


ORIGINAL ARTICLE

Critically examining the knowledge base required to mechanistically project climate impacts: A case study of Europe's fish and shellfish

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Abstract

An amalgam of empirical data from laboratory and field studies is needed to build robust, theoretical models of climate impacts that can provide science-based advice for sustainable management of fish and shellfish resources. Using a semi-systematic literature review, Gap Analysis and multilevel meta-analysis, we assessed the status of empirical knowledge on the direct effects of climate change on 37 high-value species targeted by European fisheries and aquaculture sectors operating in marine and freshwater regions. Knowledge on potential climate change-related drivers (single or combined) on several responses (vital rates) across four categories (exploitation sector, region, life stage, species), was considerably unbalanced as well as biased, including a low number of studies (a) examining the interaction of abiotic factors, (b) offering opportunities to assess local adaptation, (c) targeting lower-value species. The meta-analysis revealed that projected warming would increase mean growth rates in fish and mollusks and significantly elevate metabolic rates in fish. Decreased levels of dissolved oxygen depressed rates of growth and metabolism across coherent species groups (e.g., small pelagics, etc.) while expected declines in pH reduced growth in most species groups and increased mortality in bivalves. The meta-analytical results were influenced by the study design and moderators (e.g., life stage, season). Although meta-analytic tools have become increasingly popular, when performed on the limited available data, these analyses cannot grasp relevant population effects, even in species with a long history of study. We recommend actions to overcome these shortcomings and improve mechanistic (cause-and-effect) projections of climate impacts on fish and shellfish.

KEYWORDS

aquaculture, climate change, experiments, fisheries, gap analysis, meta-analysis

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1 | INTRODUCTION

Climate change (CC), particularly global warming, is having demonstrable impacts on the distribution and regional productivity of both terrestrial and aquatic organisms (IPCC, 2014). International policy initiatives have been created in the hope of limiting future changes, particularly those jeopardizing global food security (e.g., FAO climate change initiatives; FAO, 2017). The projected effects of CC on aquatic habitats and species, although fraught with uncertainty (Payne et al., 2016), are particularly relevant to society because of the importance of finfish and shellfish to food security, cultural heritage and/or the economies of dependent human communities (Allison et al., 2009; Callaway et al., 2012; Cinner et al., 2012; Hidalgo, Mihneva, Vasconcellos, & Bernal, 2018; Peck & Pinnegar, 2018). In 2016, global fish and shellfish production reached a record 171 million tons and employed around 200 million people either directly or indirectly (FAO, 2018). The quantity of finfish and shellfish used for direct consumption from aquaculture has surpassed that from wild fisheries and this gap is expected to widen as aquaculture continues to expand (FAO, 2018).

Fish and shellfish are potentially impacted by climate-driven changes in a suite of abiotic factors beyond warming including the acidification of marine and freshwaters (Caldeira & Wickett, 2003; Weiss et al., 2018), deoxygenation (Altieri & Gedan, 2015) and altered precipitation and river flow rates in freshwater habitats (Ficke, Myrick, & Hansen, 2007; Markovic et al., 2014; Pletterbauer, Melcher, & Graf, 2018; Poff, Brinson, & Day, 2002; Ward, Anderson, Beechie, Pess, & Ford, 2015). Several studies have reviewed the effects of these physical changes on fish and shellfish in these habitats (e.g., Callaway et al., 2012; Petitgas et al., 2013; Robins et al., 2016). Warming has been associated with increased rates of growth (Baudron, Needle, Rijnsdorp, & Tara Marshall, 2014; Jonsson & Jonsson, 2009), poleward or deeper shifts in spatial distribution (Morrison, Nelson, Griffis, & Hare, 2016; Rose, 2005) and phenological shifts in migration (Myers et al., 2017) and reproduction (Asch, 2015; Nunn, Harvey, & Cowx, 2007; Tao et al., 2018) in fish as well as increased variation in rates of growth, calcification and reproduction in commercially important mollusks (Mackenzie et al., 2014; Montalto et al., 2016). In fish and shellfish, decreased pH can impair behavior, and either increase or decrease rates of mortality and growth (including calcification; Harvey, Gwynn-Jones, & Moore, 2013; Kroeker et al., 2013) while low dissolved oxygen can reduce the extent of suitable habitat causing forced migrations, increase vulnerability to predation and elicit sublethal effects such as reductions in growth (reviewed in Vaquer-Sunyer & Duarte, 2008). Finally, in a few species of finfish and shellfish, synergistic responses to interacting abiotic stressors have been documented (Freitas et al., 2017; Miller, Breitburg, Burrell, & Keppel, 2016; Pörtner, Langenbuch, & Michaelidis, 2005).

The direct effects of CC on aquaculture are conceptually easier to grasp compared to those on capture fisheries. Within semi-extensive and some intensive (ponds, cage) systems, changes in local

1 INTRODUCTION	502
2 MATERIAL AND METHODS	503
2.1 Species selection	504
2.2 Literature search and inclusion criteria	504
2.2.1 Data extraction protocol	504
2.2.2 Inclusion criteria and quality control	504
2.3 Gap Analysis	504
2.4 Meta-analysis	506
3 RESULTS AND DISCUSSION	506
3.1 Gap analysis	506
3.2 Meta-analysis	509
3.2.1 Effect of increased temperature	510
3.2.2 Effect of decreases in pH	511
3.2.3 Effect of deoxygenation	511
3.2.4 Heterogeneity	512
3.2.5. Moderator analysis	513
4 CONCLUSIONS AND RECOMMENDATIONS	513
ACKNOWLEDGEMENTS	513
REFERENCES	514
SUPPORTING INFORMATION	517

conditions (e.g., temperature, pH, salinity, turbulence) will have direct, measurable, physiological impacts on a species which will alter its productivity in aquaculture. Empirical data from controlled laboratory experiments can be directly used to improve the reliability of models projecting the impacts of CC on local culture conditions. The case is more complex, however, for species targeted by capture fisheries since these species are embedded in ecosystems where indirect effects of CC are important such as changes in species interactions (Milazzo, Mirto, Domenici, & Gristina, 2013), altered habitat connectivity/availability for or between specific life stages (Petitgas et al., 2013), habitat modification (Nagelkerken, Russell, Gillanders, & Connell, 2016), flow regulation (Sundt-Hansen et al., 2018), and/or the alteration of modification of species- and life stage-specific prey resources (e.g., reviewed in Hoegh-Guldberg & Bruno, 2010). Harvesting, particularly over-exploitation, adds an extra pressure, and disentangling the potential effects of CC from those caused by direct and indirect impacts of fisheries exploitation is a further challenge (Brander, 2007; Rijnsdorp, Peck, Engelhard, Mollmann, & Pinnegar, 2009).

The further development and refinement of process-based models are needed to advance our capacity to project how CC-driven changes in temperature, pH, and dissolved oxygen will impact individuals, populations and ecosystems (Koenigstein, Mark, Gößling-Reisemann, Reuter, & Poertner, 2016; Persson, Van Leeuwen, & De Roos, 2014). There is a long list of potential prediction tools that can benefit from more or better-quality laboratory

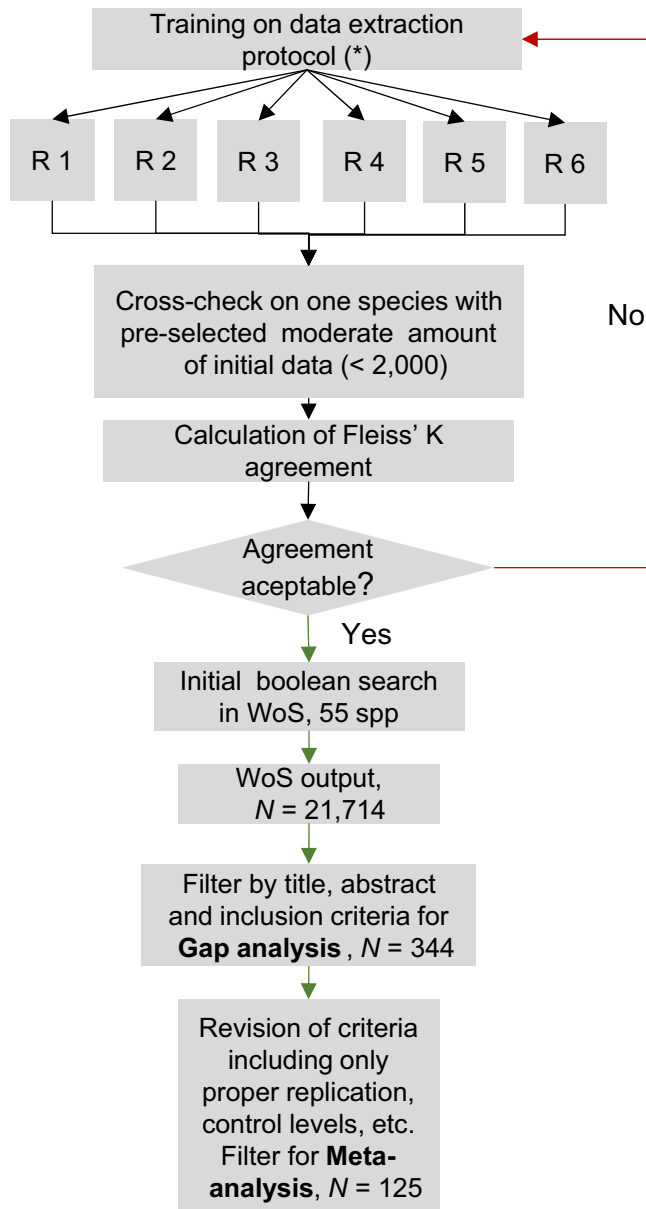


FIGURE 1 Protocol for structured literature review performed in WoS. R1, R2, ... R6 are researchers involved. (*) protocol for data extraction described in the text. Specific number of results by species are provided in Supporting Information Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]

and field data including single and multispecies population dynamics models, species distribution models, trait- and individual-based models, bioenergetics models and coupled end-to-end models (Peck et al., 2018; Teal, Marras, & Domenici, 2018). Arguably, projections from models based on physiological first principles are best suited for extrapolating beyond conditions historically observed in specific regions, which may be necessary when projecting impacts of a future climate. To be correctly parameterized, physiological-based models demand robust, empirical data and benefit from close collaboration with experimentalists (e.g., Fernandes et al., 2017; Peck, Reglero, Takahashi, & Catalán, 2013;

Teal et al., 2018). Although Herculean efforts have been made to collect information on climate impacts on fish and shellfish, the majority of recent summaries have focused on either specific (single) drivers or contain information gained from relatively few, well-studied (not always commercial) species (e.g., Harvey et al., 2013; Hendriks, Duarte, & Álvarez, 2010; Kroeker et al., 2013; Vaquer-Sunyer & Duarte, 2008).

Europe represents the largest single market for fish and bivalves worldwide (FAO, 2018). Given the high economic as well as cultural importance of these aquatic resources (Poulsen, 2016), more than a century of research has examined how the environment regulates the productivity of species targeted by fisheries (Farrugio, 1993; Froese et al., 2018; Jennings et al., 2002) and aquaculture (Shields, 2001). Several aquatic regions within Europe have been identified as climate hotspots (e.g., Hobday & Pecl, 2014), and the EU has responded by investing in research actions designed to provide advice supporting sustainable “Blue Growth” policies (Pauli, 2010). In Europe, therefore, there is a wealth of information and a clear awareness of CC-related effects on fish and shellfish resources as well as the adaptation and mitigation challenges facing management (e.g., Hidalgo et al., 2018; Peck & Pinnegar, 2018). This region, therefore is an excellent test bed to critically evaluate the knowledge base available to inform models designed to project impacts of climate change on the distribution and productivity of fish and shellfish.

We critically examined the data available in the published literature on the effects of environmental factors on 55 of the most economically important marine and freshwater finfish and shellfish species targeted by European fisheries and/or aquaculture sectors. Some of the species included here have a cosmopolitan distribution or are widely distributed across ocean basins. A global semi-systematic literature review (Kitchenham, 2004) was conducted followed by a Gap Analysis (Winch, Usmani, & Edkins, 1998) to explore potential bias in the available information by species, life stage and region. Next, we employed a meta-analysis (Assink & Wibbelink, 2016) to quantify the effects of three key climate drivers (changes in temperature, pH and/or dissolved oxygen) on the vital rates of finfish and shellfish. We provide a set of recommendations to help eliminate imbalance, bias and other potential shortcomings in the knowledge base needed for robust projections of climate impacts on these living aquatic resources.

2 | MATERIAL AND METHODS

We followed most criteria of Systematic Literature Reviews (explicit protocols for literature search, data selection and extraction, meta-analytical techniques, etc. Kitchenham, 2004). This procedure enables reproducibility and intercomparison of the analyses derived from the literature search and has become common practice (Hillebrand & Gurevitch, 2016). However, a few criteria were not met for logistical reasons: not all papers were viewed by all researchers, and only one common database was used (see below). Therefore, we use the term semi-systematic literature review to describe our approach (Kitchenham, 2004).

2.1 | Species selection

For our analyses, we initially selected 55 species representing valuable resources to three key European aquatic food production sectors (Marine Aquaculture, Marine Fisheries and Inland Waters) taking into account regional differences in commercial targets (from the Barents Sea down to the Mediterranean Sea). The widespread distribution of some species offered opportunities for regional comparison. Some species of high cultural value to artisanal fisheries and in freshwater areas were also included. The top-landed (by value) marine fisheries targets were included (see Supporting Information Table S1) such as small pelagics (four species of Clupeidae and Engraulidae), larger pelagics (two species of Scombridae and one of Coryphaenidae), demersals (six species in the families Gadidae, Mercuroidae, Soleidae, Pleuronectidae and Mullidae) and shellfish (two species in the families Loliginidae and Aristeidae). The sector Marine Aquaculture included three key finfish (families Salmonidae, Moronidae, and Sparidae) and six bivalves (two species in Ostreidae, Veneridae, and Mytilidae; Supporting Information Table S1). The Inland Waters sector included five key finfish species for either freshwater aquaculture or inland fishing (including Cyprinidae, Anguillidae, Salmonidae, Percidae and Clupeidae) and two groups of several species caught together (twenty species of *Coregonus* spp (Salmonidae) and ciprinids other than the common carp (*Cyprinus carpio*, *Cyprinidae*; six species in total, see Supporting Information Table S1). For the sector Inland Waters, species important to aquaculture and mixed fisheries were often analyzed as one unit in contrast to marine waters.

2.2 | Literature search and inclusion criteria

Six different raters, researchers with expertise in freshwater and marine fisheries and aquaculture, were each allocated a similar number of species to conduct the data extraction for the Gap Analysis and meta-analysis. Web of Science (WoS V.5.29) was used as it was the only available tool common to all raters. They were first trained in the data extraction protocol, and a cross-validation exercise was conducted on a species with a relatively high number of initial outcomes (common sole *Solea solea*, Soleidae, Figure 1). Gray literature was not considered to avoid bias in the data appraised by each rater.

2.2.1 | Data extraction protocol

The data extraction protocol consisted of:

1. A search in the WoS for ("Latin species name" OR "common species name1" OR "common species name2" etc.) AND (temperature OR climate change OR climat* shift OR acid* OR pH OR oxygen OR hypox* OR hypercapn* OR O2 OR salinity OR freshening OR stress* OR thermal) AND (tolera* OR limit* OR critic* OR lethal OR threshold* OR growth OR weight OR mass OR diameter OR develop* OR mortality OR surviv* OR metaboli* OR respir* OR oxygen consumption OR prefer* OR thermal window OR aerobic scope OR metabolic scope OR

sensitivity) NOT (chem* OR engine* OR technology). The specific text for "Latin name species" and "common name species" is specified in Supporting Information Table S1. This search term was applied to all years through December 2017. Due to workload constraints, in cases where >3,000 outcomes were returned, an additional term "exper*" was added to focus the search on published results stemming from laboratory experiments, but the new outcomes were only accepted if at least 40% of the initial literature was obtained.

2. The outcome screen from WoS was saved for a quality check. After an initial subjective revision of titles and abstracts, any paper potentially containing results that matched the objective of the present study was kept.
3. Papers were then checked for relevance according to the inclusion criteria (Table 1), noting reasons for exclusion.
4. A quality check of the initial number of hits from step 2 and the reasons for exclusion in step 3 were discussed and agreed between raters.
5. Data were finally collected into a common spreadsheet according to the inclusion criteria (Table 1).

2.2.2 | Inclusion criteria and quality control

A set of inclusion criteria was used for the Gap Analysis, a subset of which was used for the meta-analysis following more strict criteria (Table 1). Besides species and stages, these inclusion criteria accounted for the correct type of drivers, effect levels, controls, true replicates, and issues of independence. A final common revision of the selected datasets was conducted by the researchers involved in data extraction, and the conflicting datasets eliminated.

Prior to the final search and data extraction, an inter-rater calibration exercise was performed through a cross-check search on *Solea solea* (Figure 1). For this search, the Fleiss' kappa (K) parameter was calculated where $K < 0$, 0.01–0.20, 0.21–0.40, 0.41–0.60, 0.61–0.80 and 0.81–1.0 represented poor, slight, fair, moderate, substantial and nearly perfect agreement, respectively (Landis & Koch, 1977). This exercise yielded an acceptable agreement (see results), so each rater was considered apt to conduct the search.

2.3 | Gap Analysis

A Gap Analysis is a technique frequently used in management to determine what steps need to be taken in order to move from a current state (e.g., knowledge on a particular problem) to a desired, future state. The approach consists of (a) identifying the differences between the desired status (e.g., knowledge of a particular CC-related driver, often termed stressor in the literature) on a particular species, life stage, region, etc.) and the present status (degree of information available), and (b) analyze the potential solutions to move from present to desired status (Brown & Dodd, 1998; Winch et al., 1998). Broad categories were re-coded for the Gap Analysis. The main factors explored were sector (Marine Aquaculture, Marine Fisheries, Inland Waters), geographical region (e.g., Barents and Norwegian

TABLE 1 Inclusion criteria applied to the initial set of articles filtered by title and abstract by the raters (see also Figure 1)

Inclusion criteria	Explanation	Applied for Gap analysis	Applied for Meta-analysis
Subject studied	All species as defined in Supporting Information Table S1	Y	Y
Life stages	All life stages were included. They were separated into embryo (eggs and non-feeding larvae), feeding larvae, juveniles, and adults. Combinations of the above were used if required by the dataset	Y	Y
Response	We divided the responses into coherent groups: Growth/size (measured as mass, length, diameter, Von Bertalanffy (VBG) growth parameters, weight-length relationships), developmental rate, mortality/survival, metabolic rate (Standard metabolic rate (SMR), Resting metabolic rate (RMR), specific dynamic action (SDA), mean metabolic rate (MMR), aerobic scope (AS)), and optimal/critical/lethal/preferred treatment conditions (including limits, thresholds, ranges). Combinations of Responses that were not independent within a study were also recorded (e.g., Growth_development)	Y	Y
Control treatment	For Ambient temperature, we assumed the median treatment to be the temperature control if not specified in the paper. For pH, we followed the author's "ambient conditions" (7.9–8.21 or lowest µatm treatment for CO ₂ in seawater; for fresh water, we used 7.0–7.8 as a control). For oxygen, 50%–100% saturation or respective value in mg/L (in case of multiple potentially matching values, the one closer to 80% saturation was used). Salinity conditions were excluded due to scarcity of data.	N	Y
CC effect treatment	For non-ambient temperature, we used a range of 2–5°C warmer than the control. For pH, we used up to 0.6 less than control for seawater, and up to 1.5 less in fresh water. For oxygen, we used 20%–50% reduced oxygen (in case, the criteria were met by multiple values, treatments with 30%–40% reduction were favored). Salinity conditions were excluded due to scarcity of data	N	Y
Comparator	A true control treatment must exist (see exception). Only data from sources where a relationship between a CC-related stressor and the impact on potential organismal traits/parameter, such as growth, was revealed, were recorded, but not the data from studies in which a trait/parameter was measured at one single temperature	An exception is optimal/critical/lethal/preferred treatment conditions including limits, thresholds, ranges, these can be reported without a comparator	Y
Type of study	We included any primary studies with appropriate comparators and variance measures (number of true replicates [<i>n</i> !], standard deviation of the mean [<i>SD</i>]). If standard error (<i>SE</i>) instead of <i>SD</i> was reported, we calculated <i>SD</i> from <i>SE</i> and <i>n</i> ($SD = SE \cdot \sqrt{n}$)	N	Y
Non-independence criteria	Non-independence issues: In cases of multiple measures of outcome, the single most relevant one was chosen. In cases of multiple treatments with a common control, new variance was derived for several common experimental designs. In cases of repeated measures, only a single time point (final measurement) was used, and a linear effect over time was selected. Finally, phylogenetic distance was considered as a potential confounding moderator in later analyses (see meta-analysis)	Y	Y

Seas, Baltic Sea, etc.), species group (marine pelagic, marine demersal, shellfish, etc., see figures), species and stage (as defined in Table 1), CC-related driver, and measured response (Table 1). In some cases, some categories had to be pooled together (e.g., measuring the effect of temperature on the growth along the non-feeding and feeding period). The analysis was purely descriptive (graphical), and interpretations are made on the basis of comparative outputs and the literature used.

2.4 | Meta-analysis

A meta-analysis is a quantitative approach for comparing outputs of multiple primary studies investigating a common driver-response relationship and for generating a common effect size (ES). It can be a powerful technique for more broadly contextualizing the results of species or stage-specific studies and has been frequently used to summarize and quantify potential effects of CC on organisms (Daufresne & Boët, 2007; Givan, Edelist, Sonin, & Belmaker, 2018; Harvey et al., 2013; Kroeker et al., 2013). We conducted the meta-analysis following the guidelines and procedures of Assink and Wibbelink (2016). Pairs of measures having appropriate “controls” and “CC_conditions” (Table 1), variance measures and true replicates were extracted. For pH and oxygen, we used only one pair of measurements per experiment. In contrast, multiple pairs (accounting for different seasons) were extracted for temperature treatments when, according to the authors of the study, the treatment levels represented different seasons. Our ranges of values used to define treatments and controls were selected in order to maximize the number of studies included in the Meta-analyses while still being plausible with respect to future changes depicted in scenarios of CC. Some studies included treatment extremes based on global projections, whereas others included extreme values of regional projections (e.g., temperature, pH). In the case of deoxygenation, we selected studies testing moderate effects that might resemble coastal events of hypoxia (Table 1). The analysis was based on a standardized effect size metric (Ln response ratio, LnRR; Hedges, Gurevitch, & Curtis, 1999). This metric is often used in ecological analyses (Harvey et al., 2013; Lajeunesse & Forbes, 2003) and is considered to be accurate for small sample sizes, as was the case here. We used a multilevel model to account for dependence of multiple effect sizes (ES) from the same studies and dependence of multiple studies within the same species. Alternative approaches would have been to average multiple study outcomes or ignore dependence of outcomes. The former, however, would have resulted in a loss of information while the latter might have inflated specific outcomes (Nakagawa & Santos, 2012). A four-level, meta-analytic model (experiment (L1), study (L2), species (L3) and functional group (L4)) was generated for each functional group. For the meta-analysis, functional groups were “Freshwater fish,” “Pelagic fish,” “Demersal fish,” and “Mollusk.” Model parameters were estimated iteratively using Restricted Maximum Likelihood (REML), recommended by Viechtbauer (2005, 2010). The variance encompassed four

different components distributed over the model levels: within an experiment (L1), between experiments of the same study (L2), between studies of the same species (L3) and between species within a functional group (L4). Subsequently, we generated forest plots for visualizing ES of overall model results per functional group.

In order to test the consistency of effects, the heterogeneity (I^2 , ranging 0%–100% and describing the amount of unexplained variance) was calculated at different levels. As a log-likelihood ratio test might be affected by a power problem at low study numbers (Assink & Wibbelink, 2016), the I^2 was calculated for different levels following Cheung (2014). As an example, the following formula (1) explains the heterogeneity at level three (within-species variance/between-study variance):

$$I^2_{(3)} = \frac{\tau^2_{(3)}}{\tau^2_{(2)} + \tau^2_{(3)} + \tau^2_{(4)} + \tilde{v}} \quad (1)$$

where \tilde{v} describes the basic sampling variance and τ^2 represents the variance at the given level. Moderating effects of life stage (eggs, larvae, juveniles and adults) and season (only for temperature studies), distinguished by the expressions “summer,” “winter,” “intermediate,” and “other” (season not mentioned in the study), were tested by using omnibus-tests. Results on moderating effects were supposed to provide potential explanations for high levels of unexplained heterogeneity. Furthermore, profile plots were used to assess the potential over parameterization of the models, resulting from high levels of complexity at low numbers of ES (Viechtbauer, 2010).

3 | RESULTS AND DISCUSSION

During the semi-systematic literature review, the inter-rater search agreement for common sole ($n = 51$ in the first search, see Supporting Information Table S1) yielded “substantial agreement” ($k = 0.681$, $p = 0.001$, Landis & Koch, 1977), so all raters were assumed to extract comparable information. The initial search in WoS yielded an initial number of hits of 21,714 articles, of which only 331 and 89 were relevant for the Gap Analysis, and meta-analysis, respectively. From these papers, often more than one dataset was extracted, so the final number of datasets used for the Gap Analysis and meta-analysis was 344 and 140, respectively (Figure 1, Supporting Information Table S1).

3.1 | Gap Analysis

In total, 37 species yielded 344 datasets from experiments that met the inclusion criteria (see Supporting Information Table S1) which included 13 species in Marine Fisheries, 15 species in Inland Waters and nine species in Marine Aquaculture categories, each with similar number of datasets (Figure 2). As expected, more information was available for high-value and/or easy to culture (non-oceanic) species

than for the rest (Peck et al., 2013; Pörtner & Peck, 2010). The top five species in terms of the number of datasets corresponded to freshwater fish such as rainbow trout (*Oncorhynchus mykiss*, Salmonidae)

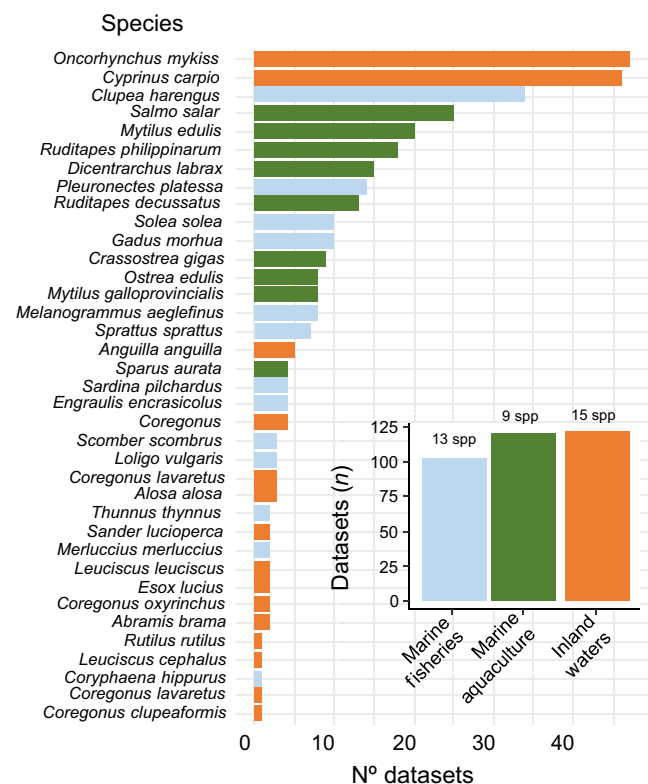
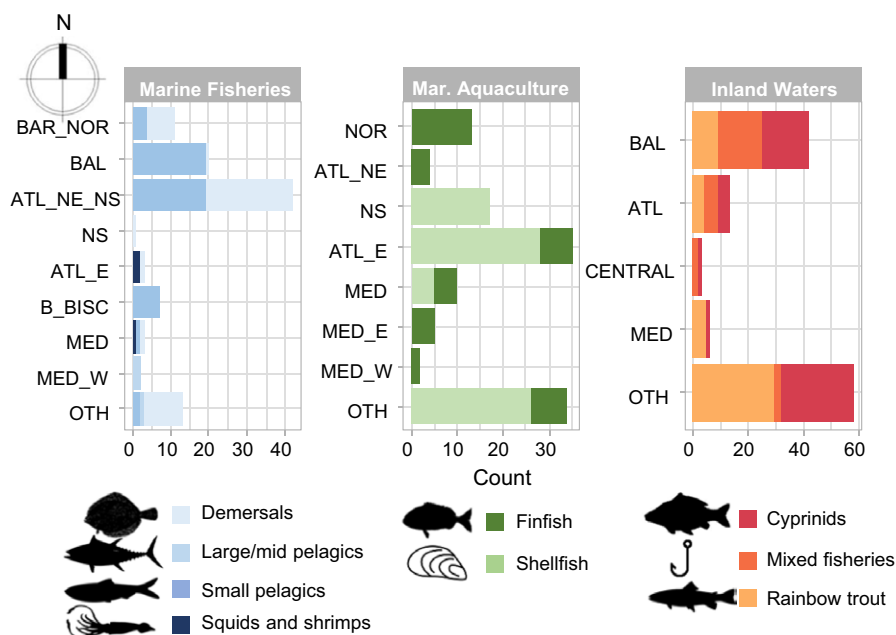


FIGURE 2 Number of datasets extracted for the Gap Analysis for each species and sectors (inside bar plot). Useful datasets were included even if they were not collected in the European Region [Colour figure can be viewed at wileyonlinelibrary.com]

and carp (47 and 46 datasets, respectively), followed by Atlantic herring (*Clupea harengus*, Clupeidae; 34 datasets), Atlantic salmon (*Salmo salar*, Salmonidae; 25 datasets) and blue mussel (*Mytilus edulis*, Mytilidae; 20 datasets, Figure 2, Supporting Information Table S1).

A strong latitudinal imbalance existed in the information available on the direct effects of CC on species of interest for fisheries and aquaculture (Figure 3, see Supporting Information Table S1 for functional classification). For the categories Marine Fisheries and Inland Waters, information was biased toward relatively high latitudes (Barents and Norwegian Seas, Baltic countries). Demersal fish (e.g., hake [*Merluccius merluccius*, Merlucciidae], haddock *Melanogrammus aeglefinus* [Gadidae], and common sole) and small pelagics (Clupeidae such as European sardine *Sardina pilchardus*, Atlantic herring *Clupea harengus*, European sprat *Sprattus sprattus* and the Engraulidae *Engraulis encrasicolus*) yielded the largest number of datasets for Marine Fisheries. For Inland Waters, datasets were approximately evenly separated among cyprinids (mainly common carp), rainbow trout, and mixed fisheries (Figure 3, Supporting Information Table S1). In the case of Marine Aquaculture, Atlantic salmon dominated datasets obtained from higher-latitude areas, and considerable information on North Sea and North East Atlantic and Mediterranean Sea areas was available for shellfish and some finfish such as European sea bass (*Dicentrarchus labrax*, Moronidae). The number of studies on large pelagics (Atlantic bluefin tuna *Thunnus thynnus*, Scombridae, dolphinfish *Coryphaena hippurus*, Coryphaenidae) was relatively low and studies on the European squid (*Loligo vulgaris*, Loliginidae) and blue and red shrimp (*Aristeus antennatus*, Aristeidae) were scarcer. Notably, considerable information was available from experiments conducted in non-European areas on some key species within the Marine Aquaculture and Inland Fisheries groups (categorized as OTH, Figure 3). This implies that these data could be appropriate for

FIGURE 3 Number of independent datasets for each sector category (Inland waters, Marine Aquaculture or Marine Fisheries), broad geographical region (European origin, y-axis, see below), and species group (color bar). Regions: ATL, Atlantic; ATL_E, North Eastern Atlantic, south of the North Sea; ATL_NE, North East Atlantic; ATL_NE_NS, regions of North Sea and North East Atlantic; BAL, Baltic; BAR_NOR, Barents and Norwegian Sea; B_BISC, Bay of Biscay; CENTRAL, central Europe; MED, Mediterranean (unspecified); MED_E, Eastern Mediterranean; MED_W, Western Mediterranean; NOR, Norwegian Sea. OTH, other world regions [Colour figure can be viewed at wileyonlinelibrary.com]



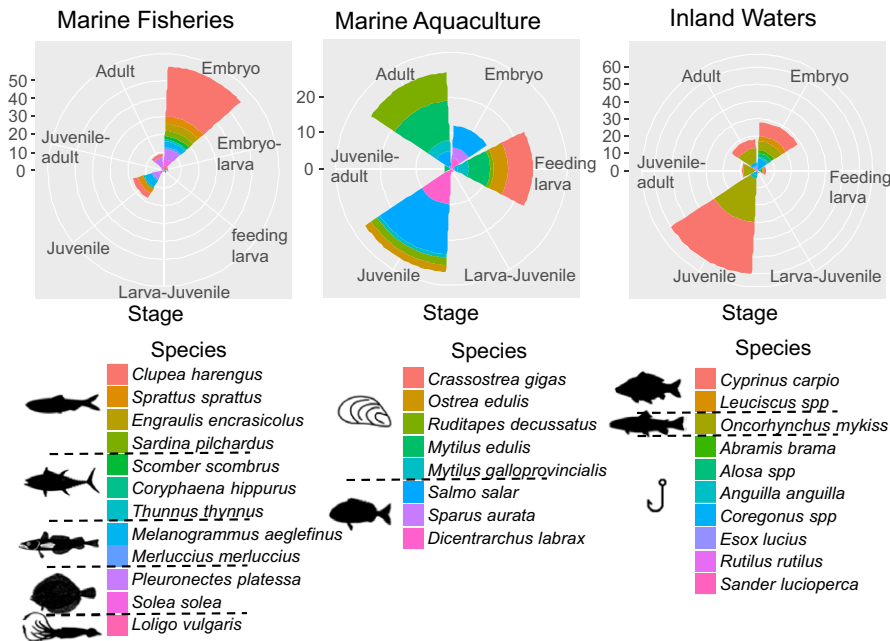


FIGURE 4 Number of studies by sector for each species and life stage (including all regions). For Inland Waters, the hook symbol represents capture inland fisheries, to distinguish them from the two fish that are typically farmed in fresh water. Note that y-axis scales are different and that each sector has its own color legend [Colour figure can be viewed at wileyonlinelibrary.com]

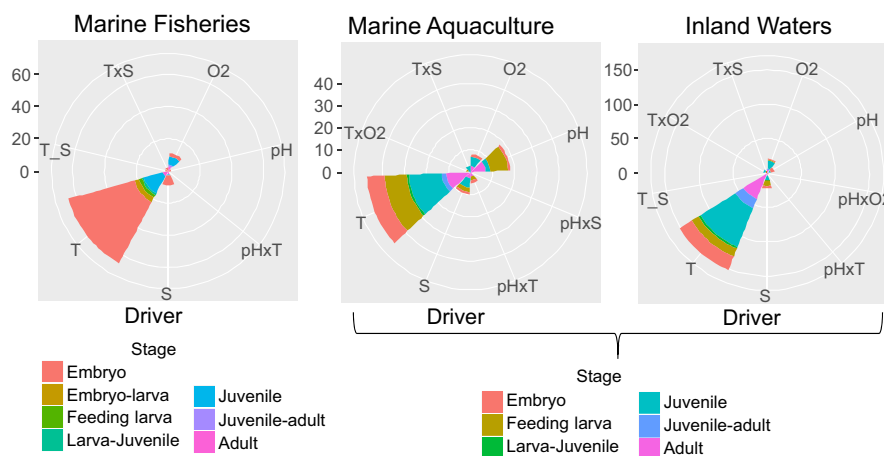


FIGURE 5 Number of studies by sector (Marine Fisheries, Marine Aquaculture, and Inland Waters), CC-related drivers (inside each graph) and life stage, including all regions. A combination of life stages was used if these were pooled by studies. The y-axis scales differ. O₂, deoxygenation effect; pH, acidification effect; pHxS, combined effect of pH and salinity; pHxT, combined effect of pH and temperature; S, salinity; T, temperature; T_S, effect of temperature and salinity in the same experiment, but not in combination [Colour figure can be viewed at wileyonlinelibrary.com]

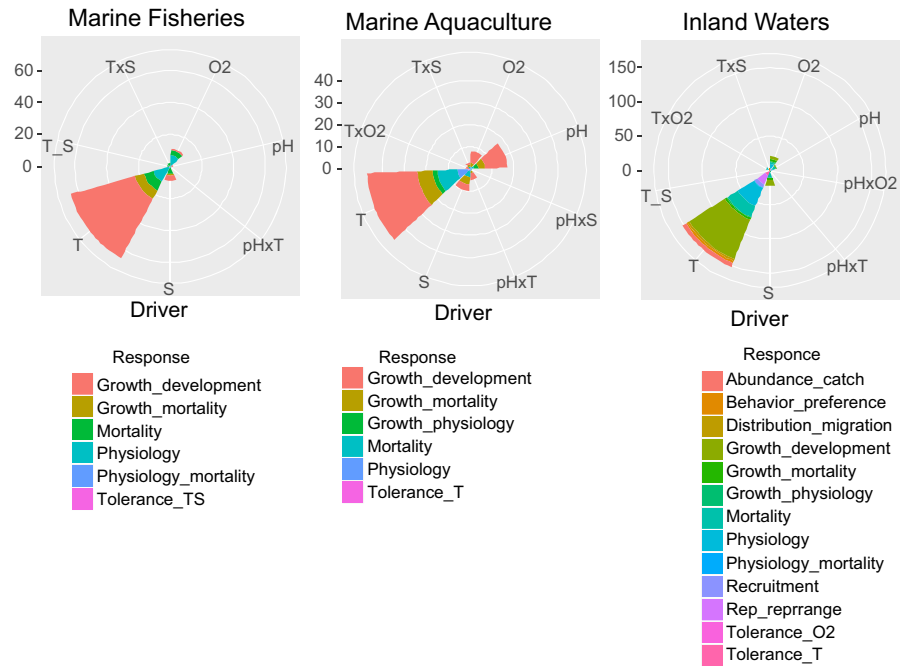
some modeling purposes as long as potential regional attributes (e.g., local adaptation, etc.) are not of interest.

In each of the three sectors, laboratory experiments examining CC-related drivers were imbalanced with respect to life stage. In Marine Fisheries, embryonic stages, particularly of small pelagics, were overwhelmingly studied compared to other life stages (Figure 4). In Marine Aquaculture, a similar number of datasets was available for adults (mainly bivalves), juveniles (mainly Atlantic salmon and European seabass) and feeding larvae (mainly oysters and mussels), whereas information on embryonic stages was only available for finfish. Datasets collected on Inland Water species stemmed mostly from studies conducted on juveniles and embryos of common carp and rainbow trout.

Laboratory studies conducted on species in each of the three sector categories were also largely imbalanced in that 58% of all datasets, temperature was the only factor examined (Figure 5). Within Marine Fisheries, the effect of O₂ (13%) and salinity (9%) were the next most-studied factors after temperature (66%). In Marine Aquaculture, the effect of temperature (50%) was equally examined across all life stages while pH (examined in 18% of the studies) was studied mainly on feeding larvae. Relatively little empirical data have been collected on the effects of salinity (12%) and oxygen (7%). For Inland Waters, fewer studies examined salinity (8%) and oxygen (16%) compared to temperature (61%).

The responses to the CC-related drivers were often difficult to separate into single, independent factors because more than one

FIGURE 6 Number of studies for each sector according to the driver (see Figure 5 for explanations) and the responses (color legend). Datasets shown here are independent (e.g., if an experiment measured both mortality and growth, the response is “Growth_mortality”). Responses which require clarification are as follows: Tolerance_TS, experiments which concurrently measure the tolerance to temperature and salinity; Rep_reprange, studies that analyze a reproduction measure or the reproduction range, measured at the scale of the driver (e.g., temperature); Physiology embraces any metabolic measurement (usually some level of oxygen consumption). The y-axis scales differ, and each sector has its own color legend [Colour figure can be viewed at wileyonlinelibrary.com]



key response was measured in the same replicate. Therefore, in many of those cases, the responses were reported together (e.g., growth/mortality, Figure 6). However, the most typical responses examined with respect to temperature included growth/development (50% in Marine Fisheries, 42% in Marine Aquaculture, 39% in Inland Waters) and mortality as a separate response in all sectors (17% in both Marine Fisheries and Marine Aquaculture and 27% in Inland Waters). A striking lack of information was available on the effect of combined drivers (e.g., 7%, 7% and 13% of Marine Fisheries, Inland Waters and Marine Aquaculture datasets, respectively), a fact that has been previously highlighted in the literature for some species (Harrod, 2016; Peck et al., 2013; Teal et al., 2018).

The imbalance that we have detected in terms of species, life stage, drivers and responses severely limits our ability to understand and model the potential effects of CC. A thorough analysis of the available data suggests an urgent need to broaden the information base available on stage- and region-specific responses to CC drivers (Pörtner & Peck, 2010; Rijnsdorp et al., 2009). Having more results from similar studies conducted in different regions is important if we hope to be able to detect local/regional adaptation, which has been documented in various species (Baumann & Conover, 2011; Crozier & Hutchings, 2014; Ojaveer & Kalejs, 2005). These gaps in knowledge must be acknowledged when parameterizing mechanistic (i.e., physiological-based) models to project climate impacts across species and regions (Koenigstein et al., 2016; Teal et al., 2018). Climate projection is inherently uncertain (Payne et al., 2016) and, until these gaps in our knowledge base are filled, one could argue that it may not be possible to generate robust, regionally specific “climate-ready” advice needed for the strategic or tactical management of aquatic resources. Many previous studies have employed meta-analyses to draw conclusions on the climate sensitivity of various taxa or groups and, in our opinion, most studies do not adequately discuss the

potential limitations imposed by stage- and regional bias in available datasets.

Our Gap Analysis did not consider information from field monitoring (e.g., time series data), which certainly offer valuable insight on the effects of CC on aquatic living resources (Heino, 2011; Parmesan & Yohe, 2003; Walther et al., 2002) including distributional shifts (Perry, Low, Ellis, & Reynolds, 2005), phenological changes (Asch, 2015) or estimates of the rate of regional extinction (Cheung et al., 2009). We argue that the tripartite approach of combining knowledge gained from laboratory experiments, field data, and models to project climate impacts (Cury et al., 2008) will be markedly stronger if bias in data collected in laboratory studies is identified, as we have done here, and addressed.

3.2 | Meta-analysis

The goal of our meta-analysis was to use data from existing laboratory experiments to generate quantitative knowledge on the effects of climate drivers on commercially important fish and shellfish. In total, 140 multiple effect sizes (ESs) were calculated from 89 studies conducted on 26 species that fulfilled the inclusion criteria (Table 1). These ESs were not evenly distributed among temperature ($n = 92$ ES/61 species), pH ($n = 23$ ES/19 studies) and O_2 ($n = 25$ ES/16 studies). Note that some studies included more than one driver. These ESs could be further separated into several response variables, functional groups, life stages and additional moderators (see Effect of increased temperature) which, naturally, further reduced the number of studies per analysis (see also Supporting information Table S2). In agreement with the Gap Analysis, the overarching finding from the meta-analysis was a general scarcity of appropriate studies, particularly those providing datasets on the effects of acidification on metabolism and the effects of deoxygenation on mortality (Figure 7).

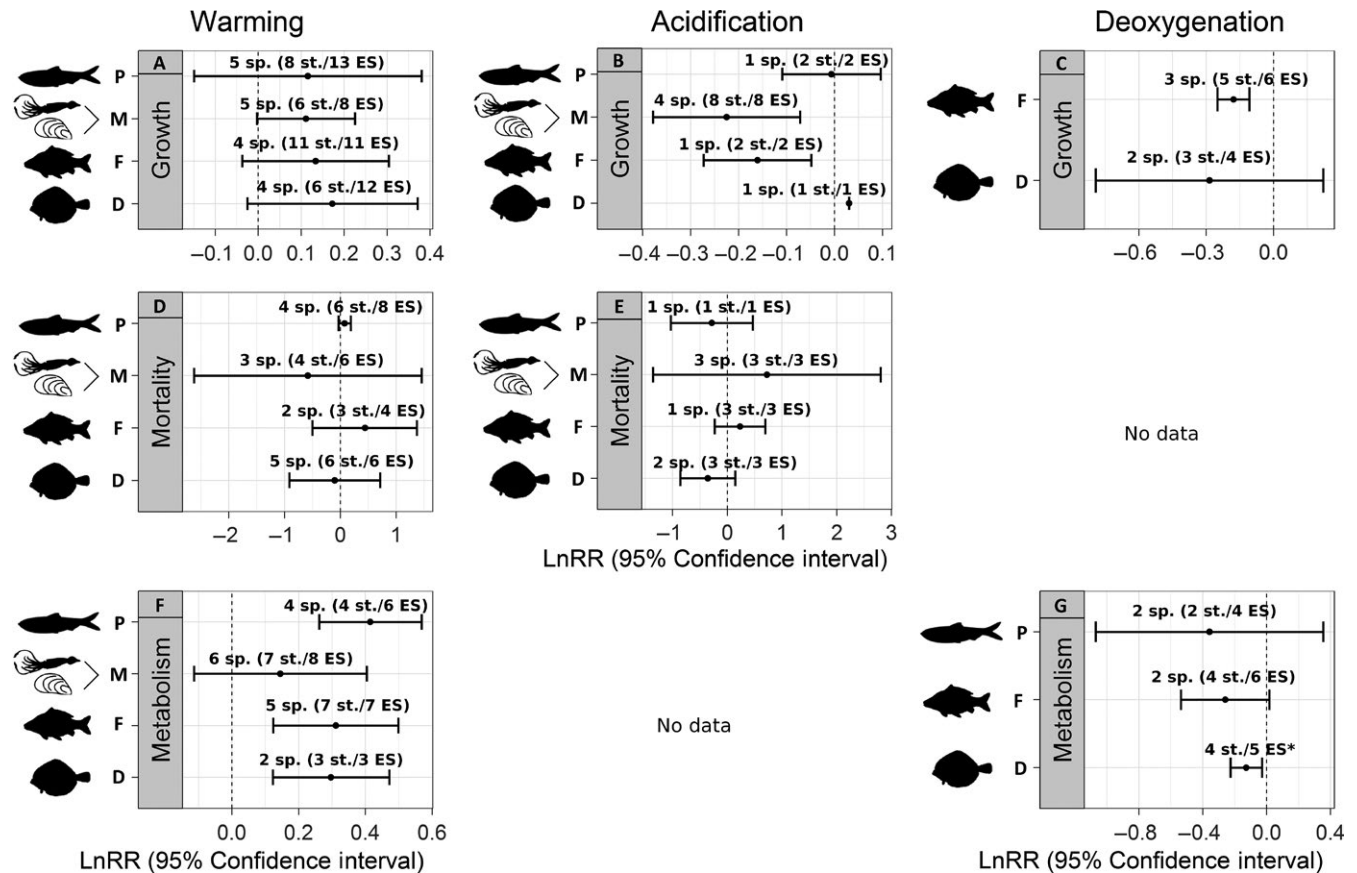


FIGURE 7 Modeled standardized effect sizes (Ln response ratio, LN RR) and 95% confidence intervals displaying climate change-related effects on growth, metabolism (oxygen consumption) and mortality for different functional groups. Sp. = number of species, St. = number of studies, ES = number of effect sizes. Functional groups: P = Pelagic fish, M = Mollusks, F = Freshwater fish and D = Demersal fish. The asterisk (Figure 7g), missing species level related to model convergence issues. Model parameters of functional groups consisting of a single ES were derived from a single-level fixed effects model

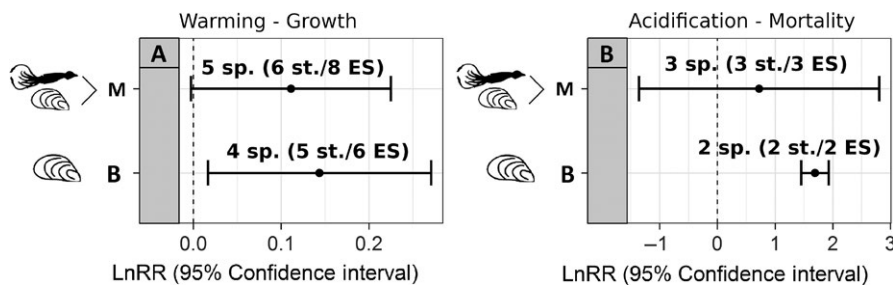


FIGURE 8 Comparison of the functional groups "Mollusks" (M) and "Bivalves" (B). (a) describes the effect of elevated temperature on growth. (b) depicts the response of mortality to lowered pH. For other abbreviations, see Figure 7

However, in some cases, the similar direction of the effects enables some generalizations of CC-related drivers on the selected groups.

3.2.1 | Effect of increased temperature

The level of warming projected for a variety of aquatic habitats worldwide under a "business as usual" scenario (2–5°C, RCP 8.5) was associated with a consistent (but not significant) increased somatic growth across the different functional groups (Pelagic fish, Freshwater fish, Demersal fish and Mollusks; Figure 7a, d & f). These results partly differ from those reported by Harvey et al. (2013) who

employed a meta-analysis to identify that warming caused a significant increase in growth of fish and reduced growth of mollusks. One explanation for the discrepancy may be due to the species included within the mollusk group which, in the present study, were several bivalve species and the European squid. When analyzed separately, warming was associated with a significant increase in the growth of bivalves (Figure 8a). Moreover, Harvey et al. (2013) did not restrict their data to commercially important species in European waters. Furthermore, sensitivity varies with ontogenetic stage and will depend on which temperature was considered to represent the "present condition" (see Moderator Analysis). Warming significantly

increased the metabolic rate of all functional groups except mollusks (Figure 7f). Increased metabolic rates under elevated temperatures were expected as warming (within tolerable limits) increases rates of biochemical reactions (Fry & Hart, 1948; Gillooly, Brown, West, Savage, & Charnov, 2001).

The effect of warming on mortality was relatively variable both within the functional groups (resulting in broader confidence intervals) as well as between ESs of functional groups. In general, none of the mean effects were significant. The variability in the effect of temperature on mortality is likely due to differences in experimental design (tank size, culture conditions, rearing expertise), species, ontogenetic stage compared, and the number of datasets that could be included. As temperature effects are mainly related to the relative position of treatments within the tolerable thermal window of the species and the respective period of the year represented (e.g., winter or summer), the results strongly depend on the season of the subset of experiments. A general increase of temperature in winter might reduce the risk of episodic die-offs from unusually low temperatures (cold-snaps) as reported for fish by Hurst (2007). In contrast, when a population exists near the lower latitudinal limit of the species, elevated summer temperatures can cause mortality (Bailey, 1955). Therefore, including the moderating effect of season can help interpret results with respect to climate-driven warming (see Moderator Analysis). However, a sufficient dataset covering all seasons for each subgroup was not available to thoroughly explore seasonal vs. climate impacts.

3.2.2 | Effect of decreases in pH

The analysis of the effect of reduced pH (reduction of ≥ 0.6 in seawater and ≥ 1.5 in fresh water, see Table 1) was limited to growth and mortality (Figure 7b, e). The number of studies was relatively low, with \leq seven ESs per functional group. The mean growth was negatively affected by reduced pH in freshwater fish and mollusks. The results for mollusks are in line with those reported in previous meta-analyses conducted on mollusk/bivalve species worldwide (Harvey et al., 2013; Hendriks et al., 2010; Kroeker et al., 2013). For fish, very few data were included in previous meta-analyses examining pH impacts. Harvey et al. (2013) reported increased growth in acidified water. Our results included only five datasets (ESs) for fish across functional groups suggesting a limited ability to discern clear impacts on functional groups. The positive effect of acidified conditions on demersal fish growth was derived from a single experiment and thus further investigations are required. The remaining functional groups were not significantly affected by reduced pH. An important factor influencing the results might have been the life stage. Stiasny et al. (2016) provided evidence for increased mortality in the larval stage of Atlantic cod (*Gadus morhua*, Gadidae) under acidified conditions. In other studies, however, no increased mortality was found in larval fish exposed to acidified conditions (Bignami, Sponaugle, & Cowen, 2013; Munday, Donelson, Dixon, & Endo, 2009). Thus, larval sensitivity toward acidification might be relatively species-specific. Another source of uncertainty is that very

little is known about potential CC-driven changes of pH in freshwater. Recently, Weiss et al. (2018) reported a decrease in pH of 0.01 per annum within four different lakes in Germany. As this value by far exceeds the rate of acidification of marine waters, we included data from treatments using a sharp reduction in pH for species in the Inland Waters sector. The meta-analysis run for bivalves only, instead of mollusks, suggests a significant increase in mortality at lowered pH conditions (Figure 8b). Similar results were depicted for mollusks in Harvey et al. (2013) and Kroeker et al. (2013). In contrast, Hendriks et al. (2010) reported that mortality was decreased in bivalves under acidified conditions. In general, responses of calcifiers toward increasing acidification were found to be very species-specific (Fabry, 2008; Whitman Miller, Reynolds, Sobrino, & Riedel, 2009). In the present study, one of the two ES originated from a study on larval Manila clam (*Ruditapes philippinarum*, Veneridae) which is, according to the authors, an especially sensitive species (Munari et al., 2016). A key message from our meta-analysis is that, in general, meta-analyses on CC-related drivers pay little attention to the confounding factors that we have detected here. In particular, for studies with low sample size, species-specific effects might have a large influence on the summarized ES.

3.2.3 | Effect of deoxygenation

The analysis of impacts of decreased dissolved oxygen (DO; lowered by 20%–50%) included only two functional groups for growth responses and three functional groups for metabolism (Figure 7). Our meta-analysis suggested that decreased DO caused decreased growth in freshwater fish and significantly reduced the metabolic rate in demersal fish. Only a three-level model was used to examine demersal fish (species level was excluded) as the results for the two species did not allow a common model estimate to be generated when including all four levels. This model convergence issue may reduce confidence in this analysis. To the authors' best knowledge, the effect of decreased DO on marine fish growth, metabolism and mortality has not been previously examined using meta-analytic techniques. Vaquer-Sunyer and Duarte (2008) reported large reductions in survival of selected benthic species under hypoxic conditions, especially at relatively warm temperatures. Fishes are considered to be among the most hypoxia-sensitive taxa (Rogers, Urbina, Reardon, McKenzie, & Wilson, 2016). Thus, the reductions in growth and metabolism found in the present study (after a 20%–50% reduction in DO level) are in line with existing knowledge. Global climate models project a 1%–7% decline in the ocean oxygen inventory over the next century (Keeling, Körtzinger, & Gruber, 2010) and some oceanic regions have experienced stronger deoxygenation exceeding 4% per decade (Schmidtke, Stramma, & Visbeck, 2017). Although these global, average declines are alarming, of primary concern is understanding how fish and shellfish will respond when hypoxic waters encroach on historically normoxic habitats, which is captured by our choice of treatments compared in the meta-analysis. The declines in growth and metabolic rates in response to reduced oxygen saturation shown in our analysis suggest that deoxygenation is an

important, albeit understudied impact of climate change on fish and shellfish.

Climate-driven warming, acidification and/or deoxygenation will not be uniform and local aquatic habitats will display large differences in the magnitude of change. Given this spatial variability in the magnitude of changes in abiotic factors, it is challenging to link significant, general responses found in our meta-analysis to direct climate impacts on field populations. Moreover, there are shortcomings in every laboratory experiment and critics often object to using these relatively “naïve” studies to directly project climate impacts, particularly because the potential plasticity and long-term adaptive capacity of field populations are not taken into account (Crozier & Hutchings, 2014). Recent studies, however, have documented that CC-related changes in aquatic habitats (e.g., strong heat waves) have had rapid (within generation) impacts on populations (Oliver et al., 2018). In such cases, empirical data from controlled laboratory studies (e.g., survival time at suboptimally warm temperatures), may be well suited to anticipating future climate impacts (Gobler, Merlo, Morrell, & Griffith, 2018; Peck et al., 2013; Portner & Farrell, 2008; Woodward, Perkins, & Brown, 2010). In most cases, however, the

results of laboratory studies and field observations should be combined to gain a mechanistic (cause-and-effect; Cheung et al., 2013; Portner & Farrell, 2008) understanding to be used in theoretical models projecting climate impacts.

3.2.4 | Heterogeneity

Following Higgins, Thompson, Deeks, and Altman (2003), the I^2 measurements (Supporting information Table S3) suggested a high degree of heterogeneity within the models. A similarly large amount of heterogeneity is considered normal in ecological meta-analyses (Senior et al., 2016). More remarkable, however, was the contribution of the variance at specific levels to the overall heterogeneity. In some cases, the variance was highest between species within a functional group whereas, in other cases, it was highest within a study or within a species. These inconsistencies further emphasize the need for additional research. Some variance within a species or within a study (in a few cases, results from multiple experimental sites were published within one study) might be related to local adaptation (Kroeker et al., 2013; Sanford & Kelly, 2011). For highly motile

Stressor	Response	Functional group	Test of moderators (p-values)	
			Season	Life stage
T	Growth	Pelagic species	<0.0001	0.9122
		Freshwater fish	0.3955	0.8410
		Demersal fish	0.4349	0.4966
		Bivalvia	<0.0001	0.4744
	Mortality	Pelagic species	<0.0001	0.1857
		Freshwater fish	0.0022	0.9285
		Demersal fish	0.1495	0.7149
		Bivalvia	0.0004	NA
	Metabolism	Pelagic species	0.0021	0.0230
		Freshwater fish	0.2124	0.2642
		Demersal fish	NA	0.0590
		Bivalvia	0.2343	0.2343
pH	Growth	Pelagic species	—	<0.0001
		Freshwater fish	—	0.3733
		Demersal fish	—	NA
		Bivalvia	—	0.6956
	Mortality	Pelagic species	—	NA
		Freshwater fish	—	NA ^a
		Demersal fish	—	0.6511
		Bivalvia	—	0.1901
O ₂	Growth	Freshwater fish	—	NA
		Demersal fish	—	NA
	Metabolism	Freshwater fish	—	0.0396
		Demersal fish	—	NA ^a
		Bivalvia	—	NA

TABLE 2 Omnibus-test of moderators. NA describes cases where only one moderator level is present

^aRepresents models for which the model optimizer did not achieve convergence.

species such as fish, however, the spatial scales for local adaptation are much broader than for species with relatively small home ranges that lack extensive migration patterns. An analysis of regional differences in potential climate change effects was not conducted in the present study due the lack of comparable data collected in different geographical areas (see Gap Analysis). The heterogeneity in the data could also have been increased by differences in the life stage tested and in the season when experiments occurred, two moderators specifically tested (below).

3.2.5 | Moderator analysis

The interpretation of model results, including the effect of moderators, has to be approached with some caution as some signals of over parametrization were detected (e.g., interrupted or flat variance estimate profiles, see Supporting information Figure S1, Table S4, Viechtbauer, 2010). The moderators “life stage” and “season,” the latter only used for temperature, had significant effects on the model outcomes (Table 2). For instance, season was a significant moderator of the effect of temperature on mollusks. These findings underscore the importance of taking season into account when interrogating data informing on the potential effects of climate-driven warming on fish and shellfish. In terms of the effect of temperature, life stage was less relevant and significant in only one group (pelagic fish). For the effects of lowered pH and DO, moderating effects were analyzed on a restricted number of life stages. An increased sensitivity of early life stages toward acidification, as denoted in Kroeker et al. (2013) for mollusks, was not found in the present study. A primary reason for the discrepancy is that our study did not include calcification but only somatic growth and mortality as response variables. More delayed responses or indirect responses such as increased susceptibility toward parasites or diseases related to a weakened immune defense were not resolved in the laboratory experiments analyzed herein. In our opinion, it is critical to thoroughly examine potential moderators and the low number of datasets available placed severe limitations on this type of analysis.

4 | CONCLUSIONS AND RECOMMENDATIONS

The present study used a semi-systematic literature review including a Gap Analysis and a meta-analysis to examine the state of knowledge of direct climate impacts that can be derived from controlled laboratory experiments conducted on Europe's high-value fisheries and aquaculture targets. Our Gap Analysis identified a large imbalance in the data available on fish and shellfish. First, there was bias toward single-factor studies with only an extremely low number of studies examining the interaction of abiotic factors (e.g., temperature \times pH, etc.). Second, the poor spatial coverage of experiments performed on commercially important species with many distinct populations precludes attempts to account for

local adaptation. Third, efforts focused on relatively few, key species (e.g., salmon, rainbow trout, carp or herring) and life stages. Further, through the meta-analyses, new knowledge on key exploited species responses was generated.

The results of our meta-analysis highlight the species-specific nature of effects of CC-related drivers. Increased temperature was generally associated with increased rates of growth and metabolic losses in all functional groups. Differences in experimental designs influenced observed responses in mortality. In general, meta-analyses need to take into account seasonal effects when exploring the potential impacts of climate-driven warming. Projected acidification was associated with reduced rates of growth in freshwater fish and mollusks. Generalizing the impacts of acidification across commercially important finfish and shellfish is unwarranted due to the species-specific responses documented here. Declines in DO to levels associated with mild to severe hypoxia depressed rates of growth in freshwater fish and reduced metabolism in marine demersal fish. A larger number of studies would have potentially allowed us to distinguish effects due to life stage and season as well as regionally specific impacts of changes in hydrographic factors. Furthermore, more data from controlled laboratory experiments examining the synergistic or antagonistic effects of multiple factors are woefully lacking and are needed to make more realistic projections of how future environmental conditions impact aquatic living resources.

Based on the results of this review, we recommend

- Prioritizing research effort to fill key gaps in knowledge, particularly by:
 - Obtaining more data on interacting CC-related drivers.
 - Widening the diversity of species, life stages and local populations tested, and
 - Applying a common framework for the design of experiments aiming at exploring projected effects of CC, so that meta-analytical approaches are easier to conduct (e.g., consistency in the definition of ambient conditions).
- Fostering the creation of a worldwide, open-access physiological database with entries based on rigorous inclusion of laboratory data usable for CC analyses, with importance conceded to geographic stock origin and season of experiment, correct definition of baselines, replicates, and projected conditions.
- Promoting policies that support the transfer of non-confidential data from the aquaculture and fishing industries to help increase the amount of empirical data available in the public domain, buttressing efforts to evaluate and project climate impacts on fish and shellfish.

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CONFLICTS OF INTEREST

We have no conflicts of interest to disclose.

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