrin (1.0 µg L^{-1}) had significant negative impacts on larval survival at very low concentrations, but chlorpyrifos (1,000 µg L^{-1}), 1-naphthol (1,000 µg L^{-1}), and carbaryl (10,000 µg L^{-1}) did not have measurable effects until applied at much higher concentrations. PAHs appear to have negative effects on larval survival at relatively low concentrations. Benzo(a)pyrene had significant negative effects at 10 µg L^{-1}, which was the only concentration examined, and anthracene and phenanthrene negatively impacted larval survival and settlement at 9.4 µg L^{-1} and 56.3 µg L^{-1}, respectively.

Larval settlement success (i.e., metamorphosis) was examined in response to five metals, nine pesticides, and two PAHs. Metals either impacted settlement at relatively low concentrations (i.e., copper at 24 µg L^{-1} and tin at 10 µg L^{-1}), or they did not have any impact until applied at very high concentrations (i.e., gallium at 2,150 µg L^{-1}, aluminum at 1,960 µg L^{-1}, and vanadium at 564 µg L^{-1}). Similarly, pesticides either affected settlement at low concentrations or did not have an apparent effect until they were applied at high concentrations. Naled, an insecticide, had no significant impacts on settlement at the concentrations examined, and diuron, a herbicide, had negative effects at concentrations of 300 µg L^{-1}. Carbaryl, an insecticide, negatively impacted settlement at 3.0 µg L^{-1}, while the insecticides chlorpyrifos, endosulfan, and permethrin all had negative impacts at 1.0 µg L^{-1}, as did the fungicide MEMC. Chlorpyrifos-oxon and profenofos (both insecticides) showed negative effects on settlement at concentrations as low as 0.3 µg L^{-1}.

Coral Juveniles: The only response examined for juvenile, post-settlement corals (i.e., recruits) was survival, which was assessed after exposure to tin, diuron, naled, and permethrin. Tin significantly decreased the likelihood of juvenile survival at 2.5 µg L^{-1}. The insecticides naled and permethrin did not have any significant effect on juvenile survival at the maximum concentrations examined, 9.59 µg L^{-1} and 6.04 µg L^{-1}, respectively. Diuron had no effect on juvenile survival at concentrations up to 1,000 µg L^{-1}.

Coral Adults: Tissue loss, growth rates, and adult mortality were examined in response to four metals, eight pesticides, two PAHs, and a PCB. Mortality increased following exposure to low concentrations of some pollutants (e.g., copper) and higher concentrations of others (e.g., manganese), but growth rates typically declined at much lower concentrations. Copper reduced growth rates at 4 µg L^{-1} and increased adult mortality at concentrations as low as 40 µg L^{-1}. Coral growth rates also declined at low concentrations of nickel (3.52 µg L^{-1} when combined with temperature stress), tin (0.4 µg L^{-1}), and cobalt (0.22 µg L^{-1}). Mortality increased after exposure to higher concentrations of lead (320 µg L^{-1}), and tissue loss and mortality increased at even higher concentrations of manganese (1000 µg L^{-1} and 5,000 µg L^{-1}, respectively).

Diuron decreased growth rates at 1 µg L^{-1} and caused tissue loss and adult coral mortality at 10 µg L^{-1}, while another herbicide, 2,4-D, caused mortality at 19,300 µg L^{-1}. None of the fungicides or insecticides (i.e., MEMC, carbaryl, chlorpyrifos, endosulfan, permethrin, and profenofos) caused tissue mortality at the maximum concentration examined, 10 µg L^{-1}, but profenofos and MEMC reduced tentacular activity at 10 µg L^{-1}. Fluoranthene, a PAH, increased tissue mortality at low concentrations (30 µg L^{-1}), while 1-methylnaphthalene increased tissue mortality and decreased tentacular activity at much higher concentrations (5,427 µg L^{-1} and above). Aroclor 1254, a PCB, did not affect mortality or growth at the concentration examined, 0.29 µg L^{-1}. Estrone, which is a naturally produced hormone used in pharmaceutical applications, decreased coral growth rates at concentrations as low as 0.002 µg L^{-1}, but mortality rates were not reported.

Bleaching was also examined as a stress response to two metals, eight pesticides, two PAHs, and one PCB. No bleaching was seen in response to cadmium at concentrations up to 50 µg L^{-1}, but bleaching was seen after exposure to copper concentrations of 30 µg L^{-1}. Aroclor 1254, a PCB, did not cause bleaching at the concentration examined (0.29 µg L^{-1}). Bleaching after exposure to PAHs and pesticides was variable. Bleaching occurred at 15 µg L^{-1} of fluoranthene but not at concentrations of up to 100 µg L^{-1} of benzo(a)pyrene. Bleaching also occurred in response to four pesticides at 10 µg L^{-1}: the fungicide MEMC; the herbicide diuron; and the insecticides permethrin and profenofos. No bleaching response was seen, however, after exposure to 10 µg L^{-1} of the insecticides carbaryl, chlorpyrifos, or endosulfan, and even when combined with temperature stress, bleaching was only seen after exposure to very high concentrations of the herbicide glyphosate (10,800 µg L^{-1}).

Symbiont density was also measured in response to six metals, nine pesticides, and one PAH. As seen with other coral responses, symbiont density decreased with exposure to metals at a range of concentrations that varied by metal. Cadmium had no significant effect on symbiont density at the maximum concentrations examined, 5 µg L^{-1}, while nickel decreased symbiont density at 3.5 µg L^{-1} when combined with temperature stress. Symbiont density decreased with exposure to mercury (180 µg L^{-1}), lead (75.6 µg L^{-1}), copper (12.6 µg L^{-1}), iron (10 µg L^{-1}), and benzo(a)pyrene, a PAH, (100 µg L^{-1}). Symbiont density decreased following exposure to 10 µg L^{-1} of profenofos (insecticide), MEMC (fungicide), and diuron (herbicide), but there was no significant change in symbiont density following exposure to the same concentration of the insecticides carbaryl, chlorpyrifos, endosulfan, naled, and permethrin. Symbiont density also decreased after exposure to very high (19,300 µg L^{-1}) concentrations of the herbicide 2,4-D.

The impact of pollutants on chlorophyll content was also examined. This assessment included studies focusing on five metals, four pesticides, and one PAH. As seen in other coral responses, chlorophyll content decreased after exposure to metals at a range of concentrations that varied by metal. Cadmium had no significant impact on chlorophyll at concentrations up to 50 µg L^{-1}, but chlorophyll content decreased with exposure to mercury (180 µg L^{-1}), lead (75.6 µg L^{-1}), and copper (5 µg L^{-1}). Benzo(a)pyrene, a PAH, reduced chlorophyll content at 9.02 µg L^{-1}, and when combined with temperature stress, the herbicide glyphosate decreased chlorophyll content at 10,800 µg L^{-1}. Atrazine, diuron, and hexazinone, all herbicides that inhibit photosystem II (Table 1), did not significantly impact chlorophyll content at the maximum concentrations examined (12.0 µg L^{-1}, 0.84 µg L^{-1}, and 3.8 µg L^{-1}, respectively).

Effective quantum yield (EQY) was measured as a response in studies that focused on the effects of copper, 1-methyl-naphthalene (a PAH), and fifteen pesticides (Table 3). However, maximum quantum yield (MQY) is the primary photosynthetic response considered herein (see Methods). MQY was examined in response to copper (see meta-analysis), cobalt, lead, nickel, Aroclor 1254 (PCB), and four herbicides. Cobalt and nickel had no significant impact on MQY at the highest concentrations examined, 0.22 µg L^{-1} and 3.52 µg L^{-1}, respectively. Copper had negative effects on MQY at concentrations as low as 1 µg L^{-1}, and lead also affected MQY at higher concentrations of 320 µg L^{-1}. Aroclor 1254 had no significant impact on MQY at the highest concentration examined, 0.29 µg L^{-1}. The herbicide, 2,4-D, similarly had no effect on MQY at 100,000 µg L^{-1}, the highest concentration examined. Atrazine and diuron did have negative effects on MQY at 3 µg L^{-1} and 1 µg L^{-1}, respectively.

4. DISCUSSION

Reduced water quality can be a root cause of extended and extensive coral-reef loss. Pollutants are major components of water quality, and as reviewed herein and elsewhere (Cooper et al., 2009; Fabricius, 2005; Gregg, 2013; Shaw et al., 2010), can cause reductions in coral reproductive function, recruitment, growth rates, and survivorship of both larvae and adults, while increasing disease susceptibility. Cumulatively, these effects diminish coral populations' persistence and replenishment capacity. To address this concern, we estimated thresholds of coral health in response to pollutants using a meta-analytical approach (Table 2). This required adapting Bayesian hierarchical dose-response meta-analysis models, originally developed for biopharmaceutical research (Thomas et al., 2014; Wu et al., 2018), for use with complex ecological datasets. Given the diversity of pollutants, coral responses, and experimental approaches, however, thresholds could not be estimated for most combinations of pollutants and responses (Table 4). Some pollutants, such as copper, have 14 different responses examined with up to 9 papers examining a single pollutant-response pair. Other pollutants and pollutant classes have received far less attention, which limits the capacity for meta-analysis to be used to develop more robust guidelines for these stressors. This is a particularly urgent need for pollutants with known impacts in other systems, such as estrogenic compounds and pesticides (Hayes and Hansen, 2017). In contrast to the coverage for copper, the three most widely used herbicides – 2,4-D, atrazine, and glyphosate – have only 7 studies among them included in this quantitative review (Table 3) (Hayes and Hansen, 2017).

Our study highlights the need to reassess the way in which pollution thresholds are examined on coral reefs and in other systems. Typically, the responses measured during early coral life-history are ‘terminal’ in that failure to fertilize or survive to the settlement-stage effectively precludes the capacity of a coral population to persist and rebound after stressful events, but these impacts can also compound through the life stages of a coral and affect various life stages differently. The varied and in some cases cumulative impacts of pollutants at different life stages have been demonstrated in other organisms such as Chinese cabbage (Luo et al., 2019), zebrafish (Brion et al., 2004), and albatross (Goutte et al., 2014). Understanding how these potentially additive impacts manifest is important in identifying high risk time periods or locations for management. This is especially important in corals which have unique, complex life cycles that are intimately linked to the health of their holobiont (i.e., associated symbionts, bacteria, fungi) (Vega-Thurber et al., 2009).

One example of the compounding effect of pollutant exposure specific to this study is illustrated in Fig. 4, in which exposure to just 40 $\mu g\ L^{-1}$ copper during the first week post-fertilization leads to less than half the number of coral recruits, as compared to uncontaminated conditions (27% vs. 59% of starting gametes). Copper exposure at 100 $\mu g\ L^{-1}$ effectively eliminates all coral larvae from settling to the reef. Thus, assigning a management threshold at EC_{50} values for responses of immature corals will likely be inadequate to prevent reef decline. A greater diversity of responses to stressors is measured for adult corals, which offers an opportunity to consider sublethal effects when estimating pollution thresholds that are more conservative than those estimated from lethal effects only. Regardless, additional studies are needed that evaluate the effect of more pollutants across the coral life cycle before truly effective management thresholds can be assigned. In the meantime, a conservative approach should be adopted when data suggest that a pollutant adversely affects corals at any stage.

Our quantitative review indicates that some pollutants impact corals more than other pollutants, which can offer insight and guidance into mitigating the risks of multiple, co-occurring chemicals (see Table 3). For example, the lowest concentrations (LOAELs) at which copper adversely affected fertilization was 6 $\mu g\ L^{-1}$, while settlement was impacted at 24 $\mu g\ L^{-1}$ and adult survival at 40 $\mu g\ L^{-1}$. Zinc similarly affects fertilization at just 10 $\mu g\ L^{-1}$. Conversely, tin does not impact fertilization at concentrations up to 318 $\mu g\ L^{-1}$, but does negatively affect settlement and juvenile survival at much lower concentrations of 10 $\mu g\ L^{-1}$ and 2.5 $\mu g\ L^{-1}$, respectively. Other metals, such as cadmium, only reduce fertilization at much higher concentrations (5000 $\mu g\ L^{-1}$). Different classes of pollutants, such as herbicides that inhibit photosystem II (e.g., diuron), may differentially impact coral life stages (Table 1). Diuron has a LOAEL for larval settlement of 300 $\mu g\ L^{-1}$, but negatively impacts photosynthesis at concentrations as low as 0.3 $\mu g\ L^{-1}$ (Negri et al., 2005). Conversely, another herbicide, chlorpyrifos (an acetylcholinesterase-inhibitor), does not inhibit fertilization or adult coral function at the concentrations measured, but does impact larval settlement at just 1 $\mu g\ L^{-1}$ (Table 3). Compared to metals and pesticides, the impacts of PAHs, PCBs, and pharmaceuticals on corals are understudied. However, within those studies that do exist, there is variability in the impacts among life stages. These differences highlight the importance of examining impacts at different life stages to understand the breadth of potential effects and develop management strategies that specifically target the greatest threats at the most vulnerable stages.

Many pollutants also degrade in the environment and in organisms, yielding a myriad of different breakdown products that may be harmful to corals and other animals (ATSDR, 1995). However, breakdown products present in the environment are not well documented for many pollutants, making it difficult to assess their potential impact (Hayes and Hansen, 2017). Further, most studies examine one pollutant at varying concentrations and then measure a single biological response. In the environment, however, corals and other organisms are exposed to a diverse array of pollutants that may be found in combination with other stressors such as fluctuations in sediment, freshwater, temperature, and pH (Banc-Prandi and Fine, 2019; Donovan et al., 2020; Hédouin et al., 2016; Negri et al., 2011a). These combinations may produce synergistic and additive effects that are difficult to isolate, quantify, and manage. For example, zinc can be harmful to corals and other organisms in isolation, but it is also known to interact with other metals, such as lead and copper, exacerbating negative impacts (Eisler, 1993). This further highlights the need for conservative guidelines that account for multiple stressors, sublethal impacts, and compounding effects throughout the life cycle of an organism.

Future studies examining the impacts of pollutants on corals and other marine organisms should consider environmentally relevant concentrations of pollutants, which means including ambient, background levels as well as those that are enhanced significantly by human activity. For example, nickel is found at high concentrations in the environment from natural sources such as volcanic rock, but it is found in unnaturally high levels on coral reefs adjacent to locations with land use that causes runoff of nickel-rich sediments (Hédouin et al., 2009). Environmentally relevant concentrations may also lend insight into the importance of exposure duration in experimental studies. For instance, we found that diuron may have impacts that vary depending on exposure duration (Fig. 3). This may be of particular importance in areas with limited water flow to flush out pollutants, such as enclosed bays. Understanding the relative importance of exposure concentration, duration, and frequency is important for local management strategies. Thus, increasing the number of studies that examine the impacts of acute vs. chronic pollutant exposures will increase the capacity to compare across stressors and more accurately model their interactions on reefs.

The difference between acute exposure and chronic impacts is often considered in the development of consumption limits in the context of human health (e.g., ATSDR Minimal Risk Levels or US EPA Reference Doses), so these guidelines may offer insight into how to more effectively develop thresholds for pollutant impacts on wildlife. In the human health context, ‘Reference Doses’ are developed by taking the highest concentration at which there is no observable adverse effect (NOAEL) in response to a pollutant and dividing it by an uncertainty factor, which can range from 10 to 3000 (US EPA, 1993; US EPA, 2009). Resource managers may want to model habitat conservation guidelines off of this approach to account for the sublethal, synergistic, and compounding impacts of pollutant stressors on corals and other marine organisms. Further, this would aid in addressing the often undocumented differences in responses between species and morphology, where some taxa are better equipped than others to manage exposure to certain stressors. In many cases, we do not have species-specific guidelines, and this is an area that is ripe for additional research, especially in locations where resource managers seek to develop place-based strategies. In the meantime, however, setting conservative limits modeled after human health approaches would ensure that the most vulnerable taxa are better protected, even in cases where their responses are not well documented.

Tools that identify sublethal stress in corals, including molecular techniques such as proteomics, genomics, and transcriptomics, also allow for both the diagnosis and evaluation of the effectiveness of management interventions at both individual and population levels. These molecular biomarkers can be used to identify those specific toxicants that affect homeostasis, metabolic condition, reproductive function, and DNA integrity, potentially before declining coral health is evident (Cantin et al., 2007; Parkinson et al., 2019; Tisthammer et al., 2021). When such molecular data are evaluated and applied, interventions can be designed, implemented and evaluated in periods of weeks to months, rather than years to decades, as is done with ecological indicators such as percent coral cover (Cooper et al., 2009). These qualitative and quantitative tools can identify key stressors of biological relevance, threshold levels at which effects occur, and antagonisms/synergisms with other stressors. Furthermore, research frameworks exist for the discovery, validation, and implementation of molecular biomarker tools in corals (Parkinson et al., 2019).

These molecular tools now allow researchers and managers to rapidly identify the biological relevance of chemical contaminants, not just their presence and concentration, which when measured in the field are ephemeral and change with tides, wind, rainfall, and water characteristics such as flushing and residence times. Corals and other reef organisms serve as sensitive and accurate integrators of toxicant exposure in the field. For example, coral lipids can act as living semipermeable membrane devices for accumulating lipophilic/hydrophobic substances, such as PAHs and pesticides (Caroselli et al., 2020; Porter et al., 2018). Additionally, molecular tools allow managers to identify both sensitive and resistant genotypes, and of critical importance to reef resilience, genotypic diversity within coral populations (Tisthammer et al., 2021). This is a very important indicator of impending local extinction events in which specific stressor thresholds are exceeded and genotypic diversity is lost.

Based on apparent gaps in our understanding and approach-to-date, we recommend that researchers target a broader set of pollutant types. We also recommend defining critical threshold values for toxicants on coral reefs by targeting a broad range of stressor concentrations that reflect toxicant levels seen in the environment and elicit sublethal (e.g., physiological, behavioral, molecular, or microbial) responses in corals, so that stress can be quantified and mitigated before corals experience mortality. We also encourage experimental designs that result in a dose-response curve to enable estimation of the inhibitory concentration thresholds (EC_x). Furthermore, we recommend that researchers attempt to standardize the units in which they report both toxicant levels (e.g., $\mu g\ L^{-1}$) and coral responses (e.g., bleaching, see Grottoli et al., 2020), and that raw data is made available whenever possible. These efforts will improve our ability to synthesize comparable information across studies, locations, species, and stressors, thus resulting in data-rich meta-analyses that better inform management decisions.

As the availability of data that addresses a range of pollutants at environmentally relevant concentrations over the complete life cycle of corals becomes available, it is important to update and adapt management strategies as appropriate. In the cases where sufficient data do not exist to inform management and policy decisions, the approach of public health officials should be followed to develop guidelines that employ the precautionary principle. Many pollutants are co-occurring and are present in combination with other environmental stressors, such as increased temperature or ocean acidification, that may also have synergistic or additive effects (Biscéré et al., 2015; Cabral et al., 2019; Fujita et al., 2014; Kwok and Ang, 2013). With this in mind, it must be acknowledged that guidelines based on NOAEL/LOAELs or EC_{50} values are not necessarily conservative enough to protect foundational species, like reef-building corals. In addition, adopting truly conservative guidelines will better address the potential variability in the effects of exposure duration on the stress response.

Basing guidelines on the maximum concentrations present in water quality monitoring as well as those seen in extreme events, rather than the mean, is one way that resource managers can work to enact more conservative management strategies. In addition, resource managers can also take proactive steps to collaboratively work with other agencies to address pollution before it reaches the coastal zone. As an example, some pollutants are broken down by bacteria and fungi (Ceci et al., 2019), so comprehensive ridge-to-reef management strategies may consider these active remediation strategies to reduce land-based pollutant inputs. Finally, climate change impacts pose a clear threat to reefs globally, so as managers develop strategies to mitigate the risks associated with increased temperatures, bleaching events, ocean acidification, and increased storm frequency, it is important to also consider the reduced capacity for resilience and recovery in corals that are already experiencing physiological stress as a result of toxicant exposure.

5. CONCLUSIONS

When sufficient data are available, Bayesian dose-response meta-analysis provides a robust way of examining the relationship between pollutant concentrations and subsequent coral responses. The impacts of copper on fertilization are well studied and offer an example of the type of data that would be desirable for all stressor-response combinations. Because there are so few studies, it is not yet possible to disentangle the effects of species, morphology, or location, but these are important considerations for the development of place-based management strategies. In the absence of robust reference data for most pollutants, it is important to create management guidelines that are conservative and abide by the precautionary principle. Pollutants on reefs do not act in isolation. Instead, they are typically combined with other toxins and environmental stressors associated with climate change (Cabral et al., 2019; Fujita et al., 2014), and negative impacts likely compound throughout the different life stages (Fig. 4). In combination with more conservative guidelines that account for the known and unknown variability in these systems, coordinated strategies that include active remediation will also reduce impacts on reefs. Finally, it is also important to move beyond considering just lethal coral responses at single life-history stages as indicators of stress. Developing standardized approaches to measure sublethal responses will offer resources for the development of targeted, proactive interventions.

Global climate change – with the associated problems of elevated seawater temperatures and regional mass coral bleaching events, ocean acidification affecting calcification rates, enhanced tropical storm frequency and severity, and sea level rise – is clearly the major cause of coral-reef loss at the global scale. From a management perspective, however, it is strategic and essential to address local stressors now to buy time to tackle the challenge of climate change. Reducing local stressors, such as chemical pollutants, can improve resistance, resilience, and recovery for individual reefs and reef ecosystems.

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DATA STATEMENT

All data generated during this study, along with code used to analyze data and generate figures, are shared in the public repository: https://github.com/ljtuttle/coral_pollutant_thresholds

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TABLE AND FIGURE CAPTIONS

Table 1. Focal pollutants of this review that may elicit negative physiological responses in corals, grouped by class, industrial use/source, and mode of action.

Table 2. Bayesian hierarchical dose-response meta-analysis results for the stressor-response pairs with sufficient data to be included in the meta-analysis. ECx refers to the effective concentration of copper (µg L^{-1}), as derived from the meta-analytical model, that inhibited the coral response by 5% ,10%, 20%, or 50%, with model average estimates and lower (Q2.5) and upper (Q97.5) Bayesian credible intervals.

Table 3. Quantitative review of pollutants, coral responses, range of concentrations examined (not including control levels at 0 µg L^{-1}), and no- and lowest-observed adverse effect levels (NOAEL, LOAEL) from the corresponding article(s). A LOAEL is the lowest pollutant concentration experimentally tested at which a coral adversely responded, and a NOAEL is the highest pollutant concentration, less than or equal to the LOAEL, at which a coral did not adversely respond. If more than one article is listed, then the LOAEL is the most conservative (i.e., lowest) value from among the articles. See Table S3 for more details concerning species, region, and reported EC50 values from each article. Abbreviations: EQY = effective quantum yield; MQY = maximum quantum yield; P/R = production to respiration ratio.

Table 4. Relative amounts of data available (i.e., gap analysis) that address different combinations of pollutants (left two columns) with coral responses, organized by life-history stage (top). The numbers in each cell indicate the number of articles that examine the pollutant-

response pair, and the shade of the cell is scaled to the relative number of articles, with darker shades indicating more articles. Empty cells indicate no (zero) articles found in our systematic review that adequately address the pollutant-response pair.

Figure 1. Inhibitory dose-response curves for the effects of copper on coral fertilization success (n = 9 articles with 17 experiments therein) (**A**), larval survival (n = 3 articles with 6 experiments therein) (**B**), larval settlement (n = 3 articles with 4 experiments therein) (**C**), and adult maximum quantum yield (n = 4 articles with 11 experiments therein) (**D**). Each point represents a raw mean from an experimental control/treatment group included in the meta-analysis. Bayesian model results are shown as lines: the bold black lines represent the models' average curves (with 95% credible intervals as gray-shaded regions) across all studies, and the gray lines represent the model-estimated curve for each article/experiment (all lines in **D** converged along the average). The red dashed lines and corresponding numbers along the x-axis indicate the EC_{50} parameter estimate for the average curve.

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Figure 2. The relative effects of different metal concentrations (in µmol L^{-1}) on coral fertilization success, shown as Bayesian-modeled inhibitory dose-response curves (**A**) and as EC_{50} posterior distributions and estimates (points) +/- Bayesian 95% credible intervals (dark lines) (**B**). Points and lines in (**A**) are color-coded by metal as indicated in the key. The following metals were included: cadmium (n = 2 articles with 3 experiments therein); copper (n = 9 articles with 17 experiments therein); iron (n = 1 article with 4 experiments therein); lead (n = 1 article with 3 experiments therein); manganese (n = 1 article with 4 experiments therein); nickel (n = 3

articles with 5 experiments therein); zinc (n = 2 articles with 2 experiments therein); and aluminum, cobalt, gallium, tin, and vanadium (all with n = 1 experiment in 1 article).

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Figure 3. Coral maximum quantum yield as a function of diuron exposure concentration (**A**) and duration (**B**) (n = 5 with 25 experiments therein). Each point represents a raw mean (+/- standard error, shown in **B** only) from an experimental control/treatment group included in the meta-analysis. Bayesian model results are shown in (**A**) as lines: the bold black line represents the model's average curve (with 95% credible intervals as gray-shaded region) across all studies, and the gray lines represent the model-estimated curve for each article/experiment. The red dashed line and corresponding number along the x-axis indicate the EC_{50} parameter estimate for the average curve. (**B**) Shows data for three exposure concentrations across two orders of magnitude of diuron exposure duration (1-100 days), and indicates a relatively weak relationship between duration and MQY, especially at 0 and 1 μg L^{-1}.

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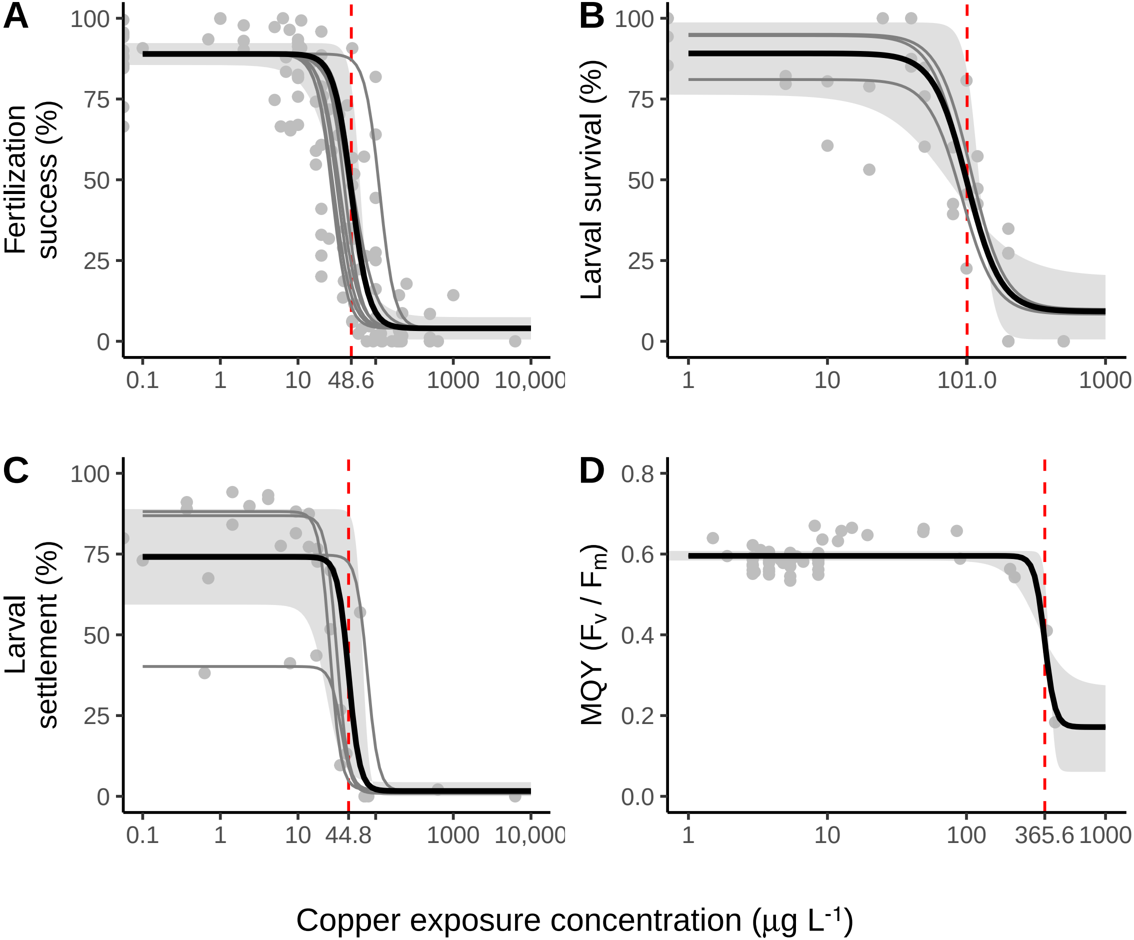
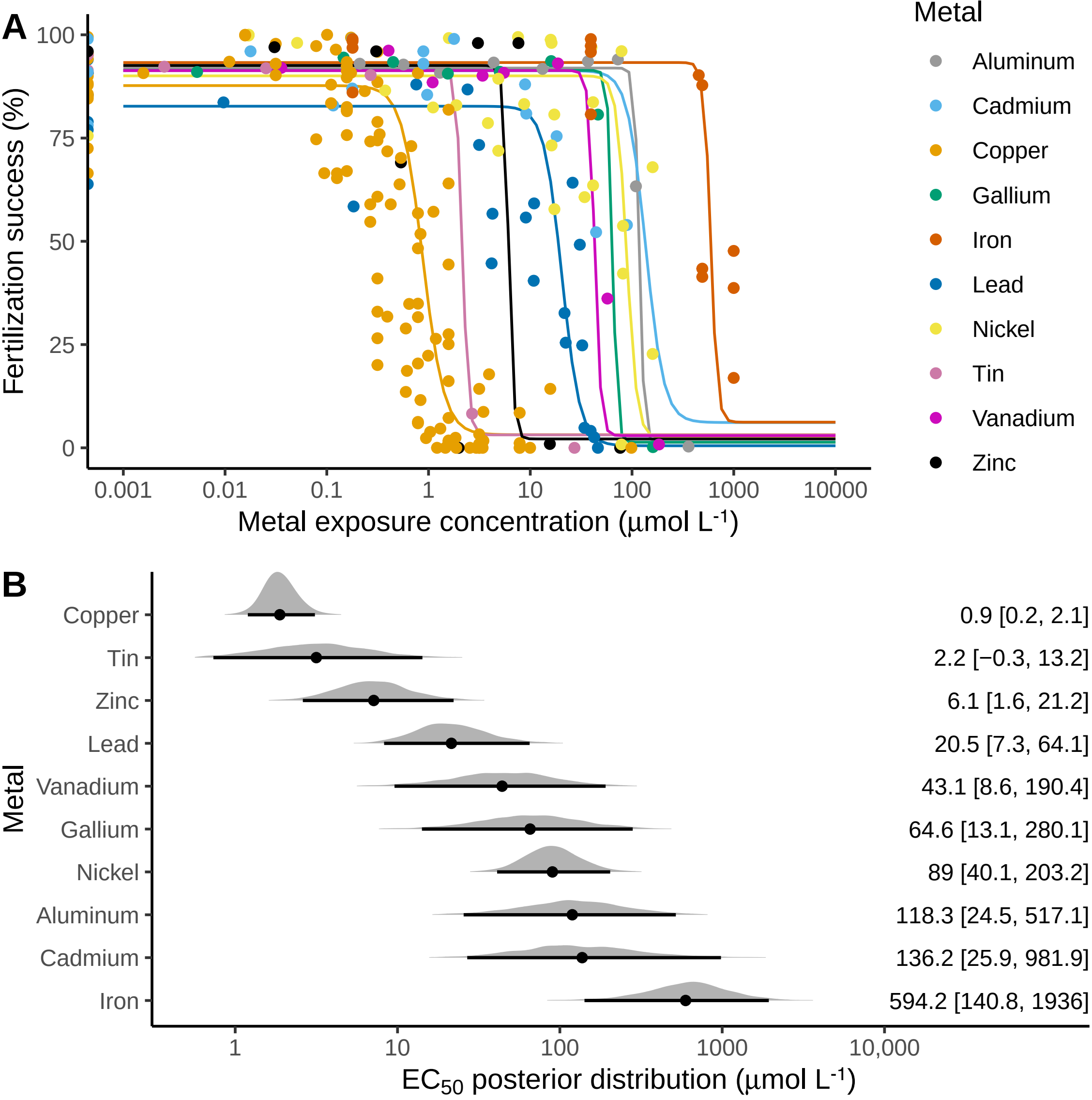
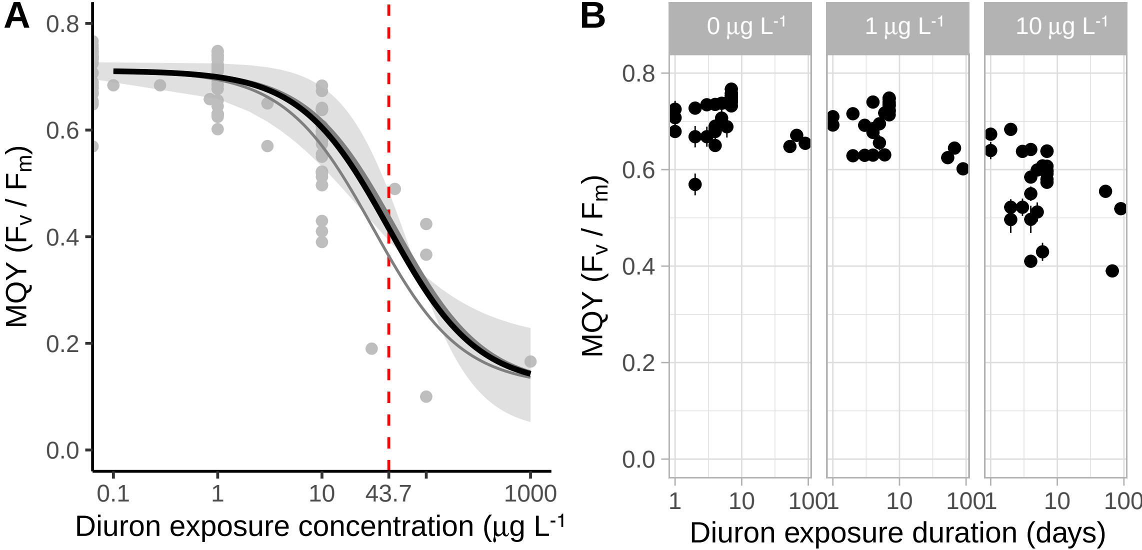
Figure 4. Illustrative representation of the compounding effects of copper during the early life stages of a coral in a simplified, closed system where only reproductive adults contribute to the population. The horizontal, colored bands correspond to systems with 0, 40, and 100 μg L^{-1} copper, respectively. "Absolute" numbers are the Bayesian model average estimates for the corresponding copper concentration and coral response. "Cumulative" numbers are the absolute percent listed at a stage multiplied by the cumulative percent from the previous stage (assuming 100% for reproductive adults). Thus, it represents the percent of individuals remaining since

release of gametes by adults. Absolute estimates (with Bayesian 95% credible intervals) at 0 µg L^{-1} are 89.0% (85.5, 92.3) for fertilization success, 89.1% (76.3, 98.7) for larval survival, and 74.1% (59.3, 88.9) for larval settlement. At 40 µg L^{-1}, the same estimates are 61.7% (38.8, 88.3), 86.4% (63.7, 98.7), and 50.0% (9.8, 88.5), respectively. At 100 µg L^{-1}, the same estimates are 9.0% (4.9, 13.9), 49.9% (42.0, 84.4), and 2.2% (1.8, 4.5), respectively.

Formatting note: 1.5 columns, color preference online only

A
Fertilization success (%)
100
75
50
25
0
0.1
1
10
48.6
1000
10,000
B
Larval survival (%)
100
75
50
25
0
1
10
101.0
1000
C
Larval settlement (%)
100
75
50
25
0
0.1
1
10
44.8
1000
10,000
D
MQY (F_v / F_m)
0.8
0.6
0.4
0.2
0.0
1
10
100
365.6
1000
Copper exposure concentration (µg L^{-1})


A
Fertilization success (%)
100
75
50
25
0
0.001
0.01
0.1
1
10
100
1000
10000
Metal exposure concentration (µmol L-1)
Metal
Aluminum
Cadmium
Copper
Gallium
Iron
Lead
Nickel
Tin
Vanadium
Zinc
B
Metal
Copper
Tin
Zinc
Lead
Vanadium
Gallium
Nickel
Aluminum
Cadmium
Iron
0.9 [0.2, 2.1]
2.2 [−0.3, 13.2]
6.1 [1.6, 21.2]
20.5 [7.3, 64.1]
43.1 [8.6, 190.4]
64.6 [13.1, 280.1]
89 [40.1, 203.2]
118.3 [24.5, 517.1]
136.2 [25.9, 981.9]
594.2 [140.8, 1936]
1
10
100
1000
10,000
EC50 posterior distribution (µmol L-1)


A
0.8
0.6
0.4
0.2
0.0
MQY (F_v / F_m)
0.1
1
10
43.7
1000
Diuron exposure concentration (µg L^{-1}
B
0 µg L^{-1}
1 µg L^{-1}
10 µg L^{-1}
0.8
0.6
0.4
0.2
0.0
MQY (F_v / F_m)
1
10
1001
10
1001
10
100
Diuron exposure duration (days)

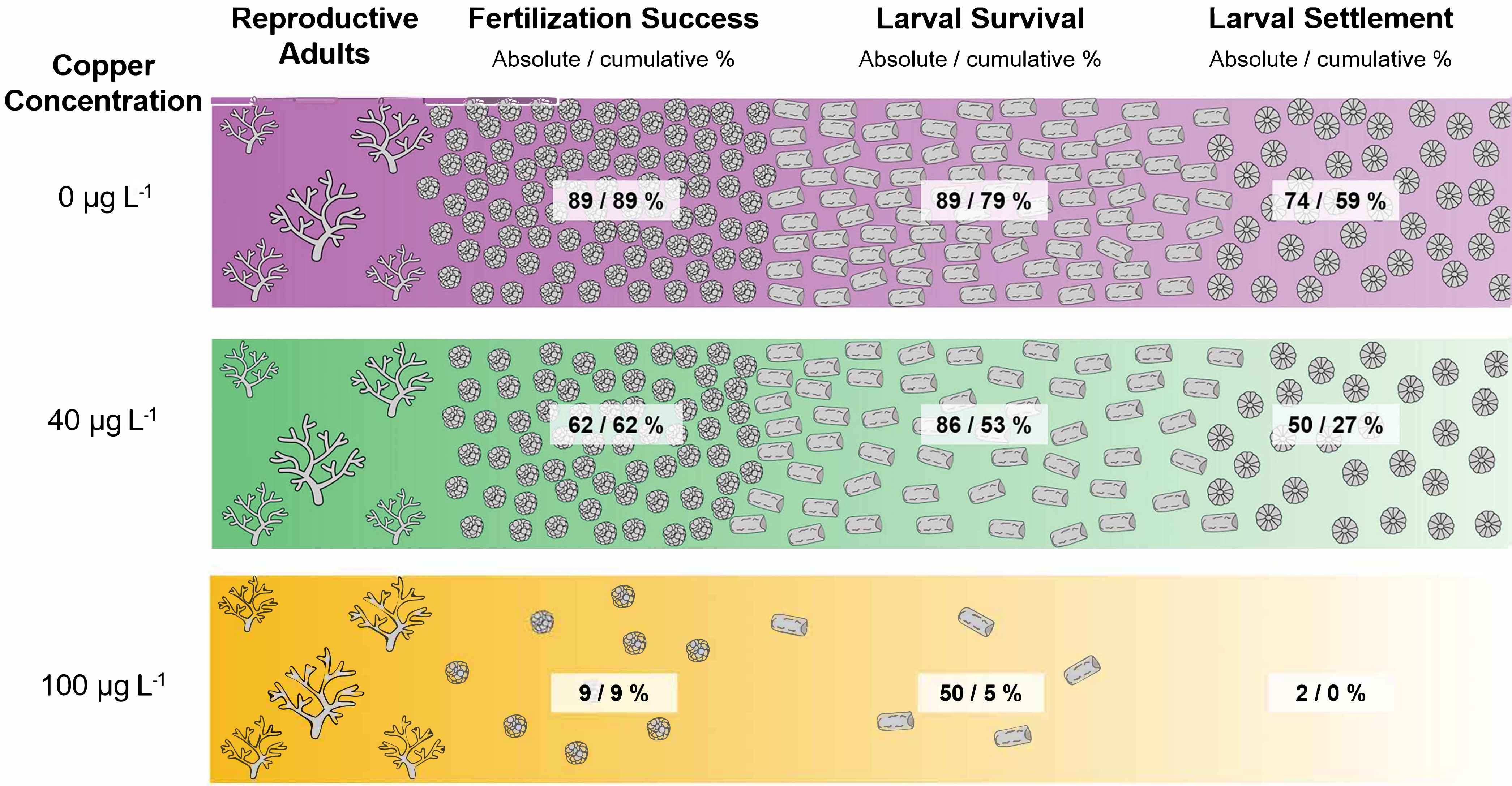

Copper Concentration
Reproductive Adults
Fertilization Success
Absolute / cumulative %
Larval Survival
Absolute / cumulative %
Larval Settlement
Absolute / cumulative %
0 µg L^{-1}
89 / 89 %
89 / 79 %
74 / 59 %
40 µg L^{-1}
62 / 62 %
86 / 53 %
50 / 27 %
100 µg L^{-1}
9 / 9 %
50 / 5 %
2 / 0 %

Table 1. Focal pollutants of this review that may elicit negative physiological responses in corals, grouped by class, industrial use/source, and mode of action.

Pollutant Class	Pollutant	Industrial Use/Source	Mode of Action
METAL	**Aluminum**	Naturally occurring but also distributed in the environment through fossil fuel combustion, agricultural spray drift, and runoff or leaching from resource extraction and wastewater treatment (EPA, 2018).	Disrupts osmoregulation at gill surface in fish, leading to cell death (Exley et al., 1991). May disrupt concentrations of specific ions, primarily resulting in a loss of sodium in invertebrates (Hornstrom et al., 1984).
	Cadmium	Naturally occurring but is also used for batteries, pigments, paints, stabilizers and coatings, and alloys (ATSDR, 2012).	Disrupts lipid composition and depletes antioxidant enzymes. Alters metabolism of other metals (e.g., zinc, iron, and copper) and can disrupt DNA transcription (ATSDR, 2012).
	Cobalt	Naturally occurring but also used to form alloys for industrial and military applications, as a colorant in dyes, and as an additive in agricultural applications (ATSDR, 2004).	Generates oxidants and causes lipid peroxidation, inducing nitric oxide synthase as a response to oxidant stress and free radical DNA damage. Can block calcium channels in mammals. Increased damage documented in combination with other stressors, like UV radiation (ATSDR, 2004).
	Copper	Used as a biocide in antifouling paints (Jones and Kerswell, 2003).	Forms reactive oxygen radicals that damage cells and proteins, and also denature enzymes (Boone et al., 2012; Yruela, 2009).
	Gallium	Naturally occurring but generated as a byproduct of aluminum manufacturing and used to make semiconductors and light-emitting diodes (Yu and Liao, 2010).	Can replace iron in iron transport proteins, disrupting the synthesis of DNA and proteins (Yu and Liao, 2010).
	Iron	Naturally occurring and required by plants and animals, but used in many manufacturing processes (US EPA, 1988).	Causes cellular oxidative stress by inhibiting antioxidants (e.g., glutathione) and increasing lipid peroxidation (Vijayavel et al. 2012).
	Lead	Naturally occurring but was widely distributed in the environment through combustion of leaded gasoline. Also occurs in paints, pesticides, pipes, and can be released through waste incineration (ATSDR, 2020).	Disrupts ion homeostasis by taking the place of metal ions (e.g., iron, calcium, zinc, magnesium, selenium, and manganese) interrupting biological processes requiring these ions or dependent enzymes and proteins (ATSDR, 2020).
	Manganese	Naturally occurring but produced through smelting, fertilizer, and gasoline (US EPA, 2003).	In mammalian studies, primarily targets the nervous system (US EPA, 2003).
	Mercury	Naturally occurring but released through burning waste and fossil fuels. Used in gold mining and as a wood preservative, fungicide, and in electrical equipment. Microorganisms convert into toxic methylmercury (ATSDR, 1999; US EPA, 2021a).	Accumulates in zooxanthellae symbionts responsible for photosynthesis, potentially leading to the expulsion of symbionts (Bastidas and Garcia, 2004).
	Nickel	Naturally occurring but found at increased concentrations due to industrial pollution (e.g., production of stainless steel) (Brix et al., 2017).	Reduces calcium available for growth, affects respiration, and can causes cytotoxicity and lead to tumor formation (Brix et al., 2017).
	Tin	Inorganic: occurs naturally in Earth's crust, also found in dyes and additives Organic: found in plastics, packaging, pipes, pesticides, paint, preservatives, & rodent repellants (ATSDR, 2005b).	Not well studied in invertebrates. In mammals builds up in the pancreas (ATSDR, 2005b).
	Vanadium	Naturally occurring but typically released through combustion of fossil fuels or via runoff (Beusen and Neven, 1987).	Inhibits ATPase, phosphotransferase, nuclease, and kinase. Also interferes with cell growth (Fichet and Miramand, 1998).
	Zinc	Naturally occurring but used to create metal alloys, pigments, and as a fungicide. Released through fossil fuel combustion and road runoff (Eisler, 1993).	Required for function, but excess concentrations can be toxic. Impacts zinc-dependent enzymes that regulate RNA/DNA. Interacts with other compounds (e.g., copper, lead), compounding effects (Eisler, 1993).

HERBICIDE	**2,4-D**	Used to control broadleaf weeds and regulate citrus growth (US EPA, 2021b).	Mimics plant growth hormone auxin leading to unregulated, disorganized cell growth (Song, 2014).
	Ametryn	Used as an herbicide to control pre- and post-emergence broadleaf weeds and grasses in pineapple, sugarcane, and banana crops (US EPA, 1984).	Photosystem II inhibitor: inhibits photosynthesis by blocking electron transfer from QA to QB (Jones, 2005).
	Atrazine	Used as a herbicide to control pre- and post-emergence broadleaf weeds and grasses in corn, sorghum, and sugarcane (US EPA, 2021c).	Photosystem II inhibitor as above.
	Diuron	Used to control weeds pre- and post-emergence (Raberg et al., 2003). Used in antifouling paints (Jones and Kerswell, 2003).	Photosystem II inhibitor as above.
	Glyphosate	Used to control broadleaf weeds and grasses (US EPA, 2021d).	Inhibits the enzyme 5-enolpyruvylshikimate-3-phosphate (EPSP) synthase and prevents creation of proteins (Shaner, 2006).
	Hexazinone	Used on broadleaf weeds and woody plants (US EPA, 2008).	Photosystem II inhibitor as above.
	Ioxynil	Used as an herbicide.	Photosystem II inhibitor as above.
	Irgarol	Used in antifouling paints (Jones and Kerswell, 2003).	Photosystem II inhibitor as above.
	Simazine	Used to control broadleaf and grassy weeds (US EPA, 2020).	Photosystem II inhibitor as above.
	Tebuthiuron	Used to control broadleaf and woody weeds, grasses, and brush (US EPA, 1994).	Photosystem II inhibitor as above.
INSECTICIDE	**1-Naphthol**	Breakdown product of carbaryl (Acevedo, 1991).	Inhibits cholinesterase, affecting the nervous system leading to paralysis (Acevedo, 1991).
	Carbaryl	Used on sugarcane, cotton, fruits, vegetables, grains, and for termite and domestic pest control (Markey et al., 2007).	Inhibits acetylcholinesterase (AChE), which leads to constant stimulation of nervous system (Markey et al., 2007).
	Chlorpyrifos	Used on sugarcane, cotton, fruits, vegetables, grains, and for termite, mosquito, and domestic pest control (Markey et al., 2007).	Inhibits AChE as above (Markey et al., 2007).
	Endosulfan	Used on cotton, fruits, vegetables, and grains (Markey et al., 2007).	Suppresses function of neurotransmitter GABA, resulting in unchecked stimulation of neurons (Markey et al., 2007).
	Naled	Used primarily for mosquito control (US EPA, 2021e).	Inhibits AChE as above (Markey et al., 2007).
	Permethrin	Used on cotton, fruits, vegetables, grains, and for mosquito and domestic pest control (Markey et al., 2007).	Inactivates nerve junctions (Markey et al., 2007).
	Profenofos	Used on cotton (Markey et al., 2007).	Inhibits AChE as above (Markey et al., 2007).
FUNGICIDE	**MEMC**	Used in seed protectants and paints (Roberts and Reigart, 2013).	Denatures proteins and inactivates enzymes (Markey et al., 2007).
PAH	**1-methyl-naphthalene**	Generated by burning fossil fuels, wood, or tobacco. Used in dyes and resins (ATSDR, 2005a).	In mammalian studies, primarily targets alveolar pneumocytes and bronchial cells (ATSDR, 2005a).
	Anthracene	Generated in volcanoes and forest fires but also found in dyes, plastics, and pesticides. Also found in fossil fuels and released during combustion (MN Dept. of Health, 2019).	Causes inflammation and buildup of fluid in tissues and can also causes tumors, reproductive issues, and damage to immune system (US EPA, 2009).
	Benzo(a)pyrene	Generated in volcanoes and forest fires but also generated through burning fossil fuels, waste, and wood (ATSDR, 1995).	Lipophilic compounds that transform to reactive intermediates which bind to DNA, causing mutation (ASTDR, 1995). Causes oxidative stress in larvae (Farina et al., 2008).
	Fluoranthene	Generated in volcanoes and forest fires but also generated through burning fossil fuels, waste, and wood (ATSDR, 1995).	Lipophilic compounds that transform to reactive intermediates which can bind to DNA, causing mutation (ASTDR, 1995).

	Phenanthrene	Generated in volcanoes and forest fires but also generated through burning fossil fuels, waste, and wood (ATSDR, 1995).	Lipophilic compounds that transform to reactive intermediates which can bind to DNA, causing mutation (ASTDR, 1995).
PCB	**Aroclor 1254**	Used in transformers, electrical equipment, heat transfer material, insulation, and adhesives (US EPA, 2021f).	PCBs interact with the 2,3,7,8-TCDD receptor protein, inhibit intercellular communication, and induce cytochrome P450c dependent monooxygenase (Eisler and Belisle, 1996).
PHARMACEUTICAL	**Estrone**	Produced in vertebrates and used in human hormone therapy. Released through untreated wastewater and sewage effluent (Atkinson et al., 2003).	Vertebrate hormone involved in female sexual development. Hypothesized to play a role in regulating reproductive process in corals, though the mechanisms are unknown (Tarrant et al., 2004).

Table 2. Bayesian hierarchical dose-response meta-analysis results for the stressor-response pairs with sufficient data to be included in the meta-analysis. EC_x refers to the effective concentration of copper (µg L^{-1}), as derived from the meta-analytical model, that inhibited the coral response by 5% ,10%, 20%, or 50%, with model average estimates and lower (Q2.5) and upper (Q97.5) Bayesian credible intervals.

Coral Age Class	Coral Response	Pollutant	Bayesian Model R^2	EC_x	Estimate	Q2.5	Q97.5
GAMETES	Fertilization success rate	Copper	0.932	EC_5	22.6	8.7	40.9
				EC_{10}	27.5	12.3	45.7
				EC_{20}	33.9	17.8	51.7
				EC_{50}	48.6	33.4	63.7
LARVAE	Settlement rate	Copper	0.844	EC_5	27.7	11.2	50.5
				EC_{10}	31.3	13.4	54.4
				EC_{20}	35.7	16.4	59.0
				EC_{50}	44.8	23.1	67.7
	Survival rate	Copper	0.973	EC_5	44.7	15.9	86.9
				EC_{10}	55.0	23.8	95.0
				EC_{20}	68.8	37.0	104.7
				EC_{50}	101.0	78.6	123.6
ADULTS	Photosynthetic efficiency (MQY)	Copper	0.717	EC_5	285.5	156.9	351.5
				EC_{10}	303.9	188.0	362.5
				EC_{20}	325.3	228.9	374.9
				EC_{50}	365.3	320.3	397.0
		Diuron	0.853	EC_5	2.5	0.6	8.0
				EC_{10}	5.1	1.5	13.8
				EC_{20}	11.3	4.1	24.9
				EC_{50}	43.7	24.0	68.5

Table 3. Quantitative review of pollutants, coral responses, range of concentrations examined (not including control levels at 0 µg L^{-1}), and no- and lowest-observed adverse effect levels (NOAEL, LOAEL) from the corresponding article(s). A LOAEL is the lowest pollutant concentration experimentally tested at which a coral adversely responded, and a NOAEL is the highest pollutant concentration, less than or equal to the LOAEL, at which a coral did not adversely respond. If more than one article is listed, then the LOAEL is the most conservative (i.e., lowest) value from among the articles. See Table S3 for more details concerning species, region, and reported EC50 values from each article. Abbreviations: EQY = effective quantum yield; MQY = maximum quantum yield; P/R = production to respiration ratio.

Pollutant Class	**Pollutant**	**Coral Response**	**Range of Concentrations Examined (µg L^{-1})**	**NOAEL (µg L^{-1})**	**LOAEL (µg L^{-1})**	**Article**
METAL	**Aluminum**	fertilization success	5.5 - 9,700	1,960	2,950	Negri et al., 2011
		settlement	15.3 - 9,700	996	1,960	Negri et al., 2011
	Cadmium	fertilization success	2 - 10,000	2,000	5,000	Reichelt-Brushett and Harrison, 2005, 1999
		bleaching	5 - 50	50	none	Mitchelmore et al., 2007
		chlorophyll concentration	5 - 50	50	none	Mitchelmore et al., 2007
		symbiont density	5 - 50	50	none	Mitchelmore et al., 2007
		tissue/colony mortality	5 - 50	5	50	Mitchelmore et al., 2007
	Cobalt	fertilization success	9.5 - 2,357	2,357	none	Reichelt-Brushett and Hudspith, 2016
		growth	0.03 - 0.2	0.03	0.2	Biscéré et al., 2015
		MQY	0.03 - 0.2	0.2	none	Biscéré et al., 2015
	Copper	fertilization success	0.1 - 6,263	2	6	Gissi et al., 2017; Kwok et al., 2016; Reichelt-Brushett and Hudspith, 2016; Puisay et al., 2015; Hédouin and Gates, 2013; Reichelt-Brushett and Harrison, 2005, 1999; Victor and Richmond, 2005; Negri and Heyward, 2001
		abnormal larval development	10 - 220	50	50	Puisay et al., 2015
		larval survival	5 - 611	5	10	Hédouin et al., 2016; Kwok et al., 2016; Kwok and Ang, 2013; Reichelt-Brushett and Harrison, 2004
		larval swimming velocity	10 - 200	50	50	Kwok et al., 2016; Kwok and Ang, 2013; Reichelt-Brushett and Harrison, 2004
		settlement	0.1 - 6,263	24	24	Kwok et al., 2016; Negri and Hoogenboom, 2011; Negri and Heyward, 2001; Reichelt-Brushett and Harrison, 2000
		adult mortality	5 - 434	20	40	Hédouin et al., 2016; Jones, 1997
		bleaching	5 - 80	20.3	30	Bielmyer et al., 2010; Mitchelmore et al., 2007; Muhaemin, 2007; Jones, 2004, 1997
		chlorophyll concentration	3.8 - 434	3.8	5	Fonseca et al., 2017; Hédouin et al., 2016; Jones, 1997; Mitchelmore et al., 2007; Yost et al., 2010
		EQY	2.4 - 20.3	2.4	4	Bielmyer et al., 2010

		growth	2.4 - 200	2.4	4.0	Kwok et al., 2016; Bielmyer et al., 2010
		MQY	1 - 434	-	1	Banc-Prandi and Fine, 2019; Fonseca et al., 2019, 2017; de Barros Marangoni et al., 2017; Hédouin et al., 2016
		production	10 - 30	11	30	Muhaemin, 2007; Alutoin et al., 2001; Nyström et al., 2001
		symbiont density	5 - 434	10	12.6	Hédouin et al., 2016; Jones, 2004, 1997; Mitchelmore et al., 2007; Yost et al., 2010
		tissue/adult colony mortality	5 - 50	5	50	Hédouin et al., 2016; Mitchelmore et al., 2007; Jones, 1997
	Gallium	fertilization success	10.2 - 11,200	1,120	3,230	Negri et al., 2011
		settlement	10.2 - 11,200	1,120	2,150	Negri et al., 2011
	Iron	fertilization success	10 - 55,800	3,000	25,300	Leigh-Smith et al., 2018
		larval survival	10 - 55,800	2,750	27,200	Leigh-Smith et al., 2018
		symbiont density	5 - 50	5	10	Harland and Brown, 1989
	Lead	fertilization success	2 - 9,577	790	855	Reichelt-Brushett and Harrison, 2005
		larval survival	100 - 20,000	320	640	Hédouin et al., 2016; Reichelt-Brushett and Harrison, 2004
		larval swimming velocity	7.7 – 20,000	405	828	Reichelt-Brushett and Harrison, 2004
		adult mortality	0.5 – 1,200	160	320	Hédouin et al., 2016
		chlorophyll concentration	0.5 – 1,200	1.9	75.6	Hédouin et al., 2016
		MQY	0.5 – 1,200	160	320	Hédouin et al., 2016
		symbiont density	0.5 – 1,200	1.9	75.6	Hédouin et al., 2016
	Manganese	fertilization success	800 - 161,100	54,200	71,200	Summer et al., 2019
		larval survival	17,000 - 163,800	-	17,000	Summer et al., 2019
		adult colony mortality	1,000 - 50,000	5,000	10,000	Summer et al., 2019
		tissue mortality	1,000 - 50,000	1,000	5,000	Summer et al., 2019
	Mercury	larval survival	10	10	none	Farina et al., 2008
		chlorophyll concentration	4 - 180	180	180	Bastidas and Garcia, 2004
		symbiont density	4 - 180	37	180	Bastidas and Garcia, 2004
	Nickel	fertilization success	5 – 9,090	5	100	Gissi et al., 2017; Reichelt-Brushett and Hudspith, 2016; Reichelt-Brushett and Harrison, 2005
		chlorophyll concentration	3.5	3.5	none	Biscéré et al., 2018, 2017
		growth	2.7 - 3.5	3.5	3.5[a]	Biscéré et al., 2018, 2017
		MQY	3.5	3.5	none	Biscéré et al., 2018, 2017

		P/R	3.5	3.5	none	Biscéré et al., 2018
		production	2.7 - 3.5	3.5	none	Biscéré et al., 2017
		respiration	2.7 - 3.5	3.5	none	Biscéré et al., 2017
		symbiont density	3.5	3.5	3.5[b]	Biscéré et al., 2018, 2017
	Tin	fertilization success	0.3 - 3,228	32	318	Negri and Heyward, 2001
		settlement	0.3 - 3,228	0.3	3.0	Negri and Heyward, 2001
		juvenile survival	0.1 - 2.5	1.0	2.5	Watanabe et al., 2007
		growth	0.1 - 0.4	0.1	0.4	Watanabe et al., 2007
	Vanadium	fertilization success	20.6 - 9,380	952	2,920	Negri et al., 2011
		settlement	20.6 - 9,380	280	564	Negri et al., 2011
	Zinc	fertilization success	2 - 5,000	10	10	Reichelt-Brushett and Harrison, 2005, 1999
INSECTICIDE	**1-naphthol**	larval survival	10 - 100,000	100	1,000	Acevedo, 1991
	Carbaryl	fertilization success	0.3 - 30	30	none	Markey et al., 2007
		larval survival	10 - 100,000	1,000	10,000	Acevedo, 1991
		settlement	0.1 - 300	1	3	Markey et al., 2007
		bleaching	1 - 10	10	none	Markey et al., 2007
		EQY	1 - 10	10	none	Markey et al., 2007
		symbiont density	10	10	none	Markey et al., 2007
		tentacular activity	1 - 10	10	none	Markey et al., 2007
		tissue mortality	1 - 10	10	none	Markey et al., 2007
	Chlorpyrifos	fertilization success	0.3 - 30	30	none	Markey et al., 2007
		larval survival	10 - 100,000	100	1,000	Acevedo, 1991
		settlement	0.1 - 300	0.3	1	Markey et al., 2007
		bleaching	1 - 10	1	10	Markey et al., 2007
		EQY	1 - 10	1	10	Markey et al., 2007
		symbiont density	10	10	none	Markey et al., 2007
		tentacular activity	1 - 10	10	none	Markey et al., 2007
		tissue mortality	1 - 10	10	none	Markey et al., 2007

Chlorpyrifos-oxon	fertilization success	0.3 - 30	30	none	Markey et al., 2007
	settlement	0.1 - 300	0.1	0.3	Markey et al., 2007
Endosulfan	fertilization success	0.3 - 30	30	none	Markey et al., 2007
	settlement	0.1 - 300	0.3	1	Markey et al., 2007
	bleaching	1 - 10	1	10	Markey et al., 2007
	EQY	1 - 10	1	10	Markey et al., 2007
	symbiont density	10	10	none	Markey et al., 2007
	tentacular activity	1 - 10	10	none	Markey et al., 2007
	tissue mortality	1 - 10	10	none	Markey et al., 2007
Glyphosate	bleaching	108 - 10,800	6,000	10,800[b]	Amid et al., 2018
	chlorophyll concentration	108 - 10,800	6,000	10,800[b]	Amid et al., 2018
Naled	larval survival	0.6 - 9.6	-	0.6	Ross et al., 2015
	settlement	0.6 - 9.6	9.6	none	Ross et al., 2015
	juvenile survival	0.6 - 9.6	9.6	none	Ross et al., 2015
	symbiont density	0.6 - 9.6	9.6	none	Ross et al., 2015
Permethrin	fertilization success	0.3 - 30	30	none	Markey et al., 2007
	larval survival	0.4 - 6.04	0.4	1	Ross et al., 2015
	settlement	0.1 - 300	0.3	1	Ross et al., 2015; Markey et al., 2007
	juvenile survival	0.4 - 6	6	none	Ross et al., 2015
	bleaching	1 - 10	1	10	Markey et al., 2007
	EQY	1 - 10	10	none	Markey et al., 2007
	symbiont density	0.4 - 10	10	none	Ross et al., 2015; Markey et al., 2007
	tentacular activity	1 - 10	10	none	Markey et al., 2007
	tissue mortality	1 - 10	10	none	Markey et al., 2007
Profenofos	fertilization success	0.3 - 30	30	none	Markey et al., 2007
	settlement	0.1 - 300	0.1	0.3	Markey et al., 2007
	bleaching	1 - 10	1	10	Markey et al., 2007
	EQY	1 - 10	10	none	Markey et al., 2007

		symbiont density	10	1	10	Markey et al., 2007
		tentacular activity	1 - 10	1	10	Markey et al., 2007
		tissue mortality	1 - 10	10	none	Markey et al., 2007
HERBICIDE	**2,4-D**	adult colony mortality	50 - 1,000,000	13,890	19,300	Sabdono et al., 1998; Glynn et al., 1984
		EQY	10,000 - 100,000	10,000	100,000	Råberg et al., 2003
		MQY	10,000 - 100,000	100,000	none	Råberg et al., 2003
		mucus production	100 - 1,000,000	1,000	1,000[c]	Sabdono et al., 1998
		P/R	10,000 - 100,000	-	10,000	Råberg et al., 2003
		production	10,000 - 100,000	-	10,000	Råberg et al., 2003
		symbiont density	100 - 1,000,000	19,300	19,300	Sabdono et al., 1998
		tentacular activity	50 - 1,000,000	100	1,000[c]	Sabdono et al., 1998; Glynn et al., 1984
		tissue mortality	50 - 1,000,000	10,000	100,000[c]	Sabdono et al., 1998; Glynn et al., 1984
	Ametryn	EQY	0.3 - 1,000	-	0.3	Jones and Kerswell, 2003
	Atrazine	chlorophyll concentration	12	12	none	Negri et al., 2011
		EQY	0.3 - 1,000	3	3	Negri et al., 2011; Jones and Kerswell, 2003; Jones et al., 2003
		MQY	0.3 - 1,000	100	100	Negri et al., 2011; Jones et al., 2003
	Diuron	fertilization success	0.1 - 1,000	1,000	none	Negri et al., 2005
		settlement	0.1 - 1,000	100	300	Negri et al., 2005
		juvenile survival	0.1 - 1,000	1,000	none	Negri et al., 2005
		adult colony mortality	1 - 10	10	10	Cantin et al., 2007
		bleaching	0.1 - 1,000	10	10	Cantin et al., 2007; Negri et al., 2005; Jones, 2004
		chlorophyll concentration	0.8	0.8	none	Negri et al., 2011
		EQY	0.1 – 1,000	0.3	0.3	Negri et al., 2011, 2005; Cantin et al., 2007; Jones, 2004; Jones and Kerswell, 2003; Jones et al., 2003; Råberg et al., 2003
		growth	0.3 - 10	0.3	1	Watanabe et al., 2007
		MQY	0.1 – 1,000	1	1	Negri et al., 2011, 2005; Cantin et al., 2007; Jones, 2004; Jones et al., 2003; Råberg et al., 2003
		P/R	10 - 100	-	10	Råberg et al., 2003
		symbiont density	0.1 - 1,000	1	10	Negri et al., 2005; Jones, 2004
		tissue mortality	1 - 10	10	10	Cantin et al., 2007

	Hexazinone	chlorophyll concentration	3.8	3.8	none	Negri et al., 2011
		EQY	0.3 - 1,000	1	3	Negri et al., 2011; Jones and Kerswell, 2003
		MQY	0.2 - 1,000	1	3	Negri et al., 2011
	Ionynil	EQY	0.3 - 1,000	1,000	none	Jones and Kerswell, 2003
	Irgarol	EQY	0.3 - 1,000	-	0.3	Jones and Kerswell, 2003
	Simazine	EQY	0.3 - 1,000	10	30	Jones and Kerswell, 2003
	Tebuthiuron	EQY	0.3 - 1,000	3	10	Jones and Kerswell, 2003
FUNGICIDE	**2-methoxy-ethylmercuric chloride (MEMC)**	fertilization success	0.3 - 30	0.3	1	Markey et al., 2007
		settlement	0.1 - 300	0.3	1	Markey et al., 2007
		bleaching	1 - 10	-	1	Markey et al., 2007
		EQY	1 - 10	-	1	Markey et al., 2007
		symbiont density	10	1	10	Markey et al., 2007
		tentacular activity	1 - 10	-	1	Markey et al., 2007
		tissue mortality	1 - 10	-	1	Markey et al., 2007
PAH	**1-methyl-naphthalene**	EQY	640 - 25,095	25,095	none	Renegar et al., 2017
		mucus production	640 - 25,095	640	5,427	Renegar et al., 2017
		tentacular activity	640 - 25,095	640	5,427	Renegar et al., 2017
		tissue mortality	640 - 25,095	640	5,427	Renegar et al., 2017
	Anthracene	larval survival	9.4 - 600	-	9.4^{d}	Overmans et al., 2018
		settlement	9.4 - 600	-	9.4^{d}	Overmans et al., 2018
	Benzo(a)-pyrene	larval survival	10	-	10	Farina et al., 2008
		bleaching	10 - 100	100	none	Ramos and Garcia, 2007
		chlorophyll concentration	9.0 - 100	-	9.0	Xiang et al., 2019; Ramos and Garcia, 2007
		symbiont density	10 - 100	10	100	Ramos and Garcia, 2007
	Fluoranthene	bleaching	15 - 60	-	15	Martínez et al., 2007
		tissue mortality	15 - 60	15	30	Martínez et al., 2007
	Phenanthrene	larval survival	14.1 - 900	28.1	56.3^{d}	Overmans et al., 2018

		settlement	14.1 - 900	28.1	56.3[d]	Overmans et al., 2018
PCB	**Aroclor 1254**	adult colony mortality	0.3	0.3	none	Chen et al., 2012
		bleaching	0.3	0.3	none	Chen et al., 2012
		growth	0.3	0.3	none	Chen et al., 2012
		MQY	0.3	0.3	none	Chen et al., 2012
PHARMACEUTICAL	**Estrone**	growth	0.002	-	0.002	Tarrant et al., 2004

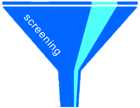
[a] when combined with temperature stress
[b] when combined with urea enrichment
[c] qualitative description
[d] when combined with UVA

Table 4. Relative amounts of data available (i.e., gap analysis) that address different combinations of pollutants (left two columns) with coral responses, organized by life-history stage (top). The number in each cell indicates the number of articles that examine the pollutant-response pair, and the shade of the cell is scaled to the relative number of articles, with darker shades indicating more articles. Empty cells indicate no (zero) articles found in our systematic review that adequately address the pollutant-response pair.

		GAMETE	LARVAE				JUVENILE	ADULT					
		Fertilization Success	Survival	Abnormal Development	Swimming velocity	Settlement	Survival	Mortality	Tissue Mortality	Tentacular Activity	Mucus Production	Bleaching	Grow
TALS	Aluminum	1				1							
	Cadmium	2							1			1	
	Cobalt	1											1
	Copper	9	4	1	3	4		2	1			5	2
	Gallium	1				1							
	Iron	1	1										
	Lead	1	2		1			1					
	Manganese	1	1					1	1				
	Mercury		1										
	Nickel	3											2
	Tin	1	1			1							1
	Vanadium	1				1							
	Zinc	2											
SECTICIDES	1-Naphthol		1										
	Carbaryl	1	1			1			1	1		1	
	Chlorpyrifos	1	1			1			1	1		1	
	Chlorpyrifos-oxon	1				1							
	Endosulfan	1				1			1	1		1	
	Naled		1			1	1						
	Permethrin	1	1			2	1		1	1		1	
	Profenofos	1				1			1	1		1	
RBICIDES	2,4-D							2	2	2	1		
	Ametryn												
	Atrazine												
	Diuron	1				1	1	1	1			3	1
	Glyphosate											1	
	Hexazinone												
	Ionynil												
	Irgarol												
	Simazine												
	Tebuthiuron												
NGICIDES	MEMC	1				1			1	1		1	
Hs	Anthracene		1			1							
	1-methylnaphthalene								1	1	1		
	Benzo(a)pyrene		1									1	
	Flouranthene								1			1	
	Phenanthrene		1			1							
Bs	Aroclor 1254							1				1	1
ARM.	Estrone												1

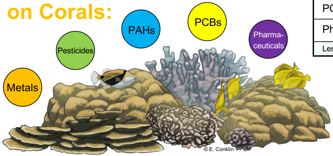
1) SYSTEMATIC REVIEW

9,332 search results

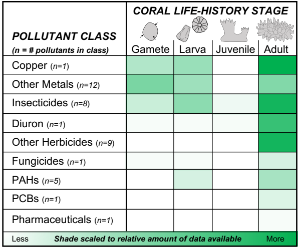


n = *55* studies in quantitative review,
n = *25* studies in meta-analysis

Pollutants on Corals:



2) QUANTITATIVE REVIEW

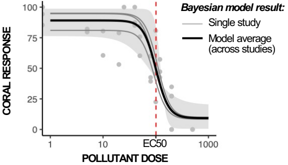


POLLUTANT CLASS *(n = # pollutants in class)*	***CORAL LIFE-HISTORY STAGE*** Gamete	Larva	Juvenile	Adult
Copper *(n=1)*	🟩	🟩		🟩
Other Metals *(n=12)*	🟩	🟩		🟩
Insecticides *(n=8)*	🟩	🟩	🟩	🟩
Diuron *(n=1)*	🟩	🟩	🟩	🟩
Other Herbicides *(n=9)*				🟩
Fungicides *(n=1)*	🟩	🟩		🟩
PAHs *(n=5)*		🟩		🟩
PCBs *(n=1)*				🟩
Pharmaceuticals *(n=1)*				🟩

Less ***Shade scaled to relative amount of data available*** More

RECOMMENDATIONS to fill research gaps and standardize reporting across studies

3) DOSE-RESPONSE META-ANALYSIS



Inhibitory exposure concentrations (EC_x) for copper and diuron across coral's life history

GOAL:

THRESHOLD ESTIMATES for coastal water quality