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Ocean acidification does not overlook sex: Review of understudied effects and implications of low pH on marine invertebrate sexual reproduction

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Sexual reproduction is a fundamental process essential for species persistence, evolution, and diversity. However, unprecedented oceanographic shifts due to climate change can impact physiological processes, with important implications for sexual reproduction. Identifying bottlenecks and vulnerable stages in reproductive cycles will enable better prediction of the organism, population, community, and global-level consequences of ocean change. This article reviews how ocean acidification impacts sexual reproductive processes in marine invertebrates and highlights current research gaps. We focus on five economically and ecologically important taxonomic groups: cnidarians, crustaceans, echinoderms, molluscs and ascidians. We discuss the spatial and temporal variability of experimental designs, identify trends of performance in acidified conditions in the context of early reproductive traits (gametogenesis, fertilization, and reproductive resource allocation), and provide a quantitative meta-analysis of the published literature to assess the effects of low pH on fertilization rates across taxa. A total of 129 published studies investigated the effects of ocean acidification on 122 species in selected taxa. The impact of ocean acidification is dependent on taxa, the specific reproductive process examined, and study location. Our meta-analysis reveals that fertilization rate decreases as pH decreases, but effects are taxa-specific. Echinoderm fertilization appears more sensitive than molluscs to pH changes, and while data are limited, fertilization in cnidarians may be the most sensitive. Studies with echinoderms and bivalve molluscs are prevalent, while crustaceans and cephalopods are among the least studied species even though they constitute some of the largest fisheries worldwide. This lack of information has important implications for commercial aquaculture, wild

fisheries, and conservation and restoration of wild populations. We recommend that studies expose organisms to different ocean acidification levels during the entire gametogenic cycle, and not only during the final stages before gametes or larvae are released. We argue for increased focus on fundamental reproductive processes and associated molecular mechanisms that may be vulnerable to shifts in ocean chemistry. Our recommendations for future research will allow for a better understanding of how reproduction in invertebrates will be affected in the context of a rapidly changing environment.

KEYWORDS

sperm, egg, fertilization, gametogenesis, fecundity, brooding, spawning, climate change

Introduction

Global climate change is impacting physical, biological, and chemical processes in the marine environment (Hoegh-Guldberg and Bruno, 2010; Howes et al., 2015; Shukla et al., 2019). Absorption of excess carbon dioxide by seawater lowers pH and reduces carbonate ion concentration and aragonite saturation state (Doney et al., 2009). These alterations in water chemistry are referred to as ocean acidification (OA) and can impact marine organisms at multiple levels of biological organization (Melzner et al., 2019). At the organismal level, changing chemistry can influence physiological processes (e.g., calcification, internal pH control, respiration and nutrient uptake), affecting performance and survival (Kroeker et al., 2010; Howes et al., 2015; Melzner et al., 2019). Although there is extensive research on the effects of OA in marine invertebrates, gaps in our understanding of how OA affects sexual reproductive processes (Figure 1) constrain predictions of species persistence, evolutionary adaptation, and biodiversity. For example, acidification could result in decoupling of biological and environmental cues, leading to reproductive failure with significant consequences for population dynamics in marine ecosystems (Shlesinger and Loya, 2019; Olischläger and Wild, 2020) (Figure 2).

Reproduction is a complex process that relies on numerous mechanisms (Figure 1, Box 1); using multiple parameters to evaluate reproductive performance is fundamental to predict how fitness may be impacted by future environmental conditions. OA research has centered around processes during early-life history stages (embryos, larvae, and juveniles), and previous reviews have synthesized trends in organismal responses to OA (Kurihara et al., 2008; Dupont et al., 2010; Albright, 2011b; Ross et al., 2011; Byrne and Przeslawski, 2013; Przeslawski et al., 2015; Ross et al., 2016; Foo and Byrne, 2017). While larval or juvenile performance can be indicative of successful reproduction, an appropriate chemical and physical

environment for gamete development, spawning, mating behavior, and fertilization success is also crucial.

In 2016, nearly 26 million tons of invertebrates were produced for consumption *via* commercial aquaculture, comprising 32% of global aquaculture and 77% of marine and coastal aquaculture that year (FAO, 2018). Invertebrate aquaculture is increasingly leveraged by restoration groups to enhance wild populations that are struggling to recover naturally (Froehlich et al., 2017; Wasson et al., 2020). Both commercial and restoration aquaculture depend upon reliable sources of viable gametes or larvae, which are either produced in controlled hatchery conditions or collected from the wild (Helm et al., 2004; Washington Sea Grant, 2015). Aquaculture production could be hampered if acidification decreases reproductive capacity (Figure 2). In contrast to aquaculture, wild fisheries depend upon an organism's ability to reproduce in the natural environment; any impact of acidification on reproduction will directly influence wild stock available for fisheries. Threatened and endangered marine invertebrates increasingly require human interventions to conserve and restore populations (Elliott et al., 2007). Success of these programs is contingent upon a population's ability to persist naturally and successfully reproduce once interventions cease. Therefore, it is critical that aquaculture, fisheries, and conservation groups identify whether reproductive processes will be impacted by low pH, and how that will impact their focal species' abundance and distribution (Figure 2).

In this review we synthesize the literature to date that has explored how OA impacts reproductive processes of five ecologically, economically, and culturally important marine invertebrate taxa: cnidarians, crustaceans, echinoderms, molluscs, and ascidians. These groups play important roles as keystone species, ecological engineers, aquaculture and fishery products, and model organisms in developmental biology. Our synthesis identifies important gaps in knowledge of the physiological mechanisms involved in reproduction in response to OA in invertebrate taxa important to aquaculture,

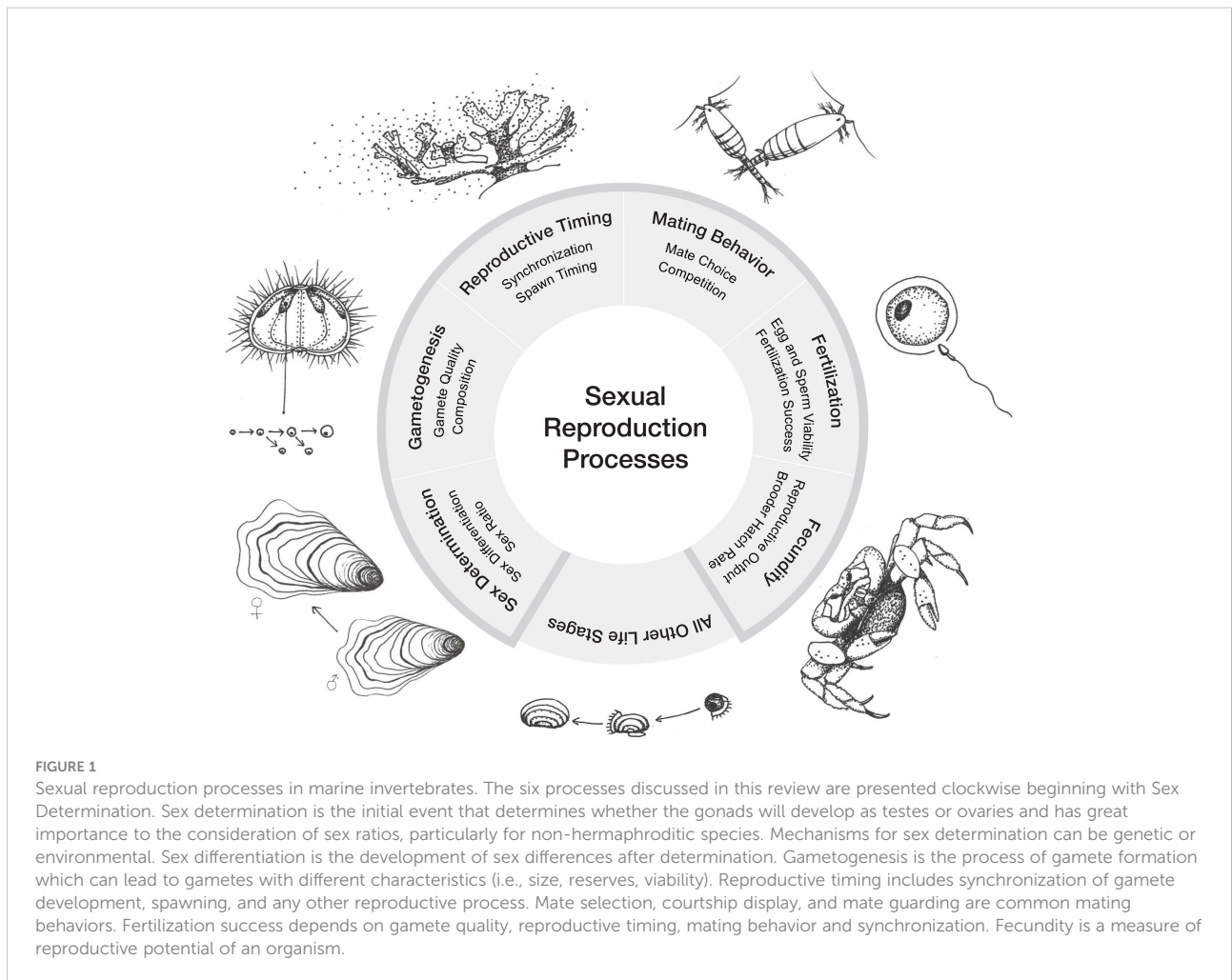
fisheries, and conservation efforts. In addition to fertilization and brooding, we focus on pre-fertilization processes (Figure 1) that are poorly understood both mechanistically and in the context of climate change. Finally, we provide recommendations for future research to better understand how invertebrate sexual reproduction will be affected in the context of a rapidly changing environment.

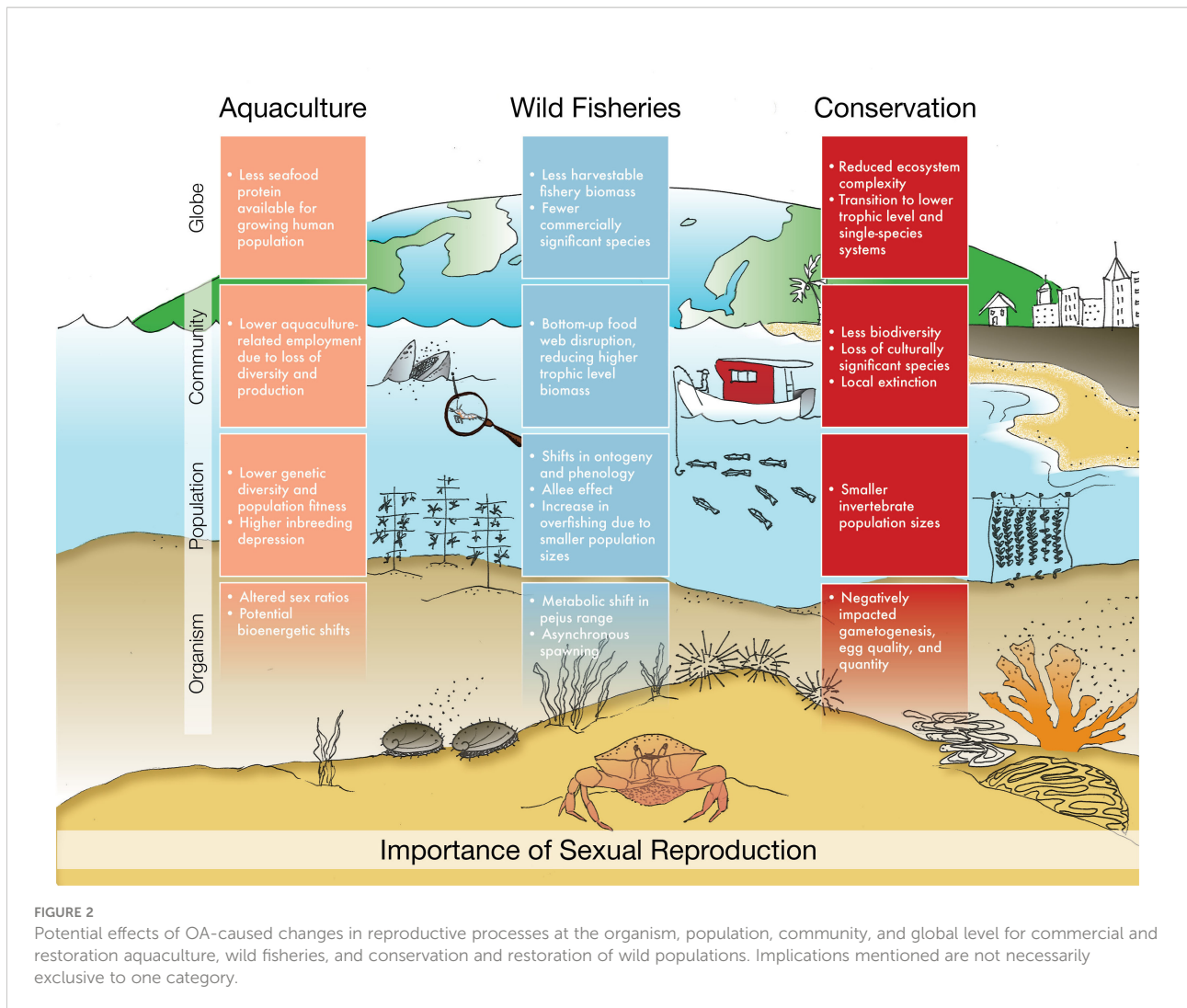
Methods

To identify empirical studies for this review, we searched the literature databases ProQuest, Web of Science, Google Scholar, and European Project on Ocean Acidification (EPOCA) for articles published in English-language journals through the end of 2021 that examined the effects of OA on reproduction in our focal taxa (Table 1). Keywords included British and American spelling for each taxonomic group. We used Boolean search operators to specify or expand our search results. ProQuest, Web of Science, and Google Scholar queries

were sorted by relevance and at minimum 350 results were manually reviewed. We searched all available papers on EPOCA. Google Scholar limits word count for each search, so we broke searches down into several iterations, using the list of common terms in each search and alternating through the taxa-specific terms. We included studies featuring experiments in laboratory and field conditions that included several spatial (m to km) and temporal (minutes to years) scales. We did not include gray literature or observational studies. Throughout the manuscript we will refer to ocean acidification, OA, low pH, or acidification interchangeably.

For each study, the effect of OA on reproduction was determined for the following processes: 1) sex determination, differentiation, and ratio, 2) gametogenesis and gamete quality, 3) fecundity and reproductive output, 4) timing of reproduction and synchronization, 5) mating behavior, and 6) fertilization (Figure 1). While we acknowledge that reproductive processes are linked, we define specific metrics associated with individual processes used to categorize all findings (Box 1). The number of independent findings per reproductive process was summarized





for each taxonomic group. If a study examined multiple reproductive processes, they were categorized independently. Studies that investigated multiple response variables within a single reproductive process (e.g., fertilization rate and sperm motility) and reported an effect of OA on at least one response variable were classified as showing an effect on reproduction.

To characterize geographic location of research, study site and collection site were assigned to one of the 12 Marine Realms of the World (Spalding et al., 2007). If organisms were collected from a different marine realm than where the experiment took place, only the collection location was considered.

Given the extensive literature that quantified and reported fertilization rate in varying pH conditions, we conducted a meta-analysis to explore the response of fertilization to reduced pH in cnidarians, echinoderms, and molluscs. Crustaceans and ascidians were excluded as no studies have directly measured fertilization rate in varying pH treatments. A generalized linear mixed model was developed to estimate fertilization rate by pH using a logit-linked beta distribution. When reported, the

following metrics were extracted from publications, then tested as candidate predictor variables for fertilization success with Analysis of Deviance and chi-squared statistics: 1) difference between experimental and control pH (Δ pH), 2) phylum, 3) lower taxonomic group (e.g. urchin, oyster, coral), 4) incubation time, 5) sperm concentration, 6) sperm:egg ratio, 7) number of sires, 8) number of dams, and 9) pH of the control treatment (Supplemental Table 3). Analysis of covariance (ANCOVA) and the Akaike Information Criterion (AIC) were used to identify the maximal predictive model using variables that significantly affected fertilization rate as sole predictors or as covariates with Δ pH. Significance of intercepts and slope estimates were determined using z-tests. Fertilization data from multiple stressor studies were included in the analysis for all treatments (i.e., all temperature, dissolved oxygen, and salinity treatments) to capture the effect of pH on fertilization rate across a range of environmental conditions. Data from treatments that combined OA and secondary metal contaminants and cocaine byproduct stressors were excluded. When necessary, fertilization rate

BOX 1 Glossary of key reproduction terms.

- Egg fertilization mechanisms:** molecular processes in eggs involved in successful fertilization, including release of egg-derived chemicals, egg-sperm fusion, egg activation and polyspermy prevention
- Egg receptivity:** the length of time an egg can be fertilized by a sperm cell
- Exogenous vs. endogenous reproductive cues:** external environmental cues vs. cues originating within the organism
- F1:** first filial generation comprised of offspring resulting from a cross between two individuals from parental generation
- Fecundity:** number of eggs (or embryos) per individual. For colonial organisms, the number of eggs or sperm per module (i.e., polyp) or number of fecund modules per weight unit, body length or projected area
- Fertilization:** union of male and female gametes during sexual reproduction to form a zygote
- Gamete quality:** size, composition, and developmental stage of gametes
- Gametogenesis:** process by which gametes are produced through meiosis and cell differentiation. Formation of ova occurs through oogenesis and spermatozoa through spermatogenesis
- Gonad condition:** Assessment of gonad development via histological examination
- Gonad Index (GI) or Gonadosomatic Index (GSI):** gonad mass as a proportion of the total body mass [(gonad weight / total tissue weight) X 100]
- Gravid:** carrying eggs or young offspring
- Hatching success:** percentage of eggs which produce viable offspring
- Indeterminate vs. determinate sex:** ability to change sex during an organism's lifetime vs having a defined sex at birth
- Mating behavior:** social interaction that prepares for, or increases the success of, copulation and fertilization
- Mass spawning:** synchronous release of gametes by many species or the majority of a mating aggregation
- Oocyte:** cell in an ovary which may undergo meiotic division to form an ovum
- Oosorption (atresia):** process of resorbing vitellogenic eggs under stress to reuse lipids for other physiological processes
- Phenology:** study of periodic events in biological life cycles and how they are influenced by local, seasonal, and interannual environmental variation
- Polyspermy:** occurs when an egg is fertilized by more than one sperm
- Reproductively inactive vs. sexually immature:** sexually mature individual not presently breeding vs. one not old or big enough to undergo gametogenesis
- Reproductive output:** number of reproductive elements (sperm or egg) per unit body volume. Can also be measured by counting embryos per unit body volume. In colonial organisms, reproductive output is the total amount of gametes released by the colony. In some cases, fecundity and reproductive output are used interchangeably
- Resource allocation:** proportion of an organism's energy budget allocated to reproduction
- Sex determination:** initial event before sex differentiation that determines whether gonads will develop as male or female
- Sex differentiation:** events after sex determination that ultimately produce either the male or female sexual phenotype
- Sire and dam:** father and mother of a genetic line
- Spawnd bundle:** sperm and/or egg clusters released to the water column for external fertilization
- Sperm activity:** sperm swimming behavior, including motility, velocity or speed, and path linearity
- Sperm linearity:** how straight the sperm is swimming, as calculated by the ratio of average velocity on a straight line from start to endpoint of the sperm's path to the curvilinear velocity along the sperm's path
- Sperm velocity:** defined by (1) curvilinear velocity along the sperm's path, (2) smoothed average sperm path velocity, (3) average velocity on a straight line from start to endpoint of the sperm's path
- Spermatocyte:** male gametocyte from which spermatozoa develop
- Standardized Gonad Index (SGI):** reproductive cycle indicator based on the differences between the observed and expected weights of the gonads for an individual of a given size. Takes into account allometric gonadal growth
- Synchronization:** coordination of reproductive events to increase mating potential, fertilization, and offspring success
- Timing of reproduction:** milestones that rely on environmental and chronological cues
- Vitellogenins:** principal precursors to the yolk proteins (the vitellins) of egg-laying animals, but not present in all marine invertebrates
- Volitional vs. strip or induced spawning:** release of gametes via natural or hormonal means vs artificially releasing gametes through anthropogenic means

estimates were extracted from published figures using WebPlotDigitizer v4.2. In addition to exploring fertilization rates across all experimental pH levels (6.0 - 8.5), we also examined the response of fertilization to pH using conditions more relevant to OA (pH >7.6) (IPCC, 2022). For all models tested, study was included as a random effect. Data were weighted by the inverse of one plus the sampling variance squared ($1/(1+\sigma^2)^2$), which was determined from the

fertilization mean, error rate (standard deviation), and number of trials conducted at each pH level. The value 1 was added to every sampling variance to prevent overinflation of low variances (between 0-1) in models (Fiorenza et al., 2020). Resultant p-values were considered significant if they were less than $\alpha = 0.05$.

Of the 70 studies that experimentally tested fertilization rates in multiple pH conditions, six were omitted (one, four, and one

in echinoderms, molluscs, and cnidarians, respectively) due to missing error rates (corresponding authors were contacted). The resulting meta-analysis included data from 35, 23, and 6 studies in echinoderms, molluscs, and cnidarians, respectively. We recognize that the fertilization rate reported by some studies may represent both fertilization rate and early embryonic development success. Other reproductive processes included in this review (Figure 1) were not considered for meta-analyses given the inconsistent metrics reported and/or the limited number of studies (Figure 3C).

Results and discussion

We identified a total of 129 studies (16 cnidarian studies, 25 crustacean studies, 69 echinoderm studies, and 56 molluscan studies) that investigated the effects of OA on reproduction in 122 species total (19 cnidarian species, 38 crustacean species, 30 echinoderm species, and 35 mollusc species; Supplemental Table 1). Only two studies examining OA impacts on ascidian reproduction were identified. In ascidian *Ciona robusta*, OA significantly decreased sperm motility, mitochondrial membrane potential (MMP), and intracellular pH (pH_i) (Gallo et al., 2019) but did not affect sperm intracellular reactive oxygen species (ROS), lipid peroxidation, nor viability (Gallo et al., 2019; Esposito et al., 2020). *In situ* and microcosm experiments showed that in *C. robusta*, OA initially decreased sperm motility, viability, MMP, pH_i, and morphology, but sperm underwent rapid recovery after within one week of exposure, suggesting that ascidian spermatozoa is resilient to OA (Gallo et al., 2019). Given the lack of ascidian studies, the remainder of this review will focus on the remaining four taxa.

Echinoderm research comprises the majority (53.5%) of OA and reproduction studies, followed by research in molluscs (43.4%) (Figures 3A, B). The same echinoderm and mollusc species are examined in multiple studies, while cnidarian and crustacean studies tend to study unique species (Supplemental

Table 1). Except for one echinoderm study published in 1924, all OA and reproduction research highlighted in this review was conducted between 2004 and 2021 (Figure 3B). The majority of the studies were performed under laboratory conditions (Supplemental Table 2) highlighting the need for more research in mesocosms and the natural environment. Life stages exposed to OA and duration of experiments were variable among taxa (Supplemental Table 2). Most studies collected organisms from the Temperate Northern Atlantic Marine Realms (Spalding et al., 2007), followed by Temperate Northern Pacific and Temperate Australasia (Figure 3A). Collection sites are reported in Figure 3A, and study sites (which in some instances differ from collection location) are included in Supplemental Table 1.

Published research suggests that the effects of OA depend on the taxa and the specific process studied (Figure 3C). Within each taxon, OA studies focus on a handful of species. Copepods dominated crustacean literature, while urchin species were prominent in echinoderm studies. All cnidarian studies examined corals. There was only one cephalopod study within molluscan research.

Impacts of ocean acidification on sexual reproduction processes

In this section, we summarize ocean acidification studies for cnidarians, crustaceans, echinoderms, and molluscs by reproductive process (Supplemental Table 1). See the Supplementary Materials for a more comprehensive synthesis of results.

Sex determination, differentiation, and ratio

The sex of many invertebrate species is sensitive to environmental conditions, which can skew populations' sex ratios (Korpelainen, 1990; Yusa, 2007). Changes to the number and proportion of mature females and males at a given time can alter a population's reproductive capacity, its effective population size, and its genetic diversity. There are no studies

TABLE 1 This review utilized specific keywords to search several literature databases.

Keywords

All Taxa	climate change, ocean acidification, carbonate chemistry, CO ₂ , hypercapnia, aragonite saturation state, reproduction, gamete*, sperm*, egg*, ovary, oocyte*, fertilization, fecund*, mating behavior, behavior, gametogenesis, reproductive output, synchronization, brood*, hatch*, spawn*, spawning, sex*, determination, differentiation, gonad development
Cnidaria	coral*, jelly*, hydroid, zoanthid*, sea pen, gorgonian, siphonophore, anemone, cnidaria*, cubozoa*, anthozoa*, scyphozoa*, hydrozoa*, myxozoa*, medusa*, medusozoa*, polipodiozoa*, staurozoa*, hexacorallia*, octocorallia*, hydromedusae*, scleractinia*, zoantharia*, corallimorpharia*
Crustacea	crustacean*, arthropod*, malacostraca*, crab*, lobster*, shrimp*, amphipod*, copepod*, barnacle*, decapod*, brachyura*, artemia*, ostracoda*, dendrobranchiata*, isopod*, branchiopoda*, mysid*, hermit*, zoea*, krill*, cyst*, prawn*
Echinodermata	echinoderm*, sea star*, starfish*, urchin*, sand dollar*, brittle star*, sea cucumber*, feather star*, crinoidea*, echinozoa*, holothuroidea*, echinoidea*, asterozoa*, ophiuroidea*, asteroidea*
Asciidacea	ascidian*, sea squirt, tunicate, tunicata, urochordata, sea tulip, sea liver, sea pork, ascidiacea, thaliacea, appendicularia, salp, doliolid

Each taxonomic group used a common list of words, which were followed by a list of taxa-specific words. Keywords unique to each taxa included both common names and Latin nomenclature for major classifications. The Boolean search operator asterisk (*) was used as a "wildcard operator" to search for words or phrases that may contain parts of that truncated word. In addition to the general terms, all taxa specific terms were given an asterisk.

that have directly examined effects of acidification on sex determination or differentiation in individuals of any taxa covered in this review. However, we identified several studies that examined effects of acidification on sex ratios. The sole crustacean study did not find differences in sex ratios in copepods when reared in OA conditions (Kita et al., 2013). Two studies that exposed oysters to low pH prior to and during gametogenesis also reported no impact on gonad sex ratios (Venkataraman et al., 2019; Clements et al., 2020). In contrast, three oyster studies indicated that acidification exposure during gametogenesis may alter populations' sex ratios by impacting egg and sperm development unequally. Sex-specific impacts of OA on gametogenesis therefore reduce the proportion of females (Boulais et al., 2017) or males (Parker et al., 2018; Spencer et al., 2020) capable of breeding in a population, thereby reducing the effective population size. These studies are challenging due to the difficulty of identifying sex without harming or destroying the organisms being investigated (Ellis et al., 2017), the lack of sex biomarkers, and the limited understanding of hormonal control on reproductive processes in marine invertebrates.

Gametogenesis and gamete quality

Environmental conditions during gametogenesis can influence population dynamics through changes to gamete

development and quality. Several metrics are associated with gametogenesis, including gamete size, stage, biocomposition, integrity, viability, developmental rate, maturation, and spawning capability. In cnidarians, OA negatively affected octocoral egg size (Rossin et al., 2019), while hexacoral studies showed no effect of OA on gamete size (Fine and Tchernov, 2007; Gizzi et al., 2017; Caroselli et al., 2019; Marchini et al., 2021) or maturation stage (Fine and Tchernov, 2007; Gizzi et al., 2017; Caroselli et al., 2019). However, Marchini et al. (2021) showed a delay in spermary development due to OA. In crustaceans, OA resulted in delayed gametogenesis and smaller spermatophores (Fitzer et al., 2012a; Cripps et al., 2014; Meseck et al., 2016; Conradi et al., 2019). OA did not affect copepod egg viability, oogenesis (Vehmaa et al., 2013; Thor et al., 2018), or barnacle and copepod gametogenesis (Smith et al., 2017; Pansch et al., 2018).

OA had negative effects on gonad growth, maturation, egg size, and gamete development in some echinoderm species (Siikavuopio et al., 2007; Kurihara, 2008; Stumpp et al., 2012; Kurihara et al., 2013; Suckling et al., 2014; Suckling et al., 2015; Verkaik et al., 2016; Dworjanyn and Byrne, 2018; Hu et al., 2018; Hue et al., 2020; Marčeta et al., 2020; Anand et al., 2021), while other studies reported no change in gamete development and quality (Wood et al., 2008; Uthicke et al., 2013; Hazan et al.,

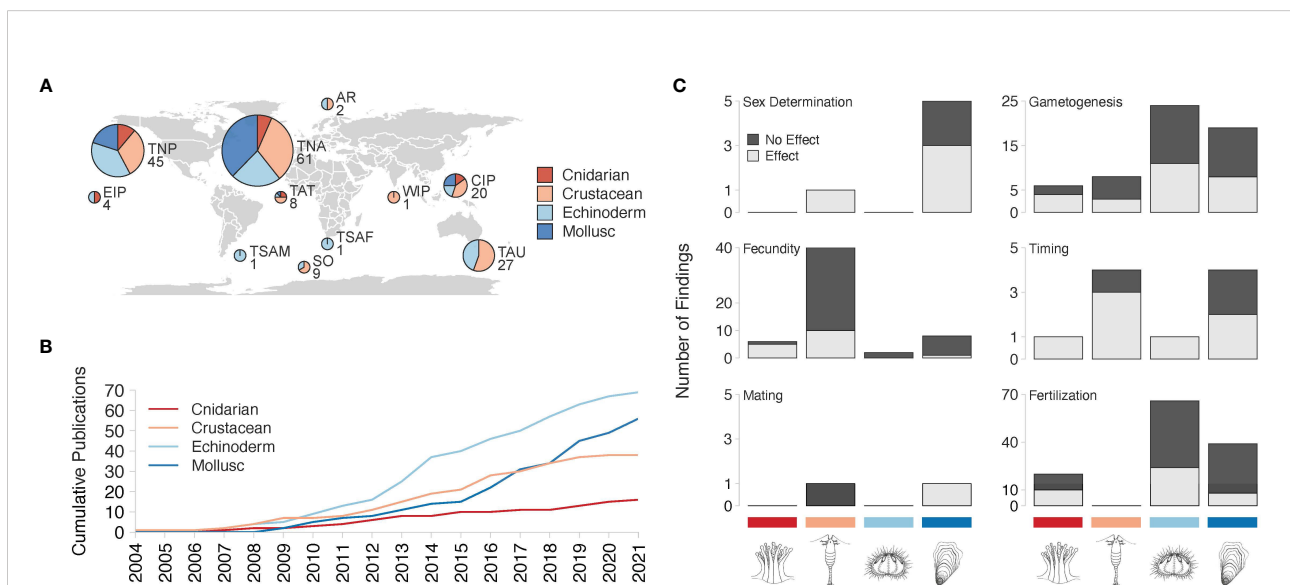


FIGURE 3

Summary of study locations, number of publications, and effects of Ocean Acidification on Reproductive Processes across taxa. (A) Graphical description of published studies used in this review. Pie charts for each geographic study locations are labeled with initials and the number of studies from that realm: Eastern Indo-Pacific (4), Temperate Northern Pacific (45), Temperate Northern Atlantic (61), Tropical Atlantic (8), Southern Ocean (9), Temperate Southern Africa (1), Arctic (2), Western Indo-Pacific (1), Central Indo-Pacific (20), and Temperate Australasia (27). There were no studies from Tropical Eastern Pacific. Pie charts represent the proportion of taxa-specific studies in which study organisms were collected in each region, and pie size and numbers underneath the pies represent the total number of studies in that region. Studies may be represented more than once in a pie chart if the study examined multiple taxa. (B) Cumulative number of papers published for each taxon from 2004 to 2021. One echinoderm study was published in 1924 but was not included in this figure. Studies may be represented more than once per year if the study examined multiple taxa. (C) Number of findings that reported an OA effect (either positive or negative, light gray) or no effect (black) for various reproductive processes by taxa (from left to right: cnidarians, crustaceans, echinoderms, molluscs).

2014; Uthicke et al., 2014; Dell'Acqua et al., 2019; Karelitz et al., 2019; Wong et al., 2019; Hue et al., 2020; Uthicke et al., 2020). One study reported a positive effect on gonad protein storage after low pH exposure (Challener et al., 2014). Suckling et al. (2015) suggests egg size is plastic in response to OA, and longer exposure to low pH can lead to larger eggs due to increased maternal provisioning.

Most studies in molluscs indicate that low pH exposure affects the rate of gametogenesis, typically by decreasing gamete development or spawning rates (Xu et al., 2016; Boulais et al., 2017; Parker et al., 2018; Zhao et al., 2019; Spencer et al., 2020; Wang et al., 2021), or less commonly by accelerating gamete development (Dell'Acqua et al., 2019; Clements et al., 2020). However, no impact of OA on molluscan gametogenesis has also been reported (Le Moullac et al., 2016; Venkataraman et al., 2019). Molluscan egg quality may be resilient to OA, as most studies report no impact to egg size or lipid content (Parker et al., 2017; Parker et al., 2018; Scanes et al., 2018; Parker et al., 2021; Reed et al., 2021; Gibbs et al., 2021a) (but see Spady et al., 2020, the sole non-bivalve study). Two studies do report increased egg size or lipid content in response to OA (Zhao et al., 2019; Gibbs et al., 2021b), which can be indicative of higher energy content and egg quality (Moran and McAlister, 2009). While other egg quality parameters are possibly vulnerable (e.g., egg rupture rate, Omoregie et al., 2019), most studies indicate that molluscan species prioritize per-egg maternal investment when exposed to low pH, in some cases over gametogenic rate. In one of the few studies utilizing naturally low pH environments, *Bathymodiolus septemdierum* mussels were collected from hydrothermal vents, which reach conditions as low as pH 5.2. These mussels can maintain similar egg sizes and gametogenic cycles compared to those living in higher pH sites, possibly at the expense of calcification (Rossi and Tunnicliffe, 2017). This study provides evidence that OA-adapted populations are capable of gametogenesis despite extreme pH conditions. Given the variable responses in gametogenesis and gamete quality across phyla, species, and even populations, broader characterizations are needed to better understand how OA will impact physiological performance and allocation to energy expensive processes such as gamete development.

Fecundity and reproductive output

The fecundity and reproductive output of individuals and populations can vary along environmental gradients. In this section we highlight studies that assess fecundity and reproductive output in varying OA conditions. We considered hatch rate as a proxy for fecundity and reproductive success in brooding organisms. Cnidarian studies report no effect of OA on fecundity in hexacorals. The number of eggs, sperm, or gamete bundles were not affected by OA in four hexacoral species (Jokiel et al., 2008; Gizzi et al., 2017; Caroselli et al., 2019; Marchini et al., 2021). Most of these studies report reduced adult growth

under OA, suggesting resources may have been allocated towards reproduction over growth. In the sole octocoral study, exposure to OA reduced the number of eggs per polyp (Rossin et al., 2019). In echinoderms, OA negatively affected egg production (Dupont et al., 2013). Three molluscan studies report negative effects of OA across reproductive modes, with decreased pH reducing fecundity and spawn rate in a broadcast spawner (Parker et al., 2018), and reducing clutch size and egg masses in two oviparous species (Dionísio et al., 2017; Spady et al., 2020). Two studies reveal the complexity of responses to OA in molluscs, including reduced fecundity but more frequent spawn events (Manno et al., 2016), and unaffected spawn frequency and number of egg capsules (Kita et al., 2013).

Studies that measure hatch rate in brooders were limited to crustaceans and molluscs, as hatch rate was not reported for brooding species in any other taxa. Several brooding crustacean species held at low pH were found to have differences in fecundity, hatch success, or number of offspring (Kurihara et al., 2004; Mayor et al., 2007; Kurihara et al., 2008; Findlay et al., 2009; Zhang et al., 2011; Vehmaa et al., 2012; Weydmann et al., 2012; Kita et al., 2013; Long et al., 2013; McConville et al., 2013; Zervoudaki et al., 2013; Cripps et al., 2014; Cao et al., 2015; Swiney et al., 2015; Thor and Dupont, 2015; Choi et al., 2016; Miller et al., 2016; Vehmaa et al., 2016; Borges et al., 2018a; Cardoso et al., 2018; Gravinese, 2018; Pansch et al., 2018; Thor et al., 2018; Lee et al., 2020). One study in copepods found that OA reduced the number of brooding females (Lee et al., 2019). Several crustacean studies, however, showed that fecundity or hatch rate were unaffected by OA (Kurihara et al., 2004; Mayor et al., 2007; Kurihara and Ishimatsu, 2008; Egilsdottir et al., 2009; Zhang et al., 2011; Weydmann et al., 2012; McConville et al., 2013; Vehmaa et al., 2013; Cripps et al., 2014; Cao et al., 2015; Isari et al., 2015; Almén et al., 2016; Rains et al., 2016; Zervoudaki et al., 2017; Thor et al., 2018; Langer et al., 2019). One study found that OA can increase fecundity, and another found that low pH increased reproductive output, but at the cost of body size and shell integrity (Fitzer et al., 2012b; Engström-Öst et al., 2014). In molluscs, OA exposure during breeding reduced bivalve brood size (Wippel, 2017; Maboloc and Chan, 2021), while a previous OA exposure resulted in increased brood size but no effect to overall larval production (Spencer et al., 2020). Instances where reproductive output increases may be a short-term stress response or may indicate adaptive potential to pH change (Engström-Öst et al., 2014). Overall, research to date suggests that OA negatively affects fecundity and reproductive output in molluscs and echinoderms, while some cnidarians appear to be less sensitive, and responses in crustaceans are variable.

Timing of reproduction and synchronization

Synchronicity and timing of reproductive maturation, spawning, hatching, and planulation are important to ensure reproductive success. In a brooding coral, OA conditions delayed planulation timing (Putnam et al., 2020). OA may

affect the timing at which brooding crustaceans reach milestones associated with hatching. When female copepods and crabs were acclimated to OA conditions, copepod hatching occurred earlier and crabs hatched for a longer duration (Long et al., 2013; Langer et al., 2019). However, there was no effect of OA on egg onset time in the barnacles (McDonald et al., 2009). On the other hand, OA did not affect the number of days that copepods needed to form mating pairs, successfully copulate, and spawn (Kita et al., 2013). A volitional spawning experiment in sea cucumbers reported no effect of OA on spawn timing (Verkaik et al., 2016). In molluscs, studies that induced spawning found reductions in spawning success in acidified conditions (Xu et al., 2016; Parker et al., 2018). Two studies examined impacts of OA on volitional spawning in a brooding molluscan species: one reported no effects to larval release timing (Spencer et al., 2020), and another reported delayed larval release onset in one of three trials (Wippel, 2017). More studies that incorporate natural spawning and planulation conditions are needed. Studies that monitor the number and timing of naturally breeding males and females would improve our understanding of ecologically relevant impacts of acidification on spawn timing and synchronicity.

Mating behavior

Marine species are diverse in their mating behaviors. However, there is a very limited number of OA studies to date examining mating behavior, limiting the number of observable behavioral metrics. We summarize two studies that measure mate selection, courtship display, and mate guarding. Male mate tracking and guarding behavior in amphipods were disrupted under OA conditions, which may have negative consequences for fertilization (Borges et al., 2018b). The ability for amphipods to detect and orient toward female pheromone cues through chemotaxis was greatly reduced under OA, suggesting potential disruptions in chemosensory cues related to food acquisition, defense, and predator avoidance behaviors under low pH. Squid mating pair behavior was unaffected by OA, even though females laid denser egg clutches after the pair were exposed to low pH (Spady et al., 2020). More studies are needed to explore the impacts of OA on invertebrate mating behavior, particularly in cephalopod, gastropod, and crustacean species with sophisticated mating behaviors (e.g., changing body patterns and textures, parallel swimming, male-male fighting, and mate guarding). It is critical that we expand our understanding of mating behavior in invertebrates exposed to OA because disruptions may have rippling effects on population fitness and ultimately, the future of the species.

Fertilization

Many marine invertebrates broadcast spawn and undergo external fertilization, which exposes gametes to the surrounding environment prior to and during fertilization. Acidification may

affect fertilization success by altering chemosensory and biochemical egg-sperm interactions, therefore directly influencing gamete activation, sperm activity, egg biochemistry and polyspermy defense (Mortensen and Mortensen, 1921; Nakajima et al., 2005; Miyazaki, 2006; Lymbery et al., 2019). The impact of OA on fertilization and gametes has been reviewed previously (Byrne, 2011; Byrne, 2012; Byrne and Przeslawski, 2013; Foo and Byrne, 2017). Here we provide an updated review of 92 studies that have assayed fertilization, sperm quality, and/or egg biochemical processes under OA conditions, the majority of which were published since prior reviews. Additionally, we conducted a meta-analysis to evaluate general trends across and within echinoderms, molluscs, and cnidarians. Crustaceans were not included in the meta-analysis as no studies have directly measured fertilization rate in varying pH treatment, likely because they undergo internal fertilization.

Fertilization rate

Reviews by Byrne (2011; 2012) found that fertilization rate is robust in pH above ~7.6. However, discrepancies were noted among studies of the same species and conspecifics from different habitats. The authors encouraged researchers to examine other taxa with standardized experimental designs. Since then, an additional 51 studies have assessed fertilization rate in varying pH conditions.

The majority of studies, which predominantly evaluate echinoderms (largely urchins) and bivalve molluscs, conclude that acidification negatively affects fertilization rate when gametes are directly exposed (Smith and Clowes, 1924; Kurihara and Shirayama, 2004; Havenhand et al., 2008; Parker et al., 2009; Ericson, 2010; Parker et al., 2010; Kimura et al., 2011; Moulin et al., 2011; Schlegel et al., 2012; Van Colen et al., 2012; Barros et al., 2013; Gonzales-Bernat et al., 2013; Uthicke et al., 2013; Foo et al., 2014; Frieder, 2014; Scanes et al., 2014; Suckling et al., 2014; Sung et al., 2014; Riba et al., 2016; Boch et al., 2017; Shi et al., 2017a; Shi et al., 2017b; Szalaj et al., 2017; Zhan et al., 2017; Basallote et al., 2018; García et al., 2018; Świeżak et al., 2018; Zhan et al., 2018; Smith et al., 2019; Sui et al., 2019; Wang et al., 2020), or parents are exposed prior to fertilization (Graham et al., 2015). The pH level at which fertilization rate becomes compromised varies considerably across taxa, and also depends on factors such as sperm and egg concentration (Ericson, 2010; Albright, 2011a; Ericson et al., 2012; Albright and Mason, 2013; Gonzales-Bernat et al., 2013; Ho et al., 2013; Frieder, 2014), gamete incubation time (Bechmann et al., 2011; Gianguzza et al., 2014; García et al., 2018; Kong et al., 2019), inter-individual and mating pair variability (Schlegel et al., 2012; Foo et al., 2014; White et al., 2014; Smith et al., 2019), collection location and time of year (Martin et al., 2011; Cohen-Rengifo et al., 2013; Pecorino et al., 2014; Riba et al., 2016; Basallote et al., 2018; García et al., 2018; da Silva Souza et al., 2019; Pereira et al., 2020; Caetano et al., 2021), and species hybridization (Striewski,

2012). Parental acclimatization to low or highly variable conditions (including pH) can either increase (Moulin et al., 2011; Suckling et al., 2014; Kapsenberg et al., 2017) or decrease fertilization rates in low pH (Graham et al., 2015).

Negative effects of OA were not universally reported (Byrne et al., 2009; Byrne et al., 2010a; Byrne et al., 2010b; Schlegel et al., 2012; Byrne et al., 2013; Chua et al., 2013; Kamyra et al., 2014; Onitsuka et al., 2014; Stavroff, 2014; Bylenga et al., 2015; Iguchi et al., 2015; Schutter et al., 2015; Foo et al., 2016; Zhan et al., 2016; Boulais et al., 2017; García et al., 2018; Armstrong et al., 2019; Lenz et al., 2019; Smith et al., 2019; Guo et al., 2020; Hue et al., 2020; Pitts et al., 2020), which indicates that fertilization in some species may be more resilient than others to the effects of acidification. Several studies report that *Mytilus* spp. mussels, for example, are capable of maintaining high fertilization rates across a broad pH range (Bechmann et al., 2011; Eads et al., 2016; Riba et al., 2016; Gallo et al., 2020). Fertilization in some molluscan and echinoderm species can persist at severely low pH (e.g., ~23% of *Crassostrea gigas* eggs were successfully fertilized at pH 6.0, Riba et al., 2016).

In rare instances, low pH can increase fertilization rate. Higher fertilization rates occur in *Mytilus galloprovincialis* when sperm are pre-exposed to low pH conditions in the presence of egg-derived chemicals (Lymbery et al., 2019). These results could be explained by a stronger attraction of sperm to egg-derived chemicals under low pH conditions, resulting in increased fertilization rates. As suggested by Lymbery et al. (2019), increased fertilization rates are not necessarily beneficial to population fitness. OA could alter chemical cues that would typically only occur among genetically compatible sperm and eggs, resulting in higher rates of fertilization among incompatible genotypes, and ultimately decreasing the overall population fitness (Lymbery et al., 2019).

Fertilization rate meta-analysis

Studies that reported fertilization rates across multiple pH levels were leveraged to perform a meta-analysis to quantify broad-scale impacts of pH on fertilization rate in cnidarians, echinoderms, and molluscs. Change in pH ($\Delta\text{pH} = \text{pH}_{\text{experimental}} - \text{pH}_{\text{control}}$) across all taxa significantly predicts fertilization success as a sole predictor ($X^2 = 22.0$, $p = 2.7e^{-6}$). Using ANCOVA we modeled fertilization rate by ΔpH and other candidate covariates. The most parsimonious model was selected using AIC criterion, and retained only the interaction between ΔpH and phylum (phylum: ΔpH , $X^2 = 34.3$, $p = 1.7e^{-7}$), and phylum as a main effect ($X^2 = 3.4$, $p = 0.18$), indicating that the response of fertilization rate is phylum-specific. The probability of successful fertilization is estimated by:

$$p(\text{fertilization success, cnidarians}) = \frac{e^{(0.92 + 2.43 * \Delta\text{pH})}}{1 + e^{(0.92 + 2.43 * \Delta\text{pH})}}$$

$$p(\text{fertilization success, echinoderms}) = \frac{e^{(1.16 + 1.92 * \Delta\text{pH})}}{1 + e^{(1.16 + 1.92 * \Delta\text{pH})}}$$

$$p(\text{fertilization success, molluscs}) = \frac{e^{(1.13 + 0.32 * \Delta\text{pH})}}{1 + e^{(1.13 + 0.32 * \Delta\text{pH})}}$$

where the ΔpH coefficient estimates for cnidarians, echinoderms, and molluscs are 2.43 ($z\text{-score} = 1.24$, $p = 0.22$), 1.92 ($z\text{-score} = 5.75$, $p = 9.0e^{-9}$), and 0.32 ($z\text{-score}=0.71$, $p = 0.48$), respectively (Figure 4). The positive ΔpH coefficients indicate that fertilization rate decreases with pH in all phyla; however, ΔpH only significantly predicts fertilization for echinoderms. While pH is not a significant factor in the cnidarian model, likely due to limited data (6 studies), the model does suggest high pH sensitivity (Figure 4) and underlines the need for more cnidarian fertilization studies. The large number of studies in the echinoderm (35) and mollusc (23) models enables more confident predictions in those two taxa. Echinoderm fertilization appears to be more sensitive than molluscs to pH changes, which could reflect habitat differences in most species studied to date (largely subtidal echinoderms and intertidal molluscs).

Using the phylum-specific models, we estimate that under the Shared Socioeconomic Pathways (SSPs) SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5 predicted for the end of the 21st century (Cooley et al., 2022; IPCC, 2022), fertilization rate will decrease by 2.9%-15.1% for echinoderms, and by a non-significant amount for molluscs (0.5%-2.3%), relative to 1995–2014 (Figure 4). Our low-confidence predictions for cnidarians estimate a decrease of 4.1%-21.0%.

Since many studies included pH levels beyond those predicted under SSP5-8.5, we reconstructed our meta-analysis using data from experimental $\text{pH} \geq 7.6$. This reduced the dataset by ~20% for echinoderms and molluscs but did not affect the cnidarian data due to the narrower range of experimental pH levels tested for cnidarians (Figure 4). In the revised analysis, ΔpH remains significant but is less predictive of fertilization rate ($X^2 = 4.39$, $p = 0.036$). The best fit model includes ΔpH only and predicts a decrease in fertilization rate across all taxa by 2.0%, 4.3%, 7.1%, and 9.9% under SSP1-2.6, SSP2-4.5, SSP3-7.0 and SSP5-8.5, respectively. Predictions from this more conservative approach support previous conclusions that marine invertebrate fertilization is more robust — albeit still negatively impacted — at pH 7.6 and above (Byrne, 2011; Byrne, 2012), which may better reflect relevant open ocean pH projections. However, many species covered in this review are coastal and periodically experience pH levels below 7.6; therefore, the full model should not be disregarded.

As noted by Byrne (2011; 2012), there are many factors found to influence fertilization success that vary across studies. Given the diversity of species and secondary variables tested (e.g.

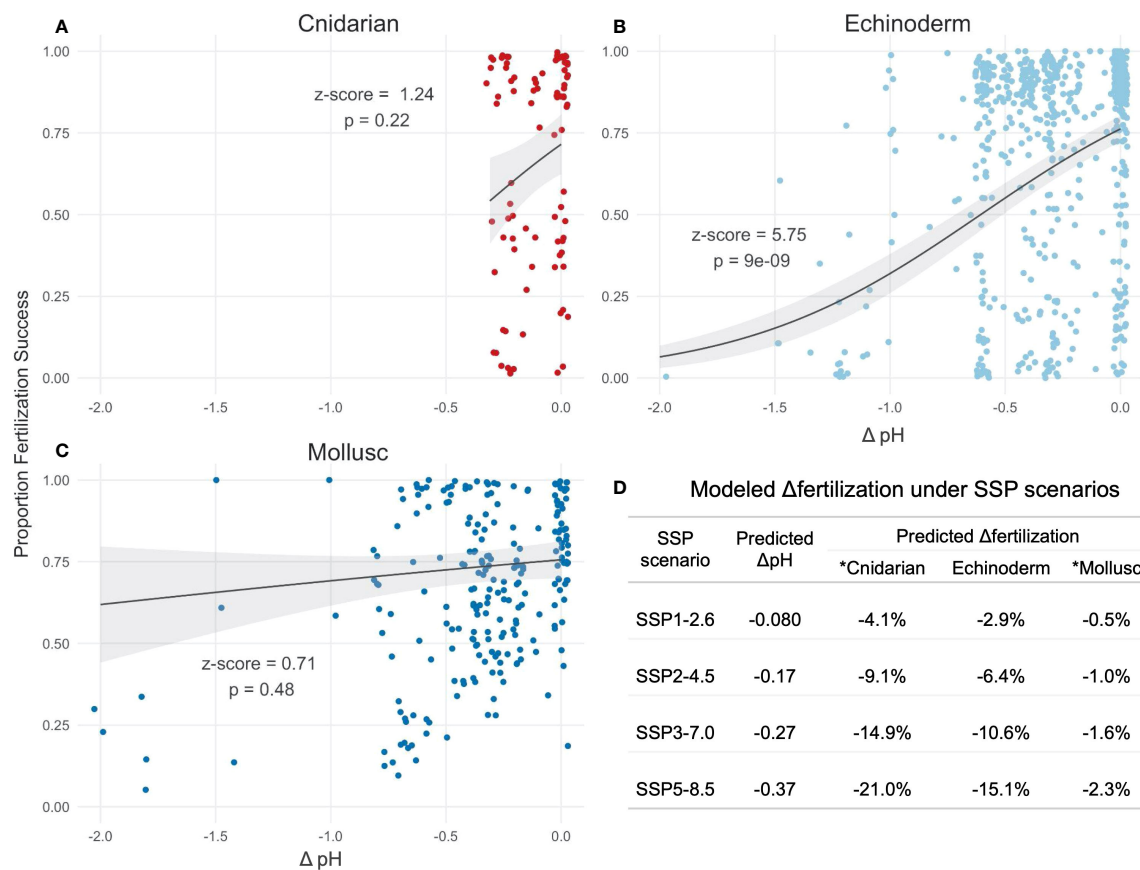


FIGURE 4

Fertilization success by Δ pH (the difference between experimental pH and control) for (A) cnidarians (6 studies), (B) echinoderms (35 studies), and (C) molluscs (23 studies). Control pH (Δ pH = 0) is defined separately by each experimental study, and typically represents present-day ambient pH at experimental location. The meta-analysis was performed using a beta regression model, and indicates that the effect of pH on fertilization rate is phylum-dependent (phylum: Δ pH interaction, $X^2 = 34.3$, $p = 1.7e^{-7}$). In all figures, each point reflects the average percent fertilization reported by one study at each Δ pH and secondary variable tested, curves indicate the fitted models, ribbons indicate 95% confidence intervals, and z-scores and p-values indicate the significance of the Δ pH coefficient estimates for each phylum. (D) Models were used to predict the change in fertilization rate under four Shared Socioeconomic Pathways (SSPs) for each phylum, which predict the pH change for the end of the 21st century (IPCC, 2022) relative to 1995–2014. *The pH coefficient was not a significant factor in the mollusc or cnidarian models, therefore these predictions should be considered descriptive, particularly for cnidarians for which there is limited data. No fertilization studies were found for crustaceans or ascidians.

warming), limiting the meta-analysis to only studies that used the same procedures was not possible. Instead, we took a broader approach, including all studies with a variety of secondary variables (Supplemental Table 3). We then tested for effects of six additional experimental variables (when reported, see Methods and Supplemental Table 3). We found that experimental sperm concentration significantly affects fertilization rates as a sole predictor but does not interact with Δ pH alone or as an additional covariate with phylum. Given that only five of the 34 studies that reported sperm concentration included multiple concentrations in the experimental design (Supplemental Table 3), the model was likely unable to fully characterize the interaction between pH and sperm concentration. In the natural environment, sperm levels can be

considerably more dilute than the optimal levels used in most studies. Whenever possible, studies should test effects of pH on fertilization across a range of sperm concentrations.

Other experimental variables that are not commonly reported or considered may interact with pH to affect fertilization rate, making it difficult to fully describe the impacts of OA. For instance, given the rapid pace of ocean change, many experimental animals likely already experienced OA, which could have affected fertilization rates through changes to their gametes (e.g. maternal effects, epigenetic changes). This is particularly pertinent because control pH levels applied by researchers often reflected conditions entering their experimental systems or the historical pH for a given region, which could differ dramatically from conditions at

the animal collection site. Future studies should strive to characterize their focal species' current and future environments to determine pH treatment levels, as they will provide the most ecologically relevant results.

In summary, our meta-analysis indicates that OA will reduce fertilization rates in many marine invertebrates, and effects are taxa specific. Fertilization rates are likely to decrease in echinoderms but remain relatively similar in molluscs. More studies are needed for cnidarians, but preliminary work indicates that their fertilization rates may be the most affected.

Gamete mechanisms that influence fertilization rate

There are five major events that typically occur during fertilization: 1) sperm chemoattraction to the egg, 2) sperm binding to the egg envelope, 3) sperm acrosomal reaction, 4) sperm penetration through the egg envelope, and 5) gamete fusion (Vacquier, 1998). Successful fertilization therefore involves a cascade of biochemical processes in both sperm and eggs, many of which include intracellular pH and calcium ion changes (Morisawa and Yoshida, 2005; Nakajima et al., 2005; Byrne, 2011; Sherwood et al., 2012). OA could alter fertilization rates through changes to chemoattractants, surface receptors, jelly coat, polyspermy defense system, and activation processes in eggs, and/or activation, motility, velocity, mitochondrial activity, chemotaxis, and fusion reactions in sperm.

Several studies examined the impact of acidification on egg fertilization mechanisms. In urchins, low pH increased the percentage of abnormally fertilized eggs (Zhan et al., 2018), polyspermy frequency, and time to completely block polyspermy (Reuter et al., 2011; Sewell et al., 2014). In molluscs, polyspermy rates increased as pH decreased when clam *Tegillarca granosa* eggs were pre-exposed to various pH treatments (Han et al., 2021). The inability to block polyspermy may be related to low pH reducing the protective egg jelly coat area, which can subsequently impair sperm chemotaxis (Foo, 2015; Foo et al., 2018). These impacts are likely species- and population-specific, with some urchins exhibiting no impact of low pH on egg jelly coat area, and populations exhibiting varied impacts depending on prior pH exposure (Foo et al., 2018). Egg intracellular pH adjusts according to the external chemical environment (Ciapa and Philippe, 2013; Bögner et al., 2014), which may also hamper egg activation by interfering with calcium signaling and actin dynamics (Limatola et al., 2020). Indeed, Shi et al. (2017b) observed that low pH disrupts the intracellular calcium ion (Ca^{2+}) activity in *T. granosa* eggs, which was associated with reduced fertilization rates.

The influence of low pH on sperm activity varies. Three cnidarian (hexacoral) studies report negative effects of pH on sperm activity (Morita et al., 2010; Albright, 2011a; Nakamura and Morita, 2012). Albright's initial examination of OA impacts on hexacoral sperm velocity showed no effect, but results from a second experiment suggested a negative effect (Albright, 2011a). OA reduced sperm swimming speed, motility, and linearity in

some echinoderms (Havenhand et al., 2008; Morita et al., 2010; Uthicke et al., 2013; Campbell et al., 2016; Caballes et al., 2017), but had no effect or positively impacted sperm swimming speed in others (Caldwell et al., 2011; Sung et al., 2014; Graham et al., 2015). Similarly, pH negatively affected sperm swimming speed, velocity, motility, and mitochondrial activity in some molluscs (Vihtakari et al., 2013; Vihtakari et al., 2016; Shi et al., 2017a; Shi et al., 2017b; Omoregie et al., 2019; Esposito et al., 2020), but had no effect on sperm motility in others (Havenhand and Schlegel, 2009; Vihtakari et al., 2016). In one population of *C. gigas* oysters, low pH increased sperm motility (Falkenberg et al., 2019).

Contrasting impacts on sperm activity could be due to varied sensitivities among genotypes within species (Schlegel et al., 2015; Campbell et al., 2016; Vihtakari et al., 2016; Falkenberg et al., 2019; Smith et al., 2019). Individual sperm characteristics can also respond differently to low pH (Schlegel et al., 2012; Graham et al., 2015). For instance, OA had a negative effect on the proportion of motile sperm, but not sperm swimming speed, in urchin *Heliocidaris erythrogramma* sperm (Schlegel et al., 2012). Impacts on sperm activity can also be influenced by experimental conditions, such as the exposure duration (e.g. Eads et al., 2016) or the method used to prepare experimental pH levels (pCO_2 vs. HCl, Shi et al., 2017b).

Implications

Our synthesis of the OA reproduction literature to date reveals the complexity of responses across and within species. For all reproductive processes there are studies that report effects of OA, while others found no effect (Figure 3C). Predicting future community-level changes at this stage is therefore not possible. There are, however, some observable trends for those well-studied reproductive processes (gametogenesis, fecundity, fertilization): for all phyla, negative effects were observed in at least one species (and typically many more), and reports of positive effects were rare. Echinoderm fertilization is quite sensitive to pH changes while molluscs are not. Gametogenesis is delayed and fecundity is reduced in many echinoderms and molluscs, but those processes are less sensitive in crustaceans. Cnidarian and ascidian studies are limited. Cnidarian studies suggest that gametogenesis and fecundity are relatively robust to OA, and fertilization may be quite sensitive. These observations provide the basis for hypotheses of the potential challenges faced by those in the aquaculture, fisheries, and conservation sectors. Not all reproductive processes will be affected in all species, but for those that are, here are some considerations.

Aquaculture

Impacts of OA on reproduction have the potential to negatively affect our marine food systems. Aquaculture programs may need to adjust their hatchery culturing

techniques to accommodate effects of OA. For example, gametogenesis in many species is delayed in OA, so conditioning them in buffered seawater could ensure or expedite gamete development. This may also improve synchronization of mature males and females in some species, as unequal impacts of acidification on oogenesis and spermatogenesis have been observed in oysters (e.g. Boulais et al., 2017). Seawater may also need to be buffered during fertilization to maintain high fertilization rates, particularly for some echinoderms and possibly cnidarian species. Alternatively, fertilization conditions could be re-optimized at a lower pH, such as by adjusting sperm concentrations. Should these measures be needed, larger facilities with more complex seawater treatment systems, more resources, and increased handling will be required, thus increasing the overall cost of production.

Wild fisheries

Wild fisheries do not have the capability of modulating the environment during reproduction, and may therefore be more susceptible to the effects of OA. Acidification may impact invertebrate fishery stocks by slowing gametogenesis, and reducing fecundity and fertilization, which could ultimately reduce reproductive output. While not covered in this review, there are many other possible indirect effects of OA on reproduction that could impact fisheries. Reproduction-related mortality may increase, as acidification can alter immune and stress-response functions, increasing vulnerability to pathogens and secondary stressors during and after reproduction (Mackenzie et al., 2014; Liu et al., 2016; Wang et al., 2016). In many invertebrates, reproductive capacity is closely tied to food availability before or during gametogenesis (Bernard et al., 2011). Changes to prey species dynamics due to acidification, such as altered phytoplankton communities' composition, abundance, and bloom timing (Cheung et al., 2011; Gao et al., 2012), may result in asynchronous invertebrate reproductive processes such that larval production and quality decreases.

Conservation and restoration

Conservation and restoration programs may need to update their strategic plans to account for impacts of acidification on reproduction. For instance, natural recovery of wild populations following removal of stressors (e.g., creation of a marine protected area following overharvest) could be impeded by decreased larval supply due to reduced reproductive success. Populations may take longer to recover, requiring programs to allocate more time and resources for longer-term interventions. Conservation and restoration approaches may need to change altogether, such as moving from passive strategies (e.g., removing disturbances and allowing succession to occur naturally), to active strategies (e.g., transplanting or augmenting wild populations) (Figure 2). For instance, programs may need to incorporate restoration

aquaculture and gamete cryopreservation to rebuild threatened populations. While preliminary studies in coral report a variety of response, some aspects of coral reproduction may be uniquely vulnerable to acidification due to their sexual reproduction strategies (Richmond and Hunter, 1990; Burke et al., 2011). In many coral species, gametes take several months to develop, and spawning occurs only a few nights a year over a few hours (Babcock et al., 1986). If OA interferes with these highly coordinated spawning events (Olischläger and Wild, 2020), sexual reproduction could be severely inhibited in the wild, but this has yet to be tested.

Genetic considerations

Genetic diversity, an important factor for species resilience to environmental stressors (Bernhardt and Leslie, 2013; Timpane-Padgham et al., 2017), could shift as a consequence of acidification-induced changes to reproduction and effective population size. Many invertebrate species are r-strategists with highly fecund females (Ramirez Llodra, 2002). Should acidification reduce the number of individuals that reproduce each season due, for instance, to delayed gametogenesis, populations could still be sustained by a few individuals that “win the reproduction lottery” (Hedgcock and Pudovkin, 2011; Sanford and Kelly, 2011). It may therefore be important for programs to actively facilitate genetic diversity and/or resistance to acidification. For commercial and restoration aquaculture facilities, broodstock may need to be collected later or conditioned longer in the hatchery to increase the number of breeding individuals. Conservation programs may need to design marine protected areas that encompass a variety of current and projected pH conditions, not just buffered areas, to enable both diversity and selection for low pH-resilient individuals. To build resilient populations and lines, restoration and breeding programs could leverage standing genetic variability to target genotypes that are reproductively viable in acidified conditions (Parker et al., 2011; Rossi and Tunnicliffe, 2017). This may include careful consideration of broodstock collection sites, such as areas with naturally low or variable pH conditions. Should the number of individuals contributing gametes become dangerously low, programs may need to begin cryopreserving gametes to preserve allelic diversity in a “seed bank” for future use (Figure 2).

Within- and inter-generational acclimatization have been observed in some species in response to acidification (Ross et al., 2016). Adult exposure to acidification may result in beneficial carryover effects for offspring and future generations (Parker et al., 2012; Wong et al., 2019; Zhao et al., 2019; Spencer et al., 2020), which could mitigate some of the negative effects to reproduction reviewed here. While additional research is needed and there may be limitations to inter-generational acclimatization (Byrne et al., 2019), these beneficial carryover effects may be leveraged to improve offspring fitness for production and breeding purposes (Parker et al., 2011; Durland et al., 2019).

Gaps in understanding for OA impacts on reproduction mechanisms

In addition to the critical need to know more about the basic biology and natural history of reproduction in marine invertebrate communities (Box 2), the most pressing need is for increased mechanistic knowledge of reproductive processes to gauge the impact of OA on marine invertebrates (Figure 5). In this section we outline mechanisms that should be explored with future research.

Fertilization mechanisms

Fertilization mechanisms are the most studied reproductive processes in marine invertebrates. Even so, there are still considerable knowledge gaps, particularly in how changes to gamete quality and sperm-egg interactions will affect fertilization (Figure 5). As a model organism for developmental biology, urchin fertilization has been well-studied, with cellular processes potentially impacted by OA reviewed in Bögner (2016). Compared to the numerous echinoderm and molluscan bivalve studies, only a handful of studies have explored OA and fertilization in cnidarians (none in non-hexacoral cnidarians) and crustaceans, and there are none in cephalopods. Considerable research on fertilization mechanisms has come from ascidians (Sawada and Saito, 2022); however, only two studies have examined ascidian fertilization under OA conditions. More studies are clearly needed for these ecologically and economically important taxa.

Gamete quality depends on maintaining an optimal intracellular pH (pH_i). Reductions in extracellular pH are thought to affect pH_i , suppress motility, and impact fertilization success (Christen et al., 1983; Alavi and Cosson, 2005; Morita et al., 2006; Boulais et al., 2018). In certain species, an increase in pH may be required for sperm activation (Nakajima et al., 2005). Explicit measurements of sperm pH_i , including those taken in the field, can help uncover the mechanism behind pH_i activation of sperm motility and its vulnerability to environmental pH conditions.

The impact of acidification on spawned eggs likely depends on their composition, structure, and intracellular conditions. Egg size is used as a proxy for well-provisioned eggs, but few studies empirically test this assumption with lipid analyses. Intracellular egg calcium content can also impact fertilization. Calcium triggers the second meiotic division in eggs, readying it to unite with sperm to complete the fertilization process (Miyazaki, 2006), and is part of the polyspermy defense (Epel, 1978). Egg calcium content can also be influenced by environmental pH (Ciapa and Philippe, 2013). More research should be conducted on energy allocation, maternal provisioning, and egg lipid and calcium content in low pH conditions.

Other structural components that could be influenced by acidification include the egg jelly coat and gamete recognition proteins. Present in echinoderms and molluscs, the jelly coat

protects the egg from intense wave action and prevents polyspermy and increases the likelihood of fertilization by increasing the size of the egg (Farley and Levitan, 2001; Podolsky, 2004). Additionally, the jelly coat is known to contain chemoattractants that activate and guide sperm or prevent polyspermy and harbor protective chaperone and gamete recognition proteins (Evans and Sherman, 2013). The dissolution of the jelly coat by low pH conditions observed in echinoderms can reduce percent fertilization, with jelly coats in some populations and species resilient to low pH. Cnidarian eggs do not have jelly coats, and similar structures have not been described in crustaceans. A general survey of gamete accessory structures in marine invertebrates will be beneficial to determine how low pH will impact eggs.

Mechanisms beyond fertilization

Mechanisms controlling pre-fertilization reproductive processes are understudied generally and in the context of OA. In many marine invertebrates, gametogenesis, spawn timing, and synchronicity is influenced by exogenous signals such as temperature, photoperiod, food, and pheromones from conspecific gametes (Galtsoff, 1938; Lawrence and Soame, 2004), and by endogenous signals such as hormones or neuropeptides (Tanabe et al., 2010; Jouaux et al., 2012). Applying knowledge of how these environmental cues are registered and acted upon by organisms may elucidate how low pH will affect these pathways.

Future studies should examine whether OA impacts biochemical cues involved in gametogenesis, coordinated spawning events, and mating behavior. Since many invertebrates are osmoconformers with open circulatory systems, reproductive hormones that circulate through the hemolymph are likely to be exposed to environmental pH changes (Tarrant, 2007; Treen et al., 2012). Structural changes have been observed in signaling peptides outside of the reproductive context (Tarrant, 2007; Roggatz et al., 2016). Exposure to acidification, for instance, resulted in protonation of three peptide signaling molecules, which was associated with behavioral impairment in shore crabs (Roggatz et al., 2016). Whether acidification alters marine invertebrate reproductive hormones is not yet known. This framework could be extended to pheromones involved in mating. Pheromones come in direct contact with the environment, and may be important for spawning synchrony, long-distance mate searches, mate guarding, and copulation dances. Out of all marine invertebrates, reproductive pheromones are best understood in decapod crustaceans. Pheromones released by female crabs instigate courtship displays and guarding behaviors in males (Kamio et al., 2022). Male crabs can distinguish female molting stages and copulation readiness based on pheromone detection (Kamio et al., 2022). Alteration of pheromone chemical composition, molecule shape, and residence time in low pH conditions could impact necessary mating behaviors and successful reproduction (Roggatz et al., 2016; Kamio et al.,

BOX 2 Experimental considerations for future OA and reproduction studies

Improve field research capability

- Spawning timing, duration, and intensity in natural settings are not easily predictable, and we lack baseline reproduction knowledge for most marine species. Additionally, physiological and reproductive responses of laboratory-raised organisms may be compromised by stress associated with captivity.
- Research initiatives should collect baseline knowledge. Technologies should be developed and integrated with biophysical models to track gametes and larvae in the natural environment.

Measure multiple reproductive traits simultaneously

- Reproduction is a complex process. It is important to examine multiple reproductive traits simultaneously to get a better understanding of overall reproductive performance.
- Reporting measures of reproductive success that integrate multiple traits will improve the predictability of demographic models (ex. fecundity and survival of mother, survival of offspring).

Incorporate diversity in test subjects and experimental design

- Studies should maximize genetic variation, as organism origin (i.e., field site, hatchery) and genotype can affect sperm and egg compatibility and confound findings.
- Future work should incorporate taxonomic diversity and multiple stressors to expand the breadth of species and conditions studied.

Account for length of gametogenic cycles

- Gametogenic cycles vary between species. Many studies only expose organisms to OA when gametes are almost fully developed.
- Accounting for gametogenic cycle length improves understanding of OA effects on gamete development and parental effects.

Test multiple sperm concentrations

- The probability of detecting a treatment effect may be dependent upon sperm concentrations. “Optimal” sperm concentration may be higher than ecologically relevant concentrations. Low sperm concentrations can exacerbate OA effects.
- Experiments should use multiple sperm concentrations and gamete incubation times, as these factors may alter the probability of fertilization and/or polyspermy.

Understand limitations of intergenerational studies

- Artificially induced fertilization methods (i.e., strip spawning, chemical/hormonal injection, etc.) used in intergenerational studies may cause organisms to release gametes before complete gametogenesis.
- Many intergenerational OA studies inherently include adult exposure during reproduction, so those studies should formally measure and report reproduction metrics.
- Future research should differentiate between within-generation carryover effects, cross-generational impacts (F0-F1), and multigenerational plasticity (F1-F2+), and determine how reproductive conditioning may impact each facet of plasticity.

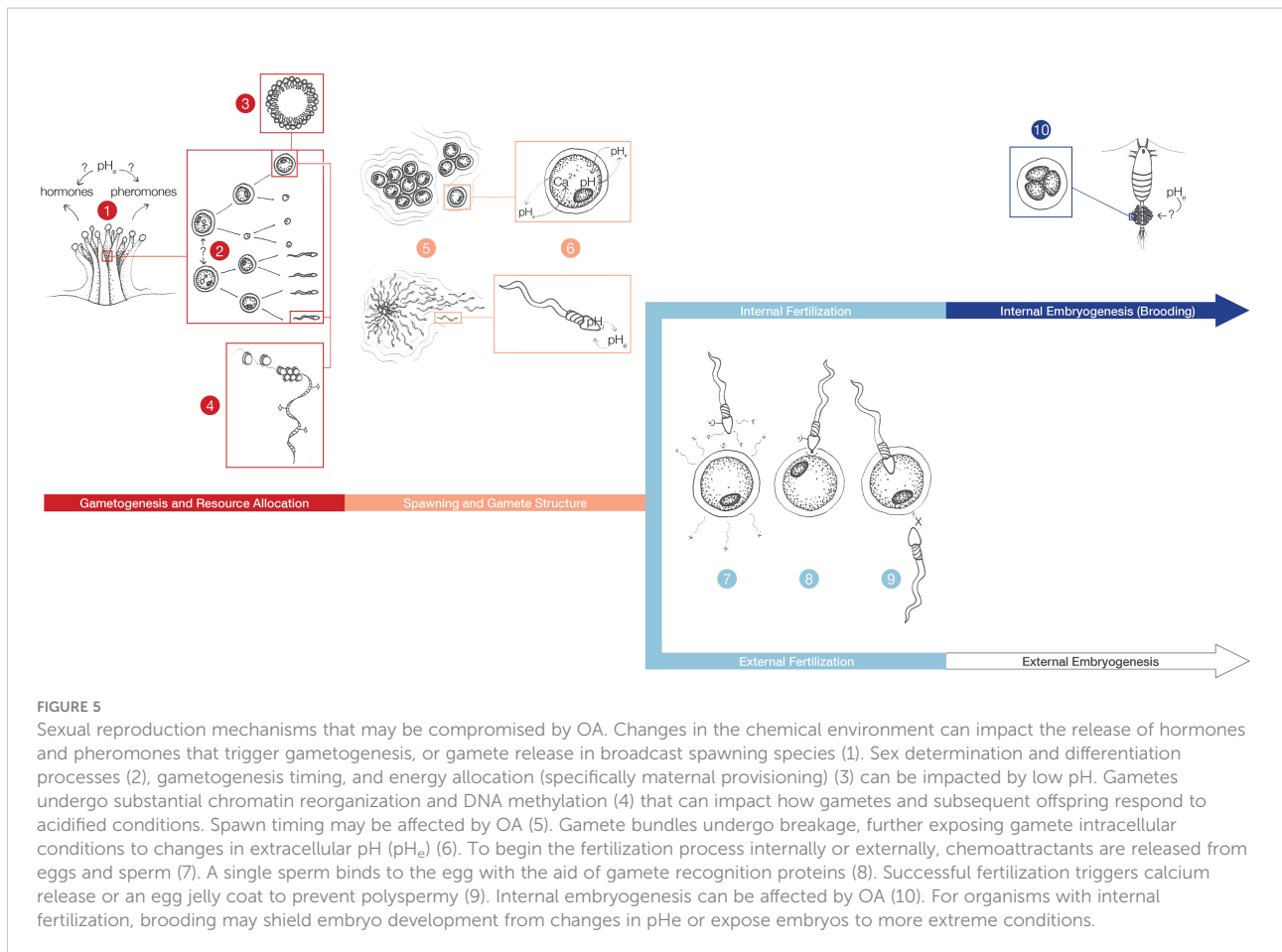
See previous reviews for additional challenges in the design and execution of ocean acidification experiments (Albright et al., 2011b; Grazer and Martin, 2012; Prezeslawski et al., 2017).

2022). Additionally, the ability of invertebrates to produce and detect these compounds may be impacted by low pH (Roggatz et al., 2016; Kamio et al., 2022). A recent hypothesis developed by Olischläger and Wild (2020) suggests that gamete release timing during periods of low water motion is possibly regulated by the carbon concentrating mechanism in corals and/or their symbionts, which may make the synchronized spawning of organisms with photo-symbionts vulnerable to OA. Future work should examine hormones, pheromones, and other factors governing reproductive cues and behavior to identify molecular signals vulnerable to OA.

For a more comprehensive understanding of changes to reproductive resource allocation in acidified conditions, future studies should examine multiple physiological metrics. OA-induced changes in sex-specific growth, tissue regeneration, and energy allocation could impact reproductive resource allocation. While there are no studies correlating internal pH at the site of gametogenesis and environmental pH, organisms that regulate their internal environment may have increased metabolic demand in low pH conditions, and less energy available for reproductive processes (Sokolova et al., 2012). In corals, tissue damage caused a reduction in coral fecundity (Rinkevich and Loya, 1989; Van Veghel and Bak,

1994; Rinkevich, 1996) and tissue regenerated at a lower rate under OA in various hexacorals (Horwitz and Fine, 2014). When exposed to acidified conditions, the intracellular fluid of the crab *Chionoecetes bairdi* did not change in low pH. However, there were significantly more dead hemolymph cells and less granular cells within acidified treatments. This suggests that metabolic demands related to increased cell apoptosis, immune response, and phagocytosis may be diverting energy away from reproduction (Meseck et al., 2016). If organisms can buffer extracellular pH to promote somatic growth or maintenance, the diversion of energetic resources to this task may impact reproduction.

There is a lack of research on how OA affects on brooding behavior in cnidarians, echinoderms, and molluscs. Brooding echinoderms may be disproportionately impacted by OA in the Southern Ocean, based on predicted changes to aragonite and calcite saturations at depths where these species are found (Sewell and Hofmann, 2011). Recent studies show that internal brooding itself may impart tolerance in these taxa. For example, pH conditions in the brood chambers of *Ostrea* spp. oysters are lower than the surrounding water (Gray et al., 2019; Gray et al., 2022). Naturally lower pH in brood chambers could make fertilization



more resilient to OA (Lucey et al., 2015; Gray et al., 2019; Gray et al., 2022), thereby providing a potential evolutionary advantage. Potential advantages from brood chambers may not apply to external brooding species like the octocoral *Rhytisma fulvum* (Lieberman et al., 2021). Further research should compare low pH impacts on external and internal brooding to determine if both reproductive strategies provide similar evolutionary advantages.

Genomic regulation of reproduction in marine invertebrates is a crucial, yet understudied, area. Determining how OA affects baseline genetic processes related to reproduction is imperative for understanding if processes can be phenotypically plastic or evolve in response to stressors. Genes specific to sex, maturation stage, early gametogenesis, sex determination, and differentiation have been identified for the oyster *C. gigas* (Dheilly et al., 2012; Cavelier et al., 2017; Yue et al., 2018). In other economically-important and edible species like the urchin *P. lividus* and scallop *Pecten maximus*, transcriptome information has been used to identify markers for sex determination (Machado et al., 2022) and gamete quality (Pauletto et al., 2017), respectively. Expressed transcriptomes of reproductively active individuals at various time points may elucidate genetic regulation of reproduction in low pH conditions. In fish, miRNA molecules regulate oogenesis genes; similar analyses should be conducted in invertebrate species to

understand other regulators of gametogenesis (Juanchich et al., 2013). If organisms experience low pH during reproductive conditioning, environmental cues may be integrated in the germline through DNA methylation and other epigenetic modifications (Bell and Hellmann, 2019). Sex-associated methylation differences have been documented in *C. gigas*, and OA exposure modified the reproductive tissue methylome in *C. gigas* and *C. virginica* (Venkataraman et al., 2020; Sun et al., 2022; Venkataraman et al., 2022). Changes to DNA methylation due to low pH may impact successful reproduction or explain intergenerational effects of these conditions on marine invertebrates. Analysis of DNA methylation enzymes during the maternal-to-zygotic transition in coral *M. capitata* embryos exposed to OA suggests that methylome programming occurs within 4 hours of fertilization (Chille et al., 2021), further emphasizing the vulnerability of molecular machinery to OA and its influence on carryover effects. Beyond DNA methylation, changes to chromatin organization may influence reproduction and carryover effects. Gametes, particularly sperm, are subject to significant chromatin reorganization and packaging that can affect the availability of genes for methylation or expression (Eirin-Lopez and Putnam, 2018). As successful reproduction hinges on the survival of offspring, understanding genetic and epigenetic

mechanisms that drive reproduction is important to elucidate changes to reproductive processes and offspring performance.

Conclusion

Despite the large body of research examining the effects of OA on reproduction, there are notable gaps in the literature (Box 2). In addition to the mechanisms described in the previous section, long-term ecological baselines for reproduction are missing for most organisms. This information is essential for understanding the impacts of OA on organismal phenology and the resilience and plasticity of reproductive processes. More ecologically relevant experimental designs are also needed. For instance, knowledge of acidification effects on spawn timing and synchronicity is, to date, largely based on rates of spawning when induced or other metrics that approximate spawn readiness, such as the number of gravid individuals. Moving forward, it will be important to monitor natural spawn rates and timing in variable pH conditions. Studies on how OA affect mating behavior and sex determination and differentiation are very limited, and additional research into the effects of OA and additional environmental stressors on reproduction are also needed (for a summary of multi-stressor studies to date, see Supplemental Materials).

It is crucial that we expand OA studies to include a more diverse set of species with aquaculture, fisheries, and conservation importance. Of the taxa discussed in this review, those that constitute the largest fisheries and cultured species are among the least studied. Crustaceans are notably underrepresented. In wild fisheries, crustacean taxa represent the largest wild-caught group (6.31 billion tons in 2017), with over half of the fishery comprising shrimp and prawn species (3.60 billion tons combined, FAO, 2019), and to date there are no studies that have looked at the effects of OA on the top farmed marine crustaceans worldwide (FAO, 2018). Cephalopods are another overlooked group. Despite 3.77 billion tons of squid, cuttlefish, and octopus harvested globally in 2017 (FAO, 2019), we identified only one cephalopod study in this review that exposed adults to OA and monitored reproductive activity (Spady et al., 2020). Finally, while cnidarians are among the most threatened by changing oceanic conditions (Hoegh-Guldberg et al., 2017), they are also among the least studied. It will be important for future studies to prioritize impacts of acidification on reproduction in species that support aquaculture and fishing communities, restoration, and those species of conservation concern.

Author contributions

JLP-G, LA, LHS, YRV, and LW contributed to conception and design of the study. LA, LHS, YRV, and LW organized the data base. LS performed statistical analyses. LW and YRV

produced the illustrations. JLP-G, LA, LHS, YRV, and LW wrote the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.977754/full#supplementary-material>

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