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Impacts of Ocean Acidification on Reproduction and Early Life Development in Marine Teleost Fish—A Synthesis

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ABSTRACT

Ocean acidification (OA) remains a major and underexplored threat to marine fishes, particularly regarding reproductive physiology and early life stages (ELS). Although research over the past 15 years has documented diverse OA effects, substantial knowledge gaps persist. Most studies focussed on a limited set of species from North America and Europe, leaving broad uncertainty across phylogenetic groups, geographic regions and multi-stressor conditions. In adult fish, especially females, elevated $p\mathrm{CO}_2$ can shift energy allocation to prioritise reproductive output at the expense of egg or clutch size. While adult and juvenile fish have well-developed acid–base balancing systems, embryos and larvae possess only rudimentary mechanisms, making them more vulnerable to OA. This article stresses the importance of understanding these physiological and mechanistic responses to predict the future of fish stocks and ecosystem health as OA intensifies due to ongoing CO_2 emissions. Our results highlight that OA responses in fish are highly variable and often specific to life stage and species, with acute and sometimes stage-specific effects not fully documented. Lastly, our recommendations on targeted research and funding are necessary to address the remaining knowledge gaps, including broadening taxonomic and geographic sampling, exploring multi-stressor scenarios and improving understanding of the downstream effects of OA on fish reproduction and development. Maintaining robust fish populations is vital for food security, employment and ecosystem functioning, making continued investigation into OA's impacts a scientific and societal priority.

1 | Introduction

Since the advent of the industrial revolution, atmospheric CO_2 concentrations have increased by 47% as a result of anthropogenic carbon emissions (i.e., fossil fuel combustion, deforestation and cement production) and have now reached their highest levels in approximately 2 million years (IPCC 2021). The ocean is an important carbon sink, having absorbed 20%–30% of the total anthropogenic CO_2 emissions within the past two decades (IPCC 2023). Ocean acidification (OA thereafter) is the phenomenon by which the dissolution of excess CO_2 into seawater causes a reduction in pH and alters ocean carbon chemistry and carbonic saturation state (Riebesell et al. 2011). In the best-case scenario where carbon emissions reach net-zero by 2050–2070, mean open ocean pH is predicted to decline by a global average of 0.08 units in 2081–2100 (Cooley et al. 2022). However, if no additional climate policies are implemented and carbon emissions continue to rise, the average global ocean pH is predicted to decrease by approximately 0.3 units towards the end of the century (IPCC 2023).

Predictions for coastal waters are more complex due to annual, seasonal and diel fluctuations in pH (Cooley et al. 2022; Strong et al. 2014). Driving forces for coastal acidification

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include CO_2-rich upwellings, freshwater and nutrient runoff and high biological productivity, calcification and respiration rates (Cooley et al. 2022; Duarte et al. 2013; Wallace et al. 2014). Already, coastal organisms can experience temporary but strong diel pH fluctuations and seasonal declines of 0.3–0.4 units (Duarte et al. 2013; Wallace et al. 2014) and elevated pCO_2 of up to ~4000 μatm (Baumann et al. 2015). Coastal waters provide important socioeconomic and ecological benefits, for example, sustaining fisheries and nursery habitats for fish and invertebrate species (Barbier et al. 2011; Jordan et al. 2012; Lefcheck et al. 2019). Therefore, OA and the subsequent impaired buffering capacity of seawater may pose a greater risk to coastal organisms by exacerbating the severity and duration of natural CO_2 cycles (McNeil and Sasse 2016; Melzner et al. 2013). This synthesis includes coastal acidification as a part of the general phenomenon of OA.

OA has deleterious effects across a wide range of marine taxa (e.g., Wittmann and Pörtner 2013) and is particularly pronounced in calcifying marine invertebrates (Ross et al. 2011), such as corals (Hoegh-Guldberg et al. 2017), bivalves (Zhao et al. 2017) and calcifying larvae (Griffith and Gobler 2017). Fish species represent a major global source of protein, and maintaining sustainable fish stocks is therefore critical for food security, employment and broader ecosystem functioning (Béné et al. 2015). Since the review by Ishimatsu et al. (2008), which noted a lack of studies investigating the effects of OA on fish reproduction and early life stages (ELS), the availability of empirical research has advanced (Figure 1); however, consensus on the exact responses and the severity of the effects remains unclear. Furthermore, there are significant knowledge gaps remaining for many taxonomic groups, oceanic regions, life stages and multi-stressor effects that we seek to address within this synthesis.

A fundamental understanding of the physiological mechanisms underlying acid–base homeostasis is necessary for interpreting the effects of OA in teleost fish, which are briefly outlined here. However, for a thorough exposition of acid–base regulation and the role of carbonic anhydrase, we recommend consulting the following reviews: Brauner et al. (2019); Gilmour and Perry (2006); Gilmour and Perry (2009); Melzner et al. (2009); Shartau et al. (2019); Zimmer and Perry (2022). To cope with short term acid–base disturbances resulting from elevated blood pCO_2 (known as hypercapnia), juvenile and adult fish use specialised ion-regulatory epithelia located in highly developed gills for CO_2 diffusion and to maintain acid–base balance (Shartau et al. 2019; Zimmer and Perry 2022). Extracellular pCO_2 values of teleost fish are approximately 3000–4900 μatm, and can reach 9900 μatm after exhaustive exercise, therefore a high diffusion gradient for CO_2 excretion to the seawater is maintained (Melzner et al. 2009). However, when environmental pCO_2 is elevated, blood pCO_2 increases to maintain the partial pressure gradient and CO_2 excretion rates (Esbaugh 2018). Respiratory acidosis occurs as elevated extracellular CO_2 is hydrated into H^+ and bicarbonate ions which reduces extracellular pH (pH_e) (Brauner et al. 2019). Although ventilation increases under elevated environmental pCO_2 to facilitate gas exchange (known as respiratory compensation), this mechanism alone is not sufficient for preventing respiratory acidosis (Gilmour and Perry 2006). Therefore, fish actively regulate their acid–base status (metabolic compensation) using energetically costly mechanisms (e.g., Na^+/K^+-ATPase in the gills) for net proton excretion through

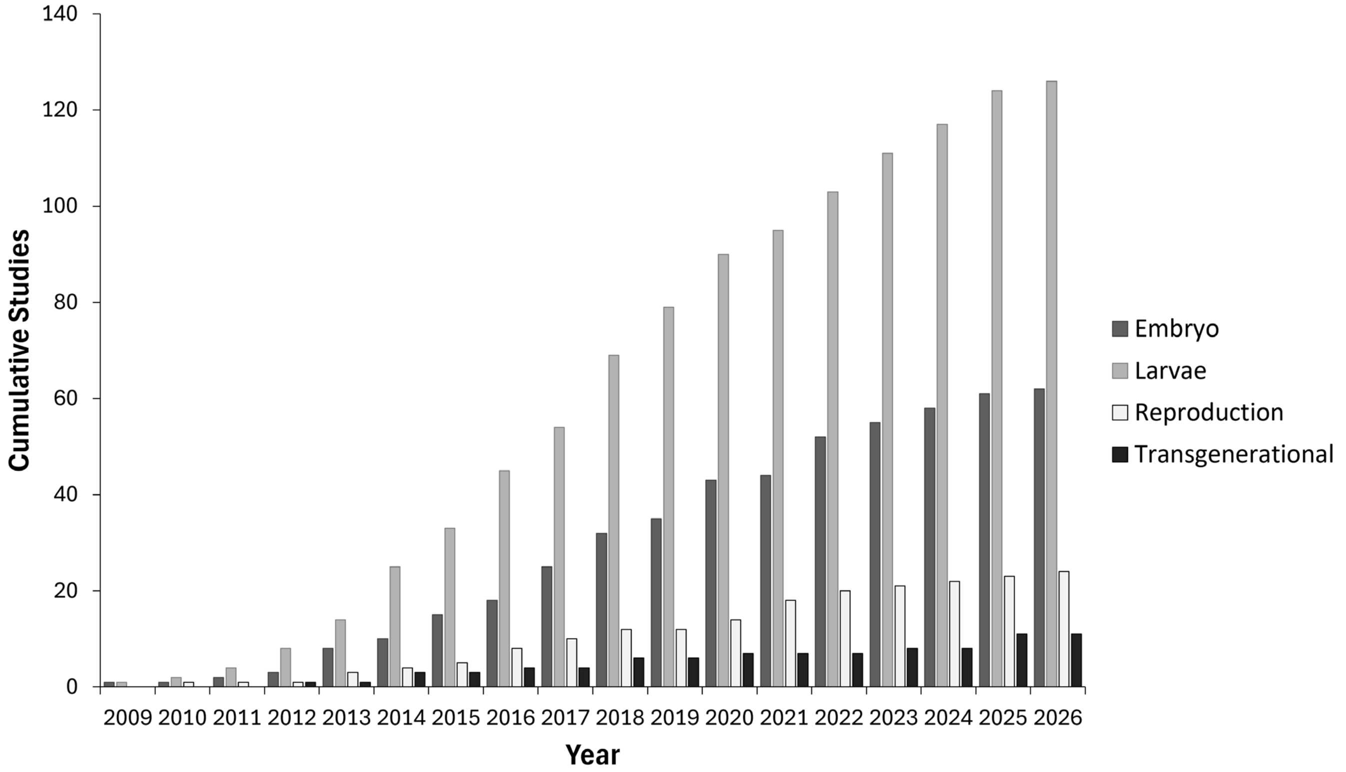

FIGURE 1 | Cumulative graph representing the number of studies published on the effect of ocean acidification on reproduction, embryonic development, larval development, and transgenerational experiments of teleost fish between 2009 and 2026. A total of 154 studies were found, and if studies experimented on multiple life stages (59 studies), the entries were counted separately for each category for the cumulative score.

the exchange of acid–base equivalents (i.e., H^+ and HCO_3^-). Alterations in pH_e can affect the structure and function of biological macromolecules as well as the activity of transporters, receptors and physiological processes such as ionic conductivity, metabolic enzyme activity and the synthesis of macromolecules (Shartau et al. 2019). Consequently, acid–base balance is tightly regulated to minimise disruptions to whole-animal performance and survival (Shartau et al. 2019).

In fish physiological research, it is important to note that the term 'ocean acidification' is often misleading since arguably the proximate environmental stressor is hypercapnia associated with a greater partial pressure of CO_2 (pCO_2) (Esbaugh 2018). Firstly, ventilatory compensation via the detection of CO_2-sensitive branchial chemoreceptors occurs in response to elevated environmental pCO_2, not reduced pH or altered blood pCO_2/pH (Perry et al. 2023). Secondly, fish can regulate the pH of extracellular fluid (i.e., blood) to remain between 7.7 and 7.8. Therefore, under end-of-century OA scenarios, the increase in extracellular pCO_2 is expected to have a greater physiological impact on fish than the accompanying reduction in environmental pH, as elevated CO_2 directly alters blood carbonate chemistry and induces hypercapnia and respiratory acidosis (Esbaugh 2018; Kwan and Tresguerres 2022). Furthermore, the energetic costs associated with hydrating CO_2^{aq} and actively excreting the resulting protons (H^+) are expected to increase, potentially diverting energy away from other metabolically demanding processes such as growth, development and reproduction (Heuer and Grosell 2014). Nevertheless, for the purpose of this synthesis, the term OA will be used to describe the general trend of ocean acidification in terms of pH under the context of climate change, as well as for experimental treatments that simulate ocean acidification by elevating seawater pCO_2. Early life stages of fish, including embryos and larvae, possess limited homeostatic capabilities, relying primarily on rudimentary structures such as cutaneous ionocytes (Dahlke et al. 2020; Kwan et al. 2021). In combination with their high surface area-to-body mass ratio, which facilitates efficient gas exchange, these characteristics can increase embryonic susceptibility to the adverse effects of OA (Dahlke et al. 2020; Kwan et al. 2021). The tolerance of early life stages to environmental conditions (e.g., temperature, pH, hypoxia and food availability) plays a key role in the recruitment and fitness of fish stocks and ecosystem functioning. Therefore, larval sensitivities can present a critical bottleneck to recruitment (Koenigstein et al. 2018; Tiedemann et al. 2021; Voss et al. 2019). It is essential to understand the mechanisms underpinning tolerance to OA and the associated vulnerability during reproduction and early life stages, helping to inform ecological and economic consequences under future OA scenarios (Migaud et al. 2013).

Prior to the targeted research into the effects of OA during embryonic development, Melzner et al. (2009) hypothesised that embryos may be less susceptible to ocean acidification since the egg fluid layer (perivitelline fluid) provides another barrier to the outward diffusion of gases. Therefore, embryos may already experience hypercapnic conditions from the accumulation of metabolically produced CO_2 and thus are more tolerant to hypercapnia. Additionally, during early embryogenesis, maternal control and defence mechanisms (e.g., maternal mRNAs and chaperones) provide protection from changes in the external environment, such as elevated pCO_2 during early embryogenesis (Dahlke et al. 2020). As development progresses, organ differentiation and the development of specialised cells (e.g., ionocytes) improve the defence mechanisms associated with acid–base balance (Dahlke et al. 2020; Kwan et al. 2021). However, there is a critical point during the maternal-zygotic transition (MZT) and gastrulation whereby maternal protection has decayed and the homeostatic plasticity is still under development where the embryo becomes increasingly susceptible to changes in environmental pCO_2 (Dahlke et al. 2020). As development continues, organ differentiation and the development of specialised cells (e.g., ionocytes) improve the defence mechanisms associated with acid–base balance (Dahlke et al. 2020; Kwan et al. 2021). Since embryonic development is a critical and vulnerable life stage, a risk assessment of embryonic development under OA is necessary for predicting how the fish populations will respond to a changing climate.

The goal of this synthesis is to comprehensively review the literature available on the physiological effects of ocean acidification on the reproduction and early life stages of teleost fish. Furthermore, we highlight the observation bias that leads to critical knowledge gaps on various taxa, oceanic regions, and lifestyle strategies. Whilst the review primarily focuses on fish physiology, there are aspects of behavioural responses which have been included in the synthesis to provide an ecological context.

2 | Scope of the Synthesis

To synthesise the current state of knowledge on the impact of ocean acidification on the reproduction and development of teleost fish (see Zemah-Shamir et al. (2022) for a detailed review on elasmobranchs), we conducted a systematic review following the PRISMA guidelines (Page et al. 2021). A literature search was conducted using Web-of-Science (WoS) with the exact search of:

1. 'ocean acidification' OR acidification OR hypercapnia (Topic)
2. fish OR teleost* (All Fields)
3. 'early life stages' OR ELS OR reproduc* OR larv* OR embryo* OR *transgen (All Fields)
4. NOT invertebrate* OR crustacea* OR bivalve* (Topic)
5. NOT freshwater (Topic)

We included papers that exposed teleost fish to OA during reproduction, embryonic development, or larval development experimentally and in the field. Papers were screened firstly by the title and abstract, followed by screening the content of the study. Review articles and book chapters were excluded from the search. Papers were excluded if: (i) there was no mention of acidification in the abstract; (ii) the pH was manipulated using acid (e.g., HCl) rather than CO_2; (iii) the research was not conducted on marine teleosts; or (iv) they used artificially bred hybrid species in aquaculture (e.g., Das et al. 2023) due to the lack of ecological relevance. Two studies used three-spined sticklebacks (*Gasterosteus aculeatus*; Devergne et al. 2023; Devergne et al. 2025) collected from a freshwater experimental mesocosm. However, as individuals were subsequently acclimated to a salinity of 34‰, their results were included in this synthesis.

The following information was extracted from each article to aid the synthesis and is available to view in Tables S1 and S2:

1. Reference and digital object identifier (DOI).
2. Year of study.
3. Species information (e.g., family, genus, species name, common name and lifestyle strategies).
4. Physiological parameters studied (e.g., growth, survival, clutch size, organ damage etc.).
5. Parameters for the control and experimental treatments.
6. Source type (e.g., wild, aquaculture, laboratory broodstock).
7. Study type (e.g., laboratory experiment, field study).
8. Continent and country the study was conducted.
9. Oceanic region the study species inhabited.
10. Climatic zone (e.g., polar, temperate, tropical).
11. Life stage studied (e.g., embryo, larvae, adult).
12. Notes on the effect of stressors on the physiological responses measured in the study and whether responses were positive, negative, neutral or variable.

Water-column positions for each species were assigned using FishBase (Froese and Pauly 2026). However, where classifications were inconsistent with current ecological understanding, assignments were revised based on primary literature evidence. Species were classified using the following definitions: benthic species live on, within or in close association with the substratum; benthopelagic species occupy the water column near the substratum and utilise both benthic and mid-water habitats; and pelagic species live predominantly in the open water with little to no association with the substratum.

This review considers directional changes observed from the physiological responses as an increase or decrease in relative metrics. Additionally, responses are referred to as neutral if there was no statistically significant directional change under OA and variable responses refer to reports where the directional change of the response varied either due to life stage, $p\mathrm{CO}_2$ intensity, or other variables included in the study. We classified these physiological responses as a directional change rather than having a positive or negative effect as the benefits or disadvantages of these responses are often unknown or may depend on the ecological context. Without further research into the long-term effects of OA, it remains uncertain whether these responses will emerge into true positive or negative effects.

As of 13/04/2026, the WoS search produced 593 results with 152 of the results meeting the appropriate criteria. References from all papers published in the last 2 years were inspected to check for any missed publications relevant to the review, yielding an additional two papers which met the appropriate criteria (154 studies in total). All publications used for this synthesis and the containing figures have been summarised in Tables S1 and S2. From 2012 to 2022, there was a substantial increase in OA research focused on embryonic and larval fish biology. However, publication rates appear to have plateaued thereafter (Figure 1), potentially reflecting the longer-term impacts of the COVID-19 pandemic, including delays to experimental work, reduced job security, and shifts in research funding priorities. These studies investigated the impacts of OA on a total of 59 species across 46 genera and 31 families, representing a coverage of ~8% across all marine teleost families (Figure 2). Throughout the literature, four teleost families (Gadidae, Pomacentridae, Atherinopsidae and Clupeidae) have received disproportionately greater attention, accounting for 44% of all research within this field. Most studies focused on benthic-associated species (70%), such as cod, seabream, and flatfish (Figure 3). Comparatively few studies (30%) tested the effect of OA on pelagic fish, representing only 12 species investigated to date. Among these, only six species are considered large pelagic fish of commercial importance (i.e., Atlantic bluefin tuna (*Thunnus thynnus*), yellowfin tuna (*Thunnus albacares*), mahi mahi (*Coryphaena hippurus*), cobia (*Rachycentron canadum*), yellowtail kingfish (*Seriola lalandi*) and garfish (*Belone belone*)).

The oceanic regions where the study species were collected for research are mapped within Figure 4. Clear disparities in research focus between oceanic regions have been identified, with the majority of fish species collected from either the Atlantic Ocean or the Pacific Ocean (47% and 40%, respectively). Only 11% of fish originated from the Arctic, Indian and Southern Oceans combined which means that many fish from diverse habitats and life histories with different ecological functions are considerably underrepresented in research. Furthermore, there is a lack of research into species inhabiting the polar regions (5%; Figure 3) even though the Arctic Ocean specifically is acidifying at a greater rate compared to other regions and has already surpassed a critical planetary boundary for ocean acidification (Findlay et al. 2025).

3 | Ocean Acidification Effects on Reproduction

The effect of OA on fish reproduction remains relatively understudied with only 24 out of 154 papers assessing reproductive responses (Figure 1). This disparity is largely due to the logistical and financial challenges of spawning fish in captivity, especially large-bodied and pelagic species which typically require larger experimental tank space. Only six studies have assessed the reproduction of a large-bodied species and only one of these assessments was on a large-bodied pelagic species: Atlantic cod (*Gadus morhua*) (Dahlke et al. 2017, 2018, 2020, 2022; Frommel et al. 2010) and garfish (Alter and Peck 2021). Whilst these studies mitigated the experimental constraints by using strip-spawning approaches, the adult fish were not maintained under OA conditions which limited their assessments to gamete quality and fertilisation success only. Thus, this leaves a particular knowledge gap regarding the longer term effect of OA on maternal investment and parental reproductive responses in large-bodied and pelagic species and funding priorities should facilitate the increased cost associated with this type of research, especially since the limited evidence from other groups suggests maternal investment may be significantly impacted by OA (Figure 5A).

Studies to date provide no evidence to suggest that fertilisation success is affected by OA alone in marine teleosts (Figure 5A), with consistently neutral responses reported across cinnamon

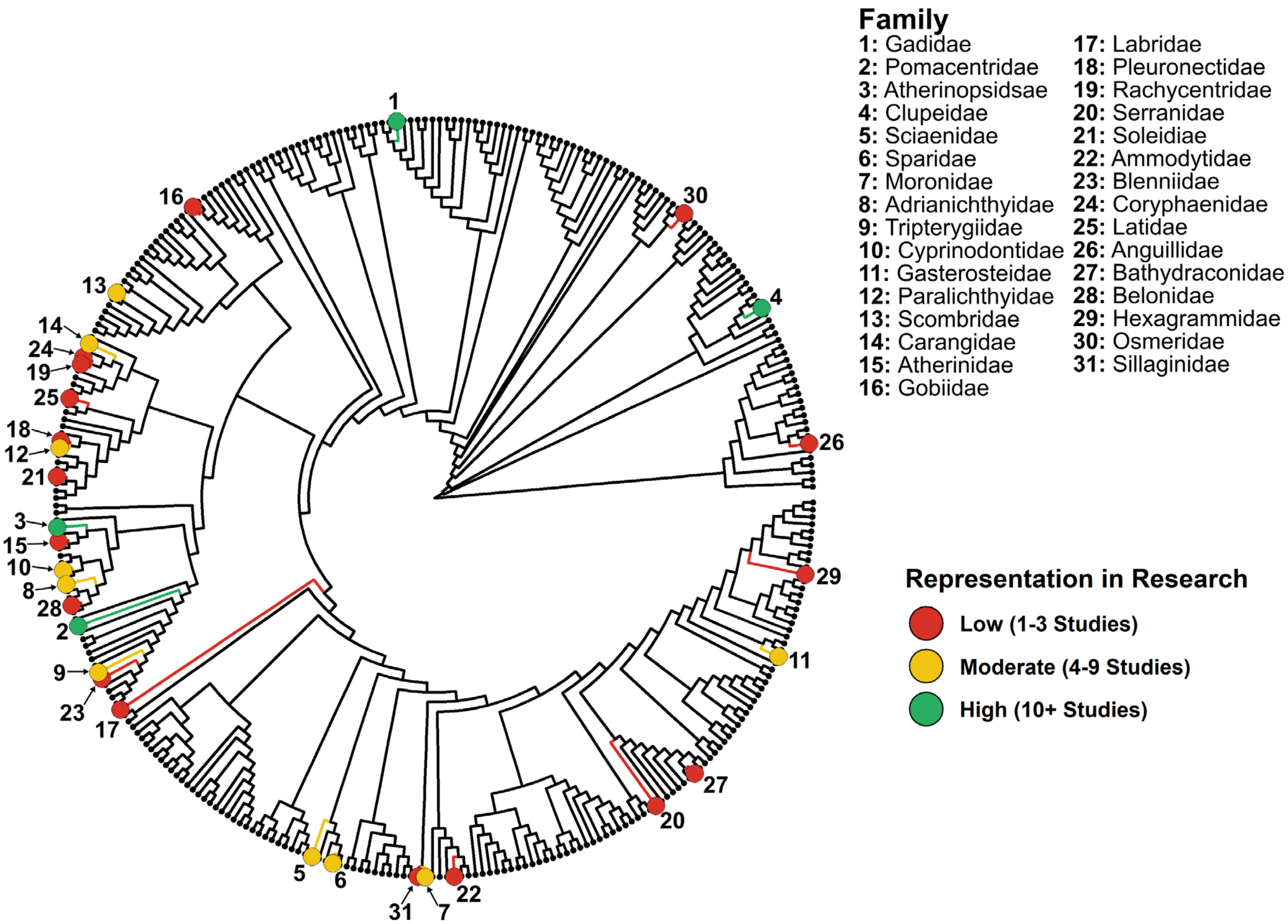

FIGURE 2 | Cladogram of marine teleost families represented in research on the impact of ocean acidification on reproduction and early life development. Coloured node tips indicate the degree of family representation in the literature, based on the number of times a species within each family has been used as a study model. Node tips are numbered (1–31) according to descending family representation in the literature. The cladogram uses phylogenetic data from The Fish Tree of Life (Chang et al. 2019).

clownfish (*Amphiprion melanopus*), Arctic cod (*Boreogadus saida*), Atlantic cod, garfish, Atlantic herring (*Clupea harengus*), and Black sea bass (*Centropristis striata*) (Alter and Peck 2021; Dahlke et al. 2018, 2020; Miller et al. 2015; Murray and Klinger 2022; Zavell and Baumann 2024). Additionally, gametogenesis and sperm motility also remained unaffected by acidified conditions in Atlantic cod, suggesting that the reproductive processes associated with gamete production and function are largely insensitive to OA in isolation (Dahlke et al. 2022; Frommel et al. 2010). However, gamete quality and fertilisation success are impaired when OA is combined with warming (Dahlke et al. 2022; Devergne et al. 2023). As fish will be exposed to ocean acidification and warming in tandem during future spawning seasons, further research is necessary to explore the interactive effects of multiple stressors on fish reproduction.

For benthic-associated species, field observations at natural CO_2 vent sites have provided an effective method for assessing reproductive responses under analogous OA conditions, with five studies identified to date (Cattano et al. 2016; Kang et al. 2026; Milazzo et al. 2016; Nagelkerken et al. 2021; Spatafora et al. 2021). These studies allow the assessment of maternal investment and parental responses under prolonged in situ exposure, making them particularly useful for identifying potential trade-offs between reproductive output, parental physiology and reproductive behaviour. However, their interpretation requires caution, as other environmental factors such as food availability often differ between vent and ambient control sites which may influence reproductive performance (Nagelkerken et al. 2021). For example, greater prey biomass around CO_2 vent sites has been shown to enhance reproductive investment (Nagelkerken et al. 2021). Additionally, responses can vary depending on the predatory niche as Nagelkerken et al. (2021) found that only competitively dominant, generalistic fish capitalised on the OA-enhanced food availability as opposed to more specialised fish. OA can cause indirect effects on food availability due to overall changes in food web stability so may not be directly applicable to future climate change conditions (Ullah et al. 2018).

An emerging trend suggests that reproductive output is favoured under OA, with 40% of studies reporting an increase in maternal investment (Figure 5A). Faria et al. (2018), Miller et al. (2013), and Welch and Munday (2016) reported a significant increase in both clutch size and the number of clutches produced in cinnamon anemonefish, orange clownfish (*Amphiprion percula*) and the two-spotted goby (*Gobiusculus flavescens*), respectively. Similarly, the prioritisation of reproductive output under OA has been identified at a transcriptional level (Kang et al. 2026).

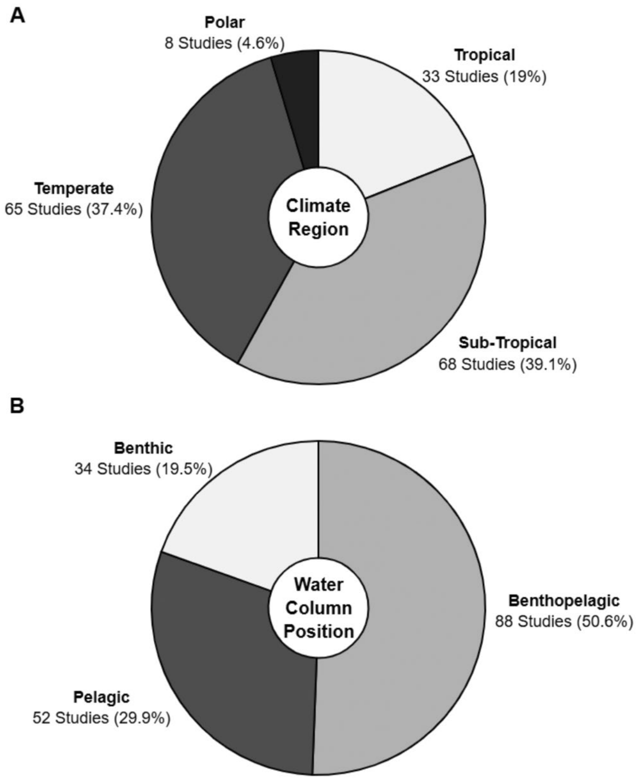

FIGURE 3 | Number (and percentage) of studies assessing the effects of ocean acidification on reproduction and early life development in marine teleosts across climatic and ecological attributes of the model species used. (A) Representation across climate regions. (B) Representation across primary water column position. Climatic region and water column positioning were compiled from FishBase and primary literature, with classifications revised where database assignments were inconsistent with current understanding (Froese and Pauly 2026). Where a single study used multiple species models, each species is represented individually.

Despite the increased reproductive output, there was no evidence in the literature of a trade-off in gamete quality, suggesting this to be maintained despite the increased production (Figure 5A). However, evidence suggests that trade-offs may still occur through altered parental behaviour. Both Nagelkerken et al. (2021) and Spatafora et al. (2021) identified reduced parental care and foraging behaviour in female common triple fins (*Forsterygion lapillum*) and ocellated wrasse (*Symphodus ocellatus*), suggesting that the increased energy allocation towards reproductive output is compensated by reducing physical activity.

Whilst studies on fish reproduction are still relatively infrequent, current findings support that OA produces varied inter- and intra-specific responses. Lopes et al. (2020) found that the hatching success, clutch size, and parental investment of the two-spotted goby were not affected by pH. However, this finding contradicts the work developed by Faria et al. (2018) in which hypercapnia stimulated reproduction of the same species, albeit a trade-off with the size of the eggs and larvae at hatching. Faria et al. (2018) noted that the variation in responses of the same species is likely due to different breeding populations used, so a population effect may exist, which should be accounted for when making predictions about the effect of OA on fish reproduction.

4 | Embryonic Development Under Ocean Acidification

Most studies assessing embryonic survival under OA reported no significant effect (65% of relevant studies); however, 29% identified reduced survival (Figure 5B), demonstrating that while some embryos are often resilient to OA, this resilience is not universal. Evidence suggests that reduced embryo survival under OA is highly species-specific, with no effects reported across multiple studies on species such as Atlantic cod (Dahlke et al. 2017; Frommel et al. 2013) and marine medaka (*Oryzias melastigma*)

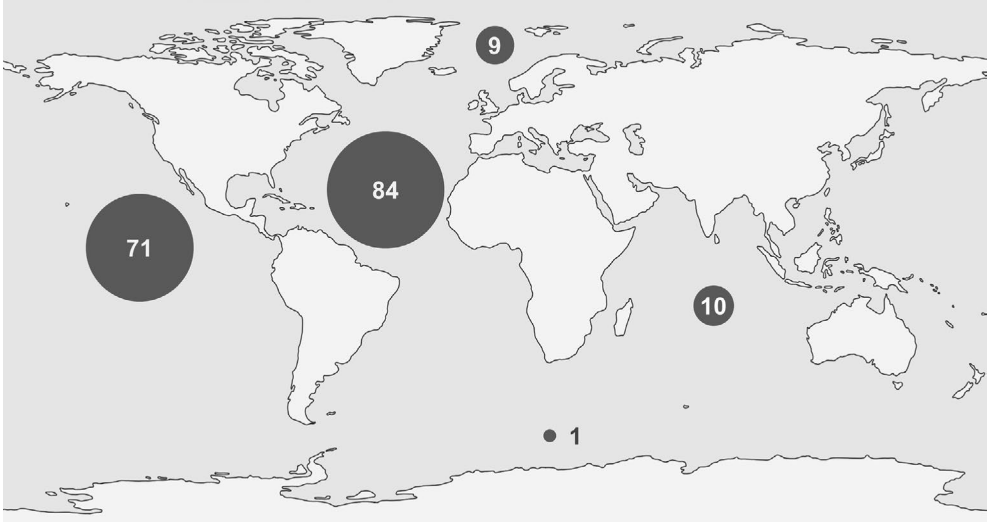

FIGURE 4 | Global distribution of study species used to assess the effects of ocean acidification on reproduction and early life development in marine teleosts. Bubble area indicates the proportional representation of study models from each oceanic region (Arctic, Atlantic, Indian, Pacific and Southern Oceans), while numeric labels indicate the total number of studies from each region. When aquaculture-sourced organisms were used, the oceanic region was assigned based on the origin of the broodstock. Where a single study used multiple species models or multiple cohorts of the same species sourced from different oceanic regions, each is represented individually. Two studies that used freshwater-sourced organisms were excluded.

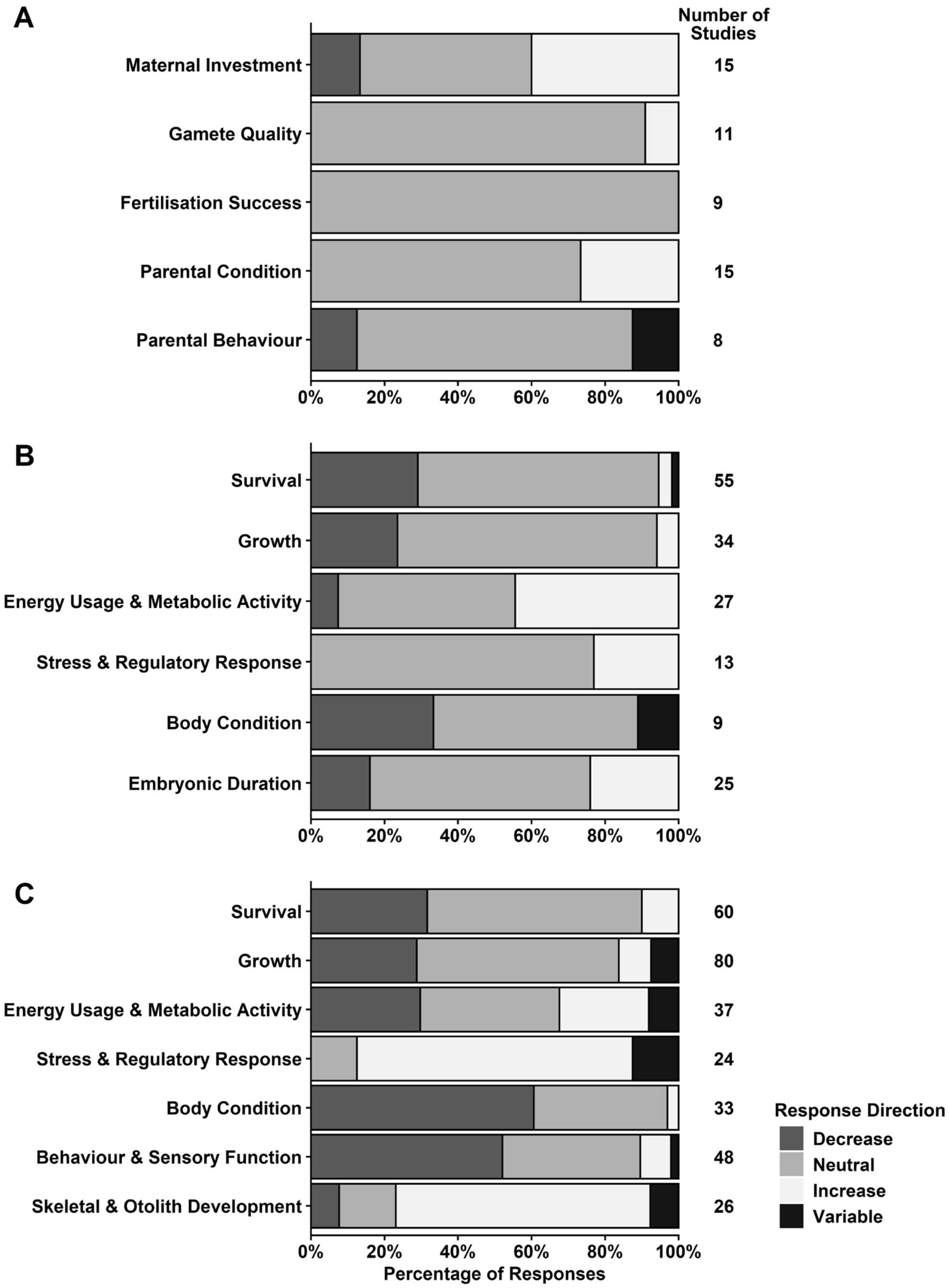

FIGURE 5 | The distribution of responses to ocean acidification across behavioural and physiological traits assessed during different developmental periods in marine teleosts. (A) Reproduction, (B) Embryonic Development, and (C) Larval Development. For each trait category, stacked bars show the percentage of reported responses classified as decreased, neutral, increased or variable, where 'variable' denotes opposing responses reported for the same trait category within a single study. Values to the right of each bar indicate the total number of studies that have assessed the trait category. Where a single study used multiple species models, each species is represented individually. Responses reflect effects attributed solely to ocean acidification, and studies that did not test ocean acidification in isolation were excluded.

(Mu et al. 2015; Wang et al. 2017), whereas reduced survival has been consistently observed across species including meagre (*Argyrosomus regius*) (Faria et al. 2017; Pimentel et al. 2016) and the northern sand lance (*Ammodytes dubius*) (Baumann et al. 2022; Murray et al. 2019). Embryonic susceptibility to OA is likely dependent on the developmental stage, with embryos being particularly vulnerable during early stages when ion-regulatory capacity is still poorly developed (Dahlke et al. 2020). For instance, Atlantic cod embryos exhibited elevated mortality during early gastrulation in response to the combined effects of OA and warming, which was associated with low activity of ion pumps and co-transporters involved in acid–base regulation (Dahlke et al. 2020). However, as this effect was not observed under OA alone, the extent to which these mechanisms contribute to OA-driven mortality may be species-specific and influenced by interactions with additional environmental stressors.

Embryonic development under OA is frequently accompanied by sub-lethal responses that are not captured by survival metrics alone. Sub-lethal responses to OA were frequently reported across embryonic studies, with an elevated stress and regulatory response identified in 23% of studies, alongside an increased energy and metabolic demand in 44% of studies (Figure 5B). For instance, while marine medaka showed no reduction in embryonic survival under OA, studies reported increased acid–base activity, heart rates and a reduced yolk size at hatching (Chen et al. 2023; Liu et al. 2025; Wang et al. 2017). Similar sub-lethal responses have been reported in meagre and cinnamon anemonefish which have both shown increased energetic demands during development, suggesting that embryos can experience increased physiological demands even when survival is not compromised (Faria et al. 2017; Miller et al. 2015). Sub-lethal physiological responses can manifest as morphological changes during embryonic development. Reduced embryonic growth in response to OA was reported in 23% of studies measuring this metric, while 33% of studies assessing embryonic body condition reported a significant decrease (Figure 5B). For example, Dahlke et al. (2017) identified an increased oxygen consumption rate and a reduction in standard length and somatic body area during embryonic development, despite no effect on survival rates. Similar responses have been identified in the ocellated wrasse which identified an increased metabolic rate and reduced total length at hatch, while an increased deformity rate was identified in the Atlantic herring despite no reduction in survival (Cattano et al. 2016; Leo et al. 2018). OA may therefore indirectly decrease offspring survival, as reduced body size is frequently associated with lower survival probabilities (Johnson 2022), potentially through elevated predation risk resulting from an extended duration within size-dependent predatory niches (Paradis et al. 1996).

Changes observed in embryonic developmental time under hypercapnia were variable between species with 24% of studies reporting increased embryonic duration, 16% reporting reduced embryonic duration and 60% reporting no significant change (Figure 5B). An increase in developmental time has been observed in the yellowfin tuna (Bromhead et al. 2015), the northern sand lance (Baumann et al. 2022; Murray et al. 2019), the black sea bass (Meseck et al. 2022) and the Pacific herring (*Clupea pallasii*) (Murray and Klinger 2022; Singh et al. 2023). A decrease in developmental time was observed in Japanese ricefish (*Oryzias latipes*) associated with a strong downregulation of genes related to metabolic pathways (Tseng et al. 2013) and the inland silverside (*Menidia beryllina*) (Morrell and Gobler 2020), whereas the orange clownfish (Munday et al. 2009) and marine medaka (Mu et al. 2015; Sun et al. 2019; Wang et al. 2017) were resilient to changes in embryonic duration. Reduced developmental time under OA may be beneficial since the period spent in the critical life stage is reduced, but the accompanying physiological, behavioural and ecological costs might produce overall negative net consequences to developing fish. The species-specific time spent in embryonic development may influence susceptibility to OA. For example, black sea bass has a short embryonic period of 48 h and (Meseck et al. 2022) found no change in hatching success after exposure to OA. As embryos spend more time in an acidified environment with ionoregulatory mechanisms still under development, species with longer development times may be more at risk to the threats posed by OA. Therefore, the time taken to develop the homeostatic mechanisms needed to regulate acid–base balance may be a key factor influencing the resilience or sensitivity to OA.

Acclimation to OA in the embryonic stage may be possible for some species (e.g., Cattano et al. 2016; Dahlke et al. 2017, 2018, 2020). In a field trial investigating embryonic development in the ocellated wrasse after transplantation to a CO_2 vent to simulate OA conditions, metabolic rates were elevated and reduced size at hatching was reduced in transplanted embryos (Cattano et al. 2016). However, nesting and development at the CO_2 vent showed no change in size or metabolic rates compared to the ambient field site (Cattano et al. 2016). Whilst embryonic acclimation to OA is possible, it is unclear how many generations are required for beneficial acclimation to occur. Additionally, Cattano et al. (2016) noted that acclimation to OA may increase the range in tolerance as transplantation from high $p\mathrm{CO}_2$ to low $p\mathrm{CO}_2$ produced no change in metabolism nor hatch size. For acclimation to occur in embryos, energy is allocated towards life-sustaining processes, such as acid–base regulation, at the expense of embryonic growth, shown by reduced larval standard length and somatic area upon hatching (Dahlke et al. 2017, 2018).

5 | Larval Development Under Ocean Acidification

Although larval fish begin to develop more sophisticated mechanisms for homeostasis and acid–base balance, they are still vulnerable to the effects of hypercapnia. Larval survival under OA is highly variable across studies, with the majority reporting neutral effects (58%) or reduced survival (32%) (Figure 5C). However, reduced body condition, as reported in 61% of the relevant studies, may have longer term consequences and carry-over effects to adulthood that may not be captured within the limited experimental time. It is important to understand the long-term effects of OA even after the larval stage since reduced survival under OA may directly translate to reduced recruitment of fish stocks (Koenigstein et al. 2018). Furthermore, larval survival is positively correlated with size, and exposure to OA can intensify this relationship, such that the mortality of larvae at smaller sizes is significantly higher when reared under OA compared to larger size classes (Johnson 2022). Therefore, there is evolutionary pressure for greater larval size; otherwise, larval recruitment is likely to decline significantly under future OA conditions (Johnson 2022).

Ocean acidification can alter larval growth; however, responses are inconsistent across studies. Most studies (55%) show no evidence that OA affects growth; however, larval growth under OA was reduced in 29% of studies and increased in 9% of studies (Figure 5C). Responses can be stage specific, and several studies have found varied responses to OA depending on the developmental stage (Hurst et al. 2016; Kim et al. 2015; Muller et al. 2020). For example, in the olive flounder (*Paralichthys olivaceus*) daily growth rates were reduced up to 14 days post-hatching (dph); however, growth rates increased during the late larval stage, and body length and weight were greater under OA (Kim et al. 2015). Additionally, Muller et al. (2020) found that the pre-flexion stage of the Roman seabream (*Chrysoblephus laticeps*) experienced reduced metabolism and growth rates, but the opposed response was observed during the flexion stage as metabolic and growth rates were increased. Stage-specific responses likely link to sensitive windows of larval development depending on how developed the organs are at the stage of sampling (Muller et al. 2020).

Identifying species that are more tolerant to OA is not straightforward, as intraspecific variation in responses has been widely reported. For example, studies on the early life stages of the Atlantic herring have revealed contrasting findings. Some studies suggest that herring larvae have a resilient proteome structure (Maneja et al. 2014) and show no evidence of altered swimming or foraging behaviour in response to OA (Maneja et al. 2015). However, other studies have found significant developmental delays and a greater instance of organ damage after 39 days post hatching (Frommel et al. 2014) and a greater instance of larval malformations indicating potential sublethal cellular damage during development (Leo et al. 2018). Despite the direct sub-lethal effects of OA recorded in larval herring, this species may also experience indirect benefits from OA-driven changes in food-web dynamics. Enhanced primary productivity under OA has been associated with increased larval survival (Sswat et al. 2018), while OA-induced shifts in predator–prey interactions have also been shown to reduce predation risk through decreases in predator biomass (Spisla et al. 2022). A longer-term study would be necessary to investigate how sublethal consequences influence fish health as individuals transition into juvenile and adult stages, as well as to assess the extent to which any apparent benefits arising from OA-driven changes in food-web dynamics persist over ontogeny.

Organ damage after development under OA has been observed in 61% of the relevant studies, such as in the Atlantic cod (Frommel et al. 2012; Stiasny et al. 2019), Atlantic herring (Frommel et al. 2014), yellowfin tuna (Frommel et al. 2016) and marine medaka (Sun et al. 2019). Frommel et al. (2012) observed greater incidences of tissue damage in the liver, pancreas, eye, and gut of the Atlantic cod larvae at 32 dph reared under OA. Additionally, fatty vacuole deposits were found in the liver and larval lipid content increased by 61% and 97% in larvae reared under medium (~1800 μatm) or high (~4200 μatm) OA treatments (Frommel et al. 2012). These results may be linked to the upregulation of genes associated with fatty acid and glycogen synthesis, causing disruption in lipid homeostasis due to stress induced changes in lipid and fatty acid metabolism (Díaz-Gil et al. 2015; Frommel et al. 2020). Interestingly, exposure to predicted end of century $p\mathrm{CO}_2$ (~1100 μatm) in Atlantic cod larvae increases mortality rates (Stiasny et al. 2016) and organ damage (Stiasny et al. 2019), but it was revealed that OA is likely a 'stealth stressor' since few genes were differentially expressed during 6–13 dph, a period of the highest mortality. In other words, a transcriptomic and cellular response could not be detected despite the high stress and mortality experienced by the cod larvae, likely due to rapid breakdown of cellular homeostasis (Mittermayer et al. 2019). OA is expected to incur additional energetic costs to maintain acid–base balance and internal homeostasis. Upregulation of acid–base regulation and increased physiological stress responses has been recorded in 75% the studies in larval fish species reared under OA (Figure 5C), such as the Atlantic cod and sheepshead minnow (*Cyprinodon variegatus*) (Dahlke et al. 2020; Enzor et al. 2020). However, impaired acid–base regulation has been observed in the Senegalese sole (*Solea senegalensis*) (Pimentel et al. 2014) and there was no change in gene expression coding for key ion transporters and ionocyte density associated with acid–base balance in the orange spotted grouper (*Epinephelus coioides*) (Lonthair et al. 2020), indicating that some species may be more resilient than others. Whilst it is expected that upregulated acid–base regulation would increase energetic costs, our literature search found that energy usage and metabolic activity were highly variable across experiments. Specifically, 24% showed increased energy usage/metabolism, 30% showed a decreased energy usage/metabolism (metabolic depression), and 40% showed no significant effect on energy usage/metabolism. Further research is needed to elucidate the capacity for acid–base regulation in various fish species to understand the energetic costs associated with living under OA. However, food availability appears to play a key role in meeting the energetic demands under OA (e.g., Gobler et al. 2018; Siegfried and Johnson 2023; Sswat et al. 2018; Stiasny et al. 2019).

There is strong, consistent evidence that OA increases size, growth rate, asymmetry and irregularity of otoliths (69% of the relevant studies) (Figure 5C) (Alter and Peck 2021; Mahé et al. 2023; Tian et al. 2022; Wexler et al. 2023). It is likely that acid–base regulation in the endolymph of fish is responsible for the increased size of otoliths, with greater hyper-calcification of otoliths in fish that possess more robust acid–base mechanisms (Kwan and Tresguerres 2022). OA treatments increased the size of otoliths in the white seabass (*Atractoscion nobilis*), but this change did not affect characteristics associated with the vestibo-ocular reflex (VOR), a behaviour stimulated by the ustricular otoliths during head movement (Shen et al. 2016). Given that otoliths play an important role in hearing and balance, changes in otolith growth and mineralisation can impact hearing and behavioural lateralisation (Holmberg et al. 2019; Lopes et al. 2016; Radford et al. 2021; Rossi et al. 2016, 2018). Altered hearing capabilities can further influence settlement behaviour and habitat selection, for example, barramundi larvae (*Lates calcarifer*) were attracted to ecologically irrelevant soundscapes (i.e., temperate rocky reefs and white noise) as opposed to the ecologically relevant tropical mangrove soundscape when they were reared under OA (Rossi et al. 2018). Larval settlement into adult habitats is a bottleneck for recruitment so alterations in the offspring's ability to sense appropriate habitats could impact overall recruitment and connectivity of populations.

Biomineralisation of the skeleton in developing fish has received much less attention, but hyper-calcification similarly observed in the otoliths has been recorded. For example, the number of ossified vertebrae in larval cod reared under OA increased (Stiasny et al. 2019), and larval sea bream exhibited faster mineralisation and reduced skeletal deformities under the severe OA treatment (~1520 μatm) (Crespel et al. 2017). Conversely, skeletal deformities were recorded in larval olive flounder despite also exhibiting enlarged otoliths, which together may have impaired consequences for eco-physiological performance (Pimentel et al. 2014). Nonetheless, the physiological and molecular mechanisms behind skeletal biomineralisation in developing fish remain a critical knowledge gap in our understanding of ELS responses to OA.

OA can have a strong effect on neurotransmission in fish, leading to behavioural impairments, as recorded in 52% of the relevant studies (see Tresguerres and Hamilton 2017) (Figure 5C). To alleviate acidosis from hypercapnia, fish accumulate $\mathrm{HCO_3}^-$ to buffer internal pH reductions back to baseline levels and to maintain ionic gradients (Brauner et al. 2019). $\mathrm{GABA_A}$ receptors rely on the transmembrane gradients of $\mathrm{HCO_3}^-$ and Cl^- but an accumulation of $\mathrm{HCO_3}^-$ can reverse ion fluxes through the receptor (Tresguerres and Hamilton 2017). Reversing the flux of these ions causes the receptor to become excitatory and lose the inhibitory function necessary for minimising overstimulation and noise. Impaired foraging behaviour in the black seabream has been linked to reduced contents of the neurotransmitters γ-aminobutyric acid (GABA) and Acetylcholine (ACh) as well as changes in the expression of olfactory transduction related genes (Jiahuan et al. 2018). Furthermore, OA-induced impairments to shoaling cohesion and lateralisation were partially reversed in sand smelt (*Atherina presbyter*) treated with gabazine, a competitive antagonist of $GABA_A$ receptors that blocks ionic fluxes of Cl^- and HCO_3^- across the synapse (Lopes et al. 2016). Therefore, it is plausible that GABAergic dysfunction as a result of ocean acidification could lead to the behavioural impairments previously identified, such as mating behaviour (Milazzo et al. 2016), foraging (Pimentel et al. 2016), swimming activity (Pimentel et al. 2016), shoaling cohesion and lateralisation (Lopes et al. 2016). These behavioural impairments could have subsequent indirect effects on larval survival and recruitment, potentially elevating their vulnerability to predation. Furthermore, altered behavioural dynamics and settlement behaviour could pose a concern for future fish stock instability predicted under future climate conditions.

Adaptation through evolutionary processes (i.e., modification and inheritance of advantageous genetic sequences) can occur over multiple generations; however, environmental change could outpace a species rate of adaptation, leading to low evolutionary potential (Bautista and Crespel 2021). Transgenerational plasticity is a mechanism by which inheritance of non-genetic factors (i.e., through maternal provisioning, microbiome transfer, epigenetic markers) can prime the offspring for coping with an environmental stressor experienced by the parent (Liu et al. 2025; Murray et al. 2014; Suresh et al. 2024). For example, transgenerational plasticity was observed in the marine medaka with F2 embryos showing enhanced adaptability to OA as transcriptional perturbations were markedly reduced alongside a partial restoration of acid–base homeostasis (Liu et al. 2025). However, factors such as variability in individual sensitivities, certain life history traits, environmental variability of a species habitat, and availability of resources can impact the capacity for acclimation over multiple generations (Bautista and Crespel 2021; Murray et al. 2014; Schunter et al. 2017; Stiasny et al. 2018; Suresh et al. 2024). For example, Stiasny et al. (2018) found a partial increase in survival in Atlantic cod larvae from hypercapnia-acclimated parents only under high food availability, which is a common factor influencing survival under future OA conditions (Koenigstein et al. 2018; Sswat et al. 2018). Understanding acclimation and adaptation to stressors over multiple generations is vital for assessing population resilience to climate change (Bautista and Crespel 2021). Transgenerational experiments in teleost fish remain limited (Figure 1), therefore, further studies are needed to elucidate the adaptive potential of fish species as environmental pCO_2 rises.

6 | Ocean Acidification and Multiple Stressors

Ocean acidification rarely—if ever—acts in isolation as climate change causes global ocean warming and increases the frequency of marine heatwaves and hypoxic events, and all these stressors cause further indirect changes through ecosystems and food webs functioning. Additionally, local stressors, particularly in coastal waters, like eutrophication, fishing, pollution and other anthropogenic activities, may add cumulative pressures particularly to fish nurseries and early life stages. Research into interactive effects of multiple stressors is growing, comprising 42% of studies included in this review. Most of the studies combine OA with warming (47 studies), followed by combined OA and hypoxia (9 studies) and OA and food availability (8 studies) (Figure 6). There is a critical knowledge gap in the effect of triple stressor studies, with only two papers investigating the combined effect of OA, warming and hypoxia on the metabolism, survival, development and thermal sensitivity of embryos (Schwemmer et al. 2020; Willis-Norton et al. 2022). Therefore, understanding how these stressors interact with other parameters remains poorly documented.

Anthropogenic pollution represents an additional stressor that has rarely been incorporated into multi-stressor studies of teleost fish development. Only six studies have investigated the effect of OA combined with marine pollutants, namely cadmium (Cui et al. 2020, 2022), crude oil (Sun et al. 2019), microplastics (Chen et al. 2023), TiO_2 nanoparticles (Milton et al. 2025) and endocrine disrupters (Devergne et al. 2025). Declines in pH can increase the bioavailability and toxicity of heavy metals and other contaminants (Hatje et al. 2022). For example, organ damage is intensified under combined exposure to OA and crude oil, while crude oil exposure in isolation does not produce the same effect in the marine medaka (Sun et al. 2019). Future research priorities should consider the combined effects of pollution and global climate change stressors since understanding how local and global stressors interact can help management authorities identify conservation priorities and develop effective mitigation strategies.

Multi-stressor experiments require complex setups and sufficient replication, which can necessitate compromising on the number of experimental treatments. Consequently, some multi-stressor studies do not test the effects of the individual stressors (e.g., Devergne et al. 2023; Mahé et al. 2023; Moreira et al. 2022; Willis-Norton et al. 2022). While these studies aimed to understand the biological effects of projected climate conditions, the interactive effects of multiple stressors cannot be accurately interpreted without first establishing the response to each individual stressor. Additionally, 100% of the biological response could be caused by one stressor dominating over the other (dominant effect) (Figure 6). For example, whilst OA alone can indirectly affect larval survival (i.e., through reduced body condition, energy assimilation etc.), warming appears to be the predominant environmental factor influencing larval recruitment when marine heatwaves occur in combination with OA (Spencer et al. 2026). However, these studies often represent a snapshot within the life cycle of the relevant species and do not test the cumulative effect of stressors over multiple life stages. Therefore, this poses a risk of underestimating other stressors, which could still add significant long-term effects.

Climate stressors often produce an additive or synergistic effect that is particularly noticeable in studies investigating ocean acidification and warming (OAW) (Figure 6). Across fish species, reproductive performance and early development are more strongly impaired under combined stressors than by OA alone

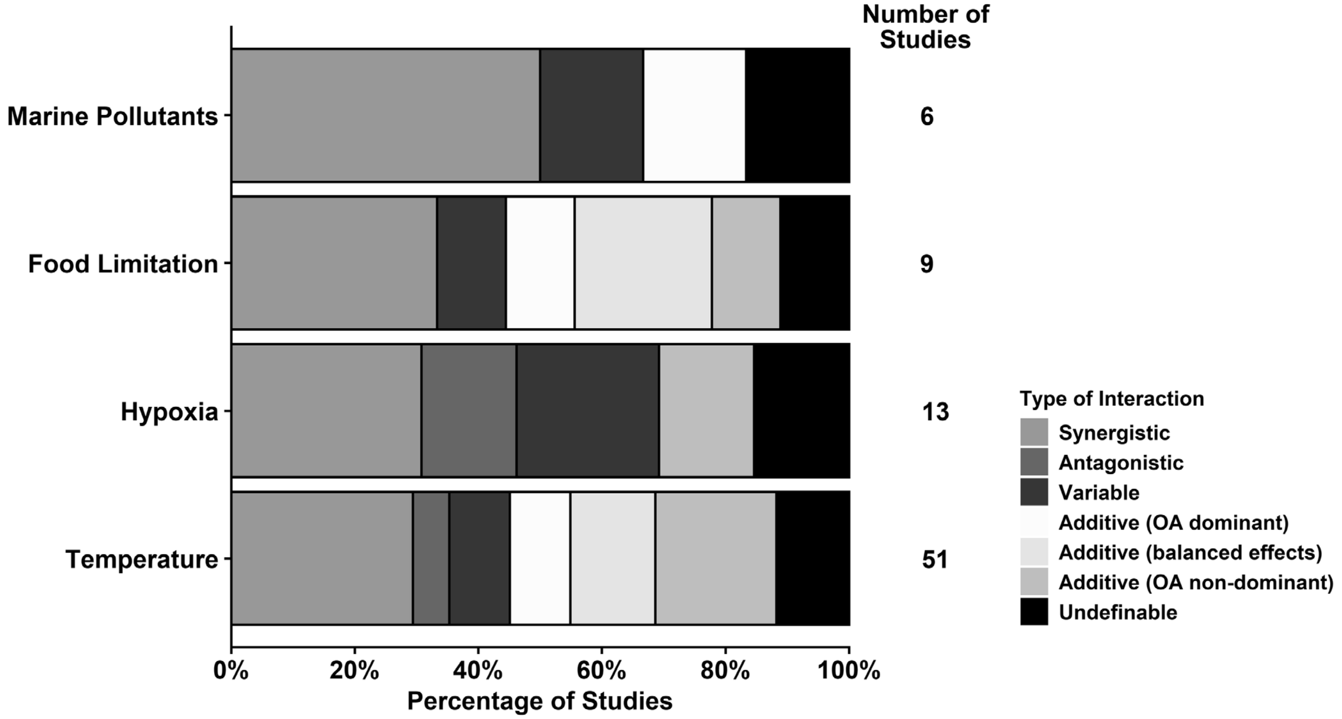

FIGURE 6 | Distribution of interactive effects between ocean acidification and additional environmental stressors on reproduction and early life development in marine teleosts. For each stressor category, stacked bars show the percentage of reported interaction outcomes classified as synergistic, antagonistic, variable, additive or undefinable. Additive effects imply that the interaction of the combined stressors were not statistically significant ($p > 0.05$). The additive categories include OA-dominant, whereby exposure to OA had a dominant effect on the response variables; 'balanced effects' where the response of combined effects is equal to the sum of the individual effects when both stressors have an effect; and 'OA non-dominant' where the response variable is influenced only by the respective combined stressor and not by OA. 'Undefinable' indicates cases where no single-stressor comparison was conducted so the interactive effects could not be delineated. Values to the right of each bar indicate the total number of studies assessing each environmental stressor in combination with ocean acidification. Where a single study used multiple species models, each species is represented individually as interactive outcomes often differed among species.

(e.g., Dahlke et al. 2022; Slesinger et al. 2025). For instance, Atlantic silverside (*Menidia menidia*) showed no significant reproductive response to OA at 17°C, but under elevated temperature (24°C), OA reduced reproductive potential and relative fecundity (Concannon et al. 2021). Additionally, long term exposure to OA under an RCP 8.5 scenario (~1510 µatm/+2°C) reduced sexual maturation, gamete quality and fertilisation rate in the three-spined stickleback (*Gasterosteus aculeatus*) (Devergne et al. 2023), while offspring quality in the cinnamon anemonefish only declined when OA occurred in combination with warming (Miller et al. 2015). Similarly, in the Atlantic cod, OA combined with warming (+3.5°C) reduced fertilisation success by a further 22% relative to warming alone (Dahlke et al. 2022).

Evidence suggests that OA can modify thermal sensitivity, thereby narrowing thermal performance windows during early development (e.g., Pimentel et al. 2014). Reduced thermal sensitivity under OA has been observed in embryonic Atlantic silversides (Schwemmer et al. 2020), while OA has been shown to constrain thermal windows in fish (Dahlke et al. 2017, 2018). In the Atlantic cod from the Barents Sea, egg loss was exacerbated under OA when spawning temperatures fell outside of their preferred range of 3°C–7°C, leading to significantly higher mortality rates upon hatching when stressors are combined compared to single stressor exposure (Dahlke et al. 2018). From an ecological standpoint, the constraining of thermal performance windows and reduced tolerance to OA may shift spawning habitats of cod to higher latitudes, while simultaneously contracting the area of suitable habitats (Dahlke et al. 2018). Furthermore, sequential exposure to warming after exposure to chronic hypercapnia may pose further challenges to larval fish. For example, Pimentel et al. (2014) found that thermal tolerance was reduced in the Senegalese sole, during developmental exposure under OA, due to impaired acid–base regulation and reduced efficiency of cellular activities.

Hypoxia can interact with OA to produce additive and synergistic effects on hatching success, survival and metabolic rates in embryos and larvae depending on the species of fish. Negative additive effects of combined hypoxia and OA have been observed in inland silversides (DePasquale et al. 2015) and Atlantic silversides (Cross et al. 2019; DePasquale et al. 2015; Morrell and Gobler 2020) where reductions in larval length and survival are greater than under OA alone. Furthermore, developing fish may become oxygen limited in acidified and hypoxic waters as metabolic costs are exacerbated by the energy requirements for homeostasis. Hypercapnia reduces the oxygen binding efficiency to haemoglobin because of the reduced pH_e (Bohr effect), causing subsequent reduction in oxygen uptake to metabolically active tissues. For example, in embryonic Atlantic silversides, resting metabolic rates (RMR) increased under OA but decreased when combined with hypoxia which can indicate that the critical oxygen tension (P_{crit}) for which RMR becomes oxygen dependent in oxyregulators is higher under OA (Schwemmer et al. 2020).

Habitats such as coastal waters undergo frequent fluctuations in stressors (i.e., pH, hypoxia and warming), due to upwellings and diel fluctuations of community metabolism. Cross et al. (2019) found that this cycling of stressor exposure, that is, OA and hypoxia, is likely beneficial to larval fish (i.e., Atlantic silversides) by providing a 'physiological refuge' for periods of recovery and promoting adaptation to future climate change. Estuarine fish that are adapted to large variations in dissolved oxygen and $p\mathrm{CO}_2$ also have well adapted physiological mechanisms for compensation. For example, exposure to OA (~2000 μatm) and hypoxia (~2 mg/L) in embryonic and larval sheepshead minnow triggered higher activity of acid–base regulatory mechanisms (Na^+/K^+-ATPase and carbonic anhydrase activity) with no apparent trade-offs in hatching success, survival, growth or body condition (Enzor et al. 2020).

Evidently, combined climate stressors may elevate the reproductive and developmental challenges fish will face in the coming years and further research should incorporate both single and multi-stressor exposure to unravel how reproductive success will be impacted.

7 | Future Directions

Despite substantial progress to date, there are still significant knowledge gaps in our understanding of how fish physiologically respond to ocean acidification. Future research should prioritise long-term, multi-generational studies to evaluate the potential for transgenerational acclimation and adaptive evolution mediated through epigenetic mechanisms and genetic change. Up to now, most studies have been short-term and focused on isolated life stages, highlighting the need to investigate the cumulative effects of chronic OA exposure across entire life cycles. Furthermore, examining OA in conjunction with co-occurring stressors (e.g., ocean warming, hypoxia and pollution) continues to be critical for accurately assessing impacts on fish physiology, fitness and survival over successive generations.

Persistent geographic and taxonomic biases further limit our current understanding, as research conducted to date has been disproportionately concentrated in North America and Europe and encompasses only a small fraction of global fish diversity. Expanding studies to underrepresented regions and taxa will be essential for capturing the full variability of OA responses across the phylogenetic tree. For instance, polar species (e.g., Nototheniidae) remain largely understudied despite experiencing some of the fastest rates of acidification globally. Additionally, many economically and commercially important fish families, such as Engraulidae (anchovies), Lutjanidae (snappers) and Anguillidae (eels), remain comparatively underrepresented in ocean acidification research (Figure 2). Addressing these gaps will require integrating physiological research with ecological and evolutionary frameworks to better understand downstream consequences and to determine whether future oceans will favour 'winners' or create vulnerable 'losers' among fish populations.

8 | Conclusion

Overall, advancing our understanding of fish responses to OA demands a shift towards more comprehensive, integrative and globally representative research approaches. Bridging physiological processes with ecological and evolutionary outcomes, while accounting for multiple stressors and long-term exposure, will be key to improving predictions of population and ecosystem-level impacts. Such efforts are essential not only for refining vulnerability assessments but also for informing conservation and management strategies in an increasingly changing ocean.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Experimental studies investigating the effects of ocean acidification (OA) on reproduction and/or early life development in teleost fishes included in this synthesis. The table includes information on study species, life stage, experimental conditions, response variables and the reported effects of OA on reproductive performance and early developmental traits. **Table S2:** Experimental studies investigating the interactive effects of ocean acidification (OA) and at least one additional stressor (e.g., warming, hypoxia or pollution) on reproduction and/or early life development in teleost fishes included in this synthesis. The interactive effects of combined stressors were classified as synergistic or antagonistic when the response was greater or less than the sum of the individual stressor effects, respectively. Additive effects indicate that the interaction between stressors was not statistically significant. Within the additive category, it is further noted whether the effects on the response variable were balanced between stressors or dominated by a single stressor (e.g., OA-dominant). The interactive effect was considered undefinable if the effect of the stressors were not tested individually.