THRESHOLDS FOR SEDIMENT STRESS ON CORALS

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A systematic review and meta-analysis

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ASSOCIATED PUBLICATIONS

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Tuttle, L.J.[1], M.J. Donahue[1] How does sediment exposure affect corals? A systematic review. In preparation for *Environmental Evidence*.

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EXECUTIVE SUMMARY

Background

Local management action to address coral-reef stressors can improve reef health and mitigate the effects of global climate change. Coastal development and runoff lead to sedimentation, which directly impacts coral recruitment, growth, mortality, and the ecosystem services that coral reefs provide. Decision making for reef resilience in the face of global and local stressors requires information on thresholds for management action. In response to needs identified by the National Oceanic and Atmospheric Administration's Pacific Islands Regional Office (NOAA PIRO), we conducted a systematic review and meta-analysis that explores the effects of both deposited and suspended sediment on corals to identify stressor thresholds. We identified levels of sediment exposure (i.e., concentration and duration) that cause adverse physical, physiological, behavioral, developmental, and ecological responses in coral. The goal of this study is to provide managers with sediment exposure thresholds that can be expected to negatively affect corals.

Methods

Our systematic review synthesized available evidence on the effects of suspended and deposited sediment on corals. The research questions were formulated with an advisory team to support management decisions concerning local reef stressors in waters under U.S. federal jurisdiction. While the advisory team is most concerned with reefs adjacent to U.S. Pacific Islands, our review included studies that examine reef-building coral species around the world. We searched online databases and grey literature to obtain a list of potential studies, assess their relevance, and critically appraise them for validity and risk of bias. We conducted meta-analyses that examined changes in coral health and survival in response to suspended and deposited sediment, with the goal to define sediment thresholds for reef managers. This protocol has been published in an open-access, peer-reviewed journal dedicated to the results of systematic reviews and meta-analyses that inform natural resource management (Tuttle et al. 2020).

Results

Our global, systematic review of corals' responses to sediment identified 86 experiments to be included in meta-analyses, after critical appraisal of over 15,000 records. Data were extracted from these experiments and grouped by sediment type, coral age-class, and coral response to identify thresholds in terms of the lowest exposure levels that induced an 'adverse effect' (physiological and/or lethal) and the probabilities of a coral experiencing an adverse effect at a range of sediment concentrations.

- Corals experience both physiological and lethal responses to concentrations below 10 $mg/cm^2/d$ and 10 mg/L, levels previously identified as 'normal' on reefs (Rogers 1990), and relatively few studies examine coral response at these sediment levels.
- In response to **deposited sediment**, adverse effects occurred as low as 1 $mg/cm^2/d$ for larvae (limited settlement rates) and 4.9 $mg/cm^2/d$ for adults (tissue mortality).

- In response to **suspended sediment**, adverse effects occurred as low as 10 mg/L for juveniles (reduced growth rates) and 3.2 mg/L for adult corals (bleaching and tissue mortality).
- Corals take at least 10 times longer to experience tissue mortality from exposure to suspended sediment than to comparable concentrations of deposited sediment, though physiological changes manifest 10 times faster in response to suspended sediment.

SEDIMENT TYPE	CORAL RESPONSE*	THRESHOLD† CONCENTRATION		THRESHOLD† DURATION	
		Larvae/Juveniles	Adults	Larvae/Juveniles	Adults
Suspended Sediment	Any adverse effect	10.0 mg/L	3.2 mg/L	1 h	2 h
	Any mortality	30.0 mg/L	3.2 mg/L	2.5 d	14 d
Deposited Sediment	Any adverse effect	1.0 mg/cm²/d	4.9 mg/cm²/d	3 d	12 h
	Any mortality	8.3 mg/cm²/d	4.9 mg/cm²/d	3 d	22 h

*See definition of *adverse effect* (coral-specific) in the Glossary, inclusive of both physiological and lethal responses. *Any mortality* is inclusive of death of tissue or the entire coral colony.
†Threshold is LOAEL, lowest-observed adverse-effect level, based on binary data of the presence/absence of coral response.

Corals exposed to deposited sediment at 10 mg/cm²/d have a 25.8 to 35.9% probability of experiencing adverse effects. At 5 mg/cm²/d, this probability drops to 18.0 to 30.4%, and at 1 mg/cm²/d, it further drops to 7.7 to 19.2%. Corals exposed to suspended sediment at 10 mg/L have an 8.2 to 10.0% probability of experiencing adverse effects. At 5 mg/L, this probability drops to 5.1 to 8.4%, and at 1 mg/L, it further drops to ~2%. These estimates were derived from meta-regressions of binary data that account for exposure duration and variability among studies and species.

We also estimated thresholds for sediment causing increased magnitudes of adverse effects. Thresholds derived from these continuous data largely match those from binary data (no-observed and lowest-observed adverse effect levels). In cases where thresholds do not match, we identify research gaps and make **four key recommendations for future studies that aim to define critical threshold values for sediment on coral reefs**:

1) *Validate thresholds from lab experiments with data from nearby coastal watersheds*;
2) *Target a lower range of experimental sediment concentrations using susceptible coral taxa*;
3) *Standardize reporting of coral responses and stressor dosage/properties*; and
4) *Test for potential synergisms between and among stressors that often co-occur.*

Conclusions

Our comprehensive synthesis uses a rigorous protocol to provide empirically based estimates of stressor thresholds on coral reefs. We compiled a global dataset that spans three oceans, over 140 coral species, decades of research, and a range of field- and lab-based approaches. Our analyses inform the no-observed and lowest-observed adverse effect levels that are used in management consultations by NOAA PIRO and supplement these with thresholds derived from meta-regressions of coral responses to deposited and suspended sediment. In the absence of more location- or species-specific data to inform decisions, our results bring to bear the best available information to protect the most vulnerable reef-building corals from sediment stress. Ongoing systematic reviews and meta-analyses for common co-stressors, including eutrophication, chemical contamination, light attenuation, and freshwater discharge, will disentangle the additive and synergistic effects of multiple local stressors on coral reefs.

Relevant Governmental Mandates, Goals, & Priorities

This report addresses the NOAA long-term mission goal of Healthy Oceans (NOAA 2010):

- *Marine fisheries, habitats, and biodiversity sustained within healthy and productive ecosystems.*

As part of its Fishery Management Plans under the Magnuson-Stevens Fishery Conservation and Management Act (MSA), NOAA National Marine Fisheries Service designates essential fish habitat (EFH) for all federally managed species. In the Pacific Islands Region (PIR), EFH includes coral reefs, which provide a complex habitat that support a wide diversity of fishes. In reporting thresholds that may be used during EFH regulatory consultations, our work further addresses two of the three strategic goals in the PIR (NOAA Fisheries Pacific Islands 2020):

- *Conserve and recover protected species while supporting responsible fishing and resource development*, and
- *Improve organizational excellence and regulatory efficiency.*

This report also addresses the Western Pacific Regional Fishery Management Council's 'island fisheries' research priority (WPRFMC 2019):

- *[Understanding and quantifying] non-fishing impacts on essential fish habitats and habitat areas of particular concern.*

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2. Tuttle and Donahue 2020 NOAA Report ESM 2 TEMPLATE.xlsx (Microsoft Excel file):
   Data coding and extraction form used for the systematic review.
3. Tuttle and Donahue 2020 NOAA Report ESM 3 DATABASE.xlsx (Microsoft Excel file):
   Database of extracted information from all studies used in the meta-analysis and list of articles excluded after full-text screening.
4. Tuttle and Donahue 2020 NOAA Report ESM 4 ARTICLES.zip with subfolders "for deposited sediment meta-analysis" and "for suspended sediment meta-analysis":
   PDF files of all the articles used in the meta-analyses for deposited and suspended sediment.
5. LINK: https://github.com/ljtuttle/coral_stressor_thresholds
   Repository of data and analysis scripts in an R Project, using R Markdown.

ACRONYMS AND ABBREVIATIONS

AIC	Akaike Information Criterion
ASFA	Aquatic Sciences and Fisheries Abstracts
AUC	Area under the curve in ROC plot (see 'ROC AUC' in Glossary)
BACI	Before-After, Control-Impact study design
DRMA	Dose-response meta-analysis (meta-regression)
DSC	Deposited sediment concentration (reported in $mg/cm^2/d$)
EFH	Essential Fish Habitat
GBRMPA	Great Barrier Reef Marine Park Authority
DSE	Databases or Search Engines
JCU	James Cook University (Australia)
LOAEL	Lowest observed adverse effect level (see Glossary)
MSA	Magnuson-Stevens Fishery Conservation and Management Act
NOAA	National Oceanic and Atmospheric Administration
NOAEL	No observed adverse effect level (see Glossary)
NPV	Negative Predictive Value (see Glossary)
NTU	Nephelometric Units
PAM	Pulse Amplitude Modulation
PECO	Population-Exposure-Comparator-Outcome framework
PIR	Pacific Island Region, under U.S. jurisdiction
PIRO	Pacific Island Regional Office
PPV	Positive Predictive Value (see Glossary)
PQDT	Dissertations & Theses Global
ROC	Receiver Operating Characteristic (see 'ROC AUC' in Glossary)
ROSES	RepOrting standards for Systematic Evidence Syntheses
SSC	Suspended sediment concentration (reported in mg/L)
UH	University of Hawai‘i at Mānoa (USA)
WAMSI DSN	Western Australia Marine Science Institute's Dredging Science Node
WoS	Web of Science

GLOSSARY

Adverse effect	EFH definition: Any impact that reduces quality and/or quantity of EFH. Adverse effects may include direct or indirect physical, chemical, or biological alterations of the waters or substrate and loss of, or injury to, benthic organisms, prey species and their habitat, and other ecosystem components, if such modifications reduce the quality and/or quantity of EFH. Adverse effects to EFH may result from actions occurring within EFH or outside of EFH and may include site-specific or habitat-wide impacts, including individual, cumulative, or synergistic consequences of actions (50 CFR § 600.810). Coral-specific: Any response of a coral individual, colony, or experimental treatment group that *may* negatively affect the coral's fitness and/or survival. These may include physiological changes and mortality. The magnitude of the effect may be sufficiently small that the fitness effect is not measurable.
Article	Any written document including scientific papers, abstracts, reports, book chapters, theses/dissertations, and other publications
LOAEL	The 'lowest observed adverse effect level,' i.e., the lowest dose/exposure level at which an adverse effect was observed
NOAEL	The 'no observed adverse effect level,' i.e., the highest dose/exposure level at which an adverse effect was NOT observed
NPV	The probability that an experimental unit (treatment group of corals, for example) with a negative result from a screening test or statistical model actually does NOT have the condition of interest (Trevethan 2017)
PPV	The probability that an experimental unit (treatment group of corals, for example) with a positive result from a screening test or statistical model actually has the condition of interest (Trevethan 2017); also called 'precision'
ROC AUC	The ROC is a plot of a model's true positive rate (*sensitivity*) against its false positive rate (1 - *specificity*); the AUC of an ROC is a measure of the diagnostic ability of a binary screening test or statistical model to discriminate between negative and positive results; values of 1 indicate perfect discriminatory ability and 0.5 indicate discriminatory ability no better than chance
Sensitivity	The ability of a screening test or statistical model to detect a 'true positive,' i.e., correctly identify experimental units (treatment group of corals) that have a condition of interest (Trevethan 2017); also called the 'true positive rate'
Specificity	The ability of a screening test or statistical model to detect a 'true negative,' i.e., correctly identify experimental units (treatment group of corals) that do NOT have a condition of interest (Trevethan 2017); called the 'true negative rate'
Study	Each article may report the results of multiple studies, which we define as a manipulative experiment that addresses a single hypothesis or research question

1 BACKGROUND

Half of the world's coral reefs have been lost in recent decades (Bellwood et al. 2004, Côté et al. 2005, Jones et al. 2017, Hughes et al. 2018), while rising sea surface temperatures and local stressors threaten a third of those remaining (Carpenter et al. 2008). This decline imperils the ecosystem services that reefs provide (Mumby et al. 2008), including a USD$36 billion annual tourism industry (Spalding et al. 2017). In the U.S. and areas under its jurisdiction, corals are protected as federal trust resources, for their value as habitat for fish, and because some corals are listed as threatened or endangered species (40 CFR § 230.44, 79 FR § 53852, Sheppard et al. 2017). The regulatory programs that apply to corals and coral reefs manage a wide variety of local stressors that include physical destruction and alteration; sediment, nutrients and chemical pollutants; and point sources of thermal pollution (40 CFR § 230.44, 79 FR § 53852, Sheppard et al. 2017). Other regulatory programs are designed to conserve species that use coral reefs as habitat and indirectly benefit reefs (50 CFR § 660.75).

Management of coastal activities can minimize the degradation of water quality and bottom habitat, and thus mitigate reef decline in the face of climate change (Mumby and Steneck 2008, Carilli et al. 2009). However, reefs face a litany of local stressors that may act synergistically and thus complicate regulatory programs (Gurney et al. 2013). Among the most damaging pollutants on coral reefs is sediment, which can remain suspended in the water or be deposited on the coral surface and can contain toxicants, pathogens, and nutrients, all of which impact coral growth, recruitment, and survival (Rogers 1990, Fabricius 2005, Erftemeijer et al. 2012b, Jones et al. 2016). There is enormous variation in the levels of exposure to deposited and suspended sediment that corals can tolerate, which may result from taxonomic differences, geographic location, sediment type, and exposure concentration, duration, and frequency. Exploring potential sources of this variation will help to quantify synergistic effects and identify critical threshold values for sediment and other anthropogenic stressors on reef-building corals, thus enhancing efforts to conserve and restore coral reefs.

The Pacific Islands Regional Office (PIRO) of the U.S. Department of Commerce's National Oceanic and Atmospheric Administration (NOAA) is in the process of developing a tool to help regulators (NOAA) and the regulated community (e.g., applicants for U.S. Army Corps of Engineers permits) assess the effects of human activities on corals in the Pacific and to develop appropriate measures to mitigate unavoidable impacts. This 'Coral Tool' will be used during NOAA PIRO's essential fish habitat (EFH) consultations with permit applicants and will become more valuable if critical threshold values for suspended and deposited sediment on coral reefs can be identified. The tool currently relies on the results of previously published literature syntheses concerning the effects of coastal development and terrestrial runoff on coral reefs, the most widely cited of which are more than a decade old (Rogers 1990, Fabricius 2005). Substantial new experimental data are now available to inform best management practices. More recent syntheses of the effects of sediment on corals (Erftemeijer et al. 2012b, Risk 2014, Jones et al. 2015, 2016) provide qualitative accounts only, thus providing a starting point for the quantitative synthesis that allows regulatory assessments to rigorously identify thresholds and quantify adverse effects.

In response to needs identified by NOAA PIRO, we conducted a systematic review and meta-analysis that identified thresholds of coral response to both deposited and suspended sediment. These thresholds may be applied to NOAA's Coral Tool and associated EFH consultations, bringing to bear the most current and comprehensive information for decision-making. Specific research questions and a protocol (section 3, Tuttle et al. 2020) were developed by the team at NOAA that is building the Coral Tool (C. Johnson, S. Kolinski, and D. Minton, hereafter referred to as the 'Coral Tool advisory team') in conjunction with a research team from the University of Hawai'i (authors L. Tuttle and M. Donahue), who conducted the systematic review and meta-analysis.

In so doing, this review and meta-analysis address the NOAA long-term mission goal of Healthy Oceans: *Marine fisheries, habitats, and biodiversity sustained within healthy and productive ecosystems* (NOAA 2010). As part of its Fishery Management Plans under the Magnuson-Stevens Fishery Conservation and Management Act (MSA), NOAA designates EFH for all federally managed fisheries species, which includes coral reefs in the Pacific Islands Region (PIR). Thus, our work further addresses two of the three strategic goals in the PIR: *Conserve and recover protected species while supporting responsible fishing and resource development* and *Improve organizational excellence and regulatory efficiency* (NOAA Fisheries Pacific Islands 2020). This report also addresses the Western Pacific Regional Fishery Management Council's 'island fisheries' research priority: *[Understanding and quantifying] non-fishing impacts on essential fish habitats and habitat areas of particular concern* (WPRFMC 2019).

1.1 Coral Life History and Sediment Exposure

The simplified coral life cycle begins with successful fertilization of gametes into an embryo, which can occur either internally, for brooding species, or externally, for broadcast-spawning species. After several days, the embryo develops into a planktonic planula larva that moves through the water column searching for suitable habitat onto which to settle. Once settlement occurs, the larva becomes a sedentary juvenile recruit. The recruit begins to asexually bud, forming a colony that develops into an adult coral when it reaches sexual maturity, at which time the coral will begin spawning and producing gametes.

Sediment can affect corals throughout their life cycle (Fig. 1). High levels of sediment exposure may depress coral health, condition, and survival along multiple mechanistic pathways (reviewed in Erftemeijer et al. 2012). First, light attenuation reduces photosynthesis of symbiotic zooxanthellae, which provide the main source of energy available to corals. Also, corals divert available energy toward sediment clearance behaviors such as mucus production/sloughing and tentacle movement. Thus, sediment may lead to sublethal responses, such as reduced rates of growth, productivity, calcification, as well as bleaching, disease susceptibility, physical damage (e.g., breaking and abrasion), and inability to regenerate following tissue damage (Meesters et al. 1992, Stafford-Smith 1993, Riegl 1995, Riegl and Branch 1995, Fabricius 2005). As the stress level intensifies, corals may experience lethal effects including tissue necrosis and colony death, which if widespread, may lead to changes in coral-reef community structure (Gilmour 1999).

Sediment exposure also affects the early life history of corals. Sediment may affect reproductive success by interfering with gamete fertilization (Ricardo et al. 2018). Even relatively thin layers of sediment not harmful to most adult corals may inhibit coral larvae from settling on otherwise suitable surfaces (Gilmour 1999, Babcock and Smith 2000, Birrell et al. 2005, Goh and Lee 2008), which can influence reef regeneration and persistence. Tolerance to sedimentation is an order of magnitude lower for coral recruits than for adults (Fabricius 2005), leading to high recruit mortality in areas of moderate to heavy sediment exposure.

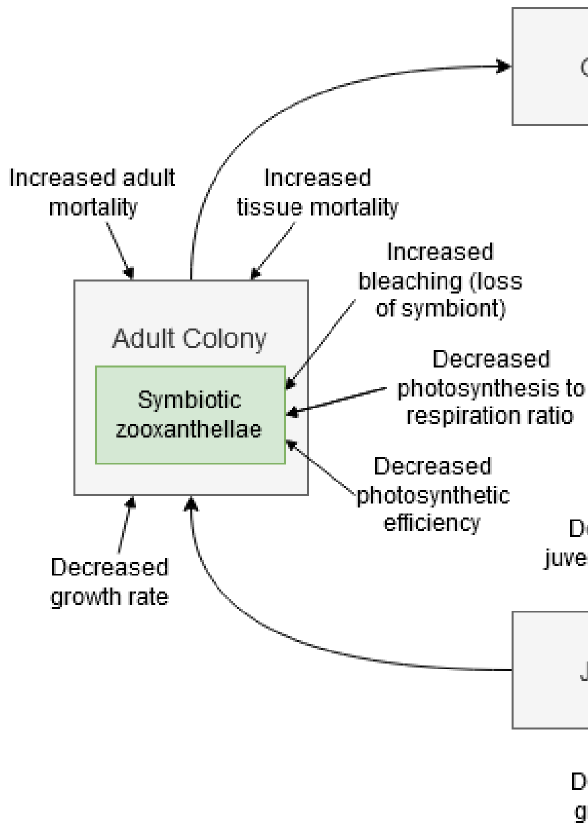

Fig. 1. A simplified coral life history. Developmental stages in gray boxes and the coral endosymbiont in the green box. Hypothesized and previously documented biological responses to sediment are shown with arrows pointing toward the affected life-history stage/process.

2 OBJECTIVE OF THE REVIEW

The primary objective of the present study is to perform a systematic review of peer-reviewed, public, and/or grey literature to develop thresholds for suspended and deposited sediment stressors that affect nearshore coral-reef ecosystems. We followed established methodologies (Pullin and Stewart 2006, CEE 2018, Haddaway et al. 2018) for systematic review in environmental management to (a) identify, collect, and evaluate sources of empirical data on the effects of sediment on corals; (b) extract relevant data from these sources; and (c) use statistical and meta-analytic procedures to identify stressor thresholds on coral reefs.

To disentangle the effects of synergistic stressors, we focused on experimental studies that quantify the causal relationship between sediment and coral response. Monitoring and other observational studies were used to contextualize experimental findings. We address the following question and sub-questions:

1) *How does sediment exposure affect corals?*
   (a) *What physical, physiological, behavioral, developmental, and ecological responses of corals are associated with sediment exposure (i.e., concentration, duration, frequency)?*
   (b) *What is the relationship between sediment exposure and the frequency and magnitude of coral responses (e.g., mortality, tissue necrosis, growth rate, photosynthetic yield, etc.)?*
   (c) *How do coral responses to sediment exposure differ between deposited and suspended sediment?*
   (d) *How do coral responses to sediment exposure differ by geography, sediment type, and coral taxonomy, morphology, and developmental stage?*

3 METHODS

Our systematic review and meta-analysis was conducted according to the Guidelines and Standards for Evidence Synthesis in Environmental Management, version 5.0 (Pullin and Stewart 2006, CEE 2018) and reported according to the procedures of ROSES (RepOrting standards for Systematic Evidence Syntheses) (Haddaway et al. 2018).

3.1 Searching for Articles

Our systematic review started with the definitive reviews on the subject, which include Rogers (1990), Fabricius (2005), Erftemeijer *et al.* (2012), Risk (2014), and Jones *et al.* (2015, 2016). We developed a list of potential sources of data, hereafter called 'benchmark studies,' from this set of reviews [ESM 1].

To supplement this list, we conducted electronic literature searches using the following databases or search engines (DSE) using the University of Hawai'I at Mānoa Library: (1) *ISI Web of Science* (*All Databases*, see Table 1), (2) *JSTOR*, (3) *Aquatic Sciences and Fisheries Abstracts*, (4) *Dissertations and Theses Global*, (5) *James Cook University Library One Search*, (6) *ReefBase's Proceedings of the International Coral Reef Symposium*, (7) *Science.gov*, (8) *Great Barrier Reef Marine Park Authority (GBRMPA) Elibrary*, and (9) *Western Australia Marine Science Institute's Dredging Science Node (WAMSI DSN) repository*. These DSE are categorized and described in Table 1, along with search specifications (e.g., full text vs. abstract only, date ranges) for each. DSE 1-3 target peer-reviewed literature produced by commercial publishers, while DSE 3-9 target 'grey' literature, including theses/dissertations, conference proceedings, and reports for governmental/non-governmental entities.

Table 1. Search specifications for each database or search engine (DSE).

DSE Category	DSE Name (Abbrev.)	DSE Scope	Search specification(s)	Search dates
Bibliographic databases:	1) *Web of Science* (WoS), *All Databases*	General science	Topic (titles, authors, abstracts, keywords); 'All Databases' include: (a) WoS Core Collection (SCI-EXPANDED, ESCI), (b) Biological Abstracts, (c) SciELO Citation Index, & (d) Zoological Record	All years (1950 - present)
	2) *JSTOR*	General academic	Abstract, All content	Any time
	3) *Aquatic Sciences and Fisheries Abstracts* (ASFA)	Aquatic and marine science	Abstract	Any time
	4) *Dissertations & Theses Global* (PQDT)	Global dissertations and theses	Abstract	Any time
Organizational databases:	5) *James Cook University One Search* (JCU)	Australian university dissertations and theses	Abstract, Dissertation/Thesis	Any time
	6) *ReefBase*	Proceedings of the International Coral Reef Symposium	Title; also Keywords for taxon-specific search terms	Any time
	7) *Science.gov*	United States federal government science	Full record (no 'Abstract' option)	Any time
	8) *Great Barrier Reef Marine Park Authority (GBRMPA) Elibrary*	Australian federal government science	All of ELibrary, Type = Report	Any time
	9) *Western Australia Marine Science Institute's Dredging Science Node (WAMSI DSN)*	Australian non-governmental reports	All reports and research articles listed at WAMSI DSN website (2020)	Any time

In developing the structure of this systematic review, we adopted the 'PECO' approach (Morgan et al. 2018), which defines the relevant Population (including species), Exposure, Comparator, and Outcomes as pillars of the research question and serve as inclusion/exclusion criteria during the screening process. For 'Population,' the following genera were specifically important because they contain species that are identified by the ESA as either threatened or endangered: *Acropora, Anacropora, Cantharellus, Dendrogyra, Euphyllia, Isopora, Montastraea, Montipora, Mycetophyllia, Orbicella, Pavona, Porites, Seriatopora, Siderastrea*, and *Tubastraea*. These additional genera were important because of their importance in the Pacific Islands Region: *Alveopora, Astreopora, Favia, Favites, Goniastrea, Goniopora, Leptastrea, Leptoria, Lobophyllia, Millepora, Platygyra, Pocillopora*, and *Turbinaria*. The following search, in English, uses Boolean operators and wildcards to improve the quality (i.e., true positive results) of search results, and was tested for its comprehensiveness [ESM 1]:

((coral AND sediment*) OR (coral AND suspend*) OR (coral AND turbidity) OR (coral AND mud) OR (coral AND terrigenous) OR (coral AND silt*) OR (coral AND plume) OR (coral AND dredg*) OR (coral AND land-based) OR (sediment* AND Acropora) OR (sediment* AND Anacropora) OR (sediment* AND Cantharellus) OR (sediment* AND Dendrogyra) OR (sediment* AND Euphyllia) OR (sediment* AND Isopora) OR (sediment* AND Montastraea) OR (sediment* AND Montipora) OR (sediment* AND Mycetophyllia) OR (sediment* AND Orbicella) OR (sediment* AND Pavona) OR (sediment* AND Porites) OR (sediment* AND Seriatopora) OR (sediment* AND Siderastrea) OR (sediment* AND Tubastraea) OR (sediment* AND Alveopora) OR (sediment* AND Astreopora) OR (sediment* AND Favia) OR (sediment* AND Favites) OR (sediment* AND Goniastrea) OR (sediment* AND Goniopora) OR (sediment* AND Leptastrea) OR (sediment* AND Leptoria) OR (sediment* AND Lobophyllia) OR (sediment* AND Millepora) OR (sediment* AND Platygyra) OR (sediment* AND Pocillopora) OR (sediment* AND Turbinaria)).

Search results were saved as BibTeX (.bib) or RIS (.ris) files and imported into open-source reference managers (e.g., *Mendeley*) with tools to identify and remove duplicates. We tested the thoroughness of our DSE searches by comparing the DSE search results with those of two other lists of potential sources of data. First, we queried *Google Scholar* with the same search string (using the Publish or Perish software tool (Harzing 2020) to export .ris files) then evaluated the top 200 search results to include only 'relevant' articles (see *Screening Process*, below) and those un-duplicated in the DSE search. Similarly, we screened the list of benchmark studies (described above) to include only relevant, un-duplicated articles [ESM 1]. We examined all relevant, un-duplicated articles within the *Google Scholar* search and the list of benchmark studies to understand why they were not also found in the DSE search.

Based on any systematic patterns of bias that we discerned, we made our DSE more inclusive. For instance, to avoid regional/language biases, we included the SciELO Citation Index in the Web of Science search [DSE 1] that targets Latin American research in many Caribbean countries where we expected relevant work to be based.

3.2 *Article Screening and Study Eligibility Criteria*

3.2.1 Screening Process

For the purposes of this systematic review, an "article" is defined as any written document including scientific papers, abstracts, reports, book chapters, theses/dissertations, and other publications. Unique articles were imported into *abstrackr* (Wallace et al. 2012), a free web application in which the results of a literature search for a systematic review are uploaded, organized, and screened. All reviewers independently screened a pilot round of 100 articles (titles and abstracts evaluated together), classified each as 'relevant,' 'irrelevant,' or 'maybe relevant' to the research question. The reviewers discussed any discrepancies in their decisions and further clarified, revised, and agreed upon the classification criteria until a consensus was reached for each conflict. Subsequently, all articles were independently screened by at least two reviewers, and any conflicts between the two reviewers were resolved by a third member of the review team. If a potential article was authored or co-authored by a reviewer, then two other reviewers determined the potential relevance of the article. This was done during the full-text screening as well (see below).

As the reviewers continue to make decisions about the articles' relevance, *abstrackr*'s machine learning protocol predicts relevant articles and presents them to the reviewer(s) in order from 'most likely' to 'least likely' to be relevant. This can increase workload savings while maintaining relatively high sensitivity and specificity and relatively low false-negative rates, thus making it a useful addition to the screening process (Rathbone et al. 2015, Gates et al. 2018). Regardless of *abstrackr*'s prediction, the reviewer(s) screened all titles and abstracts. We considered English abstracts for non-English full texts during the article screening process. When a non-English article was deemed potentially relevant, we searched for translations of full texts. If English translations were not available, the article was not screened.

The full texts for all 'relevant' and 'maybe relevant' articles were collected and reviewed according to the 'Eligibility Criteria' described below. Full-text screening was conducted by one reviewer. A second reviewer screened 10% of the full texts and compared their decisions with that of the initial reviewer. If the two reviewers had conflicting decisions, they discussed until consensus was reached and the second reviewer screened an additional 10% of full texts (and continued until there were no remaining conflicts).

Each article may report the results of multiple studies. We defined a "study" as a manipulative experiment that addresses a single hypothesis or research question. In the case of articles containing multiple studies, each study was independently reviewed according to the 'Eligibility Criteria.' To account for the non-independence of studies within articles, we considered statistical, meta-analytical models with 'study' nested within 'article' as a random effect.

In the particular case of dissertations and theses, special care was taken to ensure that there was no duplication in our review between dissertation/thesis chapters and publications based on the same data. Peer-reviewed publications and final reports took precedence over dissertation/thesis chapters of the same data. When dissertation/thesis chapters provide additional data that were not reported in the peer-reviewed document, these data supplemented that of the peer-reviewed document but remained a part of the same 'study.' Relevant, unpublished chapters were treated as independent studies.

3.2.2 Eligibility Criteria

The PECO framework helps formulate research questions that explore the association of environmental exposures with health outcomes within a relevant population in comparison to members of the population that are not exposed (Morgan et al. 2018). Thus, it is also useful in defining which populations, exposures, comparisons, and outcomes should be included or not in a systematic review and meta-analysis. We used the PECO framework to determine the inclusion or exclusion of each article for further review and analysis at the stages of title/abstract and full-text screening. To be included, an article had to meet every criterion. Otherwise it was excluded.

Population: All life stages of all shallow (photic zone, ≤80m depth) scleractinian coral genera in all warm-water ocean basins (20°-30°C).

Exposure: Exposure to concentrations of suspended and/or deposited sediment of marine or terrigenous origin. For manipulative experiments conducted in either the field or laboratory, this was the application of suspended or deposited sediment.

Comparison: Specimens experimentally exposed to suspended or deposited sediment must be compared to an appropriate experimental control in either the field or laboratory.

Outcome(s): Specific endpoints are all physical, physiological, behavioral, developmental, and ecological responses of corals associated with exposure to deposited and/or suspended sediment. These may include but are not limited to tissue/colony mortality, bleaching, and changes in rates of growth, photosynthesis, and larval settlement/survival. Outcomes were recorded as binary or continuous data, as reported in the study.

Eligible types of study design: Quantitative meta-analysis were limited to the results of experimental studies that quantify the cause-effect relationship between sediment stress and coral response (including BACI-designed studies and those conducted in the field or laboratory, mesocosms, etc.), compared to the response of corals to 'ambient' or 'control' conditions. *In situ*, observational studies were identified and used to contextualize the findings of manipulative experiments.

3.3 *Study Validity Assessment*

We critically appraised all studies that passed the full-text screening process using a number of parameters including the following, which may affect a study's external validity:

- Study setting: field or laboratory;
- Temporal extent of the study: relatively long-term monitoring or short-term measurements;

and the following, which may affect both the external and internal validity of a study:

- Study design: manipulative or observational study; presence/extent of pseudoreplication;
- Randomization: how sediment exposure levels were assigned to coral samples; and
- Confounding factors: degree of accounting for potential effect modifiers, if present.

Internal validity was further assessed per the criteria outlined by Bilotta *et al.* (2014), which adapted Cochrane's 'risk of bias' tool (Higgins et al. 2011) for environmental science applications. This "Environmental-Risk of Bias Tool" assesses selection, performance, attrition, reporting, and miscellaneous biases. With this information, we also used the "Environmental GRADE Tool" (Bilotta et al. 2014) to determine the overall quality (high, moderate, low, or very low) of each study. Studies with a low or very low overall grade (indicative of high susceptibility to bias) were excluded from further analysis. One reviewer assessed the quality of a study. A subset of five studies were appraised by the entire review team. Conflicting decisions of study-quality were resolved by the entire review team.

We used these critical appraisals and tools to organize studies into groups of comparable records across which we should (and should not) meta-analyze. This process determined the scope of inference of our meta-analysis, thus defining the extent to which our results applied to the diverse set of sedimentation events that occur on coral reefs.

3.4 *Data Coding and Extraction Strategy*

Information from studies was input into a data coding and extraction form [ESM 2] and recorded in a project database that has been made available as a supporting document [ESM 3]. The database includes study characteristics such as the sample sizes, means, and variations of coral response(s) to sediment and control conditions. When these data were not reported in the text, we extracted them from figures using open-source digitizing software that convert graph images into numerical data (e.g., Datathief III 2020). When only raw data were available, we calculated summary statistics. When information was indecipherable or missing, we contacted the corresponding author of the study for clarification. All reviewers extracted data from the same three studies, compared their results for any inconsistencies, and made adjustments to the protocol to improve the consistency of the data extraction process. After this pilot round, each study had data extracted independently by one reviewer.

3.5 *Potential Effect Modifiers and Reasons for Heterogeneity*

There are several factors that may cause variation in measured outcomes, information about which was extracted and recorded in the project database. This list of effect modifiers was compiled in consultation with the Coral Tool advisory team and includes the following: study location (ocean basin, region, and site), study species and morphological form (e.g., massive, plating, branching), time/season of sediment-exposure event, sediment composition (e.g., silt-clay vs. calcareous sand) and provenance (terrestrial vs. marine), sediment dose/concentration (and methods for measuring dose), sediment exposure duration, and possible interacting effects (e.g., light attenuation in concurrence with suspended sediment, or nutrient-enriched deposited sediment). These sources of variation were addressed as described in the following section (3.6 *Data synthesis and presentation*). While some of these effect modifiers were categorical, some were numerical and required the conversion of reported units to a common standard (e.g., for deposited sediment the standard is $mg/cm^2/d$ and for suspended sediment it is mg/L).

3.6 *Data Synthesis and Presentation*

We synthesize the results of all eligible studies that address coral responses to sediment. Our meta-analyses fall into three main categories. First, we use binary data to

1) identify levels of exposure that have been shown to cause adverse effects (Fig. 2A), and
2) estimate the probability of a coral experiencing an adverse effect at a range of exposure levels, while accounting for study and species (Fig. 2B).

Additionally, we used continuous, 'effect-size' data to

3) characterize the shape and slope of the relationship between level of exposure and the magnitude of a coral's adverse effect or response (Fig. 2C).

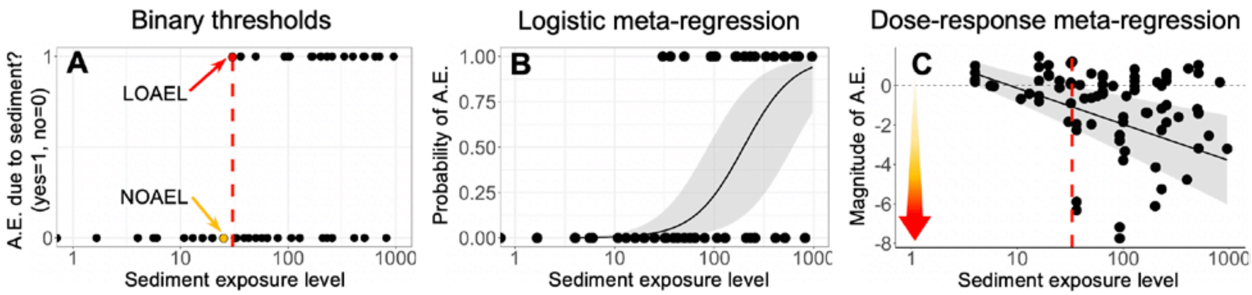

Fig. 2. Graphical summary of meta-analysis endpoints: analysis of binary data that (**A**) identifies exposure thresholds and (**B**) probabilities of experiencing an adverse effect ('A.E.'); and analysis of continuous data that (**C**) characterizes the relationship between exposure and the magnitude of an A.E. (where zero is no A.E. with respect to control). The red, dashed line in (**A**) represents the LOAEL and in (**C**) represents the dose-response threshold, where the confidence interval (in gray) no longer overlaps with zero.

3.6.1 Binary Meta-Analyses

Our quantitative meta-analyses first consider binary responses of corals by comparing corals exposed to sediment (treatment group) with corals not exposed to sediment (control group) from the same study. If the treatment group experienced a statistically significant decline in condition as compared to the control group, then that treatment group was coded as a '1' (presence of adverse effect). Conversely, if the treatment group was not significantly different from the control group (or fared better), then it was coded as a '0' (absence of adverse effect).

While 'adverse effect' is defined more broadly by the MSA in terms of EFH (50 CFR § 600.810), for the purposes of the coral-specific analyses presented herein, we define *adverse effect* as any response of a coral individual, colony, or treatment group that may negatively affect the coral's fitness and/or survival. These adverse effects may include physiological changes (e.g., reduced growth or photosynthetic rates), bleaching, tissue necrosis, and colony mortality. This definition is independent of response magnitude; while the effect may potentially reduce a coral's fitness, the reduction in fitness may not be measurable.

Once binary scores were assigned for each treatment group, we identified two thresholds, commonly used in toxicological and other regulatory contexts (Fig. 2A):

1) *LOAEL* – the 'lowest observed adverse effect level,' i.e., the lowest exposure level at which there was an observed adverse effect, and
2) *NOAEL* – the 'no observed adverse effect level,' i.e., the highest exposure level at which there was NOT an observed adverse effect.

We also performed mixed-effects logistic meta-regressions (Fig. 2B) (Simmonds and Higgins 2016, Bakbergenuly and Kulinskaya 2018). This approach estimates the probability of an adverse response given a level of sediment exposure and is useful because it can provide *specificity*, *sensitivity*, and receiver operating characteristic area-under-the-curve (*ROC AUC*) outputs (see 'Glossary') that inform choice of the most robust models for regulatory purposes.

All models were fit in *R* (R Core Team 2020) with the *lme4* package (Bates et al. 2015) function 'glmer,' which creates generalized mixed-effects models (GLMM). A regression is a set of statistical processes that estimate the relationships between a dependent variable ('response' or 'outcome') and one or more independent variables ('predictors' or 'covariates'). In the case of GLMM, each predictor is classified as either a 'fixed' or 'random' effect. Fixed effects are constant across individuals and are used to describe the direct, causative relationship with the response. Random effects vary by groups of individuals, in slope and/or intercept, and are used to attribute variability in the modeled relationship. We adopted a 'fixed slope, random intercept' approach and fit models with different structures, three for possible fixed-effects: 1) exposure concentration, 2) concentration and duration, and 3) concentration, duration, and the interaction between the two, crossed with five possible random-effects structures: 1) species, 2) study, 3) study nested within article, 4) species and study, and 5) species and study nested within article. We compared these models using Akaike Information Criterion (AIC) and likelihood ratio tests, which are used to choose the 'best-fit' model that balances parsimony with explanatory power. We inspected the residuals of best-fit models and, in all cases, used a $\log_{10}$ transformation of exposure concentration to conform with statistical assumptions and allow model convergence.

3.6.2 Dose-Response Meta-Analysis

For coral responses reported as continuous variables, we calculated the standardized difference in means for each treatment group within each study. We calculated this effect size using Hedges' *d* and the variance, *s*, thereof (Hedges and Olkin 1985), which is unaffected by unequal sampling variances in the paired groups (e.g., treatment and control conditions) and includes a correction factor (*J*) for small sample sizes:

$$d = \frac{(\bar{X}_T - \bar{X}_C)}{s} J, \qquad J = 1 - \frac{3}{4(n_T + n_C) - 9}, \qquad s = \sqrt{\frac{(n_T - 1)SD_T^2 + (n_C - 1)SD_C^2}{n_T + n_C - 2}},$$

where $\bar{X}$ is the sample mean, *T* and C are treatment and control groups, respectively, *SD* is standard deviation, and *n* is sample size.

We then explored the relationship between effect size (*d*) and stressor intensity with hierarchical mixed-effects models that fit exposure-response curves ('dose-response meta-analysis,' or DRMA, models, Fig. 2C). This model structure allowed us to examine the overall effects on corals while accounting for within- and between-study (co)variance structures (e.g., due to random effects and other effect modifiers).

All DRMA models were also fit in *R* with the *mixmeta* package and function (Sera et al. 2019). Diagnostics and comparisons of models with different fixed and random effects structures were done in the same manner as described above for binary meta-analyses. The 'dose-response threshold' for a coral response was the exposure level at which the upper bound of the 95% confidence interval of a DRMA regression did not overlap with zero (red, dashed line in Fig. 2C). Since a value of zero indicates no difference between treatment and control groups, this threshold identifies the minimum exposure that produced a statistically significant difference between treatment and control groups.

4 RESULTS

4.1 *Systematic Review*

In addition to 129 benchmark studies [ESM 1] identified within the definitive reviews (Rogers 1990, Fabricius 2005, Erftemeijer et al. 2012b, Risk 2014, Jones et al. 2015, 2016), our DSE searches returned 15,006 records (Fig. 3). After removing duplicates from these records, we screened the titles and abstracts of 10,221 records, 396 of which underwent a full-text screening. Included in our review are 65 articles, in which are the results of 86 studies (Fig. 3). Of these, we distinguish between studies that investigated the effects of deposited sediment, suspended sediment, and both deposited and suspended sediment on various responses of corals (Table 2). Because there was only one included article/study that quantified the effects of deposited and suspended sediment together (Flores et al. 2012), we do not conduct a meta-analysis of the synergistic effects of deposited and suspended sediment. Instead, we include this article/study in each of the separate analyses for deposited and suspended sediment.

Table 2. The number of articles and studies included in the meta-analysis, by sediment category.

	Deposited Sediment	Suspended Sediment	Deposited and Suspended Sediment	Total
Number of articles	44	22	1	65
Number of studies	45	42	1	86

4.2 *Coral Responses to Sediment Stress*

4.2.1 Scale of Responses

Corals respond to sediment exposure in a variety of ways, which tend to intensify as exposure concentration, duration, and/or frequency increase (Fig. 4, Fig. 5, Fig. 6):

- Immediate responses include behavioral changes that remove sediment from the coral's surface and are rarely considered adverse, unless the behaviors persist for long enough to significantly diminish a coral's energy reserves.
  Examples: Hydrostatic inflation, movement of tentacles, and increased mucus production and sloughing (green 'Signs of Sediment Removal' in Fig. 4-6).
- Short-term responses include physiological changes that are likely adverse, if they persist.
  Examples: Reduced photosynthesis (in terms of photosynthetic efficiency or ratios of photosynthesis-to-respiration; light blue in Fig. 4-6), localized bleaching (light orange in in Fig. 4-6), and reduced fertilization success (dark blue in Fig. 4-6).
- Medium- to long-term responses are usually considered adverse.
  Examples: Coral adults experience reduced growth rate (mauve in Fig. 4-6), tissue necrosis (orange in in Fig. 4-6), and colony mortality (black in in Fig. 4-6). Larvae experience limited settlement rates (yellow in Fig. 4-6) and pre-settlement mortality (red in Fig. 4-6). Juveniles also experience mortality (dark red in Fig. 4-6), and thus reduced recruitment rates.

4.2.2 Summary of Major Findings

Rogers (1990) is the first definitive review on the subject of corals' and coral-reef organisms' responses to sediment. She observes that 'normal,' background levels of sediment on coral reefs are on the order of 10 mg/cm^2/d for deposition rates and 10 mg/L for total suspended sediment concentrations, above which are considered 'high' with the potential to adversely affect corals. Other published critical thresholds on coral reefs range from 37 to 300 mg/cm^2/d for deposited sediment (Bak and Elgershuizen 1976, Pastorok and Bilyard 1985, Miller and Cruise 1995) and from 15 to 260 mg/L for suspended sediment (Mapstone et al. 1989, Rice and Hunter 1992, Hopley et al. 1993, Larcombe et al. 2001, Hoitink 2003, Thomas et al. 2003, Bogers and Gardner 2004, van der Klis and Bogers 2004).

Inclusive of all coral developmental stages, taxa, and geographic origins, **deposited sediment concentrations (DSC) as low as 1 mg/cm^2/d and suspended sediment concentrations (SSC) as low as 3.2 mg/L can adversely affect corals** (LOAELs; Table 3, Table 4). Physiological responses (e.g., reduced photosynthesis of symbionts) can **occur as quickly as 12 h and 1 h after exposure to deposited sediment and suspended sediment**, respectively (Table 3, Table 4; Fig. 7). Lethal responses (i.e., tissue necrosis) occur at DSC as low as 4.9 mg/cm^2/d and for exposure durations less than one day (22 h) (Table 3, Fig. 8). Lethal responses can occur after exposure to SSC as low as 3.2 mg/L and 12 h, though statistical models that characterize SSC's effect on the probability of partial/total mortality of all coral life-history stages do not indicate a significant relationship (Table 4, Table 5; Fig. 8; GLMM $z = 1.110$, $p = 0.267$).

When we consider only mature, adult corals, results are similar. However, **adults are slightly less sensitive to deposited sediment than immature coral stages** (cf. Fig. 7, Fig. 8 and Fig. 9), with adverse responses beginning to occur at 4.9 mg/cm^2/d and after 12 h (Table 3). Adults begin to bleach at 3.2 mg/L SSC after only 2 h exposure (Table 4; Fig. 7) and experience tissue necrosis at 3.2 mg/L after at least 2 weeks (14 d) of exposure to suspended sediment (Table 4; Fig. Fig. 8). While these minimum values at which adverse effects are observed (LOAELs) in corals appear low for suspended sediment exposure, **corals typically took an order of magnitude times longer to experience lethal effects due to suspended sediment than to comparable concentrations of deposited sediment** (cf. Table 3 and Table 4; Fig. 7–Fig. 9)).

Corals exposed to deposited sediment at 10 mg/cm^2/d have a 25.8 to 35.9% probability of experiencing adverse effects. At 5 mg/cm^2/d, this probability drops to 18.0 to 30.4%, and at 1 mg/cm^2/d, it further drops to 7.7 to 19.2% (Table 6; Fig. 10A). Corals exposed to suspended sediment at 10 mg/L have an 8.2 to 10.0% probability of experiencing adverse effects. At 5 mg/L, this probability drops to 5.1 to 8.4%, and at 1 mg/L, it further drops to 1.9 to 2.2% (Table 6; Fig. 10B). These estimates are average marginal probabilities calculated by the meta-regression analyses with binary data that hold exposure duration constant and account for variability among studies and species.

We also used dose-response meta-regression analyses (DRMA) to model the relationship between sediment exposure and the magnitude of coral responses, where available data were sufficient. The dose-response thresholds reported below are the lowest concentrations at which sediment-exposed corals ('treatment') are expected to have a lower or reduced response than corals not exposed to sediment ('controls'). These are statistically significant differences between treatment and control corals, with 95% confidence, which may not reflect biologically significant differences in some cases. Biological significance is dictated by ecological context (i.e., species, population, location, etc.), and therefore could not be easily synthesized across studies. Our key findings are summarized here, and in more detail in Table 7 and the subsequent sections for individual coral responses (sections 4.3 – 4.16):

- Coral gametes have significantly **reduced fertilization success at 30.4 mg/L SSC and greater** (Table 7; section 4.7, Fig. 11). This dose-response threshold matches exactly with the LOAEL derived from binary data (LOAEL = 30.4 mg/L, NOAEL = 25.0 mg/L).
- **Settlement rates of coral larvae** on vertically facing surfaces (those most susceptible to sediment deposition) **significantly decline at 1.3 mg/cm^2/d DSC and greater** (Table 7; section 4.9, Fig. 12). This dose-response threshold also closely aligns with the NOAEL and LOAEL derived from binary data (1 mg/cm^2/d).
- **Survival of coral juvenile recruits significantly declines at 13.8 mg/cm^2/d DSC and greater** (Table 7; section 4.10, Fig. 13). This is a less conservative threshold estimate than suggested by the NOAEL and LOAEL of 8.3 mg/cm^2/d. In this case, the dose-response threshold may be considered relatively robust because the statistical model explained over half (53%) of the variability in this coral response (I^2 = 47% residual heterogeneity).
- **Photosynthetic efficiency (maximum quantum yield, F_v/F_m) significantly declines at 3.2 mg/cm^2/d DSC and greater** (Table 7; section 4.12, Fig. 14). This estimate is much less than the NOAEL and LOAEL of 25 mg/cm^2/d. There was considerable heterogeneity unaccounted for in the DRMA model (I^2 = 81%), which may indicate that the dose-response threshold is less robust. However, most studies that measure F_v/F_m tested exposure concentrations at or above 25 mg/cm^2/d, indicating that future studies should explore the effects of lower exposure levels before a more definitive threshold can be estimated.
- We found no significant relationships between DSC and P/R ratio, growth rate, or partial mortality rate, nor between SSC and larval survival or total mortality rate (Table 7). For these relationships, there is likely **too much variability to detect an effect across studies. This may be due, in part, to the overwhelming taxonomic diversity represented within these studies, especially for those focusing on coral adults (62 species from 31 genera).**

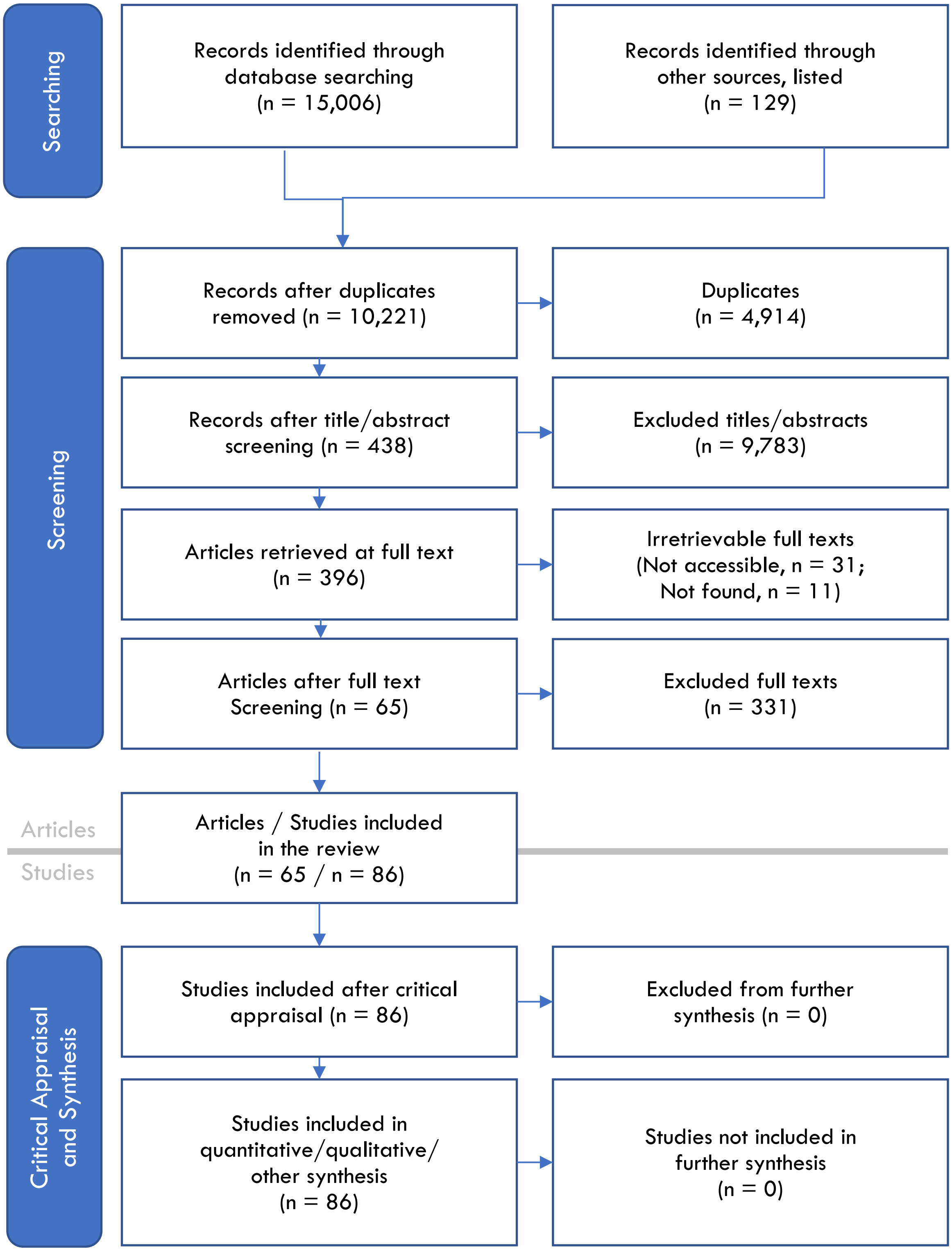

Fig. 3. ROSES flow diagram for systematic reviews, modified Version 1. (Haddaway et al. 2018) DOI: 10.6084/m9.figshare.5897389; https://www.roses-reporting.com/systematic-review-reports. Accessed 11 August 2020.

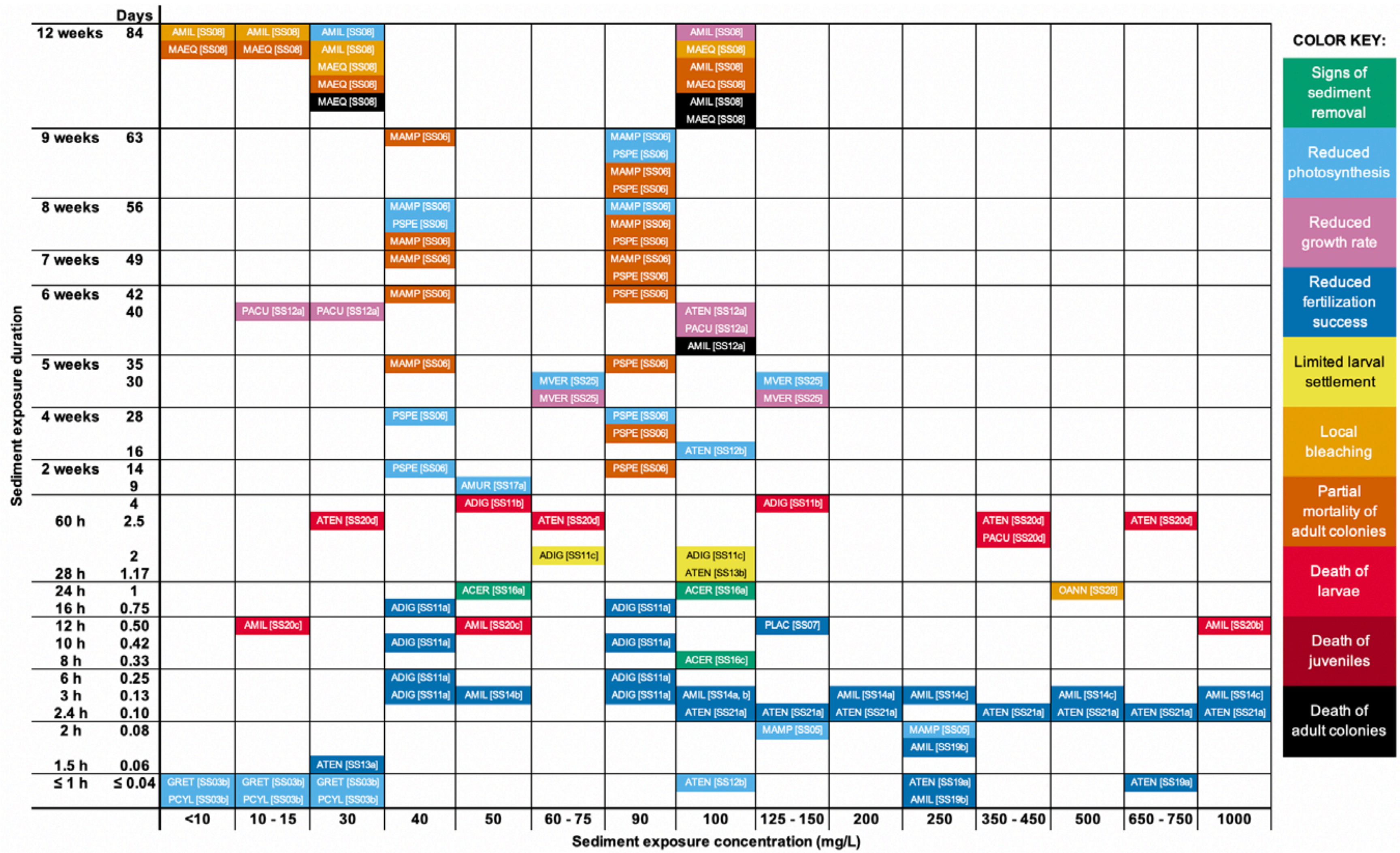

Fig. 4. Review of coral responses to varying suspended sediment concentrations at timescales ranging from minutes to months. Coral responses are color coded with a key shown at the right of this figure. Coral species are shown as four-letter codes, with a key provided at Table A-3. Key to numbered references [SS##] are provided at Table A-2.

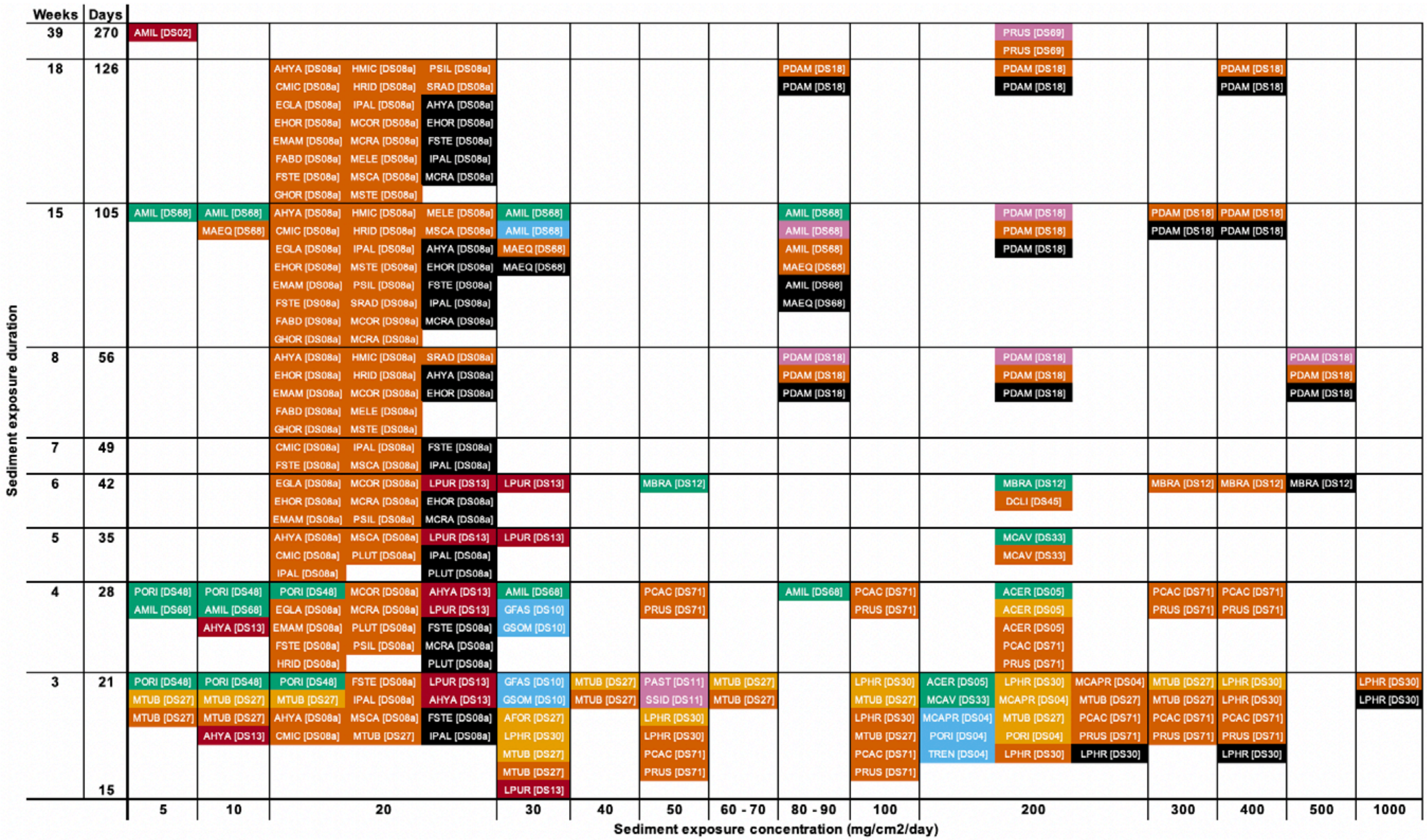

Fig. 5. Review of coral responses to varying deposited sediment concentrations at timescales ranging from 15 to 270 days (>2 weeks to 39 weeks). Coral responses are color coded with a key shown at the right side of Fig. 4. Coral species are shown as four-letter codes, with a key provided at Table A-3. Key to numbered references [DS##] are provided at Table A-1.

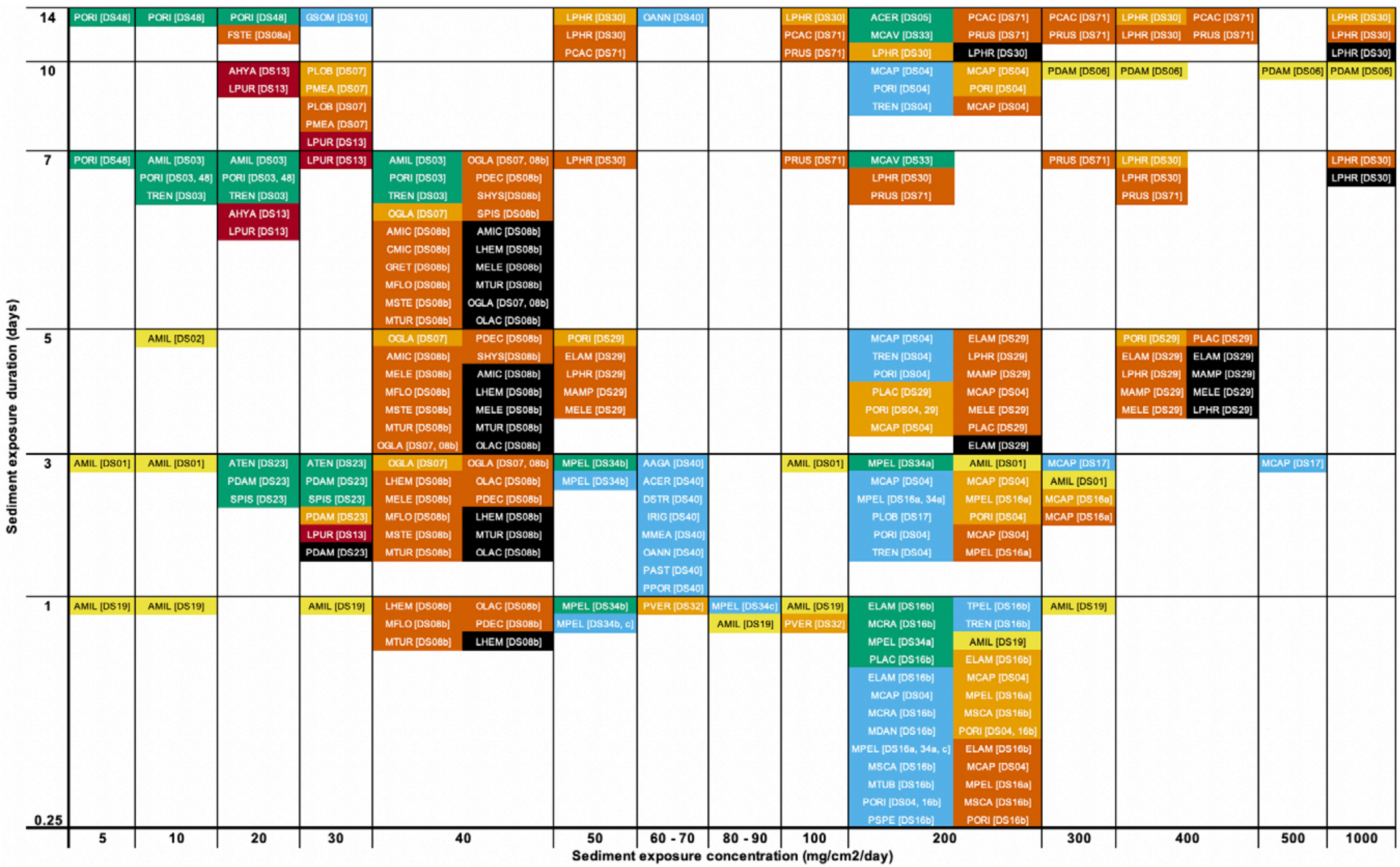

Fig. 6. Review of coral responses to varying deposited sediment concentrations at timescales ranging from hours to 2 weeks. Coral responses are color coded with a key shown at the right side of Fig. 4. Coral species are shown as four-letter codes, with a key provided at Table A-3. Key to numbered references [DS##] are provided at Table A-1.

Table 3. Results of BINARY ANALYSES of the effects of DEPOSITED SEDIMENT on corals (NOAEL/LOAELs). A '*treatment group*' is an experimental unit of corals exposed to the same exposure conditions within a study – these may be control (no sediment exposure) or treatment conditions of differing exposure concentrations and/or durations. **Bold** rows represent coral responses for which logistic meta-regression was done (for regression results, see Table 5). Double dashes '--' indicate that data were non-existent or irrelevant.

Coral age class	Binary Coral Response	# treatment groups (controls included / excluded)	# studies / articles with binary data	# species / genera with binary data	NOAEL		LOAEL	
					concentration (mg/cm²/d)	duration	concentration (mg/cm²/d)	duration
GAMETES	Reduced fertilization success?	--	--	--	--	--	--	--
LARVAE	Larval mortality?	--	--	--	--	--	--	--
	Limited settlement?	54 / 45	4 / 4	2 / 2	1.0	--	1.0	--
JUVENILES	Recruit mortality?	132 / 87	3 / 3	4 / 2	8.3	3 d	8.3	3 d
ADULTS	Reduced P/R ratio?	60 / 25	5 / 5	16 / 15	26.4	2 d	26.4	2 d
	Reduced photosynthetic efficiency?	372 / 249	9 / 9	20 / 12	25.0	12 h	25.0	12 h
	Local bleaching?	497 / 352	20 / 20	52 / 32	4.9	22 h	4.9	22 h
	Reduced growth rate?	55 / 40	10 / 10	10 / 7	38.4	21 d	53.0	21 d
	Small tissue necroses?	750 / 602	21 / 20	76 / 39	4.4	22 h	4.9	22 h
	Large tissue necroses?	657 / 522	17 / 17	75 / 39	20.8	3 d	20.8	3 d
	Total colony mortality?	678 / 509	24 / 23	84 / 46	20.8	1 d	20.8	1 d
ADULTS	**ANY MORTALITY?**	**827 / 629**	**28 / 27**	**87 / 46**	**4.4**	**22 h**	**4.9**	**22 h**
	ANY ADVERSE EFFECT?	**1085 / 783**	**34 / 34**	**101 / 50**	**4.9**	**12 h**	**4.9**	**12 h**
ALL	**ANY MORTALITY?**	**965 / 719**	**31 / 30**	**89 / 47**	**4.4**	**22 h**	**4.9**	**22 h**
	ANY ADVERSE EFFECT?	**1323 / 943**	**40 / 39**	**102 / 51**	**1.0**	**12 h**	**1.0**	**12 h**

Table 4. Results of BINARY ANALYSES of the effects of SUSPENDED SEDIMENT on corals (NOAEL/LOAELs). A '*treatment group*' is an experimental unit of corals exposed to the same exposure conditions within a study – these may be control (no sediment exposure) or treatment conditions of differing exposure concentrations and/or durations. '*Physiological limitation?*' for juvenile corals indicates either reduced P/R ratio, reduced photosynthetic efficiency, or reduced growth rate. These are combined here because they represent the physiological results from only one article. **Bold** rows represent coral responses for which logistic meta-regression was done (for regression results, see Table 5). Double dashes '--' indicate that data were irrelevant.

Coral age class	Binary Coral Response	# treatment groups (controls included / excluded)	# studies / articles with binary data	# species / genera with binary data	NOAEL		LOAEL	
					concentration (mg/L)	duration	concentration (mg/L)	duration
GAMETES	Reduced fertilization success?	110 / 86	10 / 6	4 / 2	25.0	--	30.4	--
LARVAE	Larval mortality?	63 / 52	7 / 4	5 / 2	29.5	--	30.0	--
	Limited settlement?	30 / 20	7 / 4	4 / 3	34.6	--	57.8	--
JUVENILES	Physiological limitation?	20 / 15	2 / 1	3 / 2	10.0	0	10.0	1 h
	Recruit mortality?	16 / 9	2 / 2	4 / 3	100.0	40 d	100.0	40 d
ADULTS	Reduced P/R ratio?	49 / 34	3 / 3	4 / 4	35.8	2 h	35.8	2 h
	Reduced photosynthetic efficiency?	238 / 180	6 / 5	8 / 6	35.8	56 d	35.8	56 d
	Local bleaching?	92 / 54	8 / 7	10 / 6	3.2	1 d	3.2	1 d
	Reduced growth rate?	79 / 47	7 / 5	12 / 12	49.0	31 d	58.6	31 d
	Small tissue necroses?	210 / 147	4 / 4	8 / 6	3.2	14 d	3.2	14 d
	Large tissue necroses?	210 / 147	4 / 4	8 / 6	29.1	84 d	29.1	84 d
	Total colony mortality?	272 / 176	8 / 6	17 / 14	29.1	40 d	29.1	40 d
ADULTS	**ANY MORTALITY?**	**272 / 176**	**8 / 6**	**17 / 14**	**3.2**	**14 d**	**3.2**	**14 d**
	ANY ADVERSE EFFECT?	**360 / 244**	**14 / 11**	**21 / 16**	**3.2**	**2 h**	**3.2**	**2 h**
ALL	**ANY MORTALITY?**	**376 / 261**	**19 / 11**	**21 / 15**	**3.2**	**12 h**	**3.2**	**12 h**
	ANY ADVERSE EFFECT?	**585 / 423**	**37 / 20**	**26 / 18**	**3.2**	**0**	**3.2**	**1 h**

Table 5. Classification table for the LOGISTIC META-REGRESSION models that were developed as part of this review. The '*Percent correct of model predictions*' estimates the diagnostic ability of the model by calculating the proportion of true model predictions over all model predictions. '*Sensitivity*' and '*Specificity*' refer to the percent of coral responses in the data that a model would correctly classify as having or not having the coral response of interest, respectively (see 'Glossary'). '*Positive Predictive Value*' and '*Negative Predictive Value*' estimate the probability (%) that a treatment group either with a positive result from a statistical model actually has the coral response of interest, or with a negative result from a statistical model actually does not have the coral response of interest, respectively (see 'Glossary'). The column labeled '*AUC*' represents the area under a Receiver Operating Characteristic (ROC) curve for each model (see 'Glossary'). The '*Model R^2*' represents the proportion of the variance for the '*Coral Response*' that is explained by predictors in the regression model, with fixed effects being exposure concentration (conc.) and duration (dur.) and random effects being study and species. '*ROC area under curve*' is a measure of the diagnostic ability of a logistic regression model, where values of 1 represent a perfect test and of 0.5 represent a model with no discriminatory ability. The '*Model R^2*' represents the proportion of the variance for the '*Binary Coral Response*' that is explained by predictors in the regression model. **Bold** values within '*Model p-value for conc. / dur.*' represent statistically significant ($p \leq 0.05$) model relationships between the predictor and the response.

Sediment Type	Coral age class	Coral Response	Percent (%) correct of model predictions	Sensitivity (%)	Specificity (%)	Positive Predictive Value (%)	Negative Predictive Value (%)	AUC	Model R^2		Model *p*-value for conc. / dur.
									Fixed Effects only	Fixed+ Random Effects	
DEPOSITED SEDIMENT	***Adults***	*Any Mortality*	86.8	81.5	87.3	82.3	86.6	0.949	0.124	0.843	**0.022** / 0.568
		Any Adverse Effect	83.1	74.9	85.8	83.6	78.0	0.917	0.064	0.829	**<0.0001** / **<0.0001**
	All Stages	*Any Mortality*	84.8	87.3	86.4	83.3	89.7	0.932	0.100	0.823	**<0.0001** / **<0.0001**
		Any Adverse Effect	80.5	79.8	86.8	86.1	80.7	0.888	0.052	0.778	**<0.0001** / **<0.0001**
SUSPENDED SEDIMENT	***Adults***	*Any Mortality*	89.2	40.5	96.8	70.8	89.5	0.935	0.336	0.722	**0.004** / **<0.0001**
		Any Adverse Effect	88.1	57.0	94.1	75.0	87.6	0.941	0.339	0.709	**<0.0001** / **<0.0001**
	All Stages	*Any Mortality*	87.7	60.6	94.5	71.4	92.6	0.909	0.168	0.781	0.267 / 0.379
		Any Adverse Effect	85.3	58.7	94.9	73.0	90.8	0.908	0.137	0.784	**<0.0001** / **0.011**

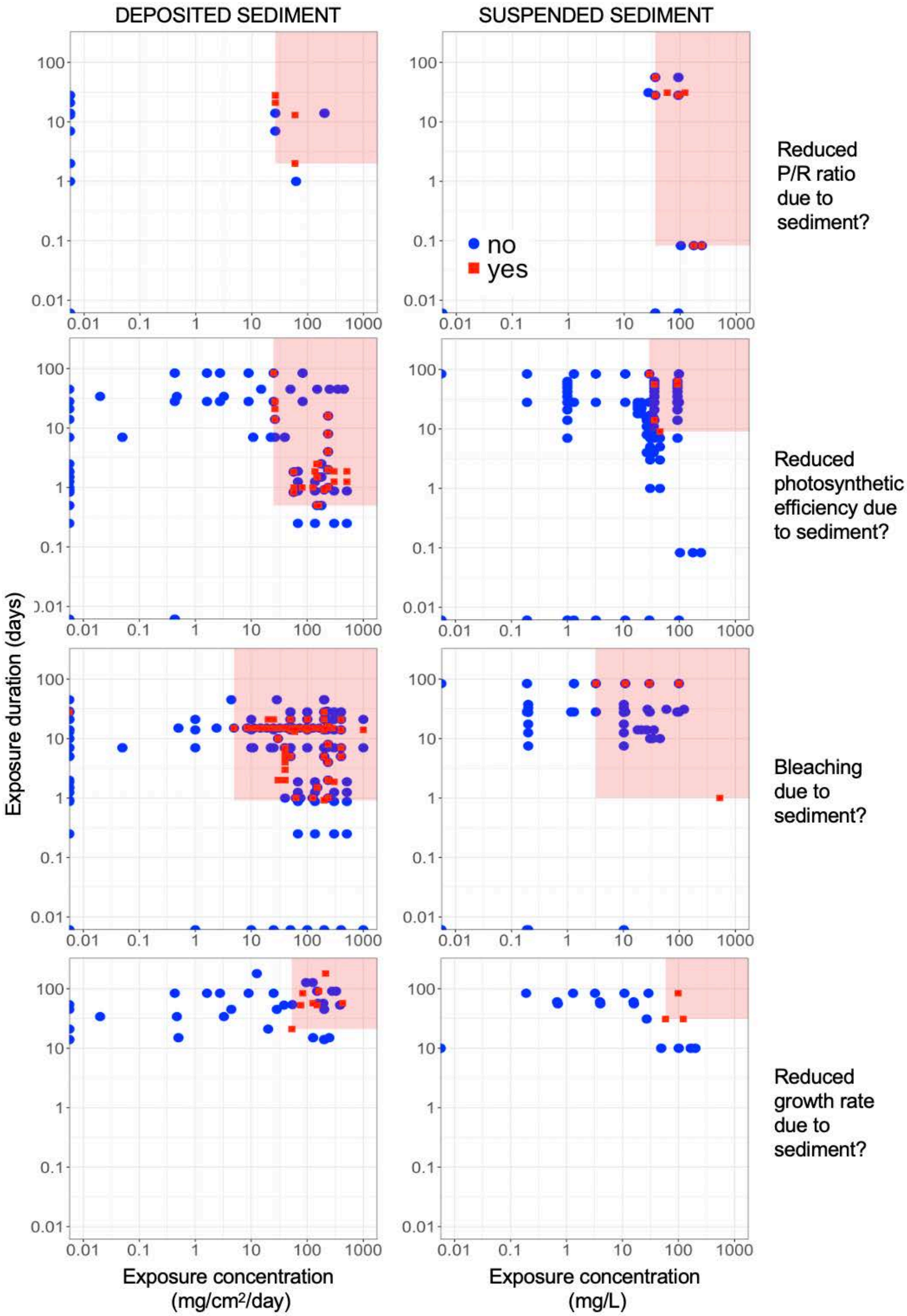

Fig. 7. Binary data for PHYSIOLOGICAL effects of sediment exposure on coral ADULTS, plotted as concentration vs. duration of exposure to either deposited sediment (left panels) or suspended sediment (right panels). Each row of panels represents a different coral response. The red, rectangular area is bounded by the LOAELs for concentration and duration, thereby representing the exposure conditions under which adverse effects have been observed in studies from our review.

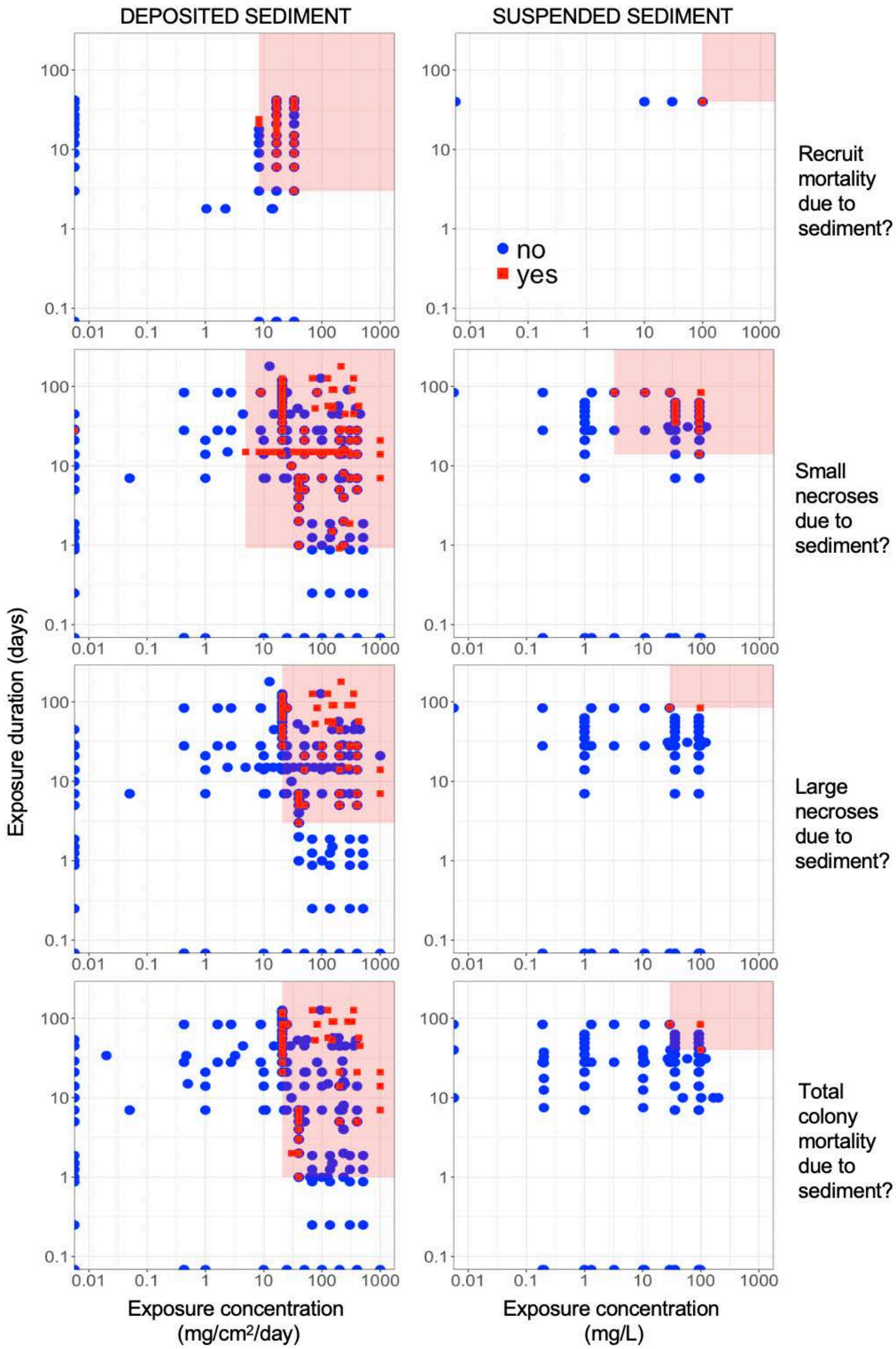

Fig. 8. Binary data for LETHAL effects of sediment exposure on coral JUVENILES and ADULTS, plotted as concentration vs. duration of exposure to either deposited sediment (left panels) or suspended sediment (right panels). Each row of panels represents a different coral response. Small necroses are <50% of adult coral tissue area, large necroses are ≥50% and <100% tissue area, and both recruit and total mortality are 100% tissue necrosis. The red, rectangular area is bounded by the LOAELs for concentration and duration, thereby representing the exposure conditions under which adverse effects have been observed in studies from our review.

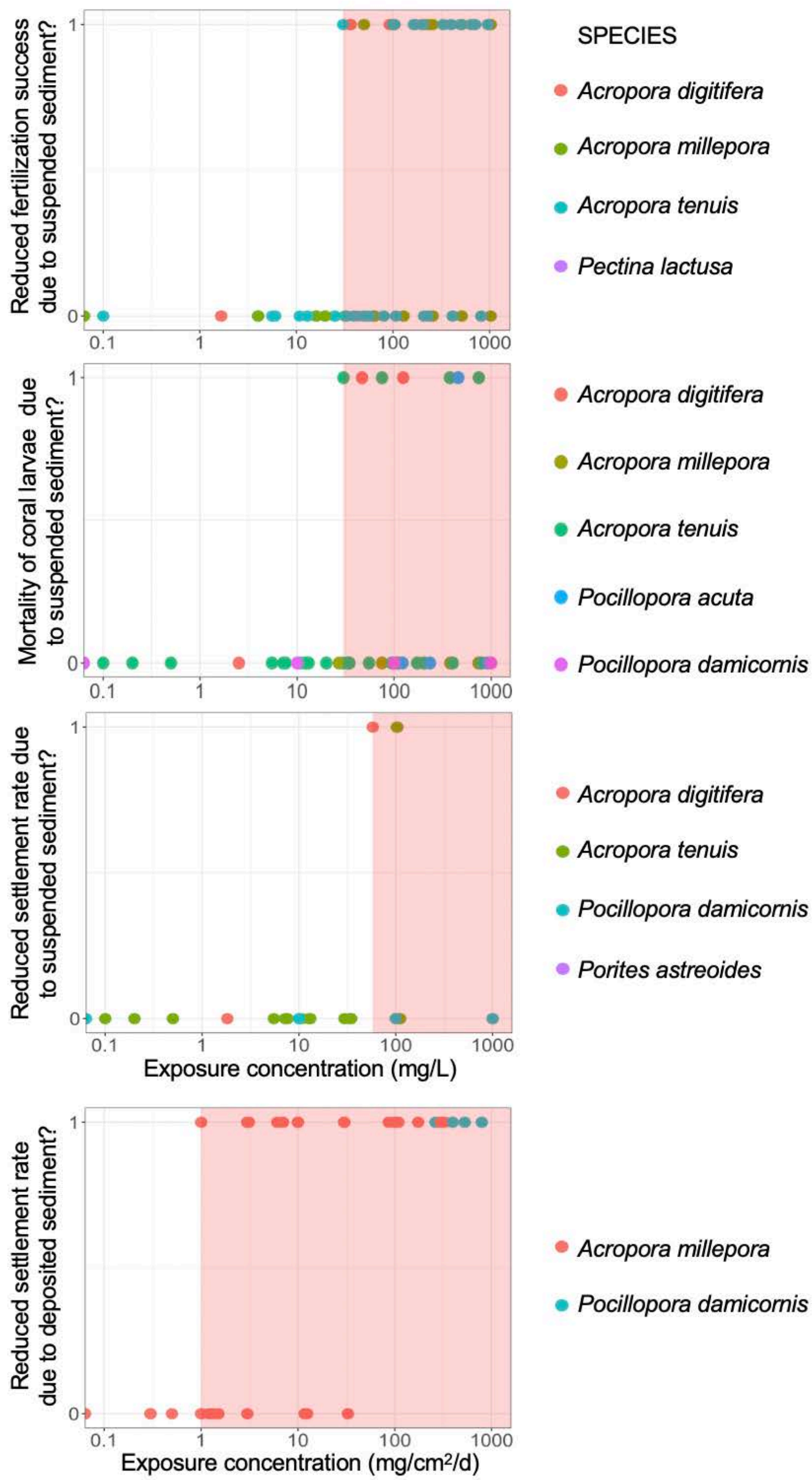

Fig. 9. Binary data for coral GAMETES and LARVAE in response to sediment exposure (0 = no, 1 = yes), plotted as a function of concentration of either suspended sediment (top 3 panels) or deposited sediment (bottom panel). The red, rectangular area is bounded by the concentration LOAEL, thereby representing the exposure concentration under which adverse effects have been observed in studies from our review. Given the short period of time that corals are in these life-history stages, exposure duration was not considered in the determination of NOAEL/LOAELs, nor in meta-analyses.

Table 6. Predicted probability of coral response at a range of sediment exposure concentrations, expressed as a proportion. Values are average marginal probabilities as a function of the best-fit, logistic meta-regression models, which held exposure duration constant and accounted for variability among studies and species. "NA" indicates that the concentration is outside of the range of model predictions. Color key: green is <0.10, yellow is ≥0.10 and <0.25, orange is ≥0.25 and <0.50, and red is ≥0.50.

			Exposure Concentration (DS: mg/cm²/d, SS: mg/L)						
Sediment Type	**Coral age class**	**Coral Response**	**1**	**5**	**10**	**50**	**100**	**500**	**1000**
DEPOSITED SEDIMENT	***Adults***	*Any Mortality*	0.077	0.180	0.258	0.452	0.522	0.639	0.680
		Any Adverse Effect	0.173	0.287	0.344	0.486	0.549	0.685	0.736
	All Stages	*Any Mortality*	0.080	0.192	0.258	0.440	0.521	0.674	0.725
		Any Adverse Effect	0.192	0.304	0.359	0.497	0.557	0.685	0.733
SUSPENDED SEDIMENT	***Adults***	*Any Mortality*	NA	0.084	0.090	0.156	0.263	NA	NA
		Any Adverse Effect	NA	0.051	0.084	0.209	0.297	0.577	NA
	All Stages	*Any Mortality (n.s.)*	0.019	0.055	0.082	0.170	0.217	0.323	0.369
		Any Adverse Effect	0.022	0.068	0.100	0.212	0.280	0.483	0.580

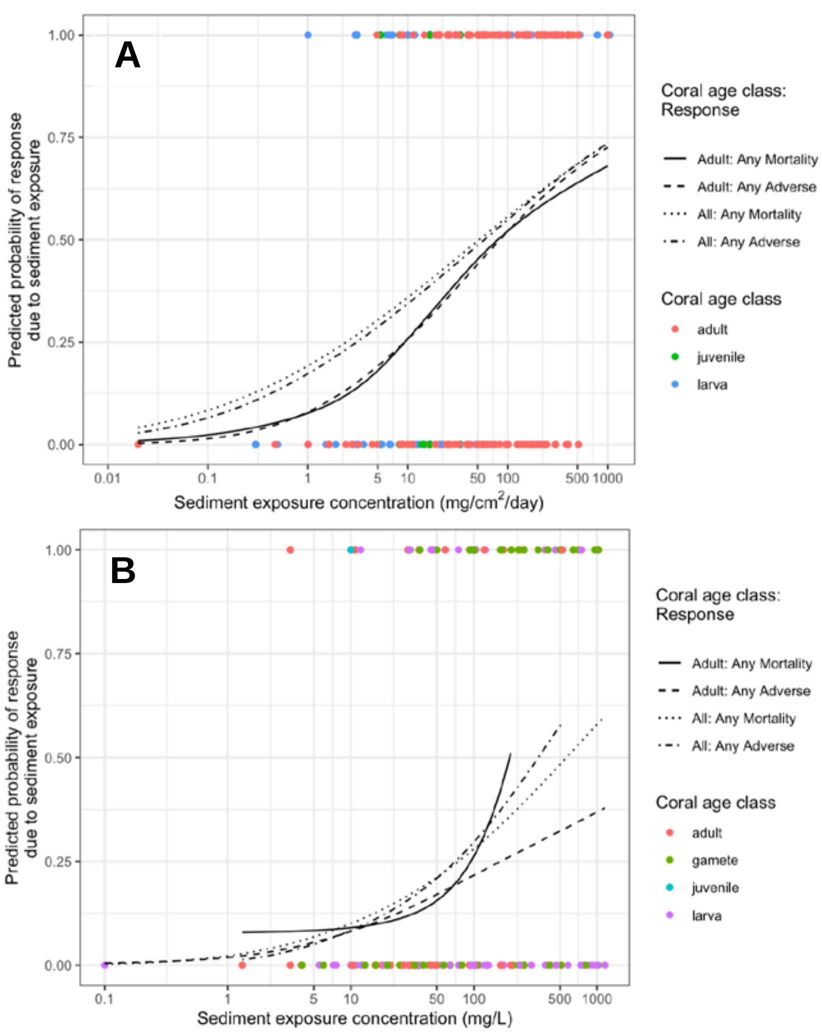

Fig. 10. Predicted probability of coral response across the range of exposure concentrations of deposited sediment (**A**) and suspended sediment (**B**). Values are average marginal probabilities, expressed as a proportion, as a function of the best-fit, logistic meta-regression models, which held exposure duration constant and accounted for variability among studies and species.

Table 7. Results of best-fit DOSE-RESPONSE META-REGRESSION (DRMA) models for coral responses where sufficient data were available to assess the relationship between sediment exposure ('dose') and magnitude of the coral response of-interest (standardized effect size, Hedges' *d*). Analyses using deposited or suspended sediment datasets are indicated as 'DS' and 'SS,' respectively. A '*treatment group*' is an experimental unit of corals exposed to the same exposure conditions within a study – these may be control conditions (no sediment exposure) or treatment conditions of differing exposure concentrations and/or durations. The '*Dose-Response I^2 Statistic*' is a measure that indicates the percentage of variance in a meta-analysis that is attributable to heterogeneity among dose-response comparisons within study. Heterogeneity is substantial when I^2 is above 75%. The '*Dose-Response Threshold*' for a coral response significantly affected by sediment concentration was the minimum exposure value at which dose-response meta-regression 95% CI no longer overlapped with zero (where zero indicates no difference between a treatment group and its control, see Fig. 2C). Rows in **bold** represent significant relationships ($p \leq 0.05$) between sediment exposure and the effect size of the corresponding coral response and '*n.s.*' indicates a non-significant relationship ($p > 0.05$).

Coral age class	Continuous Coral Response	Deposited or Suspended Sediment	# treatment groups (controls included / excluded)	# studies / articles in DRMA	# species / genera in DRMA	Dose-Response I^2 Statistic	Dose-Response Threshold (DS: mg/cm²/d; SS: mg/L)
GAMETES	**Fertilization success rate**	**SS**	**110 / 86**	**10 / 6**	**4 / 2**	**82.3%**	**30.4**
LARVAE	Larval survival rate	SS	50 / 42	4 / 3	4 / 2	73.0%	*n.s.*
	Settlement rate	**DS**	**71 / 61**	**7 / 6**	**2 / 2**	**84.6%**	**1.3**
		SS	26 / 20	6 / 3	3 / 2	88.3%	*n.s.*
JUVENILES	**Recruit mortality rate**	**DS**	**132 / 87**	**3 / 3**	**4 / 2**	**47.1%**	**13.8**
ADULTS	P/R ratio	DS	20 / 10	3 / 3	4 / 4	58.4%	*n.s.*
	Photosynthetic efficiency	**DS**	**181 / 141**	**8 / 6**	**9 / 6**	**76.8%**	**3.2**
		SS	217 / 164	5 / 4	6 / 5	21.4%	*n.s.*
	Growth rate	DS	29 / 19	8 / 8	8 / 5	41.5%	*n.s.*
	Partial tissue mortality rate	DS	140 / 115	4 / 4	11 / 8	86.9%	*n.s.*
	Total colony mortality rate	SS	47 / 33	4 / 4	6 / 4	0.0%	*n.s.*

4.3 *Coral Adults: ANY MORTALITY*

4.3.1 Biological Mechanisms of Effect

Mechanisms that mediate partial and/or total tissue mortality of adult corals in response to sediment exposure include light inhibition (Rogers 1979, Anthony et al. 2007), smothering (Fabricius and Wolanski 2000), increased energy allocation to clearance of sediment (Dallmeyer et al. 1982, Abdel-Salam and Porter 1988), and tissue damage (Riegl and Bloomer 1995). Suspended sediment decreases light availability to corals, leading to a decrease in gross photosynthesis. During periods of low light, corals can use heterotrophic feeding to meet their energetic demands, but feeding decreases when polyps retract in response to deposited sediment. A decline in autotrophic energy production of coral symbionts paired with an inability to enhance heterotrophic feeding may lead to coral starvation.

Sloughing of sediment by increased mucus production may also deplete coral energy reserves. Dead patches under sediment occur when sloughing of sediment is not possible (Bak 1978, Philipp and Fabricius 2003, Flores et al. 2012). If deposited sediment is nutrient-rich, it could enhance microbial growth and lead to flocculation of sediment (Fabricius and Wolanski 2000). Long periods of increased sediment exposure, or more frequent exposure events, have been shown to cause coral mortality (Tomascik and Sander 1987) and may lead to permanent changes in coral-reef community structure as some species adapt to high-sediment environments and others do not (Pastorok and Bilyard 1985).

For the purposes of this review, '*any mortality*' is defined as any amount of tissue necrosis as a result of sediment exposure, including both partial and total mortality of a coral colony. This response was most commonly reported as percent of live coral surface area that experienced permanent tissue loss over the course of the experiment, or in the case of total mortality, number/percent of coral replicates that died. As described in previous sections, we converted this into a binary response coded for presence/absence of any mortality.

4.3.2 Effects of Deposited Sediment

There were 29 studies from 28 articles that investigated the effect of deposited sediment concentrations (DSC) on mortality among adults of 87 coral species from 46 genera in 3 oceans (Table A-1). **When “3 oceans” is used herein, it indicates the Atlantic, Indian, and Pacific Oceans, where shallow, warm-water, scleractinian corals exist.**

Binary Meta-Analysis: For every 10-fold increase in DSC, the odds of any mortality increase by 4.0 times (95% CI 1.2, 12.8, GLMM $z = 2.300$, $p = 0.022$), while holding constant exposure duration and the interaction between concentration and duration, and after accounting for variability among studies and species. While holding exposure concentration constant, there is no significant evidence that exposure duration affects the odds of mortality (GLMM $z = -0.571$, $p = 0.568$).

4.3.3 Effects of Suspended Sediment

There were 8 studies from 6 articles that investigated the effect of suspended sediment concentration (SSC) on mortality among adults of 17 coral species from 14 genera in 3 oceans (Table A-2).

Binary Meta-Analysis: For every 10-fold increase in SSC, the odds of any tissue mortality increase by 1.06 times (95% CI 1.02, 1.11; GLMM $z = 2.896$, $p = 0.004$), while holding exposure duration constant and after accounting for variability among species. For every 10-fold increase in exposure duration, the odds of any tissue mortality increase by 1.22 times (95% CI 1.12, 1.33; GLMM $z = 4.678$, $p < 0.0001$), while holding SSC constant and after accounting for variability among species.

4.4 Coral Adults: ADVERSE EFFECTS

4.4.1 Biological Mechanisms of Effect

The mechanisms that lead to any '*adverse effect*' of adult corals due to sediment are reviewed in each of the individual sections by adult coral response (sections 4.3 – 4.16). As described in the Methods, an *adverse effect* is defined as any response of a coral individual, colony, or treatment group that may negatively affect the coral's fitness and/or survival. For the purposes of this study, these include physiological changes (decreases in photosynthetic efficiency, P/R ratio, and growth rate, as well as bleaching) and lethal changes (tissue necrosis and total colony mortality). In all cases, we converted these to binary responses coded for presence/absence of an adverse effect.

4.4.2 Effects of Deposited Sediment

There were 34 studies from 34 articles that investigated the effect of DSC on any adverse effect among adults of 101 coral species from 50 genera in 3 oceans (Table A-1).

Binary Meta-Analysis: For every 10-fold increase in DSC, the odds of an adverse effect increase by 4.4 times (95% CI 2.3, 8.6, GLMM $z = 4.358$, $p < 0.0001$), while holding exposure duration constant and accounting for variability among studies and species. For every 10-fold increase in exposure duration of deposited sediment, the odds of an adverse effect increase by 1.08 times (95% CI 1.05, 1.12, GLMM $z = 5.322$, $p < 0.0001$), while holding exposure concentration constant and accounting for variability among studies and species.

4.4.3 Effects of Suspended Sediment

There were 14 studies from 11 articles that investigated the effect of SSC on any adverse effect among adults of 21 coral species from 16 genera in 3 oceans (Table A-2).

Binary Meta-Analysis: For every 10-fold increase in SSC, the odds of experiencing an adverse effect increase by 2.4 times (95% CI 5.1, 116.7; GLMM $z = 4.013$, $p < 0.0001$), while holding exposure duration constant and accounting for variability among studies and species. For every 10-fold increase in exposure duration of suspended sediment, the odds of experiencing an adverse effect increase by 1.2 times (95% CI 1.1, 1.3; GLMM $z = 5.234$, $p < 0.0001$), while holding SSC constant and accounting for variability among studies and species.

4.5 *All Coral Life History Stages: ANY MORTALITY*

4.5.1 Biological Mechanisms of Effect

The mechanisms leading to partial and/or total mortality of all life-history stages of corals are the same as described in section 4.3.1. The only change from the above-described '*any mortality*' meta-analysis is the inclusion of mortality of both larval and juvenile coral phases. These were quantified as percent of coral replicates that died during the experiment and converted to a binary response coded for presence/absence of any mortality, as previously described.

4.5.2 Effects of Deposited Sediment

There were 31 studies from 30 articles that investigated the effect of DSC on mortality of all life-history stages of 89 coral species from 47 genera in 3 oceans (Table A-1).

Binary Meta-Analysis: For every 10-fold increase in exposure concentration of deposited sediment, the odds of any tissue mortality increase by 8.5 times (95% CI 3.6, 20.3; GLMM $z = 4.814$, $p < 0.0001$), while holding exposure duration constant and accounting for variability among studies and species. For every 10-fold increase in exposure duration of deposited sediment, the odds of any tissue mortality increase by 1.08 times (95% CI 1.05, 1.11; GLMM $z = 5.123$, $p < 0.0001$), while holding exposure concentration constant and accounting for variability among studies and species.

4.5.3 Effects of Suspended Sediment

There were 19 studies from 11 articles that investigated the effect of SSC on mortality of all life-history stages of 21 coral species from 15 genera in 3 oceans (Table A-2).

Binary Meta-Analysis: There is no significant relationship between SSC and the odds of any tissue mortality (GLMM $z = 1.110$, $p = 0.267$) after accounting for variability among articles and species.

4.6 *All Coral Life History Stages: ADVERSE EFFECTS*

4.6.1 Biological Mechanisms of Effect

The mechanisms leading to any adverse effect of any coral life-history stage are reviewed below, in each of the individual sections by coral response (sections 4.7 – 4.16). The only change from the above-described 'adverse effects' meta-analysis (section 4.4) is the inclusion of gamete, larval, and juvenile coral phases. These responses include fertilization success, larval mortality, larval settlement, and recruit mortality (see sections 4.7 – 4.10), all of which were converted to a binary response coded for presence/absence of an adverse effect.

4.6.2 Effects of Deposited Sediment

There were 40 studies from 39 articles that investigated the effect of DSC on any adverse effect at all life-history stages of 102 coral species from 51 genera in 3 oceans (Table A-1).

Binary Meta-Analysis: For every 10-fold increase in DSC, the odds of an adverse effect increase by 3.4 times (95% CI 2.2, 5.5; GLMM $z = 5.168$, $p < 0.0001$), while holding exposure duration constant and accounting for variability among studies and species. For every 10-fold increase in exposure duration of deposited sediment, the odds of an adverse effect increase by 1.05 times (95% CI 1.03, 1.07; GLMM $z = 4.559$, $p < 0.0001$), while holding exposure concentration constant and accounting for variability among studies and species.

4.6.3 Effects of Suspended Sediment

There were 37 studies from 20 articles that investigated the effect of SSC on any adverse effect at all life-history stages of 26 coral species from 18 genera in 3 oceans (Table A-2).

Binary Meta-Analysis: For every 10-fold increase in SSC, the odds of experiencing an adverse effect increase by 7.4 times (95% CI 3.2, 17.0; GLMM $z = 4.689$, $p < 0.0001$), while holding constant exposure duration and the interaction between concentration and duration, and while accounting for variability among studies and species. For every 10-fold increase in exposure duration of suspended sediment, the odds of experiencing an adverse effect increase by 1.1 times (95% CI 1.0, 1.2; GLMM $z = 2.539$, $p = 0.011$), also while holding constant SSC and the interaction between concentration and duration, and while accounting for variability among studies and species.

4.7 Coral Gametes: FERTILIZATION

4.7.1 Biological Mechanisms of Effect

Many possible cause-effect pathways may link early life-history stages of corals with sediment stress, yet these remain largely untested (Jones et al. 2015). In particular, sediments may negatively affect gamete viability or obstruct egg–sperm contact (Humphrey et al. 2008, Ricardo et al. 2015, Jones et al. 2015), leading to reduced fertilization success, thereby reducing the chance of successful recruitment, population maintenance, and recovery. Ricardo et al. (2015) revealed that fine, siliciclastic sediments cause sediment–sperm flocs, resulting in fewer available sperm to fertilize buoyant eggs. The biogeochemical mechanism by which coral sperm adhere and are stripped from the water surface in sinking flocs remains unclear.

For the purposes of this review, '*fertilization success*' is defined as successful fertilization of an egg by sperm. Fertilization is usually verified by the presence of a zygote that has begun cell cleavage within several hours of gamete-mixing and exposure to sediment. This response was most commonly reported as percent of eggs successfully fertilized after a specified time, out of those exposed to coral sperm. As described in previous sections, we converted this response into an effect size (Hedges' *d*, standardized mean difference) and into a binary response coded for presence/absence of an adverse effect.

4.7.2 Effects of Deposited Sediment

There were no studies that investigated the effect of deposited sediment on fertilization success of coral gametes.

4.7.3 Effects of Suspended Sediment

There were 10 studies from 6 articles that investigated the effect of SSC on fertilization success of gametes from 4 coral species in 2 genera: *Acropora digitifera*, *A. millepora*, *A. tenuis*, and *Pectina lactusa*, in the Indian and Pacific Oceans (Table A-2). Exposure durations were brief and relatively standardized across studies, so this factor was not considered in the meta-analyses or determination of thresholds.

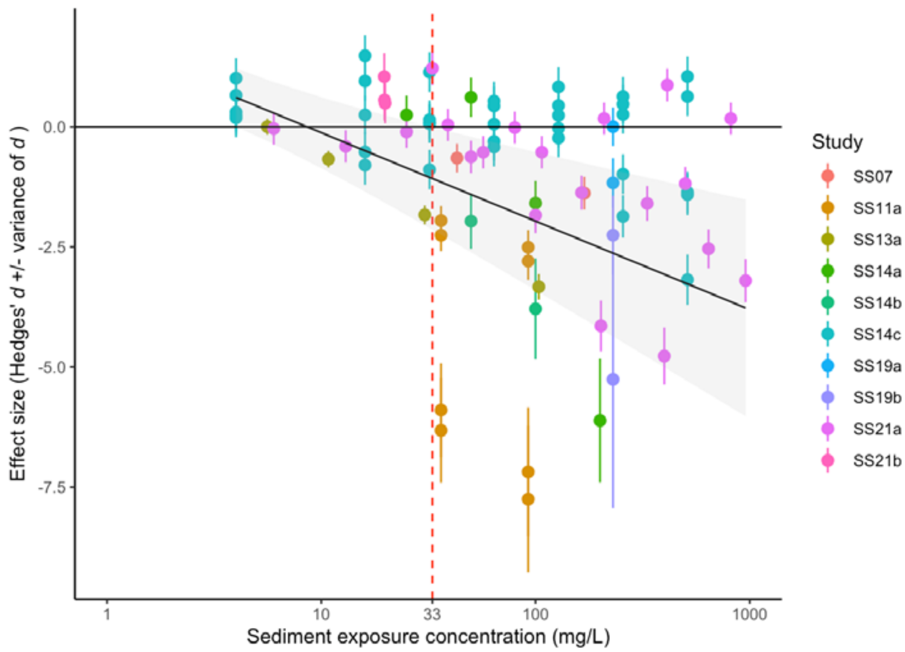

Fig. 11. Effect size for fertilization success data without outlier, by study, with the best-fit model's predictions (mean is solid, black line; 95% CI is shaded in gray) and the dose-response threshold value indicated on the x-axis, below the red, dashed line (where 95% CI no longer overlaps with zero).

Dose-Response Meta-Analysis: For every 10-fold increase in SSC, the standardized mean difference between treatment and control conditions declined by 1.9 (95% CI -2.8, -1.0; DRMA $z = -4.125$, $p < 0.0001$), after accounting for variability by article and comparison (Table 7; Fig. 10). The results were qualitatively and quantitatively similar regardless of the inclusion of an outlier. However, the best-fit model's I^2 statistic was 82%, indicating considerable residual heterogeneity unaccounted for by the model (Table 7), which could be the result of taxonomic, geographic, and/or mineralogical differences among (and within) studies.

4.8 *Coral Larvae: LARVAL MORTALITY*

4.8.1 Biological Mechanisms of Effect

Suspended sediment may reduce larval survival through decreased light availability and intensity (Rogers 1990) and physical abrasion (Gilmour 1999). Suspended sediment increases light attenuation, decreasing light availability in the water column. Planktonic coral larvae feed and receive translocated metabolites from their zooxanthellae (Richmond 1982). Decreased photosynthetic efficiency of larval symbionts from low light levels for extended periods of time may lead to larval mortality from starvation. There is evidence that mucus secretion and cilia beating protects planktonic coral larvae from suspended sediment after 60 hours of exposure (Ricardo et al. 2016).

'*Larval survival*' is measured as percent of surviving larvae after exposure to sediment in the laboratory. As described in previous sections, we converted this response to an effect size (Hedges' *d*, standardized mean difference), and into a binary response coded for presence/absence of significantly reduced larval survival.

4.8.2 Effects of Deposited Sediment

There were no studies that investigated the effect of deposited sediment on the mortality of pre-settlement, coral larvae.

4.8.3 Effects of Suspended Sediment

There were 7 studies from 4 articles that investigated the effect of SSC on the mortality of pre-settlement, larvae from 5 coral species in 2 genera: *Acropora digitifera*, *A. millepora*, *A. tenuis*, *Pocillopora acuta*, and *P. damicornis*, all in the Pacific Ocean (Table A-2). Exposure durations were brief and relatively standardized across studies, so this factor was not considered in the meta-analyses or determination of thresholds.

Dose-Response Meta-Analysis: There is no significant relationship between SSC and the Hedges' *d* effect size for larval survival (DRMA z = -1.443, p = 0.149). The best-fit model's I^2 statistic was 73%, indicating substantial residual heterogeneity unaccounted for by the model (Table 7), which could be the result of taxonomic, geographic, and/or mineralogical differences among (and within) studies.

4.9 *Coral Larvae: SETTLEMENT*

4.9.1 Biological Mechanisms of Effect

Increased light attenuation due to suspended sediment may decrease larval settlement because light quality and quantity are factors in site selection for coral larvae. Coral larvae may preferentially settle on the top of surfaces in low light levels (Birkeland et al. 1981). Settling on exposed upper surfaces increases the risk of abrasion and burial of corals by suspended and deposited sediment, which could lead to low recruit survival. Larvae avoid abrasion and smothering in the presence of sediment when they settle on downward facing surfaces (Babcock and Davies 1991). Larvae that settle in highly turbid areas that are less suitable for survival may undergo reversed metamorphosis and revert back to a swimming larva (Te 1992).

Sediment cover on the benthos can prevent larvae from sensing chemical or textural cues that induce settlement (Ricardo et al. 2017, Richmond et al. 2018), including altered bacterial cues (Goh and Lee 2008). Decreased coral settlement on sediment-covered surfaces has been previously observed for *Pocillopora damicornis* (Hodgson 1990a), *Acropora digitifera* (Gilmour 1999), and *Acropora millepora* (Ricardo et al. 2017).

For the purposes of this review, '*larval settlement*' is defined as attachment to a surface and metamorphosis. We focus on attachment to vertically facing surfaces, where exposure to sediment is concentrated. Settlement success was reported as the percent of larvae that metamorphosed after exposure to sediment in a time period specified by each study. We converted this response to an effect size (Hedges' *d*, standardized mean difference) and into a binary response as presence/absence of a significantly decreased settlement rate.

4.9.2 Effects of Deposited Sediment

There were 7 studies from 6 articles that investigated the effect of DSC on settlement rate of larvae from 2 coral species: *Acropora millepora* and *Pocillopora damicornis*, all in the Pacific Ocean (Table A-1). However, only 4 of these studies had data that were usable for the binary meta-analysis.

Dose-Response Meta-Analysis: For every 10-fold increase in DSC, the Hedges' *d* effect size for settlement rate of coral larvae declined by 2.5 (95% CI -3.6, -1.4; DRMA z = -4.494, p < 0.0001), after accounting for variability by comparison (Table 7; Fig. 11). However, the best-fit model's I^2 statistic was 84.6%, indicating considerable residual heterogeneity unaccounted for by the model (Table 7), which could be the result of taxonomic, geographic, and/or mineralogical differences among (and within) studies.

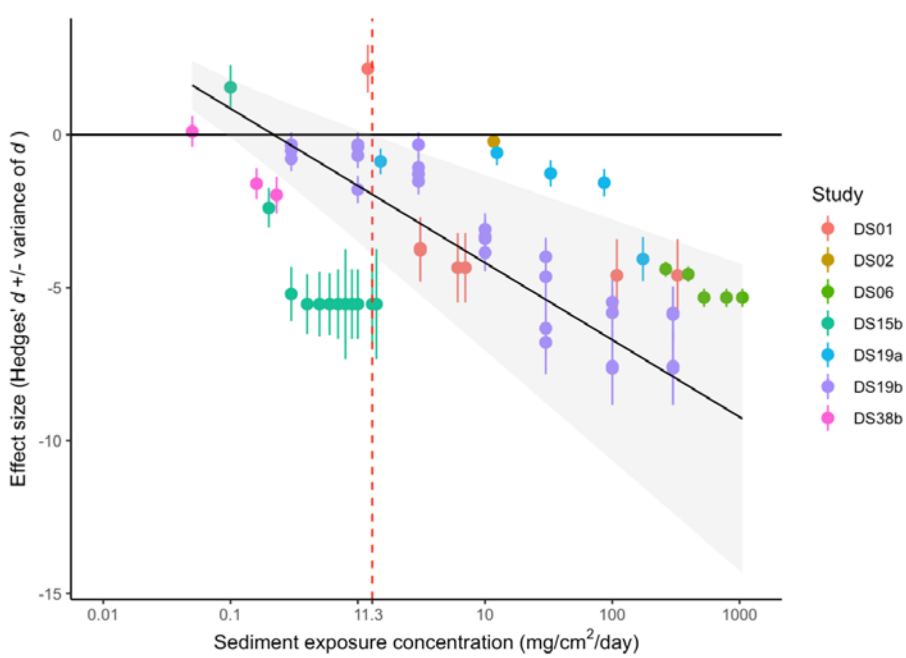

Fig. 12. Effect size for larval settlement rate data in response to deposited sediment, by study, with the best-fit model's predictions (mean is solid, black line; 95% CI is shaded in gray) and the dose-response threshold value indicated on the x-axis, below the red, dashed line (where 95% CI no longer overlaps with zero).

4.9.3 Effects of Suspended Sediment

There were 7 studies from 5 articles that investigated the effect of SSC on settlement rate of larvae from 5 coral species in 4 genera (Table A-2). However, one of these studies (Rushmore 2016) only reported turbidity in terms of NTU, without converting to the more standard unit, mg/L, and was therefore excluded from meta-analyses. Also, only 5 studies from 3 articles reported data that were usable in the binary analysis, all in the Pacific Ocean using 3 species: *Acropora digitifera*, *A. tenuis*, and *Pocillopora damicornis* (Table A-2).

Dose-Response Meta-Analysis: There is no significant relationship between SSC and the Hedges' *d* effect size for settlement rate of coral larvae (DRMA $z = -0.719$, $p = 0.472$).

4.10 Coral Juveniles: RECRUIT MORTALITY

4.10.1 Biological Mechanisms of Effect

Settlement of coral larvae onto exposed, vertically facing surfaces increases the risk of abrasion and burial by suspended and deposited sediment, which may reduce their survival as juvenile recruits. Fabricius et al. (2003) found that recruits were one to two orders of magnitude more sensitive to sedimentation than adult corals. The coral polyps of recruits may be smothered by deposited sediment (Fabricius and Wolanski 2000), the accumulation of which may prevent coral tentacles from feeding and diminish light availability for photosynthesis in symbiotic algae.

'*Recruit survival*' was measured by the percent of juvenile corals that survived an exposure to sediment after some time period specified by each study. We converted this response to an effect size (Hedges' *d*, standardized mean difference) and into a binary response as presence/absence of a significantly decreased survival rate, indicative of mortality.

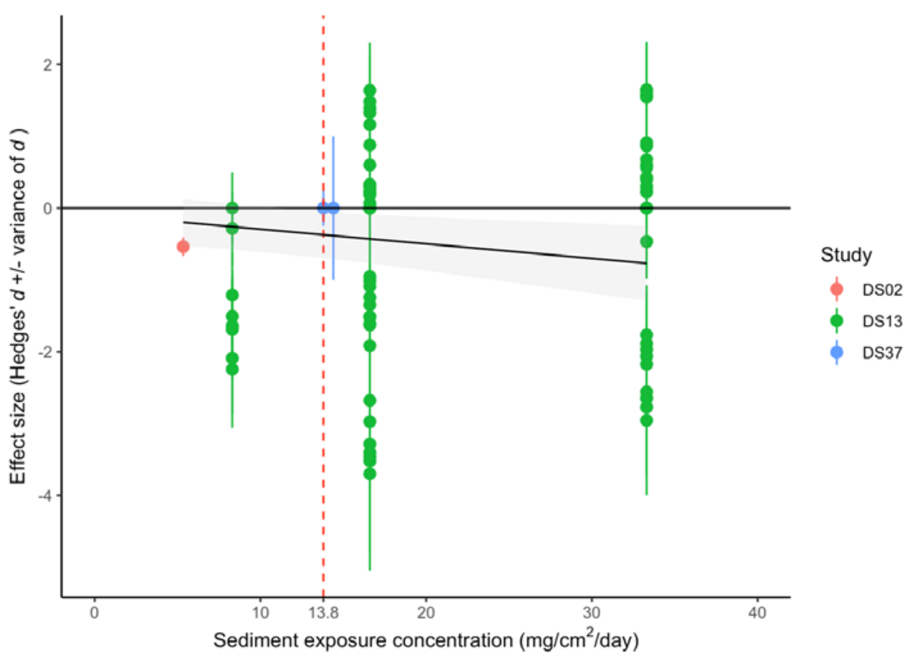

Fig. 13. Effect size for recruit survival rate data, by study, with the best-fit model's predictions (mean is solid, black line; 95% CI is shaded in gray) and the dose-response threshold value indicated on the x-axis, below the red, dashed line (where 95% CI no longer overlaps with zero).

4.10.2 Effects of Deposited Sediment

There were 3 studies from 3 articles that investigated the effect of DSC on mortality of recruits from 4 coral species from 2 genera: *Acropora hyacinthus*, *A. millepora*, *A. willisae*, and *Leptastrea purpurea*, all in the Pacific Ocean (Table A-1).

Dose-Response Meta-Analysis: For every 1-unit increase in DSC, the effect size for coral recruit survival rate declined by 0.02 (95% CI -0.04, 0.00; DRMA $z = -2.2410$, $p = 0.025$), after accounting for variability by comparison (Table 7; Fig. 12). The best-fit model's I^2 statistic was 47.1%, indicating only moderate residual heterogeneity unaccounted for by the model (Table 7).

4.10.3 Effects of Suspended Sediment

There were 2 studies from 2 articles that investigated the effect of SSC on mortality of recruits from 3 coral species from 2 genera: *Acropora millepora*, *A. tenuis*, and *Pocillopora acuta*, all in the Pacific Ocean (Table A-2). However, there were not sufficient data between these 2 studies to conduct a DRMA.

4.11 Coral Adults: PHOTOSYNTHESIS/RESPIRATION RATIO

4.11.1 Biological Mechanisms of Effect

The ratio of production to respiration (P/R) is used as an indicator of coral energy budgets. A P/R ratio below 1 indicates more energy is being used than produced. P/R ratios may fluctuate throughout the day, but a low P/R for an extended period of time means corals are using energy reserves. The P/R ratio may decrease if gross photosynthesis decreases due to low light availability in turbid water, or increased respiration rates as a result of increased metabolic activity in response to suspended sediment exposure (Riegl and Branch 1995, Telesnicki and Goldberg 1995). A decline in productivity can lead to starvation of the coral (Riegl and Branch 1995). Abdel-Salam and Porter (1988) observed decreased gross photosynthesis and increased respiration in corals smothered by sediment, leading to decreased P/R ratios.

As described in previous sections, we converted P/R ratio to an effect size (Hedges' *d*, standardized mean difference) and into a binary response as presence/absence of a significantly reduced P/R ratio.

4.11.2 Effects of Deposited Sediment

There were 5 studies from 5 articles that investigated the effect of DSC on P/R ratios among adults of 16 coral species from 15 genera in the Indian and Atlantic Oceans (Table A-1).

Dose-Response Meta-Analysis: There is no significant relationship between DSC and the Hedges' *d* effect size for P/R ratio of adult corals (DRMA $z = 1.711$, $p = 0.087$).

4.11.3 Effects of Suspended Sediment

There were 3 studies from 3 articles that investigated the effect of SSC on P/R ratios among adults of 4 coral species (Table A-2). However, there were insufficient data from these studies to conduct a DRMA, despite the inclusion of these data in the binary meta-analyses for '*any adverse effect*' of coral adults and of all coral life-history stages.

4.12 Coral Adults: PHOTOSYNTHETIC EFFICIENCY

4.12.1 Biological Mechanisms of Effect

Pulse Amplitude Modulation (PAM) Fluorometry is often used to measure the photosynthetic efficiency of Photosystem II of coral endosymbiotic zooxanthellae. Since corals rely on symbionts for up to 90% of their energy (Muscatine 1990), a decrease in their photosynthetic efficiency is used as an indicator of decreased energy availability for corals. Measurements in the literature are most often "quantum yield" (F_v/F_m), a decrease in which is believed to be an early sign of coral bleaching (Warner et al. 1999) and is often used as an indicator of health of the coral symbiont, and thus of the host coral. Declines in photosynthetic efficiency may result from physical damage of coral tissue and its symbionts due to shearing in turbid conditions, or from deposited sediment on the coral. Philipp and Fabricius (2003) observed decreases in quantum yield in corals exposed to sediment, but only in areas that accumulated sediment on the tissue. Symbionts can often recover, but recovery depends on the duration and concentration of sediment exposure (Philipp and Fabricius 2003).

In the studies included in this review, PAM data were most often provided as F_v/F_m. These data were converted to effect size (Hedges' *d*, standardized mean difference) and a binary response of presence/absence of decreased photosynthetic efficiency in terms of F_v/F_m.

4.12.2 Effects of Deposited Sediment

There were 9 studies from 9 articles that investigated the effect of DSC on the photosynthetic efficiency among adults of 20 species from 12 genera in 3 oceans (Table A-1).

Dose-Response Meta-Analysis: For every 10-fold increase in DSC, the Hedges' *d* effect size for photosynthetic efficiency of adult corals declines by 1.0 (95% CI -1.6, -0.4; DRMA z = -2.779, p = 0.005) after accounting for variability by study and comparison (Table 7; Fig. 13). The best-fit model's I^2 statistic was 77%, indicating considerable residual heterogeneity unaccounted for by the model (Table 7), which could be the result of taxonomic, geographic, and/or mineralogical differences among (and within) studies.

4.12.3 Effects of Suspended Sediment

There were 6 studies from 5 articles that investigated the effect of SSC on the photosynthetic efficiency among adults of 8 coral species from 6 genera in the Indian and Pacific Oceans (Table A-2).

Dose-Response Meta-Analysis: There is no significant relationship between exposure to suspended sediment and the Hedges' *d* effect size for photosynthetic efficiency of adult corals (DRMA $z = 1.738$, $p = 0.083$).

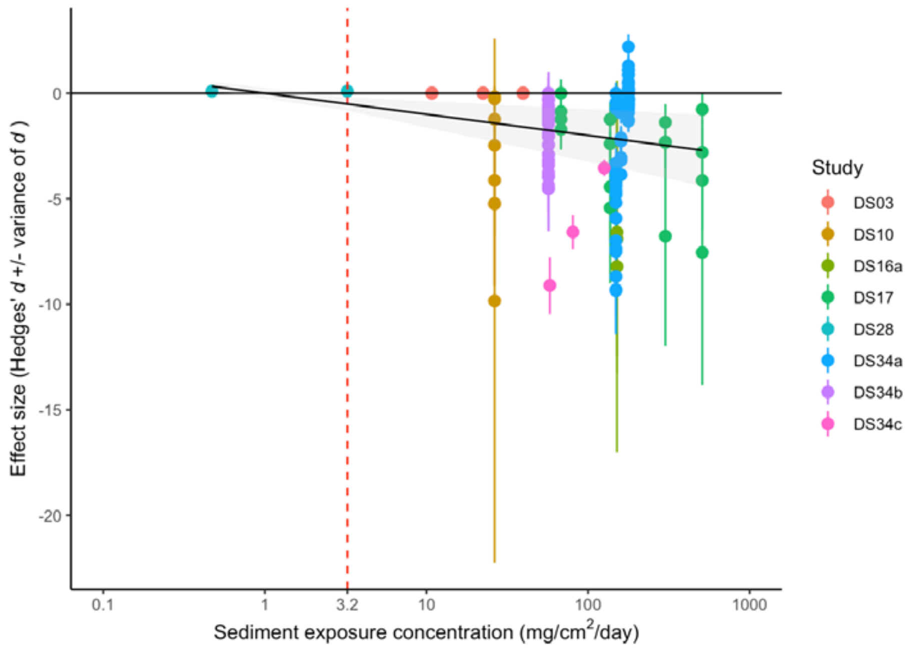

Fig. 14. Effect size for photosynthetic efficiency (F_v/F_m) data in response to deposited sediment, by study, with the best-fit model's predictions (mean is solid, black line; 95% CI is shaded in gray) and the dose-response threshold value indicated on the x-axis, below the red, dashed line (where 95% CI no longer overlaps with zero).

4.13 *Coral Adults: BLEACHING*

4.13.1 Biological Mechanisms of Effect

Large-scale coral bleaching is most strongly related to increased temperatures and irradiance levels (Jones et al. 1998, Jones and Hoegh-Guldberg 2001), but there is evidence of sediment-induced bleaching (Rogers 1979, 1983, Wesseling et al. 1999, Philipp and Fabricius 2003, Fabricius 2005, Vargas-Angel et al. 2006, Stewart et al. 2006, Piniak 2007). Deposited and suspended sediment often results in a reduced energy state for the coral due to light attenuation and the shift in resources to sediment removal (Anthony et al. 2007, Flores et al. 2012). This reduced energy state can leave corals sensitive to bleaching and may induce symbiont expulsion after prolonged sediment exposure (Bessell-Browne et al. 2017c). Bleaching is often a precursor to tissue mortality due to the accompanying stressors of deposited and suspended sediments (i.e., starvation, hypoxia, abrasion, microbially mediated tissue damage, and tissue irritation) (Wesseling et al. 1999, Philipp and Fabricius 2003, Vargas-Angel et al. 2006, Hodel 2007). However, there is some evidence that high turbidity can lead to lower susceptibility of bleaching due to shadowing when temperature is a covariate (Te 2001, Anthony et al. 2007).

In the studies included in this review, bleaching was not reported in a standardized manner. It was quantified as percent tissue experiencing total loss of pigment, as level of tissue paling, as number/density of zooxanthellae, and as number/density of chlorophyll-a. Because of these inconsistencies, we were unable to convert bleaching to an effect size for DRMA. However, we did convert these various measurements to a binary response for presence/absence of tissue bleaching.

4.13.2 Effects of Deposited Sediment

There were 20 studies from 20 articles that investigated the effect of DSC on bleaching among adults of 52 coral species from 32 genera in 3 oceans (Table A-1).

4.13.3 Effects of Suspended Sediment

There were 8 studies from 7 articles that investigated the effect of SSC on bleaching among adults of 10 coral species in 6 genera in the Atlantic and Pacific Oceans (Table A-2).

4.14 Coral Adults: GROWTH

4.14.1 Biological Mechanisms of Effect

The biological mechanisms driving the growth responses in corals are related to energy allocation and availability (Anthony and Fabricius 2000). High levels of suspended sediment result in light attenuation forcing corals to compensate via increased pigmentation or symbiont densities or shifting nutrient acquisition to more heterotrophic dependence (Anthony and Fabricius 2000). Colonies that are unable to acclimate may respond similarly to those in shaded conditions, resulting in much lower skeletal growth rates and thinner tissues due to decreased energy investment in growth and accretion (Anthony and Hoegh-Guldberg 2003). Increased turbidity and deposited sediment can also result in irritation and abrasion of coral tissue, especially if paired with wave action. This, too, may result in an energy budget with more resources put towards survival than growth. Deposited sediments also affect energy expenditures and accumulations due to disruptions in feeding mechanisms (e.g., production of mucus cords) and may shift energy spending towards self-cleaning through increased tentacle movement and mucus production (Rogers 1990, Riegl and Branch 1995, Rushmore 2016, Humanes et al. 2017a). Generally, growth rates are negatively affected by both suspended and deposited sediment, but the magnitude of the decrease is dependent on other factors or life-history strategies (Anthony and Fabricius 2000), including coral growth form, species, level of heterotrophic dependency, and sediment composition (Flores et al. 2012, Jones et al. 2016, Humanes et al. 2017a). Interestingly, the differences in response may ultimately lead to selection towards coral communities composed of branching morphologies in high sedimentation environments.

In the studies included in this review, growth rate was measured in many ways, including tissue and/or skeletal linear extension and change in weight over a specified time period. We standardized these measurements by calculating percent growth of corals in treatment vs. control conditions, then converted these to effect size (Hedges' *d*, standardized mean difference) and a binary response of presence/absence of a significantly decreased growth rate.

4.14.2 Effects of Deposited Sediment

There were 10 studies from 10 articles that investigated the effect of DSC on growth among adults of 10 coral species from 7 genera of the Atlantic and Pacific Oceans (Table A-1).

Dose-Response Meta-Analysis: There is no significant relationship between DSC and the Hedges' *d* effect size for adult coral growth rate (DRMA $z = -1.791$, $p = 0.073$), after accounting for variability by comparison (Table 7).

4.14.3 Effects of Suspended Sediment

There were 7 studies from 5 articles that investigated the effect of SSC on growth among adults of 12 coral species in 12 genera in the Atlantic and Pacific Oceans (Table A-2). However, DRMA was not done because a standardized effect size could not be reliably calculated across these studies, which had incompatible methods for quantifying growth.

4.15 Coral Adults: PARTIAL MORTALITY

4.15.1 Biological Mechanisms of Effect

The mechanisms leading to partial tissue mortality of adult corals are the same as described in section 4.3.1, above. To discern between relatively small and large amounts of tissue loss, we define '*small necroses*' as those affecting <50% of the coral tissue area. '*Large necroses*' affect ≥50% and less than 100% of coral tissue area. These were converted to a binary response coded for presence/absence of either small or large necroses, as previously described.

4.15.2 Effects of Deposited Sediment

There were 21 studies from 20 articles that investigated the effect of DSC on small tissue necroses among adults of 76 coral species from 39 genera in 3 oceans (Table A-1). There were 17 studies from 17 articles that investigated the effect of DSC on large tissue necroses among adults of 75 coral species from 39 genera, also in 3 oceans (Table A-1).

Dose-Response Meta-Analysis: There is no significant relationship between DSC and the Hedges' *d* effect size for partial mortality rate (DRMA $z = 0.778$, $p = 0.437$).

4.15.3 Effects of Suspended Sediment

There were 4 studies from 4 articles that investigated the effect of SSC on partial mortality among adults of 8 coral species in 6 genera in the Indian and Pacific Oceans (Table A-2). However, DRMA was not successful at modeling the relationship between deposited sediment and the odds of partial mortality due to extreme heterogeneity in the dataset.

4.16 Coral Adults: TOTAL COLONY MORTALITY

4.16.1 Biological Mechanisms of Effect

The mechanisms leading to total colony mortality of adult corals are the same as described in section 4.3.1, above. '*Total mortality*' is defined as 100% loss of live coral tissue area of a replicate. These were often reported as number/percent of coral replicates that died, which we converted to a binary response coded for presence/absence total mortality, as previously described.

4.16.2 Effects of Deposited Sediment

There were 24 studies from 23 articles that investigated the effect of DSC on total colony mortality among adults of 84 coral species from 46 genera in 3 oceans (Table A-1). However, DRMA was not successful at modeling the relationship between deposited sediment and the odds of total colony mortality due to extreme heterogeneity in the dataset.

4.16.3 Effects of Suspended Sediment

There were 8 studies from 6 articles that investigated the effect of SSC on total colony mortality among adults of 17 coral species in 14 genera in 3 oceans (Table A-2).

Dose-Response Meta-Analysis: There is no significant relationship between SSC and the log risk ratio of total colony mortality (DRMA $z = 0.575$, $p = 0.566$).

5 GAP ANALYSIS

5.1 Limitations

The results and thresholds that we present should be interpreted within the context of the studies that were included as part of this systematic review and meta-analysis. In particular, there are limitations inherent to the design and reporting of experiments. There are also research gaps brought to light by the interpretation of certain meta-analytical models. We discuss these limitations and gaps below, which represent opportunities to improve future work.

5.1.1 Limits of Study Design

Scope of Inference: We chose to focus on manipulative experiments so that we could directly ascribe the adverse effects experienced by corals to sediment exposure and not to other, confounding variables like nutrient-enrichment, contamination, etc. Most manipulative experiments took place in the lab where sediment exposure could be precisely measured instead of *in situ*, where sedimentation and resuspension regularly occur. Therefore, the thresholds for sediment exposure described herein may not match apparent thresholds identified in the field or in individual experiments that focus on a limited set of taxa.

The thresholds we identify are likely to be less conservative than those experienced by corals on reefs, which face multiple stressors that may cause adverse effects and diminish corals' resilience to human-caused threats. On the other hand, the thresholds we identify are more conservative than the vast majority of species- and region-specific thresholds. In fact, this highlights the utility of our synthetic approach: **in the absence of more specific information, we should adopt the most conservative threshold that uses the best available information to protect even the most vulnerable corals from stressful conditions**.

This is especially true in the Pacific Island Region (PIR) under U.S. jurisdiction where relatively few studies included in our meta-analyses took place (7 articles from Hawai'i: Hodgson 1990b, Te 2001, Piniak 2007, Piniak and Brown 2008, Jokiel et al. 2014, Perez III et al. 2014, Shore-Maggio et al. 2018; and 3 from Guam: Te 1992, HDR EOC and CSA Ocean Services 2014, Moeller et al. 2017), thus **necessitating a global review of the effects of sediment on corals across the tropical waters of the Atlantic, Indian, and Pacific Oceans**.

Coral Fragmentation: One of the original goals of this systematic review and meta-analysis was to explore how coral morphology contributes to the relative abilities of corals to cope with sediment stress. However, one aspect of experimental design – fragmentation – complicated this kind of synthesis. Experiments with corals, whether in the field or lab, often use fragments or nubbins as their experimental units so that samples are well replicated and reasonably uniform in size/shape. While fragmentation is necessary in most experimental frameworks, one consequence is that fragments often have different shapes or gross morphologies than the parent colony from which they were taken. This is especially true for massive and plating corals, the adults of which have gently sloping or flattened surfaces, respectively, which catch and entrain sediment rain. Coral fragments of massive/plating species are much smaller than their parent colony, such that sediment rain may be more easily removed, either through water flow or mucus sloughing. These kinds of differences between coral fragments and whole colonies prevented us from gaining a more mechanistic understanding of how sediment affects corals of differing morphologies. **Future studies interested in this question should account for different sizes and growth forms of corals, both within and across species**.

Disentangling Co-Stressors: Deposited and suspended sediment stressors almost always co-occur but are hypothesized to affect corals by different biological mechanisms. Unfortunately, however, it is logistically difficult to isolate the effects of these two stressors, even in the lab. In fact, no study included in our meta-analyses tested the effects of these stressors both separately and together, and only one experimental study measured total suspended solids (mg/L), turbidity (NTU), light attenuation (relative %), and deposition rate (mg/cm^2/d) during the course of their experiment (Flores et al. 2012). Despite the difficulty of separating these stressors in practice, we separated them analytically based on the unit of measurement that was reported in the text: mg/cm^2/d was indicative of deposited sediment only, while mg/L was indicative of suspended sediment only. **We encourage that future studies be designed to disentangle the effects of deposited and suspended sediment acting separately and in concert**.

5.1.2 Non-uniformity of Study Reporting

Complex Coral Responses: Our systematic review and meta-analyses describe many different responses of corals to sediment exposure across their life-history and inclusive of both physiological and lethal changes. However, many more articles exist that describe the effect of sediment on coral responses that were inadequately replicated or reported across studies. For instance, bleaching of coral tissue was a common response, but there was little uniformity in how it was reported. Proxies for bleaching included the density of zooxanthellae, the density of chlorophyll-a, the proportion of tissue without zooxanthellae, and indices of tissue paling that were specific to certain regions/species. When possible, we recorded the presence/absence of any bleached tissue as a binary response to be considered in our assignment of NOAELs, LOAELs, and probability of corals experiencing an adverse effect. Due to the non-uniformities in reporting, however, we could not standardize the differing bleaching responses to investigate the relationship between sediment exposure and the magnitude of bleaching.

Other less commonly reported responses, like gene expression, were found in too few studies to synthesize, especially considering the ongoing methodological developments in the field. **When possible, scientists interested in the effect of sediment on complex coral responses (like bleaching or gene expression) should report some kind of standardized metric that is easily repeatable across species and studies.** These metrics will depend on cooperation among scientists in the relevant field, but their creation will prove important in our ability to synthesize evidence across regions, taxa, and scientific labs with differing protocols.

Quantifying Sediment: The specifications of sediment exposure are also often reported inconsistently across studies. Most commonly, the concentration of deposited sediment is reported as $mg/cm^2/d$ in terms of how much sediment was applied within the area where coral replicates were housed. Less than a third of studies attempted to measure how much sediment came in contact with coral tissue following sediment application, as opposed to remaining in suspension or being swept away by ambient water flow. While this kind of ground-truthing can be logistically difficult, even in a relatively controlled laboratory setting, its omission from most study designs complicates comparison across studies in unpredictable ways (i.e., some studies may over- or under-estimate deposition). Because of this complication, we took reported dosages of deposited sediment at face value, as best estimates of exposure conditions.

In the case of suspended sediment and turbidity, mg/L and NTU were the most common units of measurement, respectively. Unfortunately, most studies only reported one of these units and there is no linear relationship between mg/L and NTU. This makes it very difficult and potentially misleading to convert from one unit to the other. Therefore, our review and meta-analysis use the results of studies that reported mg/L, and we exclude studies that reported only NTU. We did not do a separate meta-analysis of turbidity (NTU) thresholds because it was reported much less frequently. **We recommend that future studies report both mg/L and NTU measurements, whenever possible, so that thresholds for suspended sediment and turbidity can be disaggregated.**

Many studies tended not to report much detail concerning the sediment they used in their experiments. There is evidence that corals may be more resilient to stress from coarser, calcareous sediment from marine sources (e.g., "sand") than from finer, terrigenous sediment from land-based sources (e.g., "mud") (Weber et al. 2006). Unfortunately, however, too few articles consistently reported sediment type or comparisons among sediment types, thus limiting our ability to synthesize trends across studies. Therefore, **we recommend that all future studies attempt to quantify (with means and error estimates, when appropriate) sediment dosage, composition, grain size, and other geochemical properties.**

5.1.3 Interpretation of Statistical Model Results

Sources of Heterogeneity: Great effort was taken to include like-studies and account for potential effect modifiers and other reasons for heterogeneity across studies (see section 3.5). However, ecological meta-analyses can be fraught with often confounding sources of variability that are either too difficult or numerous to include in the meta-analytical model. In our logistic meta-regression models, the majority of variability, between 70 and 85% (R^2 values in Table 3 and Table 4), was explained by the combination of fixed and random effects. However, the fixed effects of concentration and duration of sediment exposure accounted for only 5 to 34% of this explained variability (R^2 values in Table 3 and Table 4), indicating that the random effects of species and study were the most important in determining the probability of a coral experiencing an adverse effect.

A study species is often confounded with geography and morphology. Most studies are confounded with sediment composition and are not strictly repeatable in the sense that other experimental conditions are. Therefore, **the probabilities we report from our logistic meta-regressions should be considered as starting points from which data from future studies may clarify and refine the relative roles of sediment exposure vs. experimental context (fixed vs. random effects in a model framework) in shaping corals' response**.

Gap in Tested Exposure Levels: Sometimes the results of analyses that use binary and continuous data are different, challenging our interpretation of model results. For instance, when considering the effects of deposited sediment on photosynthetic efficiency (i.e., maximum quantum yield, measured as F_v/F_m), the physiological response with the most available data, we find that the NOAEL and LOAEL are 25 mg/cm^2/d (Table 3) while the dose-response threshold is 3.2 mg/cm^2/d (Fig. 13). *Why is it that the dose-response threshold would be so much lower than the lowest reported adverse effect in the literature?* In this case, it is likely because the vast majority of studies focus on exposure concentrations greater than 25 mg/cm^2/d, with adverse effects occurring even at the lower end of tested concentrations. While the dose-response threshold of 3.2 mg/cm^2/d is relatively low, it is the result of a meta-regression of effect size by concentration that provides strong evidence that the threshold is outside of the normal range of exposure concentrations. This difference **highlights a major gap in our understanding, and the specific need for more studies to be done at exposure levels below 25 mg/cm^2/d.**

5.2 Recommendations

Opportunities to improve future experiments by addressing each of the limitations of this systematic review and meta-analysis have been bolded in the above section (5.1). Based on apparent gaps in our understanding and approach-to-date, **we make four key recommendations for those interested in defining critical threshold values for sediment on coral reefs**:

1) Pair experiments in the lab with those in nearby coastal watersheds to validate estimated thresholds in relevant environmental contexts (i.e., location, species, sediment type, etc.);
2) Target a range of experimental concentrations, between 0.5 and 50 $mg/cm^2/d$ or mg/L, which should induce physiological and lethal effects in susceptible coral taxa;
3) Standardize reporting of coral responses and stressor dosage/properties, always providing both deposited and suspended sediment levels, including turbidity; and
4) Test for potential synergisms between and among stressors that often co-occur, including deposited and suspended sediment, as well as nutrients, contamination, low salinity, etc.

Furthermore, while many studies have and will continue to investigate the effects of sediment stress on corals around the world, we recommend protocols for future work within the PIR under U.S. jurisdiction, where more specific information is needed to make the most defensible regulatory decisions.

5.2.1 Proposed Study Design to Address Research Gaps

Future studies should address key gaps that exist in our understanding of how corals respond to the independent and additive/synergistic effects of deposited and suspended sediment produced by dredging, storm event runoff, and beach nourishment. These may include both lab- and field-based studies. **We encourage the development of a network of researchers and regulators to organize parallel experiments at locations across the PIR, especially those most susceptible to sediment-producing events**, including American Samoa, Guam, the main Hawaiian Islands, and the Northern Mariana Islands. This network would be critical to test whether there are key regional differences in stressor responses that must be considered in the application of essential fish habitat (EFH) guidelines.

Lab Experiment: We recommend the use of manipulative experiments to address synergistic effects between deposited and suspended sediment/turbidity, and where possible, among other common co-stressors including light attenuation, nutrient-enrichment, contamination, decreased salinity, and increased temperature or dissolved CO_2. Here we will describe the design of an experiment aimed to disentangle the effects of deposited and suspended sediment/turbidity only.

Sediment type, exposure levels, taxa, and coral responses that are most relevant at a particular site will be informed by field monitoring and/or associated field experiments. While the set of species chosen for each PIR location may vary, we recommend using populations that are most vulnerable to future disturbances, especially coral colonies found adjacent to the impact zone of a particular stressor. As part of this location-specific set of species, we suggest the use of *Porites lobata* at all locations across the PIR to help account for differences within and among species and geographic locations. *P. lobata* has a "massive" morphology that makes it relatively susceptible to sediment rain, and has been well represented in prior studies, thus enabling comparison with other Pacific regions. Given the general interest in defining sediment exposure thresholds, we also recommend sediment levels between 0.5 and 50 mg/cm^2/d or mg/L.

Researchers may build a mesocosm array in which coral colonies will be placed in aquaria exposed to different combinations of deposited and suspended sediment (stressor-1 and -2, respectively). Stressor interactions will be assessed by monitoring corals under four treatments with all other conditions held at ambient levels: no stressor (control), stressor-1 only, stressor-2 only, and both stressors. 'Stressor-1 only' conditions could be achieved with relatively coarse sediment that sinks and does not remain in suspension for longer than 10 minutes. 'Stressor-2 only' conditions could be achieved with relatively fine sediment that remains in suspension for hours, coupled with a transparent barrier between the coral and the water column to prevent deposition on the coral surface. 'Both stressors' conditions would have no transparent barrier and combine coarse and fine sediment types. In all treatments, deposited sediment and total suspended solids would be measured intermittently, while turbidity and light levels would be measured in real-time.

We encourage the leverage of this kind of experimental setup to quantify multiple responses of control and sediment-exposed corals over the typical duration of a dredging event. Based on the results of our systematic review, candidate responses that could be measured daily are presence of mucus production and sloughing, photosynthetic efficiency (F_v/F_m with PAM), and estimates of the percent tissue area experiencing either tissue paling (on a location- and species-specific scale), total bleaching, or necrosis. Growth in terms of either change in weight or linear extension rates could be measured on a weekly or monthly basis. These responses have been most widely used to measure the health of adult corals. We recommend the use of juvenile corals as well, to broaden our understanding of the effects of sediment on immature coral stages that have been less well represented in research-to-date.

Field Experiment: A Before-After, Control-Impact (BACI) design (Green 1979) could be used to experimentally track the effects of sediment-producing events on nearby corals. As the acronym suggests, environmental conditions (i.e., sediment deposition rate, total suspended solids, turbidity, and light attenuation) and coral health (i.e., sublethal and lethal effects) could be measured before, during, and after a sediment-producing event at a range of locations inside (impacted) and outside (control) the affected area, as done previously for dredging at other tropical Pacific locations (Kaly and Jones 1997, Adjeroud et al. 2016).

This kind of study requires cooperation among regulators, scientists, and other stakeholders, but the BACI design is arguably the gold-standard for ascribing causative, *in situ* relationships between an event and a subsequent biological response. It would also provide on-the-ground monitoring of sediment plumes created by dredging or runoff, a quantitative basis for defining and testing remediation efforts, a range of realistic sediment exposure levels, and a list of vulnerable coral species and populations to be targeted in associated lab experiments.

6 CONCLUSIONS

What are the effects of sediment on corals? While a seemingly simple question, people have been observing, studying, sharing, and arguing the finer points of it for decades, making it particularly rife for quantitative review. Critical threshold values for deposited and suspended sediment on coral reefs have been determined in many regions across the world and range between 10 and 300 $mg/cm^2/d$ or mg/L (reviewed in Erftemeijer et al. 2012b). These thresholds are often determined *in situ*, where sediment co-occurs with other potential stressors.

Using a rigorous, peer-reviewed protocol (Tuttle et al. 2020), we compiled a global dataset that spans three oceans, over 140 coral species, decades of research, and 86 field- and lab-based experiments. We found that adverse effects, including mortality, occur at deposited sediment concentrations as low 1 $mg/cm^2/d$ and suspended sediment concentrations as low as 3.2 mg/L. The lowest-observed adverse-effect levels (LOAELs) for reduced settlement rates of larvae, mortality of juveniles, and bleached or necrotic tissue of adults were all below 10 mg/L or $mg/cm^2/d$. The LOAELs for other coral responses, including reduced photosynthetic/growth rates and colony mortality of adults ranged between 20 and 40 $mg/cm^2/d$ for deposited sediment and between 10 and 100 mg/L for suspended sediment. While some of these LOAELs are consistent with previously published critical threshold values above 10, they also reflect the relative paucity of studies that focus on sediment levels below 10. Given our findings, we recommend that future studies interested in experimentally deriving critical threshold values use lower concentrations of sediment than tested in most previous studies.

In addition to sediment concentration, we also report thresholds for exposure duration. Adverse effects in response to deposited sediment occur on the order of hours to days, while those in response to suspended sediment occur on the order of days to weeks. Generally, we found only modest evidence that coral adults are less sensitive to deposited sediment than are immature stages and no evidence of a developmental change in susceptibility to suspended sediment.

Using meta-regression techniques, we estimated the probabilities of corals experiencing adverse effects at a range of exposure concentrations that spanned several orders of magnitude for both deposited and suspended sediment. These probabilities will likely prove useful for the community of regulators interested in averting further decline of coral reefs. Additional meta-regressions modeled the relationship between exposure and magnitude of coral responses. While some of these regressions point to thresholds that are similar to those derived from binary data (NOAELs and LOAELs), they mostly highlight gaps in our current understanding of the effects of sediment on a diversity of coral responses.

We make several recommendations for future work, both generally and specific to the Pacific Island Region (PIR) under U.S. jurisdiction, where data are relatively sparse. In particular, we suggest updated and standardized protocol for lab experiments to be conducted by a network of researchers and regulators across the PIR. We also recommend the use of BACI-design field experiments that would provide on-the-ground monitoring of sediment plumes created by dredging or runoff, a quantitative basis for defining and testing remediation efforts, a range of realistic sediment exposure levels, and a list of vulnerable coral species and populations to be targeted in associated lab experiments.

Future experimentation has considerable potential to define more location-specific thresholds, which may also quantify the effects of other common co-stressors. In fact, systematic reviews of the individual effects of nutrient enrichment, chemical contamination, and freshwater discharge are on-going. Uniting these reviews with those of deposited and suspended sediment may result in a culminating meta-analysis that quantifies the additive and synergistic effects of multiple local stressors on coral reefs.

7 REFERENCES

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APPENDIX

Table A-1. All articles and studies included in the meta-analysis of the effects of DEPOSITED sediment (DS) on corals. Keys to species codes and coral responses in Tables A-3 and A-4, respectively. Species codes are listed when 5 spp. or fewer are in study. Exposure duration: 'short' < 1 week, 'long' ≥ 1 week.

Study ID(s)	Article Authors and Year	Species Codes	Ocean/ Region	Study site	DSC range (mg/cm²/d)	Exposure duration	Coral responses	
							Cont.	Binary
DS40	(Abdel-Salam 1989, Chapter 3)	8 spp.	Atlantic/ Caribbean	Field	59.4	Short/ Long	R, P, P/R	MO, B
DS01	(Babcock and Davies 1991)	AMIL	Pacific/ GBR	Lab	0.5 - 325	Short	SE	-
DS02	(Babcock and Smith 2000)	AMIL	Pacific/ W. Australia	Field	0.7 - 12	Long	JS, SE	-
DS03	(Bessell-Browne et al. 2017c)	AMIL, PORI, TREN	Pacific/ GBR	Lab	0 - 40	Short	CHL, CI, MQY	AM, M, TM
DS48	(Bessell-Browne et al. 2017a)	PORI	Pacific/ GBR	Lab	0 - 20	Long	-	M
DS49	(Coffroth 1985)	PAST, PFUR	Atlantic/ Caribbean	Field	5 - 78.9	Short	-	M
DS04	(Duckworth et al. 2017)	AMIL, MCAPI, TREN, PORI	Pacific/ GBR	Lab	0.5 - 235	Short/ Long	MQY	AM, B, TM
DS37	(Fabricius et al. 2003)	AWIL	Pacific/ GBR	Lab	1 - 20.3	Short	JS	-
DS68	(Flores et al. 2012)	MAEQ, AMIL	Pacific/ GBR	Lab	0.4 - 83	Long	AM, CHL, G, MPY, TM	-
DS69	(Gil et al. 2016)	APUL, PRUS	Pacific/ French Polynesia	Lab	0.4 - 83	Long	TM,G	-
DS38	(Goh and Lee 2008)	PDAM	Pacific/ Malacca Strait	Lab	0 - 2.5	Long	SE	-
DS42	(Gowan et al. 2014)	PORI	Pacific/ French Polynesia	Field/ Lab	3.8 - 12; 17 - 23	Short/ Long	B, G	-
DS71	(HDR EOC and CSA Ocean Services 2014)	PCYC, PLUT, PRUS, PCAC	Pacific/ Marianas Islands	Lab	50 - 400	Long	TM	B, M
DS05	(Hodel 2007)	ACER	Atlantic/ Florida	Lab	0 - 200	Long	-	B, M, MO, TM
DS06	(Hodgson 1990a)	PDAM	Pacific/ S. China Sea	Lab	0 - 1053	Long	SE	-
DS07	(Hodgson 1990b)	OGLA, MVER, PLOB, PMEA	Pacific/ S. China Sea	Lab	30 - 40	Short/ Long	TM	AM, B
DS08 a, b	(Hodgson 1989, Sediment Resistance Hierarchy experiment)	36 spp., 22 spp.	Pacific/ S. China Sea	Field	0 - 40	Short/ Long	AM, TM	-
DS10	(Junjie et al. 2014)	GFAS, GSOM	Pacific/ Singapore	Lab	26	Long	NP, MQY, P/R, R	-
DS11	(Lirman et al. 2008)	PAST, SSID	Atlantic/ Florida	Lab	53	Long	G	AM
DS12	(Loiola et al. 2013)	MBRA	Atlantic/ Brazil	Lab	0 - 450	Long	MO,PE, SI, TM	AM
DS13	(Moeller et al. 2017)	LPUR, AHYA	Pacific/ Marianas	Field/ Lab	0 - 1000	Long	JS	-

Study ID(s)	Article Authors and Year	Species Codes	Ocean/ Region	Study site	DSC range (mg/cm²/d)	Exposure duration	Coral responses	
							Cont.	**Binary**
DS15	(Perez III et al. 2014)	PDAM	Pacific/ Hawai'i	Lab	0 - 1.5	Long	SE	-
DS43	(Peters and Pilson 1985)	ADAN	Atlantic/ Eastern US coast	Lab	0 - 200	Long	G, NO	AM, B, M, P/R, TM
DS16	(Philipp and Fabricius 2003)	13 spp.	Pacific/ GBR	Field/ Lab	0 - 200	Short	CHL, EQY, MPY, SY	AM, B, M, TM
DS17	(Piniak 2007)	MCAPI, PLOB	Pacific/ Hawai'i	Lab	0 - 509	Short	MPY	AM, B, TM
DS18	(Piniak and Brown 2008)	PDAM	Pacific/ Hawai'i	Field	38 - 426	Long	AM, G, TM	-
DS19	(Ricardo et al. 2017)	AMIL	Pacific/ GBR	Lab	0 - 180; 0 - 300	Short	SE	-
DS20	(Riegl and Branch 1995)	FFAV, FPEN, PDAE, GINT	Indian/ SW Indian Ocean	Lab	0 - 200	Short	M, P, R	P/R
DS21	(Rogers 1979)	ACER	Atlantic/ Caribbean	Field	0 - 200	Long	G	AM, B, TM
DS45	(Rogers 1983)	APAL, OANN, ACER, DSTR, DCLI	Atlantic/ Caribbean	Field	0 - 800	Short/ Long	-	AM, B, TM
DS23	(Selim 2007)	ATEN, SPIS, PDAM	Indian/ Red Sea	Lab	0 - 30	Short	M, SY	-
DS24	(Sheridan et al. 2014)	MPAT	Pacific/ Madagas-car	Lab	62	Short	L, ME, NO, PH, P/R	-
DS25	(Shore-Maggio et al. 2018)	MCAPI	Pacific/ Hawai'i	Lab	100	Long	AM	TM
DS26	(Sofonia 2006, Chapter 3)	TMES, MDIG	Pacific/ GBR	Lab	0 - 246	Long	CHL, G, L	AM, B
DS27	(Sofonia 2006, Chapter 4)	AFOR, MTUB, PCYC	Pacific/ GBR	Field	1 - 372	Long	B	M, MO, TM
DS28	(Sofonia and Anthony 2008)	TMES	Pacific/ GBR	Lab	0 - 12	Long	G, L, MPY	AM
DS29	(Stafford-Smith 1990, Chapter 4)	10 spp.	Pacific/ GBR	Field	0 - 400	Long	AM, B, TM	TI
DS30	(Stafford-Smith 1992)	LPHR	Pacific/ GBR	Lab	0 - 800	Short/ Long	-	AM, B, TM
DS46	(Stafford-Smith 1993)	22 spp.	Pacific/ GBR	Field	200	Short	-	AM, B
DS31	(Stafford-Smith and Ormond 1992)	42 spp.	Pacific/ GBR	Field	0 - 50	Long	-	M, MO
DS32	(Stewart et al. 2006)	AHYA, PVER	Pacific/ French Polynesia	Field/ Lab	62.5 - 125	Long	SR	AM, B
DS33	(Vargas-Angel et al. 2006)	MCAV	Atlantic/ Florida	Lab	200 - 225	Long	-	AM, B, M, MO, TM
DS34	(Weber et al. 2006)	MPEL	Pacific/ GBR	Field/ Lab	33 - 160	Short	MQY	M, MO
DS36	(Zill et al. 2017)	PORI	Pacific/ French Polynesia	Field	54.2	Long	G, SR	AM

Table A-2. All articles included in the meta-analysis of the effects of SUSPENDED sediment (SS) on corals. Keys to species codes and coral responses in Tables A-3 and A-4, respectively. Species codes are listed when 5 spp. or fewer are in study. Exposure duration: 'short' < 1 week, 'long' ≥ 1week.

Study ID(s)	Article Authors and Year	Species Codes	Ocean/ Region	Study site	SSC range (mg/L)	Exposure duration	Coral response(s)	
							Cont.	**Binary**
SS01	(Anthony 1999)	GRET, PCYL	Pacific/ GBR	Lab	0.7 - 16	Long	G	G
SS03 a, b	(Anthony and Fabricius 2000)	GRET, PCYL	Pacific/ GBR	Lab	0.68 - 30.05	Short/ Long	G, P, P/R	G, AH
SS27	(Anthony et al. 2007)	AINT	Pacific/ GBR	Lab	0.2 - 10.2	Short/ Long	AM, CHL, L	B, AM
SS04	(Bessell-Browne et al. 2017b)	AMIL, MCAP, PORT	Pacific/ GBR	Lab	1.17 - 91.69	Long	TM, AM	AM, B, TM, PE, MQY
SS05	(Browne et al. 2014)	MAMP, PSPE, PSIN	Indo-Pacific/ Malacca Strait	Lab	0.00 - 242.5	Short	P/R, PE, R, NP	P/R, CHL, PE
SS06	(Browne et al. 2015)	MAMP, PSPE, PSIN	Indo-Pacific/ Malacca Strait	Lab	1.0 - 92.4	Long	MPY, NP, R, TM, P/R	P/R, PE, TM, AM
SS28	(Dallmeyer et al. 1982)	OANN	Atlantic/ Jamaica	Lab	0 - 525	Short	R, P	B
SS07	(Erftemeijer et al. 2012a)	PLAC	Indo-Pacific/ Singapore	Lab	6 - 169	Short	FS	FS
SS08	(Flores et al. 2012)	MAEQ, AMIL	Pacific/ GBR	Lab	0 - 98.2	Long	TM, AM, PE, CHL, G	TM, AM, PE, CHL, G
SS11 a, b, c	(Gilmour 1999)	ADIG	Indian/ Coastal NW Australia	Field/ Lab	1.66 - 124.01	Short	FS, LS, LE	FS, LS, LE
SS12 a, b	(Humanes et al. 2017a)	ATEN, AMIL, PACU	Pacific/ GBR	Lab	0 - 100	Long	JS, G, PE, R, NP	PE, G, AM, P/R
SS13 a, b, c, d	(Humanes et al. 2017b)	ATEN	Pacific/ GBR	Lab	0.1 - 110.7	Short	LS, SE, FS	LS, SE, FS
SS14 a, b, c	(Humphrey et al. 2008)	AMIL	Pacific/ GBR	Lab	0 - 1024	Short	FS, MO	FS, MO
SS15	(Jokiel et al. 2014)	PCOM	Pacific/ Hawai'i	Field	3.1 - 36.8	Long	G, AM, TM, SE	-
SS16 a, b, c	(Kendall Jr. et al. 1985)	ACER	Atlantic/ Florida	Field	0 - 100	Short	CAL, PRO	HI, HY, M, TE
SS17 a, b	(Liu et al. 2015)	AMUR	Pacific/ Taiwan & Coastal China	Lab	0 - 45	Long	PE, CHL, SY	PE, B
SS19 a, b	(Ricardo et al. 2015)	ATEN, AMIL	Pacific/ GBR	Lab	0 - 705	Short	FS	FS
SS20 a, b, c, d	(Ricardo et al. 2016)	AMIL, ATEN	Pacific/ GBR	Lab	0 - 1159	Short	LS	LS
SS21 a, b	(Ricardo et al. 2018)	AMIL, ATEN	Pacific/ GBR	Lab	0 - 965	Short	FS	FS
SS22 a, b, c	(Rice 1984)	8 spp.	Atlantic/ Bahamas & Florida Keys	Lab	0 - 199	Short/ Long	G, AM	G, AM
SS24 a, b	(Te 1992)	PDAM	Pacific/ Guam	Lab	0 - 1000	Long	SR	SR
SS25	(Te 2001)	MVER	Pacific/ Hawai'i	Lab	27 - 121	Long	G, AM	P/R, G, AM, B, TM

Table A-3. Key to the coral species codes reported in Tables A-1 and A-2. These were created by taking the first letter of the genus name and the first three letters of the species name. For those codes that overlapped for multiple species, a fourth letter from the species name was added.

Genus species name	Species Code
Acanthastrea echinata	AECH
Acropora cervicornis	ACER
Acropora digitifera	ADIG
Acropora florida	AFLO
Acropora formosa	AFOR
Acropora hyacinthus	AHYA
Acropora intermedia	AINT
Acropora microphthalma	AMIC
Acropora millepora	AMIL
Acropora muricata	AMUR
Acropora palmata	APAL
Acropora pulchra	APUL
Acropora spp.	ACRO
Acropora tenuis	ATEN
Acropora willisae	AWIL
Agaricia agaricites	AAGA
Astrangia danae	ADAN
Astreopora myriophthalma	AMYR
Barabattoia amicorum	BAMI
Cladocora arbuscula	CARB
Coeloseris mayeri	CMAY
Cycloseris costulata	CCOS
Cycloseris doederleini	CDOE
Cycloseris marginata	CMAR
Cyphastrea chalcidicum	CCHA
Cyphastrea microphthalma	CMIC
Cyphastrea serailia	CSER
Diaseris distorta	DDIS
Dichocoenia stokesii	DSTO
Diploastrea heliopora	DHEL
Diploria clivosa	DCLI
Diploria strigosa	DSTR
Echinopora horrida	EHOR
Echinopora lamellosa	ELAM
Echinopora mammiformis	EMAM
Euphyllia ancora	EANC

Genus species name	Species Code
Euphyllia glabrescens	EGLA
Favia favus	FFAV
Favia pallida	FPAL
Favia speciosa	FSPE
Favia stelligera	FSTE
Favites abdita	FABD
Favites pentagona	FPEN
Fungia actiniformis	FACT
Fungia crassa	FCRA
Fungia danai	FDAN
Fungia echinata	FECH
Fungia fungites	FFUN
Fungia granulosa	FGRA
Fungia horrida	FHOR
Fungia klunzingeri	FKLU
Fungia repanda	FREP
Fungia scruposa	FSCR
Fungia scutaria	FSCU
Fungia somervillei	FSOM
Galaxea fascicularis	GFAS
Galaxea horrescens	GHOR
Galaxea spp.	GALA
Gardineroseris planulata	GPLA
Goniastrea edwardsi	GEDW
Goniastrea retiformis	GRET
Goniopora lobata	GLOB
Goniopora somaliensis	GSOM
Goniopora tenuidens	GTEN
Gyrosmilia interrupta	GINT
Heliopora coerulae	HCOE
Hydnophora microconos	HMIC
Hydnophora ridgida	HRID
Isophyllastrea rigida	IRIG
Isophyllia sinuosa	ISIN
Isopora palifera	IPAL
Leptastrea purpurea	LPUR

Genus species name	Species Code
Leptoria phrygia	LPHR
Leptoseris yabei	LYAB
Lobophyllia corymbrosa	LCOR
Lobophyllia hemprichii	LHEM
Manicina aereolata	MAER
Meandrina meandrites	MMEA
Merulina ampliata	MAMP
Merulina scabricula	MSCA
Montastraea cavernosa	MCAV
Montastraea curta	MCUR
Montipora aequituberculata	MAEQ
Montipora capitata	MCAPI
Montipora capricornis	MCAPR
Montipora corbettensis	MCOR
Montipora crassituberculata	MCRA
Montipora danae	MDAN
Montipora digitata	MDIG
Montipora florida	MFLO
Montipora foliosa	MFOL
Montipora patula	MPAT
Montipora peltiformis	MPEL
Montipora stellata	MSTE
Montipora tuberculosa	MTUB
Montipora turgescens	MTUR
Montipora verrucosa	MVER
Mussismilia braziliensis	MBRA
Mycedium elephantotus	MELE
Orbicella annularis	OANN
Oulophyllia crispa	OCRI
Oxypora glabra	OGLA
Oxypora lacera	OLAC
Pachyseris gemmae	PGEM
Pachyseris rugosa	PRUG
Pachyseris speciosa	PSPE
Pavona cactus	PCAC
Pavona decussata	PDEC
Pectinia alcicornis	PALC
Pectinia lactuca	PLAC

Genus species name	Species Code
Phyllangia americana	PAMER
Platgyra sinenis	PSIN
Platygyra daedalea	PDAE
Platygyra lamellina	PLAM
Plesiastrea versipora	PVER
Pocillopora acuta	PACU
Pocillopora damicornis	PDAM
Pocillopora elegans	PELE
Pocillopora meandrina	PMEA
Pocillopora verrucosa	PVER
Porites astreoides	PAST
Porites compressa	PCOM
Porites cyclindrica	PCYC
Porites furcata	PFUR
Porites lobata	PLOB
Porites lutea	PLUT
Porites porites	PPOR
Porites rus	PRUS
Porites sillimaniana	PSIL
Porites spp.	PORI
Psammocora contigua	PCON
Sandolitha robusta	SROB
Scolymia lacera	SLAC
Seriatopora hystrix	SHYS
Siderastrea radians	SRAD
Siderastrea siderea	SSID
Solenastrea hyades	SHYA
Stephanocoenia michelinii	SMIC
Stylophora pistillata	SPIS
Symphyllia radians	SRAD
Symphyllia recta	SREC
Trachyphyllia geoffroyi	TGEO
Turbinaria mesenterina	TMES
Turbinaria peltata	TPEL
Turbinaria reniformis	TREN

Table A-4. Key to the coral responses reported in Tables A-1 and A-2.

Coral Response	Response Code
Adult mortality / colony mortality	AM
Bleaching	B
Calcification rate	CAL
Chlorophyll density	CHL
Color index	CI
Coral cover	CC
Effective quantum yield	EQY
Fertilization success	FS
Growth rate	G
High yield	HI
Histological condition score	H
Hydrostatic inflation	HY
Infection	I
Juvenile survival / recruit survival	JS
Larval survival	LS
Lipid concentration / lipid fraction	L
Maximum photosynthetic yield	MPY
Maximum quantum yield	MQY
Melanin	ME
Mucus (sheet) production	M
Net oxygen production	NO
Net photosynthesis	NP
Phenyloxidase	PH
Photosynthetic efficiency	PE
Production	P
Production/respiration ratio	P/R
Protein production/concentration	PRO
Respiration	R
Sediment removal	SR
Settlement	SE
Shift from auto- to heterotrophy	AH
Sublethal morphology	MO
Susceptibility index	SI
Symbiont density / zooxanthellae density	SY
Tentacular activity	TE
Tissue biomass	TB
Tissue injury / tissue damage	TI
Tissue mortality / partial mortality	TM
Weight	W