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Spring, Danielle; Williams, Gareth J.

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Influence of upwelling on coral reef benthic communities: a systematic review and meta-analysis

Danielle L. Spring* and Gareth J. Williams

School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK

*Correspondence: d.spring@bangor.ac.uk

Keywords

Benthic competition– nutrient flux – temperature variation – internal waves – environmental drivers – evidence synthesis

1. Abstract

Highly competitive coral reef benthic communities are acutely sensitive to changes in environmental parameters such as temperature and nutrient concentrations. Physical oceanographic processes that induce upwelling therefore act as drivers of community structure on tropical reefs. How upwelling impacts coral communities, however, is not fully understood; upwelling may provide a natural buffer against climate impacts and could potentially enhance the efficacy of spatial management and reef conservation efforts. This study employed a systematic review to assess existing literature linking upwelling with reef community structure, and a meta-analysis to quantify upwelling impact on the percentage cover of coral reef benthic groups. We show that upwelling has context-dependant effects on the cover of hard coral and fleshy macroalgae, with effect size and direction varying with depth, region and remoteness. Fleshy macroalgae was found to increase by 110% on inhabited reefs yet decrease by 56% around one well-studied remote island in response to upwelling. Hard coral cover was not significantly impacted by upwelling on inhabited reefs but increased by 150% when direct human pressures were absent. By synthesising existing evidence, this review facilitates adaptive and nuanced reef management which considers the influence of upwelling on reef assemblages.

2. Introduction

Tropical coral reefs are dynamic socioecological systems that support the health and wellbeing of hundreds of millions of people (1). Over the past few decades, coral reefs worldwide have undergone unprecedented change driven by cross-scale human impacts (2,3). These include local drivers such as overfishing and land-based pollution, and global climate change-induced ocean warming events that trigger disease outbreaks (4), mass coral bleaching and mortality (5). While governments strive to reduce greenhouse gas emissions and slow the rate of ocean warming, local resource managers are tasked with safeguarding coral reefs and the ecosystems services they provide to humanity. These efforts are necessarily undertaken against a backdrop of environmental variability that constrains reef ecosystem structure and function (6,7) and in doing so sets a natural bound on what resource managers can achieve. They therefore require evidence-based guidance on how local environmental context might constrain, support, or hinder their conservation efforts and goals.

Reef-builders on tropical coral reefs including calcifying (scleractinian) corals and crustose coralline algae (CCA) compete for space on the reef floor with non-accreting fleshy organisms such as turf algae and larger seaweeds. The outcomes of these competitive interactions are affected by changes in environmental parameters driven by biogeochemical and physical oceanographic processes (8–10). Upwelling and the breaking of deep-water internal waves cause nutrient-rich deep water to propagate into the shallows (11). Coastal upwelling is caused by two primary mechanisms: the movement of surface waters driven by wind energy moving along or away from shore; and when an island mass blocks the trajectory of current-driven water movement, causing deeper waters to shoal (11,12). In stratified waters, internal waves can form at the interface between two water masses with different densities, in much the same way that a surface wave propagates between the boundary of seawater and the atmosphere (13). Generated by strong tidal flows interacting with rough bottom topography (14), internal waves cause ocean mixing which in turn transports deep, cooler and nutrient-rich waters towards the surface (15). Wind-driven upwelling and the propagation of internal waves are exclusive processes with different mechanisms; here, ‘upwelling’ refers to all processes driving cool pulses of deep water onto shallow coral reefs.

Upwelling can have variable effects on coral reef communities (16,17). As mixotrophic organisms, reef-building corals obtain their energy and nutritional needs through a combination of autotrophy in symbiosis with the photosynthetic microalgae found within the coral tissue, and heterotrophic feeding by the coral animal through capture of particles within the water column (18,19). This strategy of trophic plasticity underpins the success of coral reefs, supporting inherent flexibility and adaptation of corals that allows reefs to thrive under variable environmental conditions (18,20). In otherwise nutrient-poor waters, increased nutrient supply may act in favour of coral productivity and growth by providing an additional energy source to supplement autotrophic feeding (21). Upwelling does not always promote coral productivity, however; cold pulses of upwelled water can have detrimental effects on scleractinian corals (22) by reducing water temperatures below the lower limit of the coral's thermal threshold (10,23–25). In tandem with less favourable temperatures for corals, upwelling can favour algal species which are able to efficiently and opportunistically utilize the influx of biologically available nutrients brought up from deeper waters (23,26,27).

The varied responses of benthic communities to biophysical drivers may be altered or entirely reversed in areas subject to direct local human impacts (28). Where background nutrient concentrations are high due to terrestrial run-off caused by poor watershed management, or herbivorous fish populations that control algal growth are removed by intensive fishing, the somewhat predictable patterns in benthic community structure on isolated reefs are disrupted (28,29). Exactly how upwelling shapes competitive interactions of benthic groups on coral reefs is unclear, and likely dependent on the spatial and temporal variability of co-occurring environmental and anthropogenic forces. The variation in study results linking upwelling to reef community structure have produced a contradictory array of conclusions, with some studies reporting upwelling resulting in algal dominance (23,26,27) and others finding coral proliferation (29,30).

Given the concerning global trajectory of coral reefs (31), active management is necessary to secure a future for reef ecosystems. Because human intervention must happen in the context of natural environmental variability, such variability should be incorporated into adaptive management plans. By focusing conservation strategies on supporting reefs' natural resilience and integrating active human intervention with natural mitigation of reef degradation, positive outcomes for maintaining coral reefs may become more likely. This is particularly true when we consider the finite financial resources available to support conservation efforts (32). Since a warming climate poses the greatest threat to coral survivability (2,33,34), environmental phenomena that reduce temperature to within the thermal tolerance range of corals may confer resistance to coral bleaching and subsequent mortality (32). Upwelling may create local scale pockets of refugia from thermal stress and may therefore be sites best placed to focus conservation efforts (14,35). Given that patterns of upwelling are likely to change in concert with global climate change, understanding biological responses to upwelling dynamics is necessary for predicting future conditions of reef communities.

This review seeks to systematically assess the existing body of evidence relating upwelling to benthic community structure on coral reefs, and to provide a policy-neutral summary of existing evidence. Systematic reviews linking reef health with anthropogenic stressors including pollution (36), sediment exposure (37), chemical pollutants (38) and anthropogenic nutrient enrichment (39) have provided valuable overview analysis of the state of evidence. Such broad evidence synthesis allows policy makers and reef managers to make informed, evidence-based decisions founded in robust science. Although upwelling affects coral reefs throughout the oceans, no such review exists which comprehensively synthesises the research linking changes in environmental parameters driven by upwelling with associated impacts on coral reef benthic communities.

The results of this study were anticipated to highlight the variability of upwelling impacts on reef communities. The hypotheses were, firstly, that benthic groups would exhibit differential responses to upwelling dependant on their functional morphology; non-calcifying organisms such as turf and fleshy macroalgae were expected to increase in abundance due to their ability to opportunistically utilize nutrient influx (23,26). Secondly, responses of benthic communities were hypothesised to differ between remote reefs and those close to human population centres, as local anthropogenic stressors are demonstrated to disrupt natural biophysical relationships (8,28,40). Hard coral cover was expected to respond positively to upwelling where local anthropogenic stressors are absent, as the potential nutritional benefits of upwelling to corals are likely to be overshadowed by the presence of human populations. By synthesising the existing body of evidence, this review will facilitate enhanced understanding of reef community responses to upwelling, supporting resource managers and decision makers in creating nuanced and informed reef management and conservation policy.

3. Methods

3.1 Study Design

This study employed a systematic review and meta-analysis to assess the impact of upwelling on the relative dominance of benthic groups on coral reefs, following guidance set out by Pullin and Stewart (41), the Collaboration for Environmental Evidence (42) and the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) (43). Key elements of the review question can be viewed using the PECO format (CEE Guidelines V.5.0., 2018):

Population – coral reef benthic communities on shallow (≤30 m) tropical reefs (between 30’N and 30’S)

Exposure – cold pulses of deep water driven by upwelling

Comparator – comparable sites not subject to the impact of cold pulses driven by upwelling, or sites that are seasonally subject to upwelling (comparing upwelling and non-upwelling seasons)

Outcome – changes in the percentage cover of benthic groups

Coral reef benthic communities were categorised into the following 6 groups, following Williams et al. (45): hard coral, fleshy macroalgae, CCA, turf algae (including filamentous cyanobacteria), other calcifying macroalgae (e.g., *Halimeda* and *Peyssonnelia*) and soft coral. These were further defined by functional group, either calcifying (hard coral, CCA, calcifying macroalgae) or fleshy (fleshy macroalgae, turf algae, soft coral) organisms. The metric used to assess the impact of upwelling on the relative dominance of groups was percentage cover, as this was the predominant unit of measurement for assessing benthic community structure within the literature.

To further investigate the nuances of upwelling impacts, this review sought to decipher variability in impacts to benthic groups dependant on remoteness (distance from human population centres); depth; magnitude of the cold pulse (measured as the resulting temperature drop in °C); and geographic location.

3.2 Literature Search and Screening

Scoping of a search strategy was undertaken using the systematic review package litsearchr (46) in R (www.r-project.org). Terms generated in litsearchr were refined and tested on an iterative basis in Web of Science (table S1) against a benchmark list of 10 key papers known to be highly relevant to the subject (table S2). Following PRISMA guidelines (43), results retrieved at each state of the search were recorded (see figure S1 for PRISMA flow diagram). The final search was undertaken on 23/06/2022, capturing all key benchmark papers: *cora*l* OR *reef** AND *upwelling* OR *"internal wave*"* OR *cooling-hour** OR "*cooling hour*"* OR "*cold pulse*"* AND *abundance* OR *assemblage** OR *alga** OR *carbon** OR *communit** OR *diversity* OR *dynamic** OR *dominan** OR *ecosystem** OR *growth* OR *nutrient** OR *pattern** OR *rate** OR *benth** OR *composition** OR *develop** OR *distribut** OR *production* OR *response** OR *seascape** OR *spatial* OR *structur** OR *zon** OR *trophic* OR *varia** OR *regime** OR "*physical driver*".*

Web of Science (Core Collection database) and Scopus were used to search for literature, with a supplementary search of the first 200 results in Google Scholar to account for grey literature (47) (table S3). Eligibility criteria were determined *a priori* (table S4)*;* to be included in the review, studies must have undertaken comparative assessment of benthic communities under upwelling and non-upwelling conditions on coral reefs between 30'N and 30'S at depths of ≤30m. This comparison could be either spatial (comparative sites, one of which is subjected to upwelling and the other not) or temporal (consideration of the same site during seasonal upwelling and during non-upwelling season). No temporal limitation was placed upon the search for literature.

Papers were screened at title (*n* = 1441) and abstract (*n* = 453) level and imported into the reference management software Mendeley for full text screening. Ultimately, 17 studies met the inclusion criteria for use in the meta-analysis (table S5): 16 peer-reviewed papers and a PhD thesis (10,14,23–27,29,30,48–55).

3.3 Data coding strategy

The following meta-data were extracted from 17 studies:

- Bibliographic information (study identifier, bibliographic source, title, author, journal, year, DOI, language and publication type)
- General description of the study (country, region, latitude and longitude coordinates, specific study location)
- Population description (benthic group, functional group)

Studies were also coded into predefined categories for the following variables:

- Functional morphology (calcifying or fleshy)
- Depth category of benthic cover assessment (shallow 0-10m, moderate 11-20m, deep 21-30m, where case studies were categorised based on the majority of sampling effort - i.e., where target benthic sampling depth was 6-12m, the study was classified as "shallow")
- Geographic location
- Remoteness: deemed 'remote' if local population <50 people and >100km from human population centres, following Williams et al. (56)
- Whether benthic cover comparison featured spatial or temporal (seasonal) upwelling

Quantitative data extracted for use in meta-analysis included: mean percentage cover of benthic groups; standard deviation of percentage cover; number of independent study replicates; and mean temperature recorded during comparative upwelling and non-upwelling (°C).

3.4 Data Extraction

Data were extracted directly from article texts, tables and figures (using Automeris WebPlotDigitizer Version 4.5) and by requesting data directly from authors where it was not readily available in the publication. A total of 188 case studies (multiple independent studies produced from a single paper, for example, where multiple benthic groups were assessed at numerous comparable locations) were extracted from 17 papers (see Data Coding and Meta-Data Extraction in Dryad data repository(57)).

Studies were critically appraised to assess for validity before being included in the meta-analysis. Studies were categorised as having ‘high’ or ‘low’ validity based on control matching of study and control conditions, habitat comparability between study and control, study replication and length and presence of confounding factors that may modify effect of upwelling, i.e., proximity to aquaculture facilities.

3.5 Data Analysis

A weighted meta-analysis was conducted on studies retrieved through the process of systematic review to assess the impact of upwelling on the percentage cover of benthic groups on coral reefs. Changes in the relative dominance of benthic groups was assessed by calculating a response ratio to quantify the proportionate change in the mean percentage cover of groups between comparative upwelling and non-upwelling conditions (58). The natural logarithm of the response ratio, ln(RR), was calculated using the following equation:

$$\ln RR = \ln\left(\frac{\bar{X}e}{\bar{X}c}\right) = \ln(\bar{X}e) - \ln(\bar{X}c)$$

where Xe is the mean percentage cover during upwelling and Xc is the mean percentage cover during non-upwelling. A negative value indicates a reduction in percentage cover during upwelling and a positive value indicates an increase in percentage cover, comparative to non-upwelling.

Potential publication bias, or the likelihood of studies with significant or positive results to reach publication, was assessed using Egger’s test for asymmetry together with a funnel plot of lnRR with standard error (59), which did not identify significant publication bias across studies (R^2 = 0.093, p = 0.545), (see figure S2). An I^2 statistic was generated to describe the proportion of variation in effect sizes across studies that is due to heterogeneity rather than chance (60); a Cochran’s Q value was used to show the level and significance of heterogeneity (61). Heterogeneity of effect sizes with associated p-values and I^2 values for all models can be viewed in table S6.

Having calculated effect size for each study (k = 180, where k represents independent case studies considered), a random effects model was used to assess the overall impact of upwelling on cover of benthic groups using the “rma.mv” function within the “metafor” package in R (62). A random/mixed effects model was chosen as effect sizes were anticipated to vary from study to study and between different groups (63). Publication ID was included as a random effect in all models to account for lack of independence of effects from the same study.

The model showed significant heterogeneity in effects between case studies. Therefore, subgroup analysis of benthic groups split by functional morphology, location, proximity to people and sampling depth was undertaken. Meta-regressions to investigate the impact of upwelling magnitude on benthic cover were conducted using mixed effects models. Magnitude of upwelling was quantified as the mean °C drop experienced during upwelling compared to non-upwelling.

4. Results

4.1 Summary Findings and Distribution of Studies

In total, 180 case studies were analysed from 15 papers, spanning 5 countries, namely Colombia (*n* = 60), Costa Rica (*n* = 12), Panama (*n* = 24), Thailand (*n* = 13) and the United States Minor Outlying Islands (*n* = 71). Eight further case studies were not included in the final meta-analysis; three due to low comparability of upwelling and non-upwelling sites, (the Philippines, *n* = 1, and Taiwan, *n* = 2), and 5 due to zero percentage cover values, as lnRR cannot be applied to values of zero (United States Minor Outlying Islands, *n* = 5). Zero percentage cover values were explored for relevance and deemed appropriate for removal (see Supplementary Information including figure S3 for exploratory analysis of these case studies). All studies were published between 2002 – 2022, with benthic community assessment spanning 1994 - 2019. Study effort was clustered around four geographic zones: Southeast Asia (*n* = 16), Pacific Central America (*n* = 36), the Caribbean (*n* = 60) and the Equatorial Pacific, specifically Jarvis Island (*n* = 76). See figure S4 for map of study locations.

4.2 Effect of Upwelling on Benthic Groups

A multivariate mixed effects model with benthic group as a moderator showed that the percentage cover of fleshy macroalgae, CCA, turf algae and soft coral was significantly different during upwelling compared to non-upwelling (figure 1). A pooled significant effect of upwelling was not detected for other calcifying macroalgae or hard coral. Upwelling had a significant positive effect on the percentage cover of fleshy macroalgae and soft coral, increasing mean percentage cover by 73 and 692%, respectively. Given that only 2 studies considered the impact of upwelling on soft coral, this result cannot be considered conclusive, but may be indicative of actual effect. Upwelling had a significant negative effect on CCA, resulting in a 32% decrease in CCA cover. Similarly, the percentage cover of turf algae decreased by 22% with upwelling compared to non-upwelling. Effect size and direction varied across studies for all groups. Hard coral cover exhibited an almost even distribution of positive and negative effects with upwelling across studies (figure S5).

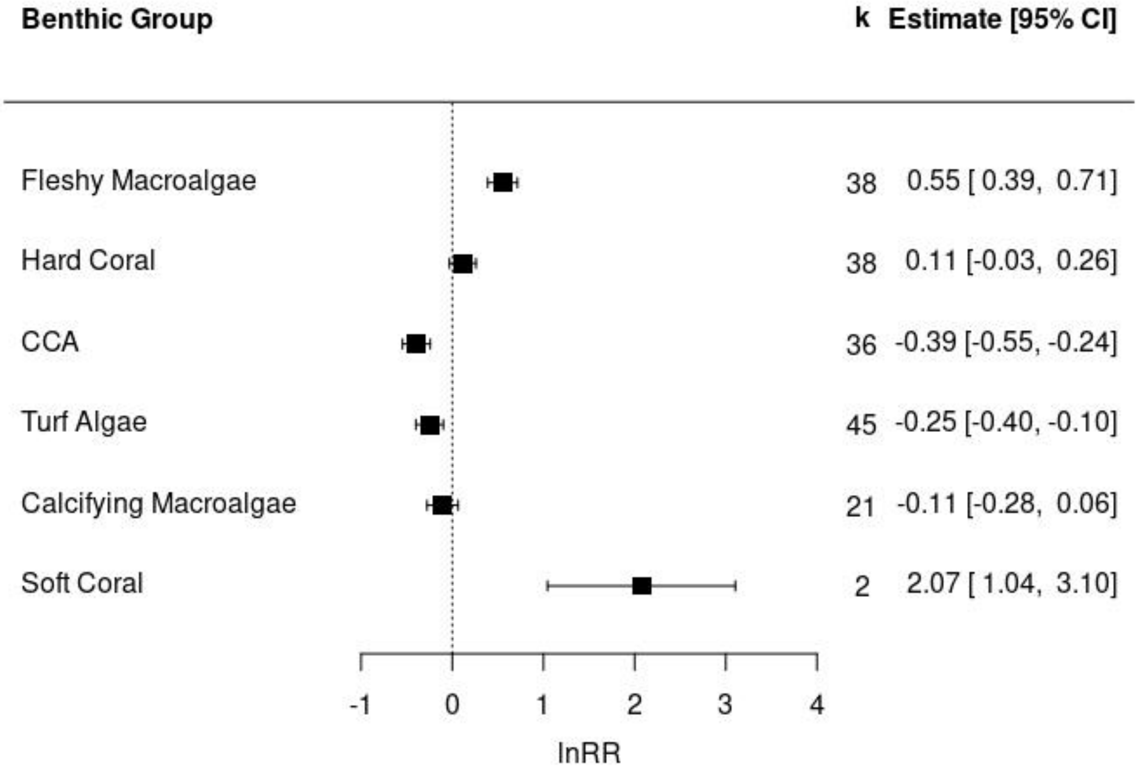

Figure 1. The lnRR (natural logarithm of response ratio) showing the effect of upwelling on the percentage cover of benthic groups on coral reefs. Boxes and error bars represent lnRR pooled effect sizes and 95% confidence intervals; values falling to the left of the dotted line indicate a negative effect of upwelling on the percentage cover of benthic groups, and to the right a positive effect. k represents the number of case studies that consider each benthic group included in the meta-analysis.

The percentage of variability in effect sizes across studies attributed to heterogeneity rather than sampling error was moderate ($I^2 = 67.6\%$) (60). Benthic group as a moderator explained a significant portion of heterogeneity within the data ($Q_6 = 379.459$, $p < 0.001$), but significant residual heterogeneity between studies remained unexplained ($Q_{174} = 1367.567$, $p < 0.001$), justifying further subgroup analysis to investigate causes of variation in effect of upwelling across studies.

4.3 Subgroup Analysis

4.3.1 Functional morphology

Categorizing groups as either calcifying or fleshy organisms did not indicate a distinct pattern of positive or negative effect of upwelling on either functional group ($p = 0.469$, $p = 0.337$, respectively) (figure S6).

4.3.2 Depth category

Benthic groups within each depth category showed variable responses to upwelling. Notably, upwelling had a significant positive effect on fleshy macroalgae in shallow sites ($p < 0.001$), a significant negative effect in moderate depths ($p = 0.017$), and a visual but non-significant negative effect at deep sites ($p = 0.053$) (figure 2).

4.3.3 Geographic location

Subgroup analysis of regionally clustered benthic groups was undertaken to explore the variability of upwelling impacts across geographic location. Upwelling in the Caribbean resulted in a significant decrease in turf algae and CCA cover ($p < 0.001$ for both groups). In contrast, fleshy macroalgae showed a mean 371% increase with upwelling in this region ($p < 0.001$). A significant positive effect on hard coral was observed at sampling locations on the Pacific coast of Central America and in the Equatorial Pacific ($p < 0.001$ for both) (figure 3).

4.3.4 Proximity to people

When categorised as inhabited or remote and with low validity studies removed, all remaining remote studies were undertaken around Jarvis Island in the Equatorial Pacific. Upwelling resulted in a 110% increase in fleshy macroalgal cover in inhabited locations, but a 56% decrease around Jarvis Island. Upwelling did not have a significant impact on hard coral cover in inhabited areas but coincided with a 150% increase on Jarvis' remote reefs (figure 4).

4.3.5 Temperature decrease

Meta-regression showed upwelling intensity measured in mean temperature drop was not a significant predictor of changes in percentage cover of benthic groups ($Q_{\text{moderator, 153}} = 1701.426$, $p = 0.654$). Further subgroup analysis was undertaken to assess the impact of temperature drop on cover of individual groups. A significant negative effect of temperature drop on the percentage cover of hard coral and calcifying macroalgae was detected ($Q_{\text{moderator, 1}} = 10.959$, $p < 0.001$, and $Q_{\text{moderator, 1}} = 5.546$, $p = 0.019$, respectively) (figure S7).

4.3.6 Temporal versus spatial comparison of upwelling

Fleshy macroalgal cover significantly increased in response to seasonal upwelling ($p < 0.001$), but significantly decreased with spatially distinct upwelling ($p < 0.001$). Hard coral cover was not significantly impacted by seasonal upwelling but significantly increased with spatially distinct upwelling (p = 0.007) (figure 5).

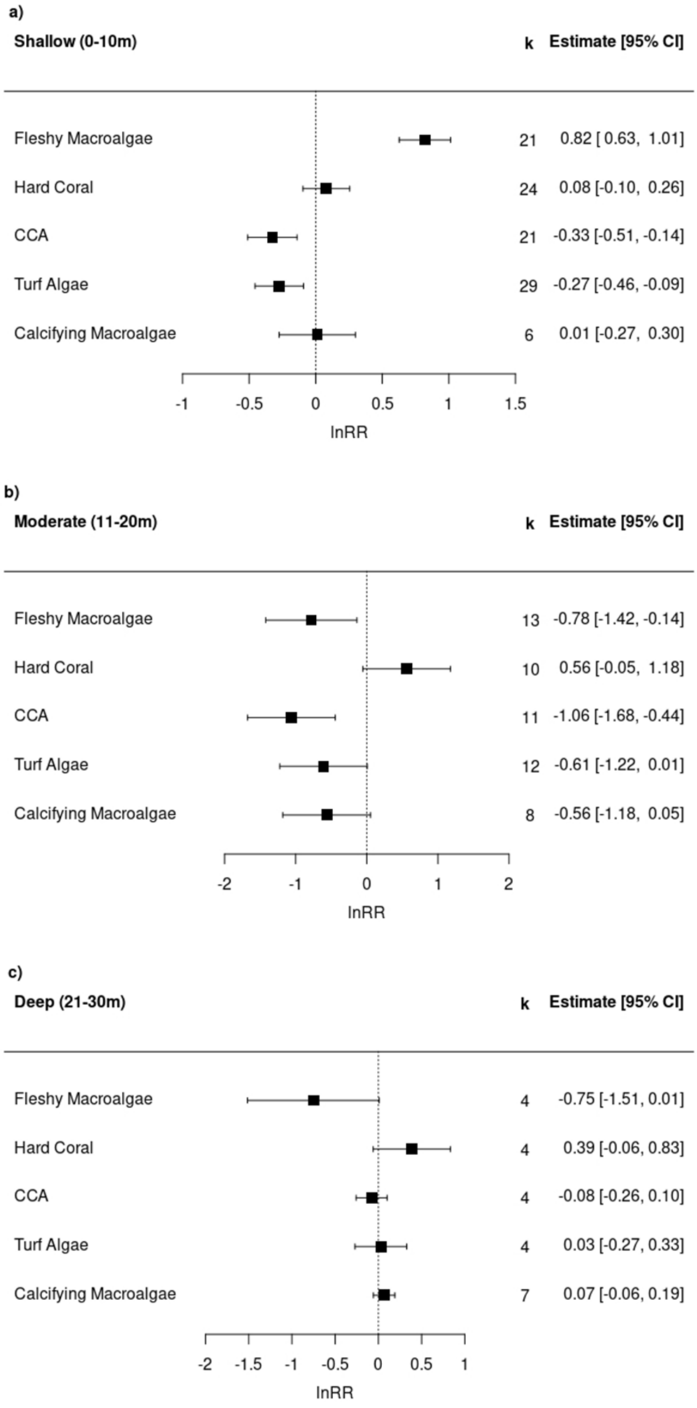

Figure 2. The lnRR (natural logarithm of response ratio) showing the effect of upwelling on the percentage cover of benthic groups separated by depth category: a) shallow, b) moderate and c) deep. Boxes and error bars represent lnRR pooled effect sizes and 95% confidence intervals; values falling to the left of the dotted line indicate a negative effect of upwelling on the percentage cover of benthic groups, and to the right a positive effect. k represents the number of case studies that consider each benthic group included in the meta-analysis. Note difference in x-axis scales across plots.

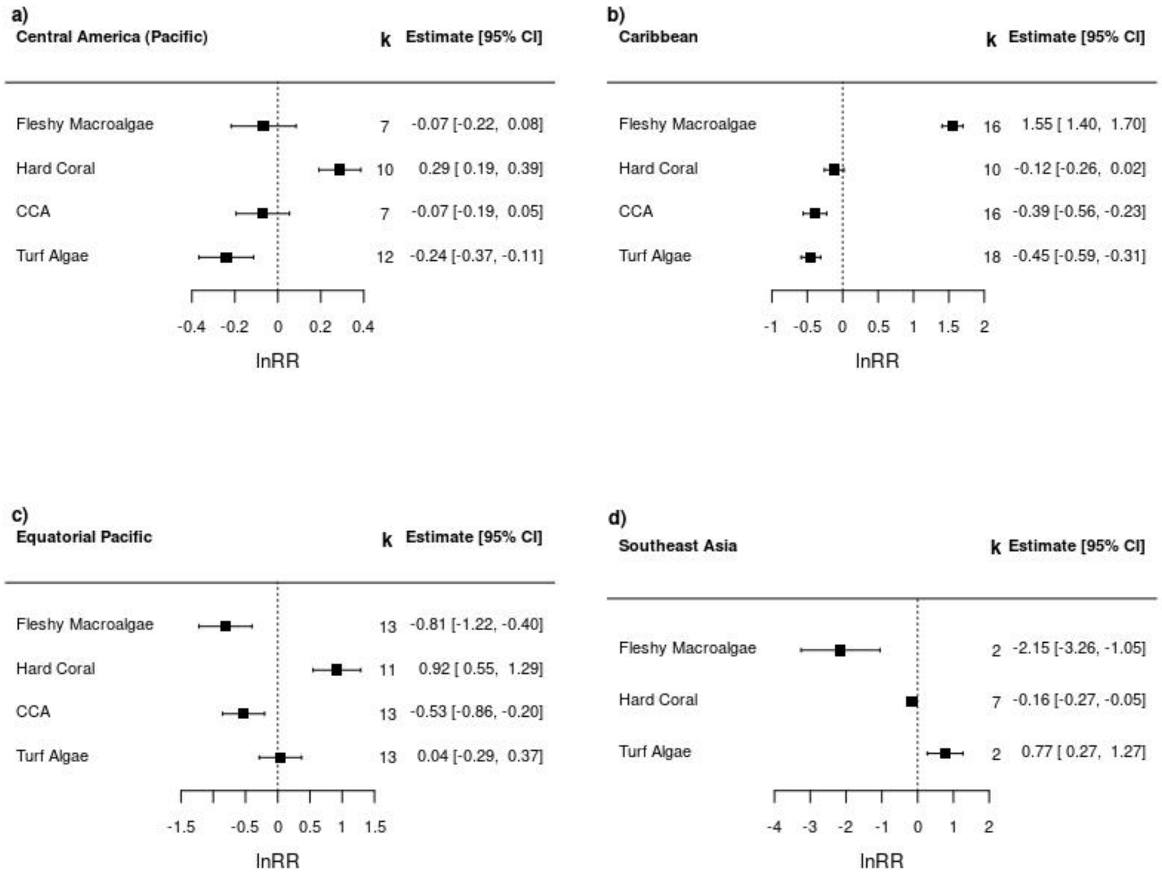

Figure 3. The lnRR (natural logarithm of response ratio) showing the effect of upwelling on the percentage cover of benthic groups separated by location: a) Central America (Pacific), b) Caribbean, c) Equatorial Pacific, d) Southeast Asia. Boxes and error bars represent lnRR pooled effect sizes and 95% confidence intervals; values falling to the left of the dotted line indicate a negative effect of upwelling on the percentage cover of benthic groups, and to the right a positive effect. k represents the number of case studies that consider each benthic group included in the meta-analysis. Note difference in x-axis scales across plots.

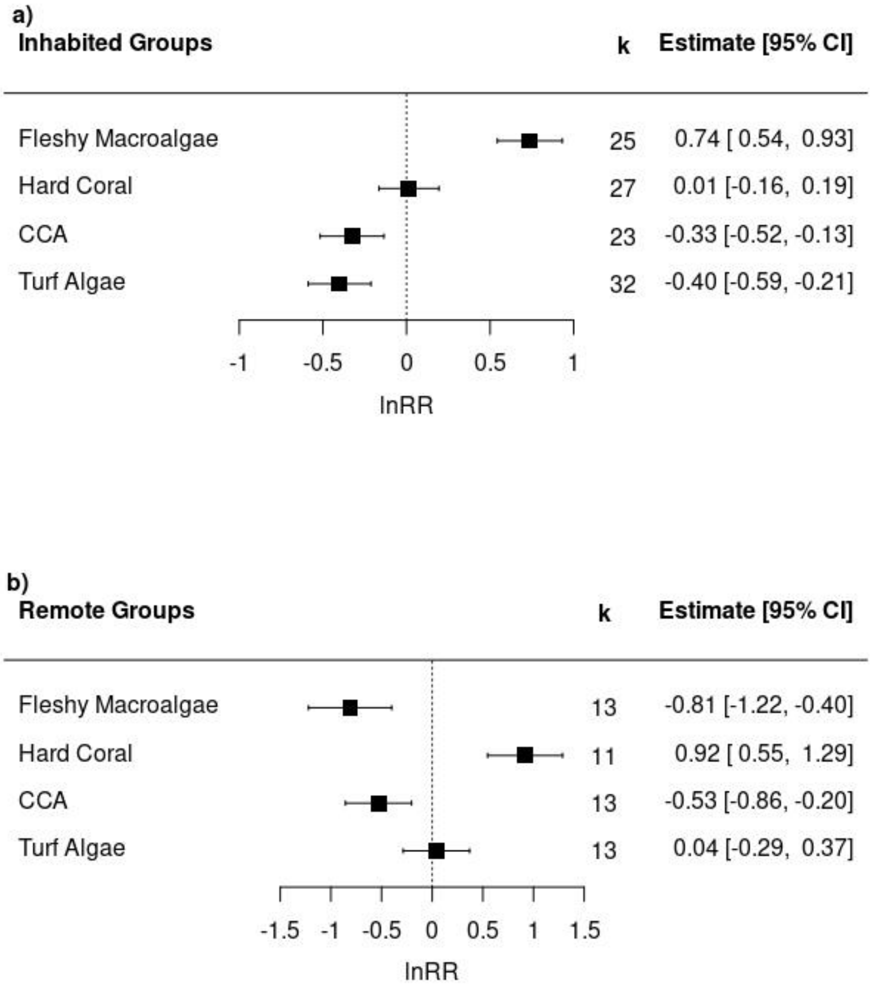

Figure 4. The lnRR (natural logarithm of response ratio) showing the effect of upwelling on the percentage cover of benthic groups separated into a) inhabited and b) remote locations. Boxes and error bars represent lnRR pooled effect sizes and 95% confidence intervals; values falling to the left of the dotted line indicate a negative effect of upwelling on the percentage cover of benthic groups, and to the right a positive effect. k represents the number of case studies that consider each benthic group included in the meta-analysis. Note difference in x-axis scales across plots.

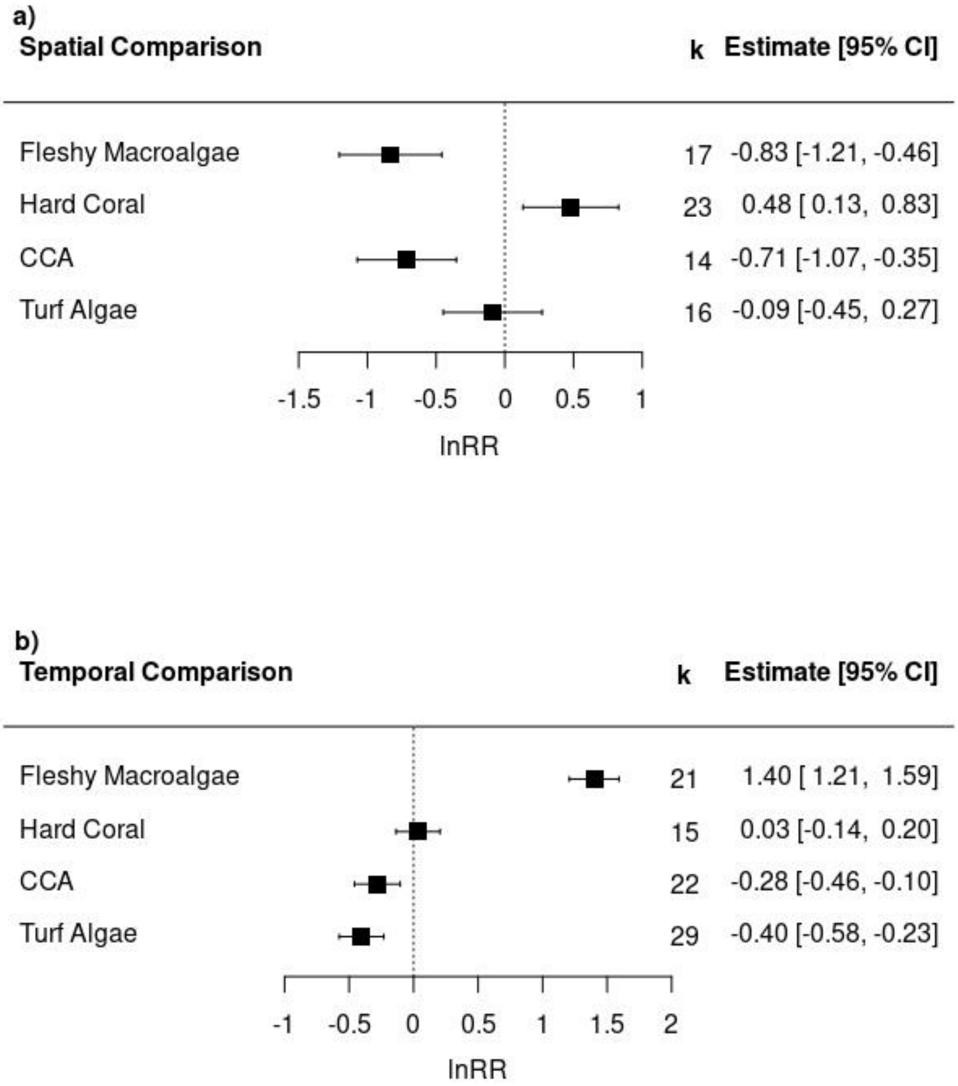

Figure 5. The lnRR (natural logarithm of response ratio) showing the effect of upwelling on the percentage cover of benthic groups impacted by a) spatial and b) temporal (seasonal) upwelling. Boxes and error bars represent lnRR pooled effect sizes and 95% confidence intervals; values falling to the left of the dotted line indicate a negative effect of upwelling on the percentage cover of benthic groups, and to the right a positive effect. k represents the number of case studies that consider each benthic group included in the meta-analysis. Note difference in x-axis scales across plots.

5. Discussion

The role of upwelling in structuring coral reef benthic communities has not been comprehensively synthesised (10,21,29). By conducting a systematic review and meta-analysis, we show that upwelling is correlated with significant changes in the percentage cover of benthic groups on coral reefs. Response patterns vary considerably when sub-analysed across geographic location, depth and, most notably, with proximity to human population centres. Responses also vary depending on whether upwelling is seasonally variable.

The pooled effect of upwelling from all studies resulted in an overall increase in fleshy macroalgal cover. This is unsurprising, given that macroalgae are well documented to be opportunistic, able to efficiently utilise heightened water column nutrient concentrations therefore outcompeting slower growing hard coral species (10,64). This trend was not observed across all geographic locations, however. When sub-analysed by study region, only in the Caribbean did fleshy macroalgal cover respond positively to upwelling. In the Equatorial Pacific (Jarvis Island) and Southeast Asia (Thai Similan Islands), upwelling had a significant negative effect on macroalgal cover. This suggests that upwelling has differential effects on fleshy macroalgae dependant on other extrinsic conditions, such as co-occurring anthropogenic stressors.

While Jarvis Island can be categorised as truly remote, the Thai Similan Islands are moderately free from local human pressure; although subject to heavy dive tourism, the closest population centre is located ~60km away. Our results support the findings of other studies that fleshy macroalgal cover increases in response to upwelling when co-occurring with other anthropogenic stressors, but not in more remote locations (29,30). The reduction in herbivorous fish abundance with increased fishing pressure that coincides with proximity to human populations is also likely facilitating the positive response of macroalgae to upwelling. On remote reefs where herbivory is high, algal responses to increased nutrient concentrations are moderated by top-down grazing pressure (65). In contrast, in the Caribbean where over-fishing is recognised as a driver of coral decline (66), upwelling was linked to fleshy macroalgal proliferation in this study. These results are suggestive of differential responses of coral reef communities to upwelling in highly populated areas compared with reefs not subject to direct human pressures. However, the paucity of evidence linking upwelling with reef communities in remote locations highlights the need for further research to disentangle the effects of gradients in natural and anthropogenic nutrient sources.

The impact of upwelling on fleshy macroalgal cover also varied with depth. Upwelling resulted in an increase in fleshy macroalgal cover in shallow depths, but a decrease in moderate and deeper depths. This may be due to the higher levels of light attenuation at depth, depriving algae of energy for photosynthesis, although this pattern is likely to be species specific (67). This highlights the need for future studies to identify macroalgal responses to upwelling with higher taxonomic or functional specificity, as different algal species will occupy ecological niches at varying depths.

Algal assemblages on coral reefs have been shown to be highly spatially and temporally variable (68), which was echoed in the results of this study. Fleshy macroalgal cover increased by 306% in response to seasonal upwelling, yet a spatial comparison of upwelling and non-upwelling sites correlated with a 56% drop in cover with upwelling. In contrast, hard coral cover was not impacted by seasonal upwelling but increased by 62% in upwelling compared with non-upwelling sites. This can likely be explained by the difference in response times of fleshy macroalgae and hard corals to increases in allochthonous energy resources, although this requires further research (69). Future studies could focus on quantifying the responses of different benthic groups to gradients in energy availability over different time-scales, particularly organisms such as hard corals that employ a mixotrophic feeding strategy (18).

Although only two studies considered soft coral response to upwelling, an overall significant positive effect of upwelling on soft coral cover was observed. Soft corals are able to lean more heavily on heterotrophy than scleractinian corals (70). Given that upwelling can increase plankton abundance resulting from enhanced nutrient concentrations, this offers an explanation for increased soft coral abundance at upwelling exposed sites (71,72).

An overall negative effect of upwelling on CCA abundance was observed, a trend that was also reflected in subgroup analysis by geographic location and remote versus inhabited areas. CCA is an important benthic calcifier on coral reefs, functioning to consolidate reef structure, binding segments of reef and contributing to overall reef accretion (73). As a biomineralizing group that requires calcium carbonate to form skeletal structure, CCA is highly vulnerable to the deleterious effects of ocean acidification (74). Upwelling can lower seawater pH, which could be preventing or diminishing CCA growth (75) despite the beneficial increase in available nutrients to the algae.

The effect of upwelling on hard coral cover was highly variable, with an almost even distribution of reported positive and negative responses in coral cover across studies. As expected, hard coral exhibited differential responses to upwelling when separated into remote and inhabited locations. Upwelling resulted in a 144% increase in hard coral cover on the remote reefs surrounding Jarvis Island, but did not have a significant effect on reefs subject to direct human pressures. Williams et al. (28) found that on remote reefs in unpopulated areas, background increases in chlorophyll-*a* (a proxy for phytoplankton biomass) coincide with a decrease in macroalgal cover and an increase in hard coral and

CCA dominance. This apparent competitive advantage to key calcifying organisms could explain some of the variation in hard coral cover in response to upwelling found in the present study. In essence, the impacts of upwelling on the abundance of hard coral are diminished when local anthropogenic stressors override the natural variation in associated biophysical parameters. The presence of human population centres drowns out natural biophysical relationships by fundamentally changing the environmental conditions within which coral reefs have evolved to thrive. Whilst natural nutrient enrichment driven by upwelling may provide a benefit to corals in terms of growth and productivity, the volume and type of nutrients deposited by anthropogenic activities surpasses the tipping point at which nutrient enrichment triggers negative impacts on coral health (17,76).

The results of this meta-analysis highlight the paucity of evidence linking physical oceanographic processes with coral reef benthic ecology. Just 17 publications directly measured the effects of fluctuations in environmental parameters associated with upwelling with changes in the percentage cover of benthic groups. Study effort was highly spatially clustered, highlighting the need for further research into the impact of upwelling on benthic community structure across scales and geographies. Our ability to develop nuanced and adaptive management strategies for maintaining coral reefs that support high biodiversity and provide key ecosystem services to people requires a thorough understanding of both natural environmental drivers and anthropogenic stressors (3,35,40). A number of studies have explored the concept of upwelling zones as potential refugia for corals from thermal stress (14,35,77,78). The present study shows that upwelling may benefit hard corals, demonstrating that upwelling results in an increase in hard coral cover in some (but not all) locations, and particularly where local anthropogenic stressors are lacking.

If thermal refugia are to be included in the arsenal of conservation scientists and reef managers, care must be taken when selecting sites. The protective capacity of upwelling seems to be localised to specific geographic areas and is unlikely to provide a failsafe guard against coral mortality under extreme temperature events. In order for upwelling to confer protection from thermal stress, Chollett et al. (78) identified two conditions that must be met; firstly, the thermal stress event and the presence of upwelling must occur synergistically; and secondly, the occurrence of upwelling during the warming event must result in a meaningful decrease in heat stress (78). In summary, upwelling cannot be considered a panacea to heat stress but may be a useful tool for managers to factor into reef management plans and the distribution of conservation resources.

This study has highlighted the differential impacts of upwelling, varying as a function of both environmental and anthropogenic context (79). In order to fully understand the interplay between physical oceanographic drivers of change on coral reefs and anthropogenic stressors, further interdisciplinary research joining physical oceanography, benthic ecology and social science is needed to effectively manage coral reefs in the Anthropocene (3,80).

Should such an evidence synthesis exercise be undertaken again in a decade, a more robust and comprehensive understanding of the interplay between upwelling and benthic community structure could be obtained. Future research should aim for more detailed quantification of upwelling parameters, including changes in *in situ* water column nutrient concentrations during upwelling events. Further, by identifying species within benthic groups to a higher taxonomic resolution, the variability in responses of individual species could be explored, particularly algae which perhaps do not fall neatly into ‘fleshy macroalgae’ and ‘calcifying macroalgae’. And finally, developing manipulative experiments that seek to separate the synergistic impacts of temperature drop and nutrient increase associated with upwelling events would allow greater understanding of the mechanisms driving benthic community structure. If these aims are met, such research may provide further clarity to decision makers on the impacts of natural oceanographic forcing on coral reefs, so that these may be taken into consideration when managing anthropogenic stressors and selecting reefs for focused conservation efforts. Reef management that does not account for natural variation and environmental drivers of change is limited by a lack of understanding of environmental context and natural carrying capacity of the reefs they are trying to preserve (6). The results of this review can be utilized by policy and decision makers when determining spatial bounds for reef management, aiding optimal resource allocation and informed reef conservation policy that accounts for the impacts of environmental variation.

Data Accessibility

Data can be obtained from Dryad repository (doi:10.5061/dryad.w0vt4b8wg); the R script is available as supplementary information.

Author’s Contributions

DLS and GJW jointly conceptualized this research; the systematic review and meta-analysis was designed by DLS. Data acquisition, literature screening and data extraction was undertaken by DLS with support from GJW. Data analysis and manuscript drafting was undertaken by DLS. Interpretation of results of the meta-analysis and critical manuscript revision was undertaken jointly by DLS and GJW, with final manuscript approval performed by both authors.

Competing Interests

We declare no competing interests related to this research.

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Influence of upwelling on coral reef benthic communities: a systematic review and meta-analysis

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Supplementary Information

Danielle L. Spring* and Gareth J. Williams

Proceedings of The Royal Society B, Biological Sciences

School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK

*Correspondence: d.spring@bangor.ac.uk

Overview of Content

A systematic review and meta-analysis were undertaken to investigate the impact of upwelling on coral reef benthic groups. The search string to capture relevant literature was developed through an iterative process (table S1) and tested against a list of 10 key benchmark papers known to be highly relevant (table S2). A PRISMA flow diagram reporting the number of studies identified through the searching process and retained at each stage of screening can be viewed in figure S1. The databases utilized in the search are specified in table S3. To be included in the meta-analysis, studies had to meet *a priori* defined eligibility criteria (table S4). All studies that met the eligibility criteria can be viewed in table S5. A funnel plot for asymmetry was used in combination with an Egger's test to check for publication bias (figure S2). Random effects models were used to assess the pooled effect of upwelling on benthic groups across all studies, then rerun with the following moderators: morphology (fleshy or calcifying organisms), depth, remoteness (distance from human population centres), geographic location and mean temperature drop. Table S6 shows heterogeneity in effect for moderators and residual heterogeneity (i.e., remaining heterogeneity not explained by the included moderators). Case studies with zero mean percentage cover values were removed from the meta-analysis; justification for this can be found on page 16-17, along with figure S3. A world map showing study locations can be seen in figure S4. Effect sizes and direction for all studies considering hard coral are shown in figure S5. A forest plot showing effect of upwelling on organisms grouped by functional morphology (calcifying or fleshy) can be seen in figure S6. Meta-regressions assessing the impact of temperature drop on the percentage cover of hard corals and calcifying macroalgae can be seen in figure S7.

Table S1. Search string development table, showing iterative process of refining search string to capture all key benchmark papers and striking a balance between specificity (not including irrelevant results) and sensitivity (including all potentially relevant results). Following page:

PECO	Version	Search string	Results retrieved	Comprehensiveness (key papers)	Comments
Population (identified in litsearchr)	#1	coral* OR reef* AND shallow AND tropical NOT temperate	62,685	Not tested	Terms *'shallow' AND 'tropical' NOT 'temperate'* were removed as any paper referring to both tropical and temperate reefs would be excluded; shallow was deemed ambiguous and unhelpful to the search string. By searching for 'coral* AND reef*' it is anticipated that all studies relating to coral reefs will be caught, and screening will remove papers relating solely to cold water/temperate/deep etc coral studies.
Population (refined)	#2	coral* OR reef*	86,546	Not tested	
Exposure (identified in litsearchr)	#3	upwelling OR "internal wave*" OR tidal OR tide* OR wave* OR mixing OR "cold pulse*"	3,697,968	Not tested	
Outcomes (identified in litsearchr)	#4	"benthic communit*" OR "benthic structure" OR benth* OR communit* OR structure OR assemblage OR spatial OR zonation OR zone OR zoning	9,464,330	Not tested	
Population + Exposure	#5	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave*" OR "cold pulse*"))	1,077	Not tested	Removal of 'wave', 'tide', 'tidal' and 'mixing' as deemed too broad and not directly relevant to upwelling or cold pulses caused by internal waves

Outcome revised (litsearchr)	#6	abundance OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR spatial OR structur* OR varia*	34,185,714	Not tested	
Exposure + Outcome	#7	TS = ((upwelling OR "internal wave*" OR "cold pulse*") **AND** (abundance OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR spatial OR structur* OR varia*))	30,068	10/10	
Population + Exposure + Outcome	#8	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave*" OR "cold pulse*") **AND** (abundance OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR spatial OR structur* OR varia*))	1046	10/10	
Population + Exposure + Outcome	#9	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave*" OR "cold pulse*") **AND** (abundance OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR spatial OR structur* OR varia*))	1048	10/10	Added ‘zon*’
Population + Exposure + Outcome	#10	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave* AND break*" OR "internal wave* AND island*" OR cooling-hour* OR "cooling hour*" OR "cold pulse*") **AND** (abundance OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR doninan* OR ecosystem* OR growth OR nutrient* OR pattern*	905	8/10	Refined expose to reduce body of literature on internal waves, so as only to catch results that deal with internal waves interacting with shallow ecosystems:

		OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR seascape* OR spatial OR structur* OR zon* OR trophic OR varia* OR ‘regime*’ OR “physical driver*”)) = 905 results			added ‘internal wave AND ‘break’ and ‘internal wave AND ‘island’
Population + Exposure + Outcome	#11	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave* AND break*" OR "internal wave* AND island*" OR cooling-hour* OR "cooling hour*" OR "cold pulse*") **AND** (abundance OR alga* OR communit* OR dominan* OR diversity OR dynamic* OR ecosystem* OR nutrient* OR pattern* OR benth* OR composition* OR develop* OR distribut* OR seascape* OR spatial OR structur* OR zon* OR trophic OR varia* OR ‘regime*’ OR “physical driver*”))	855	8/10	Refined
Population + Exposure + Outcome	#12	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave*” OR cooling-hour* OR "cooling hour*" OR "cold pulse*") **AND** (abundance OR alga* OR communit* OR dominan* OR diversity OR dynamic* OR ecosystem* OR nutrient* OR pattern* OR benth* OR composition* OR develop* OR distribut* OR seascape* OR spatial OR structur* OR zon* OR trophic OR varia* OR ‘regime*’ OR “physical driver*”))	1027	10/10	
Population + Exposure + Outcome	#13	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave* AND break*" OR "internal wave* AND island*" OR “internal wave*" AND "sub-surface” OR cooling-hour* OR "cooling hour*" OR "cold pulse*") **AND** (abundance OR assemblage* OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR dominan* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR seascape* OR spatial OR structur* OR	908	8/10	Additional terms suggested by GW

		zon* OR trophic OR varia* OR ‘regime*’ OR “physical driver*”))			
Population + Exposure + Outcome	#14	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave* AND break*" OR "internal wave* AND island*" OR “internal wave*" AND "sub-surface” OR cooling-hour* OR "cooling hour*" OR "cold pulse*" OR ENSO OR “El nino”) **AND** (abundance OR assemblage* OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR dominan* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR seascape* OR spatial OR structur* OR zon* OR trophic OR varia* OR ‘regime*’ OR “physical driver*”))	2075	8/10	Added in ‘El Nino’ terms to see if this catches additional relevant papers
Population + Exposure + Outcome	#15	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave* AND break*" OR "internal wave* AND island*" OR cooling-hour* OR "cooling hour*" OR "cold pulse*") **AND** (abundance OR assemblage* OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR dominan* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR seascape* OR spatial OR structur* OR zon* OR trophic OR varia* OR ‘regime*’ OR “physical driver*”))	907	8/10	Adding El Nino related terms makes search too broad – removed. Removed *OR “internal wave*" AND "sub-surface”* as it added only 1 additional paper. removed *OR ENSO OR “El nino”* because it doubles search results for papers that are referring to ENSO but not directly looking at the impacts of internal waves or upwelling – outside the scope of this limited review considering primarily upwelling impacts

Population + Exposure + Outcome	#16	TS = ((coral* OR reef*) **AND** (upwelling OR "internal wave*" OR cooling-hour* OR "cooling hour*" OR "cold pulse*") **AND** (abundance OR assemblage* OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR dominan* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR seascape* OR spatial OR structur* OR zon* OR trophic OR varia* OR ‘regime*’ OR “physical driver*”))	1052	10/10	Removal of qualifiers _AND break*_ and _AND Island :_ removal of these qualifying terms adds only 145 articles and including them risks missing relevant articles

Same search undertaken in Scopus: TITLE-ABS-KEY (coral* OR reef*) AND TITLE-ABS-KEY (upwelling OR "internal wave*" OR cooling-hour* OR "cooling hour*" OR "cold pulse*") AND TITLE-ABS-KEY (abundance OR assemblage* OR alga* OR carbon* OR communit* OR diversity OR dynamic* OR dominan* OR ecosystem* OR growth OR nutrient* OR pattern* OR rate* OR benth* OR composition* OR develop* OR distribut* OR production OR response* OR seascape* OR spatial OR structur* OR zon* OR trophic OR varia* OR 'regime*' OR "physical driver*") (06/07/2022 – additional 189 results after duplicates removed for abstract screening)

Same search entered directly into Google Scholar (08/07/2022 – additional 18 results after duplicates removed for abstract screening)

Table S2. Benchmark list of key papers used in search string development for systematic review assessing impact of upwelling on coral reef benthic functional groups.

#	Title	Author	Journal	Date
1	Scale-dependent spatial patterns in benthic communities around a tropical island seascape	Aston et al	Ecography	2019
2	Trophic response of corals to large amplitude internal waves	Order et al	Marine Ecology Progress Series	2010
3	Intermittent upwelling and subsidized growth of the scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica	Leichter and Genovese	Marine Ecology Progress Series	2006
4	Biophysical drivers of coral trophic depth zonation	Williams et al	Marine Biology	2018
5	Upwelling and the persistence of coral-reef frameworks in the eastern tropical Pacific	Enochs et al	Ecological Monographs	2021
6	Benthic primary production in an upwelling-influenced coral reef, Colombian Caribbean	Eidens et al	PeerJ	2014
7	Multi-scale processes drive benthic community structure in upwelling-affected coral reefs	Eidens et al	Frontiers in Marine Science	2015
8	Dynamics in benthic community composition and influencing factors in an upwelling-exposed coral reef on the Pacific coast of Costa Rica	Stuhldreier et al	PeerJ	2015
9	Coral community composition and reef development at the Similan Islands, Andaman Sea, in response to strong environmental variations	Schmidt et al	Marine Ecology Progress Series	2012
10	Upwelling buffers climate change impacts on coral reefs of the eastern tropical Pacific	Randall et al	Ecology	2020

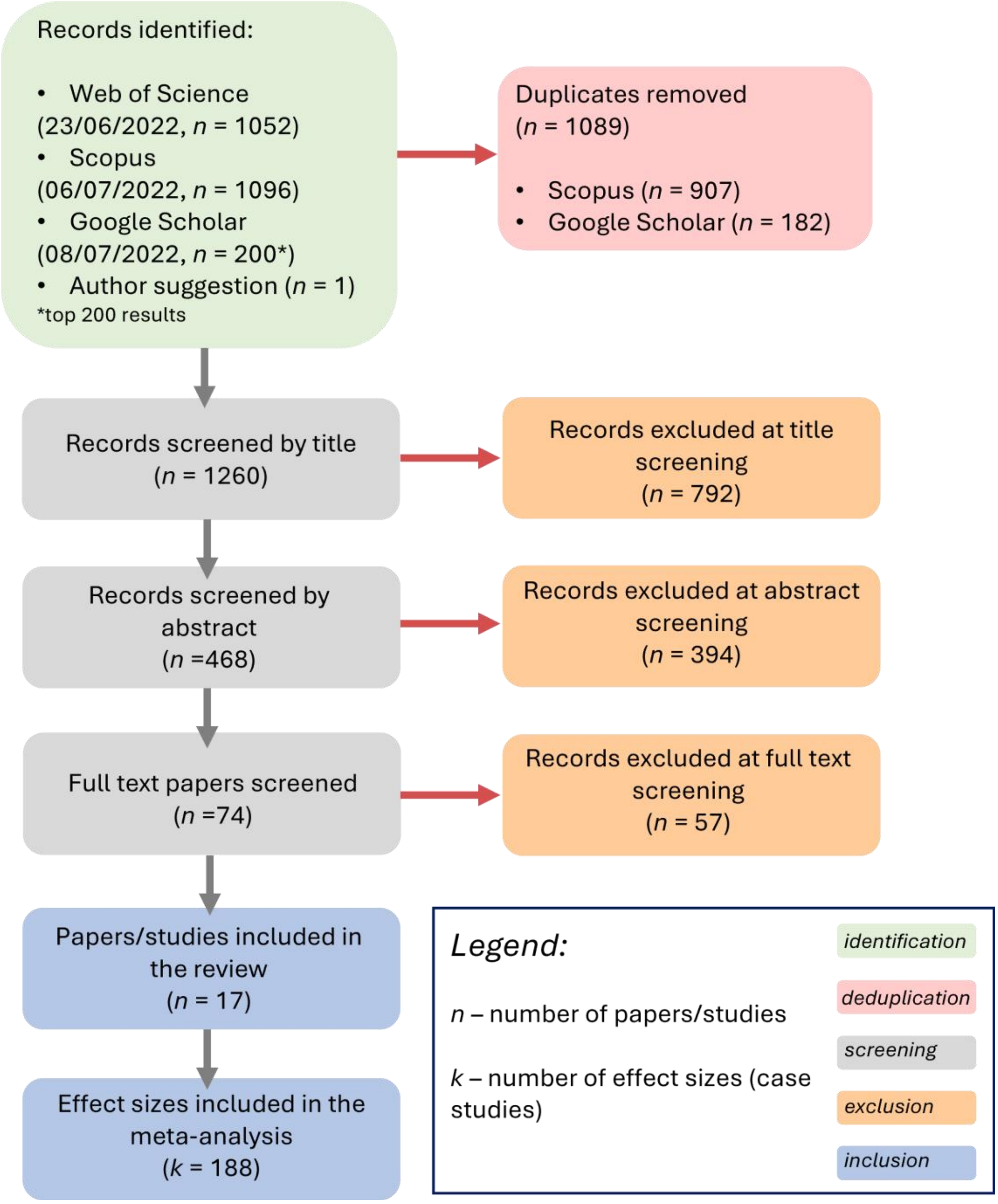


Figure S1 – PRISMA flow diagram reporting number of studies identified through the searching process and retained at each level of screening

Table S3. List of bibliographic databases used in the literature search for systematic review.

Search Engine	**Database**	**Provider**	**Date range available**	**Subscription Institution**	**# Results**	**Date of Search**
Web of Science	Core Collections	Clarivate Analytics	1970-present	Bangor University, UK	1052	23/06/2022
Scopus	Scopus	Elselvier	1788-present	Bangor University, UK	189 additional results	06/07/2022
Google Scholar	Internet search	Google		Open access	18 additional results*	08/07/2022

* - top 200 results in Google Scholar considered, following Haddaway et al., (2015) *The role of Google Scholar in evidence reviews and its applicability to grey literature searching,* PLoS ONE 10(9): e0138237

Table S4. Eligibility criteria for inclusion in the systematic review and meta-analysis, in the form of ‘PECO’ – population, exposure, comparator and outcome.

Include	**Exclude**
Population	
Coral reef benthic communities on shallow (≤30m), tropical (between 30’N and 30’S) coral reefs. Main benthic groups falling within two pre-identified categories: reef builders (hard coral, CCA, other calcifying macroalgae) and fleshy organisms (fleshy macroalgae, turf algae, soft coral); including individual species falling within the above benthic groups	Other reef organisms including reef fishes, other groups of invertebrates (molluscs, polychaetes etc). Studies looking at mesophotic or deep coral reefs (>30m); studies considering sub-tropical reefs
Exposure	
Reefs or sections of reef exposed to cold pulses of deep, nutrient rich water due to upwelling or breaking of internal waves	Studies exclusively considering cold pulses due to downwelling; studies considering other physical processes such as wave exposure but not upwelling
Comparator	
Studies must include a control site of a comparable reef or section of reef not impacted by upwelling, or consider the same area of reef during seasonal upwelling compared to non-upwelling season	Studies considering benthic communities on upwelling-impacted reefs without making comparison to a control site not impacted by upwelling
Outcome	
Structure of benthic community groups; relative dominance of major groups (i.e., percent cover)	
Language	
All studies written in English	
Document type	
Journal articles, academic book chapters, reports, conference proceedings, PhD and MSc theses	
Study type	
In situ observational studies	Review papers and meta-analyses will not be included in the review.

Table S5. Publications used in meta-analysis; benthic groups abbreviated to HC (hard coral), FMA (fleshy macroalgae), CCA (crustose coralline algae), TA (turf algae), CMA (calcifying macroalgae) and SC (soft coral).

<table>
<tr><th>Publication ID</th><th>Author(s) and year [citation]</th><th>Benthic group assessed</th><th>Ocean</th><th>Country</th><th>Number of case studies</th></tr>
<tr><td>1</td><td>C Eidens et al., 2014</td><td>HC, FMA, CCA, TA</td><td>North Atlantic</td><td>Colombia</td><td>10</td></tr>
<tr><td></td><td colspan="5">Eidens C, Bayraktarov E, Hauffe T, Pizarro V, Wilke T, Wild C. Benthic primary production in an upwelling-influenced coral reef, Colombian Caribbean. PeerJ 2014 Sep 2;2014(1):e554.</td></tr>
<tr><td>2</td><td>Jantzen et al., 2013a</td><td>HC, TA</td><td>Indian Ocean</td><td>Thailand</td><td>4</td></tr>
<tr><td></td><td colspan="5">Jantzen C, Schmidt GM, Wild C, Roder C, Khokiattiwong S, Richter C. Benthic Reef Primary Production in Response to Large Amplitude Internal Waves at the Similan Islands (Andaman Sea, Thailand). PLoS One. 2013 Nov 29;8(11):e81834</td></tr>
<tr><td>3</td><td>Gertraud M. Schmidt et al., 2012</td><td>HC</td><td>Indian Ocean</td><td>Thailand</td><td>3</td></tr>
<tr><td></td><td colspan="5">Schmidt GM, Phongsuwan N, Jantzen C, Roder C, Khokiattiwong S, Richter C. Coral community composition and reef development at the Similan Islands, Andaman Sea, in response to strong environmental variations. Mar Ecol Prog Ser. 2012 Jun 7;456:113–26.</td></tr>
<tr><td>4</td><td>Fernández-García et al., 2012</td><td>FMA</td><td>North Pacific</td><td>Costa Rica</td><td>3</td></tr>
<tr><td></td><td colspan="5">Fernández-García C, Cortés J, Alvarado JJ, Nivia-Ruiz J. Physical factors contributing to the benthic dominance of the alga Caulerpa sertularioides (Caulerpaceae, Chlorophyta) in the upwelling Bahía Culebra, north Pacific of Costa Rica. Rev Biol Trop (Int J Trop Biol ISSN. 2012;60:93–107.</td></tr>
<tr><td>5</td><td>Diaz-Pulido & Garzon-Ferreira, 2002</td><td>FMA, TA, CCA</td><td>North Atlantic</td><td>Colombia</td><td>18</td></tr>
<tr><td></td><td colspan="5">Diaz-pulido G, Garzón-ferreira J. Seasonality in Algal Assemblages on Upwelling-influenced Coral Reefs in the Colombian Caribbean. Bot Mar. 2002;45:284–92.</td></tr>
<tr><td>6</td><td>Ines Stuhldreier et al., 2015a</td><td>HC, TA, CCA, FMA</td><td>North Pacific</td><td>Costa Rica</td><td>4</td></tr>
<tr><td></td><td colspan="5">Stuhldreier I, Sánchez-Noguera C, Roth F, Cortés J, Rixen T, Wild C. Upwelling increases net primary production of corals and reef-wide gross primary production along the pacific coast of costa rica. Front Mar Sci. 2015;2</td></tr>
<tr><td>7</td><td>Aston et al., 2019</td><td>HC, FMA, CCA, TA</td><td>South Pacific</td><td>U.S Minor Outlying Islands</td><td>4</td></tr>
<tr><td></td><td colspan="5">Aston EA, Williams GJ, Green JAM, Davies AJ, Wedding LM, Gove JM, et al. Scale-dependent spatial patterns in benthic communities around a tropical island seascape. Ecography (Cop). 2019 Mar 1;42(3):578–90.</td></tr>
<tr><td>8</td><td>Tkachenko & Soong, 2017</td><td>CCA. HC</td><td>Western Pacific</td><td>Taiwan</td><td>2</td></tr>
<tr><td></td><td colspan="5">Tkachenko KS, Soong K. Dongsha Atoll: A potential thermal refuge for reef-building corals in the South China Sea. Mar Environ Res. 2017 Jun 1;127:112–25.</td></tr>
</table>

9	I Stuhldreier et al., 2015b	HC, CCA, FMA, TA	North Pacific	Costa Rica	5
	Stuhldreier I, Sánchez-Noguera C, Roth F, Jiménez C, Rixen T, Cortés J, et al. Dynamics in benthic community composition and influencing factors in an upwelling-exposed coral reef on the Pacific coast of Costa Rica. PeerJ. 2015 Nov 24				
10	Wall et al., 2015	HC, SC, FMA	Indian Ocean	Thailand	6
	Wall M, Putchim L, Schmidt GM, Jantzen C, Khokiattiwong S, Richter C. Large-amplitude internal waves benefit corals during thermal stress. Proc R Soc B Biol Sci. 2015 Jan 22;282(1799).				
11	Reyes, Robles, & Licuanan, 2022	HC	North Pacific	Philippines	1
	Reyes M, Robles R, Licuanan WY. Multi-scale variation in coral reef metrics on four Philippine reef systems. Reg Stud Mar Sci. 2022 May 1;52:102310.				
12	Smith, 2006	HC, TA, CCA, FMA	North Pacific	Panama	17
	Smith TB. The dynamics of coral reef algae in an upwelling system. Dissertation Abstracts International Part B: Science and Engineering. University of Miami; 2006.				
13	Vargas-Ángel et al., 2019	CCA, HC, FMA, TA, CMA	South Pacific	U.S Minor Outlying Islands	54
	Vargas-Ángel B, Huntington B, Brainard RE, Venegas R, Oliver T, Barkley H, et al. El Niño-associated catastrophic coral mortality at Jarvis Island, central Equatorial Pacific. Coral Reefs. 2019 Aug 15;38(4):731–41.				
14	Huntington et al., 2022	CCA, HC, FMA, TA, CMA	South Pacific	U.S Minor Outlying Islands	18
	Huntington B, Weible R, Halperin A, Winston M, McCoy K, Amir C, et al. Early successional trajectory of benthic community in an uninhabited reef system three years after mass coral bleaching. Coral Reefs. 2022 Apr 19				
15	Eidens, Hauffe, Bayraktarov, Wild, & Wilke, 2015	TA, HC, CCA, FMA	North Atlantic	Colombia	32
	Eidens C, Hauffe T, Bayraktarov E, Wild C, Wilke T. Multi-scale processes drive benthic community structure in upwelling-affected coral reefs. Front Mar Sci. 2015;2:2.				
16	Enochs et al., 2021	FMA, CCA	North Pacific	Panama	2
	Enochs IC, Toth LT, Kirkland A, Manzello DP, Kolodziej G, Morris JT, et al. Upwelling and the persistence of coral-reef frameworks in the eastern tropical Pacific. Ecol Monogr. 2021 Nov 1;91(4):e01482.				
17	Randall et al., 2020	HC, TA	North Pacific	Panama	5
	Randall CJ, Toth LT, Leichter JJ, Mate JL, Aronson RB. Upwelling buffers climate change impacts on coral reefs of the eastern tropical Pacific. Ecology. 2020;101(2).				

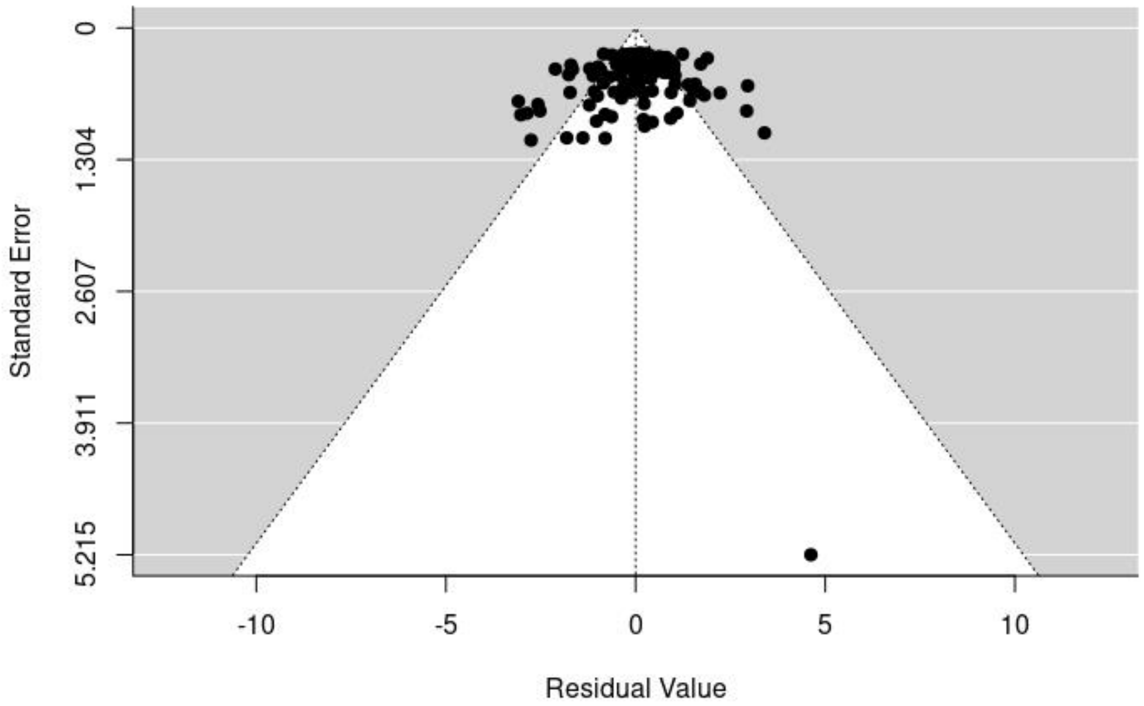


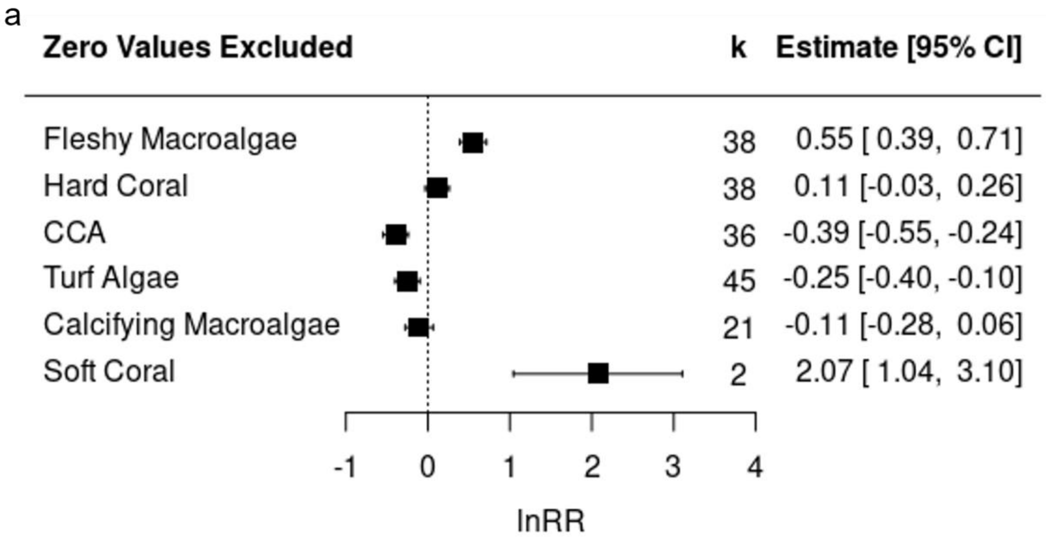
Figure S2. Funnel plot of LnRR vs Standard Error and output from Egger's test for asymmetry used to determine potential publication bias. Outlier was investigated and deemed to be a valid data point, so kept in analysis. Egger's test signified no publication bias ($R^2 = 0.09$, $p = 0.86$)

Table S6. Heterogeneity of effect sizes of upwelling on coral reef benthic groups, given as Cochran's value (Q), and the degrees of freedom (DF) and associated p-value for both the moderator included in the mixed effect meta-analysis model, and also Q, FD and p-value for residual heterogeneity from each model. Wald's Value (I^2) represents the proportion of variation in effect sizes due to heterogeneity rather than chance.

Model	**$Q_{moderator}$**	**DF**	**p-Value**	**$Q_{residuals}$**	**DF**	**p-Value**	**I^2 (%)**
All Studies	379.4594	6	<0.0001	1367.5674	174	<0.0001	67.6
Morphology	1.0924	2	0.5791	1798.0282	178	<0.0001	72.1
Depth	5.6697	3	0.1288	1776.0906	177	<0.0001	70.0
Remoteness	2.6735	2	0.2627	1779.3070	178	<0.0001	71.0
Ocean	6.5006	4	0.1648	1767.8362	176	<0.0001	67.7
Temp drop	0.2005	1	0.6543	1701.4263	153	<0.0001	74.1
Temporal/ Spatial	0.8803	2	0.6493	1786.8906	178	<0.0001	71.5

Dealing with zero percentage cover values in meta-analysis:

Five case studies were removed from the analysis due to mean percentage cover values of 0. These case studies considered hard coral (n = 2) and calcifying macroalgae (n = 3), both from the Equatorial Pacific Island of Jarvis. These values were investigated to see if their inclusion in the meta-analysis model would have greatly affected results. Following Thapa et al (18), a minimum possible value (in this case a hypothetical value of 0.001) was substituted for zero mean values, and the analysis was re-run. A visual comparison of the effects of inclusion can be viewed in Fig S3 below:



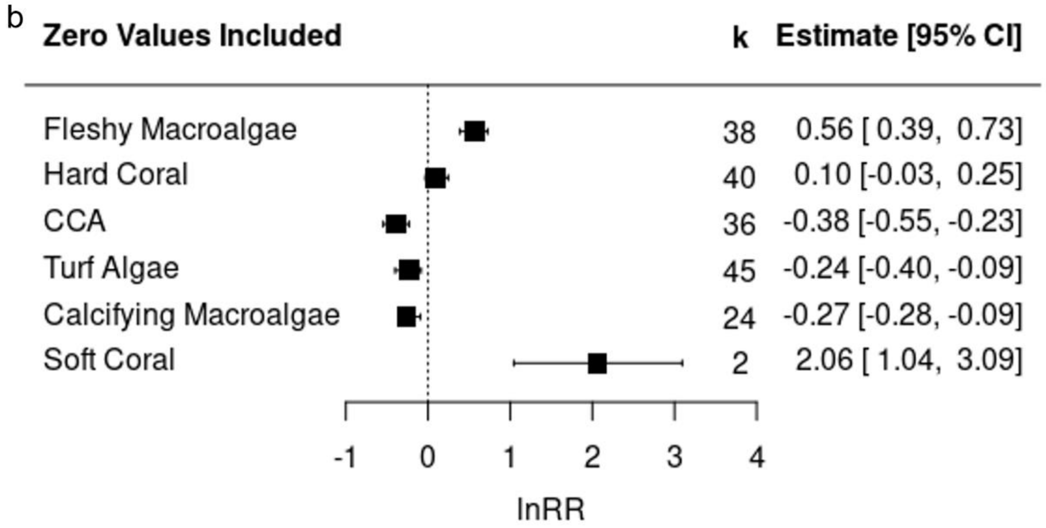


Figure S3 - The lnRR (natural logarithm of response ratio) showing the effect of upwelling on the percentage cover of benthic groups on coral reefs; a) shows the effect of upwelling on benthic groups when 5 case studies with zero mean percentage cover values are excluded from the analysis; b) shows effect when these case studies are included by replacing 0 values with 0.001 percentage cover. Boxes and error bars represent lnRR pooled effect sizes and 95% confidence intervals; values falling to the left of the dotted line indicate a negative effect of upwelling on the percentage cover of benthic groups, and to the right a positive effect. K represents the number of studies considering each benthic group included in the meta-analysis.

All five case studies featured 0 percentage cover values during upwelling and very small percentage cover values during non-upwelling (≤1.3%); the number of replicates for non-upwelling cover assessment were notably higher than for upwelling conditions (see Supplementary Data). It is possible, therefore, that with equal study effort during both upwelling and non-upwelling, a small amount of these benthic groups would have been found under both conditions. Due to the low cover values under non-upwelling conditions and the low comparative replication of benthic survey during upwelling conditions, it was decided that these 5 case studies should be excluded from the meta-analysis rather than imposing fictitious minimum values to allow for comparison. The effect of including these studies on the analysis of hard coral cover was found to be minimal and did not significantly impact hard coral cover response. Including these five case studies resulted in a significant decrease in calcifying macroalgal cover ($p = 0.002$) which was not found ($p = 0.221$) when studies were excluded.

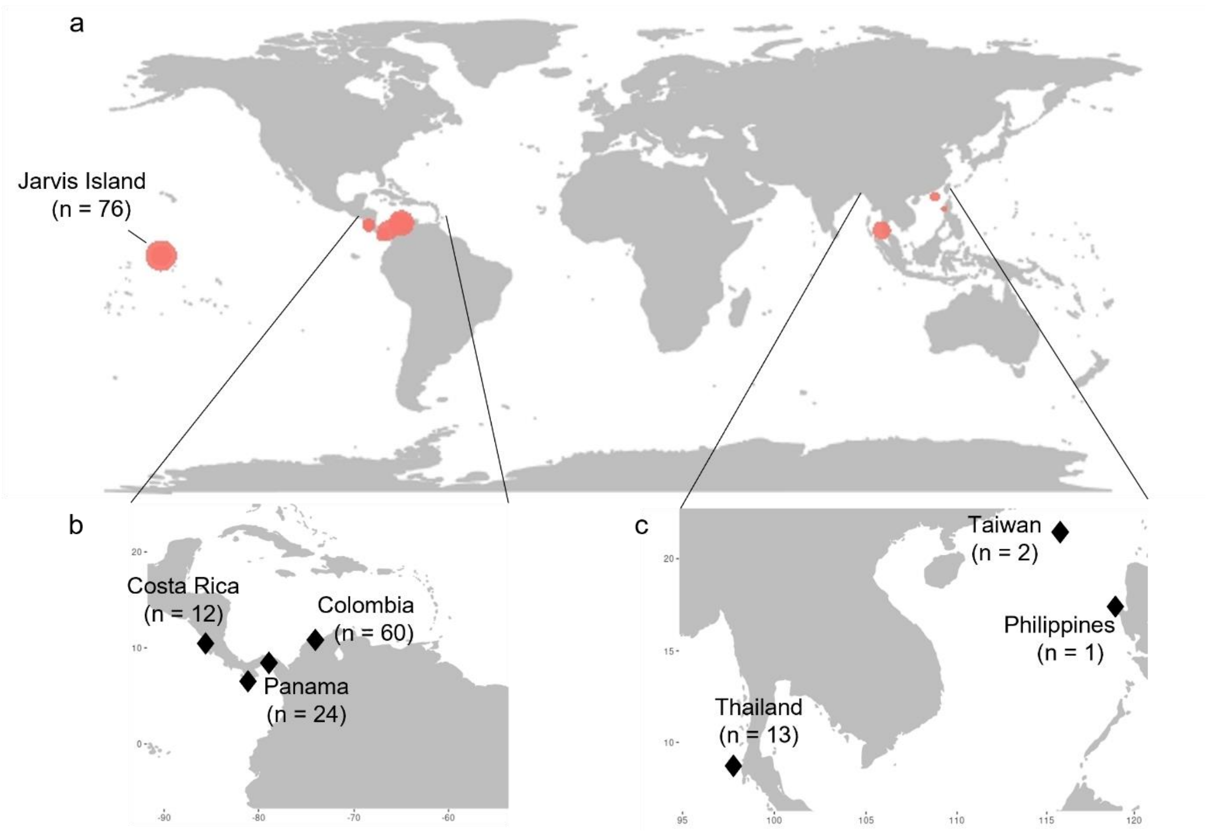


Figure S4 – a) World map showing location of studies used in meta-analysis linking upwelling to benthic community structure on coral reefs. Size of red dots indicates number of case studies undertaken in each geographic location. b) Study locations in Central America, labelled with number of studies per country. c) Studies in Southeast Asia, labelled with number of studies per country.

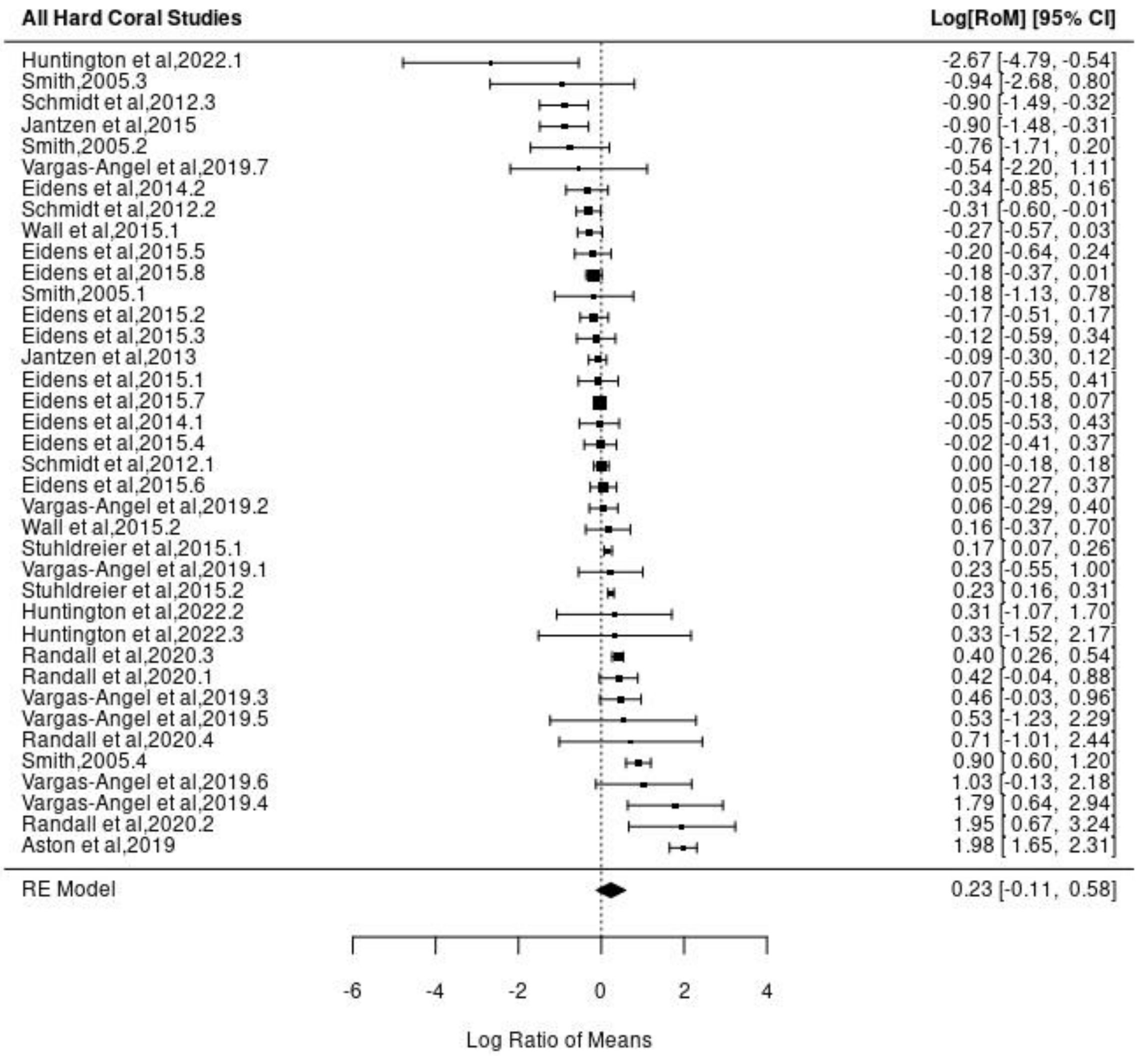


Figure S5. Random effect model displaying effect of upwelling on hard coral cover across studies. Boxes and error bars represent the natural log of response ratio values and 95% confidence intervals; values falling to the left of the dotted line indicate a negative effect, and to the right a positive effect.

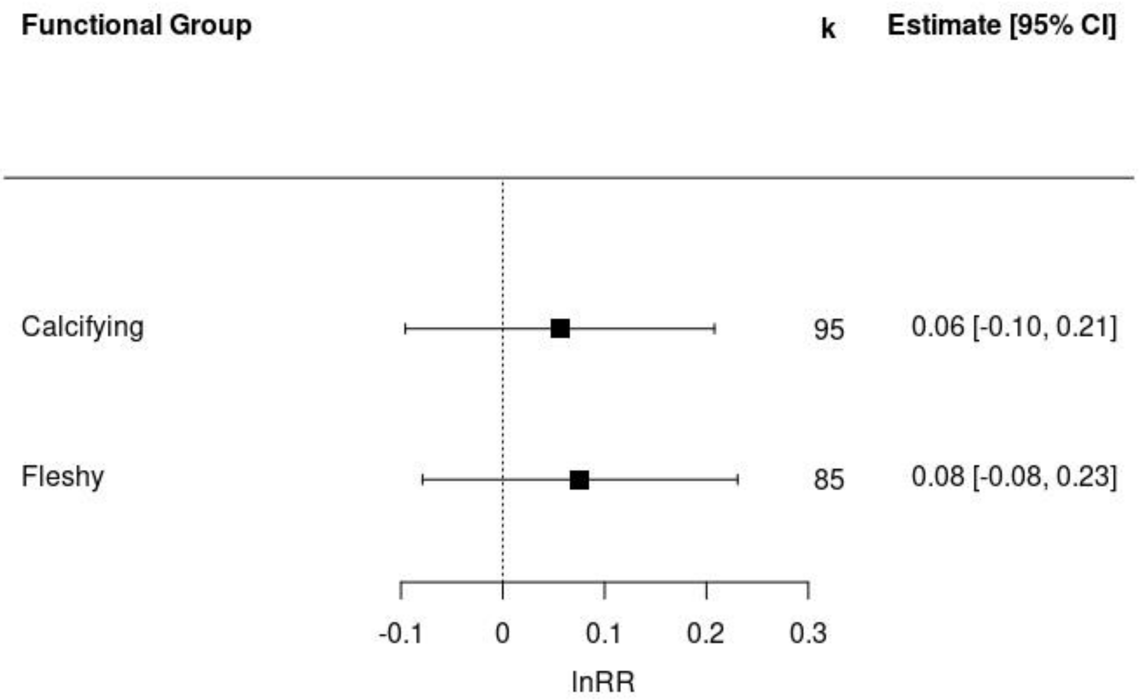


Figure S6. The lnRR (natural logarithm of response ratio) showing the effect of upwelling on the percentage cover of calcifying and fleshy organisms on coral reefs. Boxes and error bars represent lnRR pooled effect sizes and 95% confidence intervals; values falling to the left of the dotted line indicate a negative effect of upwelling on the percentage cover of organisms, and to the right a positive effect. K represents the number of case studies that consider each functional group included in the meta-analysis.

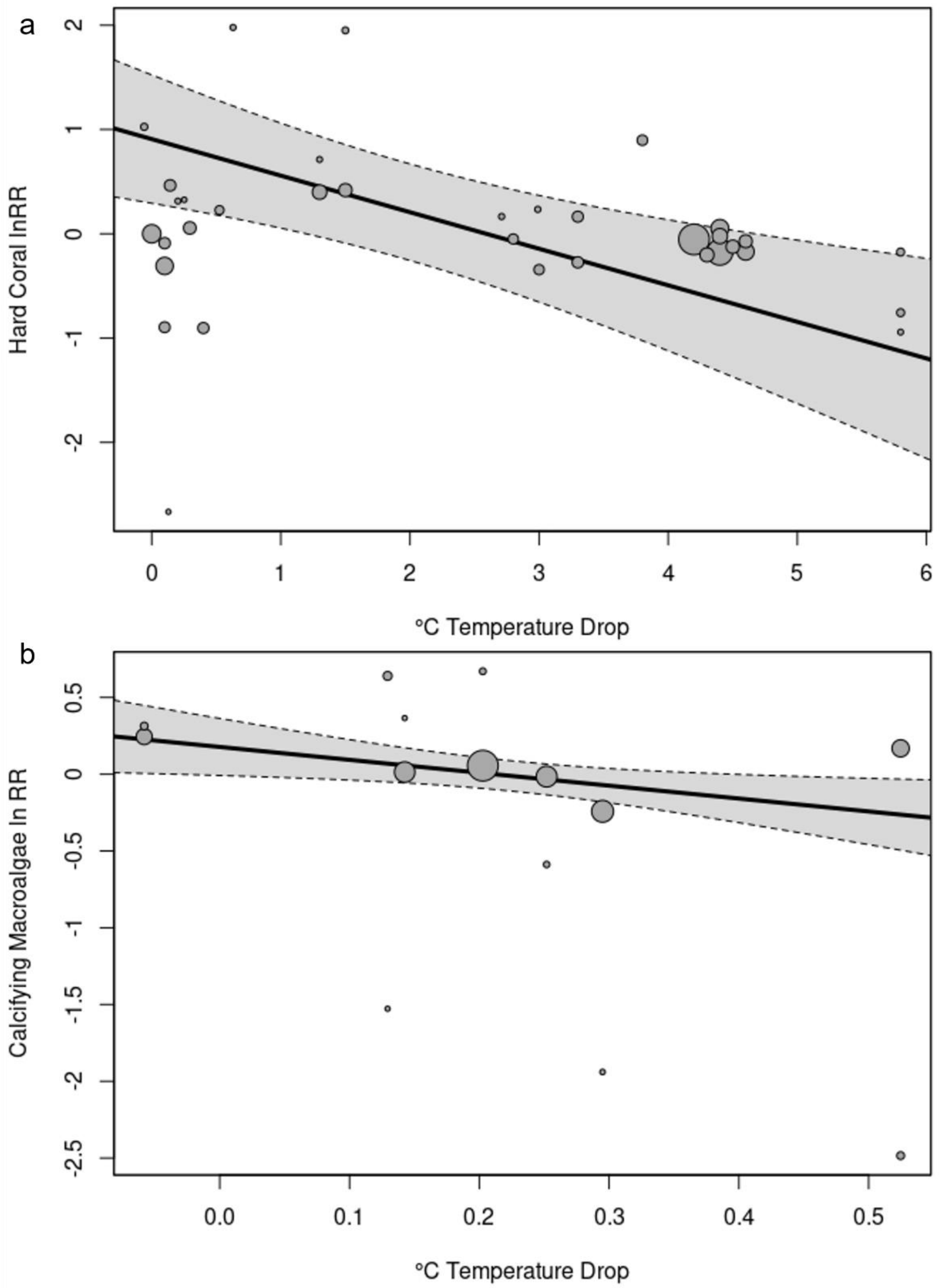


Figure S7. Meta-regression analysis on a) hard coral and b) calcifying macroalgae assessing the effect of degrees temperature dropped during upwelling events on the percentage cover of each group.

References for Supplementary Information

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