Sex analysis in marine biological systems: insights and opportunities

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The ocean is facing unprecedented challenges due to the escalating impacts of climate change and other pressures threatening ecosystems and the many benefits they provide. Effective strategies for reversing the loss of biodiversity rely on knowledge of how marine organisms, populations, and communities respond to environmental change. A fundamental but often overlooked biological characteristic of organisms is sex, which is distinct from sociocultural gender. Here, we examined how sex influences marine organisms, populations, and communities, through a review of sex analysis applications in marine biological research. We found that sex broadly affects the morphology, physiology, behavior, and distribution of organisms and populations across taxa, with evidence of sex-specific differences in survival to thermal stress, timing of biological mechanisms, and energetics. To facilitate further integration of sex into marine biological research, we synthesize current approaches, discuss methodological and logistical challenges, and lay out guidelines for future research.

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Effective ocean management and mitigation of climate-change impacts depend on understanding how organisms and ecosystems respond to anthropogenic and environmental change (Frazão Santos *et al*. 2020). Improving this understanding and increasing the capacity to produce useful and usable knowledge is a major focus of the UN Decade of Ocean Science for Sustainable Development (2021–2030) and the UN Sustainable Development Goals (particularly Goal 14, Life Below Water; Singh *et al*. 2021) and will require the formulation of novel frameworks and technologies. We argue that sex analysis (Panel 1) provides opportunities for innovation and for advancing our understanding of how marine biological systems respond to environmental change.

In a nutshell:

- Sex analysis incorporates biological sex in each step of the research process, from establishing priorities to formulating questions, designing methodologies, and interpreting results
- Although integrating sex into research design and analysis has produced new insights and solutions in biomedicine, artificial intelligence, and other disciplines, this has yet to occur for marine biology
- A review of marine biological research into sex-based differences revealed that sex analysis is most commonly applied at the scale of organisms and populations, but not communities
- In 90% of studies that explicitly considered biological sex, physiological, morphological, and behavioral mechanisms were found to be influenced by sex
- We provide guidelines for incorporating sex analysis into future marine research and highlight examples of methodological approaches in data collection, laboratory and field experiments, modeling, and meta-analyses

Sex refers to biological attributes of living organisms. Notably, it is distinguished from gender, which refers to psychological, social, and cultural factors that shape attitudes, behaviors, stereotypes, technologies, and knowledge in human societies (Tannenbaum *et al*. 2019). Sex describes differences in sexual characteristics within living organisms that go beyond their reproductive functions and affect appearance and physiology, as well as neuroendocrine, behavioral, and metabolic systems (Tannenbaum *et al*. 2019). In marine organisms, sex takes many forms (eg male, female, simultaneous or sequential hermaphrodite), which are influenced by genetic and molecular mechanisms (eg sexual or asexual reproduction) and environmental factors (eg ambient temperature). Sex is often overlooked in laboratory experiments investigating the response of a variety of marine organisms to ocean acidification (Ellis *et al*. 2017) and temperature increase (Pottier *et al*. 2021). In the broader field of biological sciences, recent studies have addressed the role of sex in research on mammals (Woitowich *et al*. 2020; Garcia-Sifuentes and Maney 2021). However, the extent to which sex-based differences have been explicitly addressed across taxa (including species), populations, and communities in marine biology has not been examined. Discipline-specific guidelines are needed to support researchers in considering sex when formulating hypotheses and methods in their own fields (Tannenbaum *et al*. 2019; EC 2020). To date, such guidelines do not exist in marine biology, or in biology in general.

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Panel 1. Sex analysis

Sex analysis is the process of incorporating biological sex considerations into research design and analysis (EC 2020). In sex analysis, sex is integrated not only as a covariate into an experimental treatment but also as a factor that can influence (or confound) research design and analysis, as well as interpretation of results. The purpose of sex analysis is to understand how sex should be considered in each step of the research process, from strategic considerations for establishing priorities to formulating questions, designing methodologies, and interpreting data (Schiebinger 2014). The ultimate goal of sex analysis is to increase research rigor, reproducibility, and generalizability, and enhance the accuracy of findings (Woitowich *et al.* 2020; White *et al.* 2021). Sex analysis can take many forms depending on the specific research field, topic, system, or organism. Sex analysis is applied not only to investigate sex-based differences in biological mechanisms but also to identify research objectives and expected outcomes that – if sex and sex-based differences were otherwise not taken into account – may not be achieved or may yield erroneous or incomplete insights (Tannenbaum *et al.* 2019). Researchers should ensure that sex is an integral component of the research rationale, experimental design, methods, analysis, and knowledge translation (Duchesne *et al.* 2017), and if not relevant to the study that it can be justifiably excluded (Tannenbaum *et al.* 2019). Ruling out sex without assessing its influence in research design can lead to erroneous results.

These potential knowledge gaps have direct implications for environmental management. For example, management of certain fisheries may fail to achieve sustainability if sex-based differences in stock assessments are ignored (Williams *et al.* 2012; Easter *et al.* 2020). Fisheries that catch large individuals (Easter *et al.* 2020) may de facto target females in species where females grow larger than males (Pauly 2019). Disproportionally high mortality among large fecund females can greatly reduce stock productivity (Hixon *et al.* 2014). Ignoring sex could therefore have unintended negative consequences for marine populations and ocean management outcomes.

We reviewed studies that addressed sex-based differences in marine biology research to highlight the need for greater consideration of sex in biological research across marine and terrestrial systems. We focused on marine systems because of the urgent environmental challenges and large knowledge gaps associated with the ocean. Our primary objectives were to (1) understand the role of sex in influencing morphological, physiological, behavioral, and ecological processes across marine taxa and at different levels of biological organization – specifically the organism, population, species, and community levels; and (2) examine the methodological approaches and experimental techniques researchers use to address sex-based differences. We conducted a critical review of research design and methods from studies applying sex analysis (Methods are presented in WebTables 1–3 and WebFigure 1). We also identified best practices for sex analysis. From this review, we propose a set of guidelines for integrating sex analysis into field research, laboratory and field experiments, mathematical modeling, and meta-analyses. Finally, we discuss the challenges and opportunities for applying sex analysis in future biological research, including the methodological and logistical challenges of considering sex.

Results

Sex-based differences across taxa and levels of biological organization

In all of the studies included in our analysis, sex was integrated into the research design, and sex-specific differences in biological processes were examined, predominantly at the organismal and population levels (Figure 1; see WebTable 4 for specific examples). Sex-based differences were found in individual appearance, morphology, and physiology, as well as in individual age and growth within or between populations (Fairbairn 2016). Sex influences numerous individual and population behaviors, including foraging and predator avoidance (Cherry *et al.* 2020). Sex-specific individual and population behaviors are driven by sex-based morphology (Montoya *et al.* 2019) or different energy requirements associated with the reproductive investment of males and females (Elliott Smith *et al.* 2015). Sex-based differences also influence courtship, competition, communication, and care of offspring (Cherry *et al.* 2020). At the species level, sex can influence segregation of species across space and time. Females and males likely segregate spatially because of preferences for temperature or salinity range (Péron *et al.* 2015) or because of sex-specific habitat preferences driven by differences in energetic requirements (Acevedo *et al.* 2014). None of the studies included in our analysis addressed the role of sex at the community level in food webs or in interspecific interactions.

A majority of the studies (90.4%, $n = 384$) detected sex-based differences in biological processes (Figure 1). The proportion of studies detecting sex-specific differences varied from a minimum of 83.0% in studies of distribution and sexual segregation of species ($n = 18$) to a maximum of 95.2% in studies of sex-specific differences in genetic mechanisms at the organismal level ($n = 62$). When grouped by taxa, we found that, on average, sex-based differences were detected in 89.7% of the studies, ranging from 87.1% of studies of elasmobranchs ($n = 31$) to 95.1% of studies of crustaceans ($n = 41$) (Figure 2; WebTable 5).

Sex-based differences have been studied more frequently in some taxa than others (Figure 2). With respect to movement ecology, for instance, we found that spatial and temporal sexual segregation have been most frequently examined in chordates, such as teleost fishes (eg Borg *et al.* 2014), seabirds (eg Paiva *et al.* 2017), and marine mammals (eg Briscoe *et al.* 2018), than in other taxa. In contrast, the role of sex-specific differences in physiological processes has been investigated more frequently in

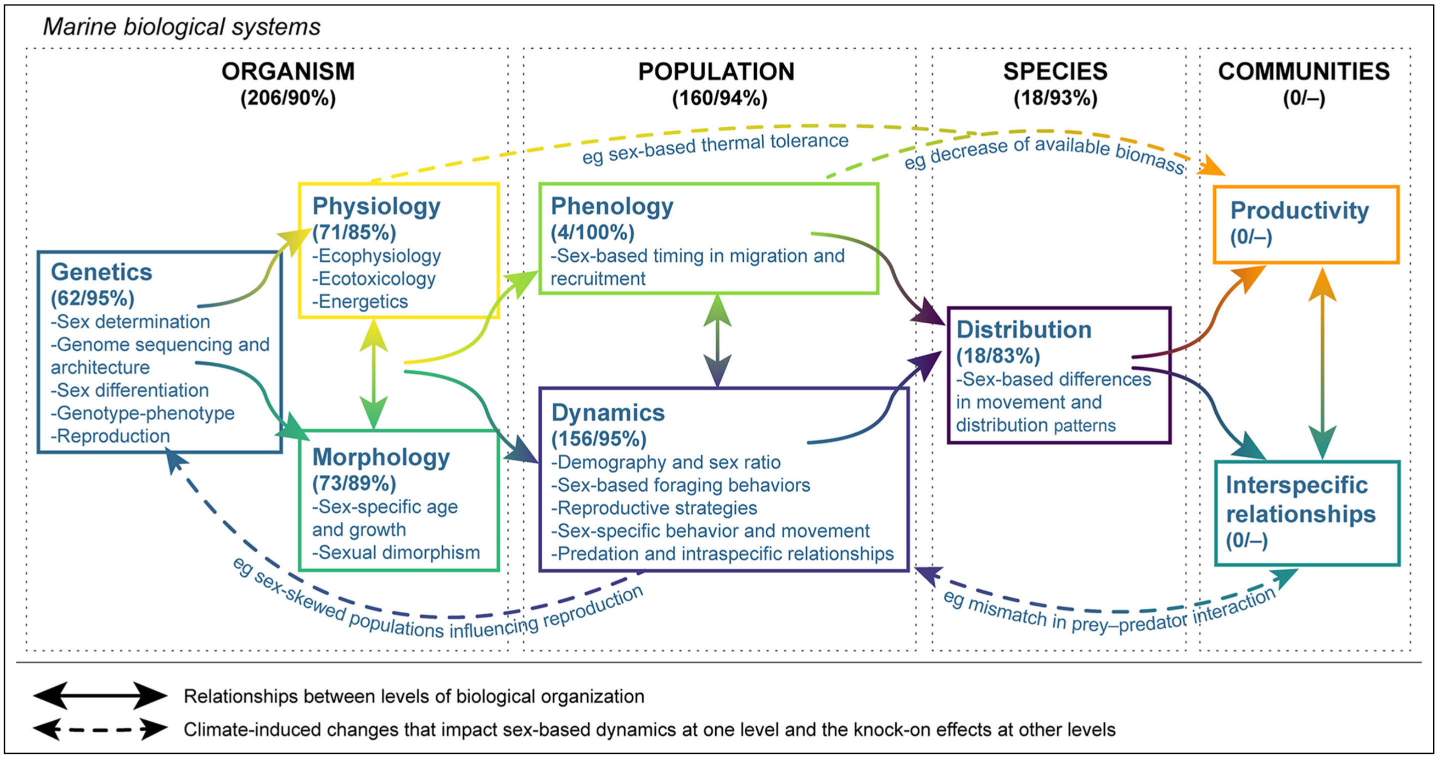

Figure 1. Sex analysis in marine biology research sorted by subfield and level of biological organization. Values within parentheses are depicted as (i/ii%), where i represents the total number of studies and ii% represents the percentage of studies within each group in which sex-based differences were detected. Details are reported in WebTable 4.

fish (eg Murray and Baumann 2020) and invertebrates (eg Rocha *et al*. 2019) than in mammals, birds, and reptiles (WebTable 4).

Methodological approaches to sex analysis

In the following sections, we provide an overview of research design approaches and methods from studies applying sex analysis, with additional detailed examples of practical applications presented in WebTable 6. In Table 1, we synthesized the same research design approaches and methods in the form of guidelines.

Data collection in field research (Table 1a)

Studies that addressed sex-based differences employed a suite of strategies and techniques to collect data about the sex of marine organisms. With data disaggregated and reported by sex, researchers were then able to consider sex as a covariate in subsequent research phases. Techniques to determine the sex of targeted organisms spanned from morphometric measurements of specific body organs (Mutalipassi *et al*. 2018) to analysis of genetic markers for molecular sex identification (Brown *et al*. 2016; Rees *et al*. 2017). Combining genetics and genomics has been productive in sex determination in many species (eg sea turtles [Banerjee *et al*. 2021], crustaceans [Shi *et al*. 2018]); in studies involving the tagging and tracking of marine organisms, multiple techniques (such as flipper tagging, satellite tracking, and analysis of genetic markers) were often used in combination for collecting data and determining sex (Rees *et al*. 2017).

Researchers have also addressed how data collection can result in skewed sex ratios of surveyed organisms or collected data. Skewed sex ratios in data can depend on sex-specific biological mechanisms or sex-specific selectivity of data collection techniques. For instance, in a study of white sharks (*Carcharodon carcharias*) off the coast of central California, Kanive *et al*. (2015) speculated that greater numbers of older males were observed because of higher mortality among younger females or that fewer females were observed due to differences in behavior between males and females. By innovatively combining detections from acoustic tags and dorsal fin photographic identifications, Chapple *et al*. (2016) determined that sex-specific patterns in white shark migrations resulted in disparate capture probabilities between males and females, which affected the observed sex ratio. Their results suggested that the greater numbers of older males observed by Kanive *et al*. (2015) were likely due to behavioral differences between males and females, not higher female mortality (Chapple *et al*. 2016).

Another approach to incorporating sex and sex analysis in field studies requires determining potential sex bias in existing datasets. Data collected through fishery-dependent surveys can be biased toward females or males, depending on species and fishery type. For instance, in the highly dimorphic snow crab (*Chionoecetes opilio*) in the eastern Bering Sea, females that are smaller than males have no commercial value and are

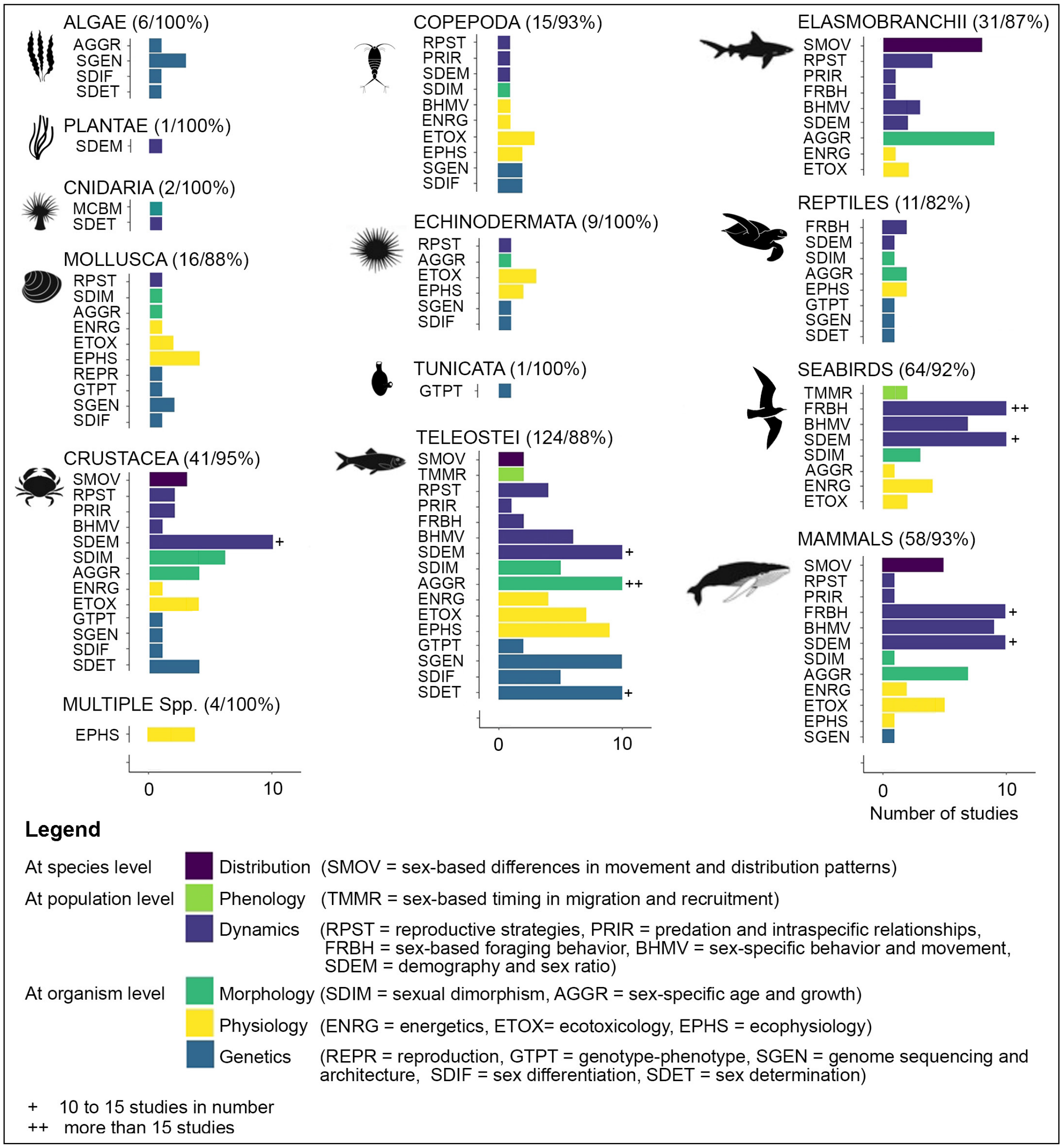

Figure 2. Studies applying sex analysis within marine taxa sorted by level of biological organization and subfield. Values within parentheses are depicted as (i/ii%), where i represents the total number of studies and ii% represents the percentage of studies within each group in which sex-based differences were detected. Details are reported in WebTable 5.

consequently underrepresented in fishery-dependent survey data because this fishery only targets large males (Murphy *et al.* 2018). To fit sex-specific state-space models, Murphy *et al.* (2018) used data collected by the annual US National Marine Fisheries Service bottom trawl summer survey in combination with fishery survey data to obtain robust data for both males and females.

Laboratory and field experiments (Table 1b)

Studies conducting experiments in controlled or natural environments either included organisms of each sex or determined sex of the organisms included in the experiment. Examples involved crustaceans (Yli-Renko *et al.* 2018) and fish species (Dessen *et al.* 2016).

Another approach to considering sex in experiments is to account for sex-specific differences between male, female, and hermaphroditic organisms under baseline conditions – that is, before experiments are performed. Baseline studies of model species were conducted to statistically determine sex-based intraspecific variation prior to experimentation because variation between sexes may be greater than variation related to the experimental treatment. In ecotoxicology, for instance, behavior has been increasingly examined as a response variable linking the biochemical effects of

Table 1. Guidelines for integrating sex analysis into field data collection; laboratory or field experiments; mathematical modeling; and meta-analysis

(a) Data collection in field research

- Design appropriate sampling strategies and techniques to consider sex of targeted organisms
- Report and archive data on sex of sampled organisms
- Explore new non-invasive techniques for determining sex of organisms in the field
- Combine genetics and genomics and related techniques for sex determination
- Combine multiple techniques to determine sex-based population dynamics and patterns
- Question how sex can affect the process of data collection
- Question whether sampling may result in skewed sex ratios
- Analyze survey data protocols and sampling techniques to determine potential sex bias

(b) Laboratory and field experiments

- Include organisms of each sex
- Proceed in determining sex of organisms included in the experiment
- Consider sex-based differences under baseline conditions
- Consider the influence of sex-based intraspecific variation on response variables
- Consider confounding effects or failures due to sex differences

(c) Mathematical modeling

- Input data disaggregated by sex (see previous sections)
- Include sex as an explanatory variable
- Check any significant differences in the response variables by sex
- Question whether the selected modeling approach or statistical method considers sex
- Question whether the model or statistical analysis can include sex-based factors

(d) Meta-analysis

- Consider sex when formulating the research question
- Question why sex was not included in the set of studies explored
- Run sex-based sensitivity analysis on original studies
- Explore sex-based variance of the results
- Analyze the role of sex in the set of original studies

Notes: see WebTable 6 for examples of applications.

contamination with the physiology of individuals (Saaristo *et al*. 2018). In a laboratory study of baseline conditions for ecotoxicological analysis, Cherry *et al*. (2020) found sex-based differences in the behavior of the intertidal amphipod *Echinogammarus marinus* stimulated by altering periods of light and dark. Ignoring sex-based differences in baseline conditions may therefore result in erroneously considering behavioral differences as a result of the biochemical effect of contamination (Cherry *et al*. 2020).

Studies have also considered the role played by sex when evaluating potential explanations for sex-based differences in response variables. For instance, Nørregaard *et al*. (2018) studied gill and liver pathologies in sculpins (*Myoxocephalus* spp) as health indicators of the possible effects of mining activity at two sites in waters off of Greenland, with sex-specific differences in heavy metal concentrations detected in fourhorn sculpins (*Myoxocephalus quadricornis*) but not in shorthorn sculpins (*Myoxocephalus scorpius*). The authors questioned whether these results depended on the skewed female-to-male sample ratio, on differences in metabolism and physiology between species, or on differences in environmental conditions between sites (Nørregaard *et al*. 2018). Further investigation of factors causing differences in heavy metal concentrations between male and female sculpins is needed, however, as confounding effects can lead to misinterpretation of ecotoxicological responses in these species and in the implications of the results for pollution mitigation (Kaarsholm *et al*. 2018; Nørregaard *et al*. 2018).

Mathematical modeling (Table 1c)

Studies that developed mathematical models of biological processes have accounted for sex-based differences by including sex as an explanatory variable. Models were fitted by aggregating or disaggregating data by sex and then comparing model outputs. Doing so allowed researchers to determine differences between sexes in biological and/or environmental explanatory variables and to assess the role of sex and sex-based differences in modeled processes. For instance, Tsai *et al*. (2015) compared single- and two-sex demographic models of shortfin mako shark (*Isurus oxyrinchus*) in the Northwest Pacific. They found that single-sex demographic models that ignored sexual dimorphism and mating mechanisms underestimated the risk of population decline (Tsai *et al*. 2015).

Another approach for considering sex-based differences is to examine statistically significant differences in the data disaggregated by sex before fitting models. For instance, in the case of finetooth sharks (*Carcharhinus isodon*) in the western North Atlantic Ocean, application of analysis of covariance (ANCOVA) revealed significant differences in length-to-mass conversions, for which sex-specific growth models were fitted, but not in body length measurements, for which one model was fitted with aggregated data (Vinyard *et al*. 2019).

To account for the role of sex when modeling population dynamics, researchers have also upgraded existing modeling approaches (such as stock assessment models or age-at-growth models) by including sex-based differences influencing the modeled biological processes. For instance, to estimate the performance of stock assessments of blue marlin (*Makaira nigricans*) in the Pacific Ocean, Su *et al*. (2011) applied Monte Carlo simulations to an assessment method that accounts for seasonal movement and sexual dimorphism. A population dynamics model that includes spatial structure, sex structure, and age structure was constructed and fitted to fisheries data, along with information on the relative density of the population over space (Su *et al*. 2011). From this, the authors determined that previous assessments that ignored seasonal movement and sexual dimorphism overestimated maximum sustainable yield and related spawning stock biomass (Su *et al*. 2011).

Meta-analysis (Table 1d)

Studies have explored the potential role of sex as a biological variable when defining meta-analysis research questions.

Meta-analyses have identified potential research gaps about the role of sex and sex-based differences in specific research fields, as well as in biological or environmental mechanisms. For instance, by analyzing the role of sex in experimental ocean acidification research, Ellis *et al.* (2017) found that only 3.9% of studies statistically assessed sex-based differences in ocean acidification responses but that, in the majority of the studies where tested, sex was shown to have a significant influence on marine organism response to ocean acidification.

Meta-analyses were also applied to explore the variability of sex-specific differences across species and biological mechanisms. A systematic review of sex-based differences in thermal acclimation capacity across ectotherms, for example, revealed that females had greater heat tolerance plasticity than males in some species and not in others (Pottier *et al.* 2021). Sensitivity analyses were also used to explore variation of synthetic findings (Lortie *et al.* 2015) by disaggregating studies that included or excluded sex-based differences, or female and male organisms (Ellis *et al.* 2017; Pottier *et al.* 2021).

When collecting studies for inclusion within meta-analyses, researchers have examined how sex and sex-specific differences were considered in the original studies. Because meta-analyses statistically synthesize results from individual studies (Vetter *et al.* 2013), results can be sex-biased if sex-specific differences are not considered in the original studies. For example, in a meta-analysis investigating sex-specific differences in contaminant concentrations in fish, Madenjian *et al.* (2016) discarded studies reporting sex-specific differences in contaminant concentrations based on determinations in just one body part (eg muscle or liver tissue), because the spatial distribution of contaminants within fish bodies may vary between the sexes. Consequently, a sex-specific difference in contaminant concentrations based on determinations in just one part of the fish may not accurately capture the sex difference in whole-fish contaminant concentrations (Madenjian *et al.* 2016).

Discussion

This review highlights that sex-based differences have been documented for a broad array of biological processes in marine systems, with sex-based differences detected in over 90% of studies in which sex was explicitly considered. Although this result may overestimate the influence of sex (as, for example, researchers may be more likely to apply sex analysis in systems where previous research has highlighted sex-specific differences), this high percentage nevertheless supports the prediction that sex can potentially influence the vast majority of biological processes – from development to physiology and behavior. The sex-based differences we documented across levels of biological organization and taxa may depend on species characteristics or the methodological approaches used to include sex in marine biology research. Our results may also be influenced by our approach of targeting only studies about sex-based differences in biological processes and excluding search terms such as "gender", which scientists occasionally use erroneously to refer to the sex of living organisms (Madsen *et al.* 2017).

Nonetheless, our findings of the prevalence of sex-based differences across taxa and subfields highlight the importance of considering whether and how sex can influence research design, analysis, and results (Tannenbaum *et al.* 2019). If sex does not play a role, this is valuable information that must be reported, and sex may be omitted in subsequent research. If sex is difficult or impossible to determine or control for, we suggest that challenges and limitations related to considering sex in the study be reported. These challenges may be addressed through future advances in methodological approaches or theory. Reporting sex will help improve transparency in study design and ultimately the accuracy of findings (Woitowich *et al.* 2020), as required by funding agencies (White *et al.* 2021) and peer-reviewed scholarly journals (eg Editorial Board 2022).

The guidelines we report in Table 1 can provide a framework for researchers to approach sex analysis in marine biological research design. More broadly, these guidelines can be relevant for research design and hypothesis development in other biological systems, such as terrestrial ones, that share similar processes and challenges (Ruckstuhl and Clutton-Brock 2006; Pinsky *et al.* 2022). For instance, specific aspects of sex-based differences have been studied in both terrestrial and marine domains to improve understanding of the many different forms and possible causes of sexual segregation in vertebrates (Ruckstuhl and Clutton-Brock 2006), of adult sex ratios in wild animal populations (Ancona *et al.* 2017), and of thermal responses in ectotherm species (Pottier *et al.* 2021).

When collecting and reporting data by sex, numerous challenges must be addressed, which may account for why sex is not always included in research design. Methodologically, a fundamental requirement for analyzing sex in biological research is that data are disaggregated by sex. When collecting data or observing species in their natural environment, it can be difficult to determine sex in species for which sex differences are not apparent, have not been previously assessed (Fairbairn 2016), or vary geographically or due to environmental factors (Nam *et al.* 2018). For many species, histological and genetic analyses may be necessary (Medeiros *et al.* 2012), but such techniques may be expensive, invasive, and time consuming. In many cases where determining sex of organisms in the field is methodologically possible, sampling organisms of both sexes along the whole of their life cycle can be logistically challenging (Griffiths *et al.* 2018), as in the case of wide-ranging species (Kanive *et al.* 2015). The trade-off between obtaining an adequate sample size and sampling costs can be critical (Ryan 2013).

Despite many difficulties, not considering sex may lead to erroneous results (Tannenbaum *et al.* 2019). Sex-based differences could be approached incrementally. Even small sample sizes can lead to insightful sex-based differences in living organisms, especially for species or biological processes for which knowledge is limited or unavailable (Sequeira *et al*. 2019). The sample size can then be increased to address new research questions and may lead to new knowledge about a species' natural history.

Technological advances may also offer solutions to these methodological and logistic challenges. For example, the miniaturization of tagging equipment has facilitated the expansion of sex-specific research on seabirds to include juveniles as well as adults (Fay *et al*. 2015). The use of drones to collect blow "snot" from whales has drastically reduced the time and cost associated with the manual collection of tissue samples via biopsy crossbows (Atkinson *et al*. 2021) while providing a better understanding of sex, health, pregnancy status, genomic structure, and microbiotic communities in individual whales (Bennett *et al*. 2015; Keller and Willke 2019).

Marine community ecology is a subfield of marine biology research where sex-based differences have been understudied, most likely because the logistical and methodological challenges discussed above are amplified when analyzing sex across multiple interacting species. However, ignoring the role of sex in community ecology studies is particularly problematic given that communities are likely to restructure as a consequence of climate-induced changes at individual and population levels (Rilov *et al*. 2019). In addition, responses to climate stressors by organisms and populations can be sex-specific (Ellis *et al*. 2017; Pottier *et al*. 2021). Although interest in intraspecific differences in biological processes has increased among community ecologists (Start and De Lisle 2018), community-level consequences of sex-specific differences remain poorly understood (De Lisle *et al*. 2022). Community ecology models tend to assume "asexual" adult organisms (Violle *et al*. 2012) and – as such – do not capture, for instance, sex-specific behaviors or resource use of females, males, or hermaphrodites, and consequently sex-based differences in consumer-resource relationships of species interactions (De Lisle *et al*. 2022). The effects of sex-based differences on the structure and dynamics of ecological communities represent a vast field for future investigation.

Conclusions

Sex fundamentally influences a suite of biological mechanisms across taxa and levels of biological organization. Challenges like determining the sex of marine organisms, particularly in offshore or deep ocean habitats, have impeded sex analysis in marine biology. Overcoming these challenges and integrating sex analysis more broadly into biological research holds promise for more effective solutions to global change and biodiversity loss. To unlock this potential, the cultural biases likely affecting theories and research design (Orr *et al*. 2020) need to be questioned and addressed by researchers, funding institutions, and peer-reviewed journals.

On the basis of this review and synthesis, we provide guidelines to facilitate future incorporation of sex in research design and analysis. Understanding specifically how to integrate sex analysis across the research process can increase the robustness of results and spark research innovation and technological advances.

While scientists are called to consider sex and sex analysis in their research hypothesis and design, funding agencies will also need to incentivize fundamental research aimed at uncovering differences between sexes and how these may influence biological systems across multiple levels of biological organization. This knowledge is needed to better inform global-scale analyses – which necessarily reduce the complexity of ecosystems or models – by accounting for natural history traits shaped through evolution. Uncovering nuances in species' sex-specific life-history traits and behaviors, and how they shape communities, will help broaden our knowledge and inform effective conservation.

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Data Availability Statement

Empirical data were not used in this research.

References

Acevedo J, Mora C, and Aguayo-Lobo A. 2014. Sex-related site fidelity of humpback whales (*Megaptera novaeangliae*) to the Fueguian Archipelago feeding area, Chile. *Mar Mammal Sci* **30**: 433–44.

Ancona S, Dénes FV, Krüger O, *et al*. 2017. Estimating adult sex ratios in nature. *Philos T Roy Soc B* **372**: 20160313.

Atkinson S, Rogan A, Baker CS, *et al*. 2021. Genetic, endocrine, and microbiological assessments of blue, humpback and killer whale health using unoccupied aerial systems. *Wildlife Soc B* **45**: 654–69.

Banerjee SM, Stoll JA, Allen CD, *et al*. 2021. Species and population specific gene expression in blood transcriptomes of marine turtles. *BMC Genomics* **22**: 346.

Bennett A, Preston V, Woo J, *et al*. 2015. Autonomous vehicles for remote sample collection in difficult conditions: enabling remote sample collection by marine biologists. Proceedings of the Institute of Electrical and Electronics Engineers (IEEE) Conference on

Technologies for Practical Robot Applications (TePRA); 11–12 May 2015; Boston, MA. New York, NY: IEEE.

Borg JPG, Westerbom M, and Lehtonen H. 2014. Sex-specific distribution and diet of *Platichthys flesus* at the end of spawning in the northern Baltic Sea. *J Fish Biol* **84**: 937–51.

Briscoe DK, Fossette S, Scales KL, *et al*. 2018. Characterizing habitat suitability for a central-place forager in a dynamic marine environment. *Ecol Evol* **8**: 2788–801.

Brown JK, Taggart JB, Bekaert M, *et al*. 2016. Mapping the sex determination locus in the hapuku (*Polyprion oxygeneios*) using ddRAD sequencing. *BMC Genomics* **17**: 448.

Chapple TK, Chambert T, Kanive PE, *et al*. 2016. A novel application of multi-event modeling to estimate class segregation in a highly migratory oceanic vertebrate. *Ecology* **97**: 3494–502.

Cherry T-R, Kohler SA, and Ford AT. 2020. Sex specific differences recorded in the behavior of an amphipod: implications for behavioral toxicology. *Front Mar Sci* **7**: 370.

De Lisle SP, Schrieber SJ, and Bolnick DI. 2022. Complex community-wide consequences of consumer sexual dimorphism. *J Anim Ecol* **91**: 958–69.

Dessen JE, Arge R, Thomassen MS, and Rørvik KA. 2016. Differences in fat accumulation between immature male and female Atlantic salmon *Salmo salar* after dietary administration of tetradecylthioacetic acid. *J Fish Biol* **89**: 2085–97.

Duchesne A, Tannenbaum C, and Einstein G. 2017. Funding agency mechanisms to increase sex and gender analysis. *Lancet* **389**: 699.

Easter EE, Adreani MS, Hamilton SL, *et al*. 2020. Influence of protogynous sex change on recovery of fish populations within marine protected areas. *Ecol Appl* **30**: e02070.

EC (European Commission). 2020. Gendered innovations 2: how inclusive analysis contributes to research and innovation. Brussels, Belgium: EC.

Editorial Board. 2022. *Nature* journals raise the bar on sex and gender reporting in research. *Nature* **605**: 396.

Elliott Smith EA, Newsome SD, Estes JA, and Tinker MT. 2015. The cost of reproduction: differential resource specialization in female and male California sea otters. *Oecologia* **178**: 17–29.

Ellis RP, Davison W, Queirós AM, *et al*. 2017. Does sex really matter? Explaining intraspecies variation in ocean acidification responses. *Biol Lett-UK* **13**: 20160761.

Fairbairn DJ. 2016. Sexual dimorphism. In: Kliman RM (Ed). Encyclopedia of evolutionary biology. Cambridge, MA: Academic Press.

Fay R, Weimerskirch H, Delord K, and Barbraud C. 2015. Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. *J Anim Ecol* **84**: 1423–33.

Frazão Santos C, Agardy T, Andrade F, *et al*. 2020. Integrating climate change in ocean planning. *Nat Sustain* **3**: 505–16.

Garcia-Sifuentes Y and Maney DL. 2021. Reporting and misreporting of sex differences in the biological sciences. *eLife* **10**: e70817.

Griffiths CA, Patterson TA, Blanchard JL, *et al*. 2018. Scaling marine fish movement behavior from individuals to populations. *Ecol Evol* **8**: 7031–43.

Hixon MA, Johnson DW, and Sogard SM. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J Mar Sci* **71**: 2171–85.

Kaarsholm HM, Verland N, Nørregaard RD, *et al*. 2018. Histology of *Sculpin* spp in east Greenland. II. Histopathology and trace element concentrations. *Toxicol Environ Chem* **100**: 769–84.

Kanive PE, Rotella JJ, Jorgensen SJ, *et al*. 2015. Estimating apparent survival of sub-adult and adult white sharks (*Carcharodon carcharias*) in central California using mark–recapture methods. *Front Mar Sci* **2**: 19.

Keller B and Willke T. 2019. SnotBot: a whale of a deep-learning project. *IEEE Spectrum* **56**: 41–53.

Lortie CJ, Stewart G, Rothstein H, and Lau J. 2015. How to critically read ecological meta-analyses. *Res Synth Methods* **6**: 124–33.

Madenjian CP, Rediske RR, Krabbenhoft DP, *et al*. 2016. Sex differences in contaminant concentrations of fish: a synthesis. *Biol Sex Differ* **7**: 42.

Madsen TE, Bourjeily G, Hasnain M, *et al*. 2017. Sex- and gender-based medicine: the need for precise terminology. *Gender Genome* **1**: 122–28.

Medeiros RJ, King RA, Symondson WOC, *et al*. 2012. Molecular evidence for gender differences in the migratory behaviour of a small seabird. *PLoS ONE* **7**: e46330.

Montoya JCH, Juárez-Rodríguez M, Méndez-Sánchez F, *et al*. 2019. Sexual dimorphism and foraging trips of the Laysan albatross (*Phoebastria immutabilis*) on Guadalupe Island. *Animals* **9**: 364.

Murphy JT, Rugolo LJ, and Turnock BJ. 2018. Estimation of annual, time-varying natural mortality and survival for eastern Bering Sea snow crab (*Chionoecetes opilio*) with state-space population models. *Fish Res* **205**: 122–31.

Murray CS and Baumann H. 2020. Are long-term growth responses to elevated pCO_2 sex-specific in fish? *PLoS ONE* **15**: e0235817.

Mutalipassi M, Maibam C, and Zupo V. 2018. The sex change of the caridean shrimp *Hippolyte inermis* Leach: temporal development of the gonopore morphology. *Zoomorphology* **137**: 377–88.

Nam HY, Lee SY, Cho SY, *et al*. 2018. Effectiveness of morphological sex determination in the East Asian barn swallow (*Hirundo rustica gutturalis*) on spring migration. *Zool Stud* **57**: 43.

Nørregaard RD, Dang M, Bach L, *et al*. 2018. Comparison of heavy metals, parasites and histopathology in sculpins (*Myoxocephalus* spp) from two sites at a lead–zinc mine in north east Greenland. *Environ Res* **165**: 306–16.

Orr TJ, Burns M, Hawkes K, *et al*. 2020. It takes two to tango: including a female perspective in reproductive biology. *Integr Comp Biol* **60**: 796–813.

Paiva VH, Pereira J, Ceia FR, and Ramos JA. 2017. Environmentally driven sexual segregation in a marine top predator. *Sci Rep-UK* **7**: 2590.

Pauly D. 2019. Female fish grow bigger – let's deal with it. *Trends Ecol Evol* **34**: 181–82.

Péron C, Welsford DC, Ziegler P, *et al*. 2015. Modelling spatial distribution of Patagonian toothfish through life-stages and sex and its implications for the fishery on the Kerguelen Plateau. *Progress* **141**: 81–95.

Pinsky ML, Comte L, and Sax DF. 2022. Unifying climate change biology across realms and taxa. *Trends Ecol Evol* **8**: 672–82.

Pottier P, Burke S, Drobniak SM, *et al*. 2021. Sexual (in)equality? A meta-analysis of sex differences in thermal acclimation capacity across ectotherms. *Funct Ecol* **35**: 2663–78.

Rees AF, Carreras C, Broderick AC, *et al*. 2017. Linking loggerhead locations: using multiple methods to determine the origin of sea turtles in feeding grounds. *Mar Biol* **164**: 30.

Rilov G, Mazaris AD, Stelzenmüller V, *et al*. 2019. Adaptive marine conservation planning in the face of climate change: what can we learn from physiological, ecological and genetic studies? *Global Ecol Conserv* **17**: e00566.

Rocha F, Baião LF, Moutinho S, *et al*. 2019. The effect of sex, season and gametogenic cycle on gonad yield, biochemical composition and quality traits of *Paracentrotus lividus* along the North Atlantic coast of Portugal. *Sci Rep-UK* **9**: 2994.

Ruckstuhl KE and Clutton-Brock TH. 2006. Sexual segregation and the ecology of the two sexes. In: Ruckstuhl KE and Clutton-Brock TH (Eds). Sexual segregation in vertebrates: ecology of the two sexes. Cambridge, UK: Cambridge University Press.

Ryan TP. 2013. Sample size determination and power. Hoboken, NJ: John Wiley & Sons.

Saaristo M, Brodin T, Balshine S, *et al*. 2018. Direct and indirect effects of chemical contaminants on the behaviour, ecology and evolution of wildlife. *P Roy Soc B-Biol Sci* **285**: 20181297.

Schiebinger L. 2014. Gendered innovations: harnessing the creative power of sex and gender analysis to discover new ideas and develop new technologies. *Triple Helix* **1**: 9.

Sequeira AMM, Heupel MR, Lea MA, *et al*. 2019. The importance of sample size in marine megafauna tagging studies. *Ecol Appl* **29**: e01947.

Shi X, Waiho K, Li X, *et al*. 2018. Female-specific SNP markers provide insights into a WZ/ZZ sex determination system for mud crabs *Scylla paramamosain*, *S tranquebarica* and *S serrata* with a rapid method for genetic sex identification. *BMC Genomics* **19**: 981.

Singh GG, Harden-Davies H, Allison EH, *et al*. 2021. Will understanding the ocean lead to "the ocean we want"? *P Natl Acad Sci USA* **118**: e2100205118.

Start D and De Lisle S. 2018. Sexual dimorphism in a top predator (*Notophthalmus viridescens*) drives aquatic prey community assembly. *P Roy Soc B-Biol Sci* **285**: 20181717.

Su NJ, Sun CL, Punt AE, *et al*. 2011. Evaluation of a spatially sex-specific assessment method incorporating a habitat preference model for blue marlin (*Makaira nigricans*) in the Pacific Ocean. *Fish Oceanogr* **20**: 415–33.

Tannenbaum C, Ellis RP, Eyssel F, *et al*. 2019. Sex and gender analysis improves science and engineering. *Nature* **575**: 137–46.

Tsai WP, Liu KM, Punt AE, and Sun CL. 2015. Assessing the potential biases of ignoring sexual dimorphism and mating mechanism in using a single-sex demographic model: the shortfin mako shark as a case study. *ICES J Mar Sci* **72**: 793–803.

Vetter D, Rücker G, and Storch I. 2013. Meta-analysis: a need for well-defined usage in ecology and conservation biology. *Ecosphere* **4**: 1–24.

Vinyard EA, Frazier BS, Drymon JM, *et al*. 2019. Age, growth, and maturation of the finetooth shark, *Carcharhinus isodon*, in the western North Atlantic Ocean. *Environ Biol Fish* **102**: 1499–517.

Violle C, Enquist BJ, McGill BJ, *et al*. 2012. The return of the variance: intraspecific variability in community ecology. *Trends Ecol Evol* **27**: 244–52.

White J, Tannenbaum C, Klinge I, *et al*. 2021. The integration of sex and gender considerations into biomedical research: lessons from international funding agencies. *J Clin Endocr Metab* **106**: 3034–48.

Williams AJ, Farley JH, Hoyle SD, *et al*. 2012. Spatial and sex-specific variation in growth of albacore tuna (*Thunnus alalunga*) across the South Pacific Ocean. *PLoS ONE* **7**: 39318.

Woitowich NC, Beery AK, and Woodruff TK. 2020. A 10-year follow-up study of sex inclusion in the biological sciences. *eLife* **9**: e56344.

Yli-Renko M, Pettay JE, and Vesakoski O. 2018. Sex and size matters: selection on personality in natural prey–predator interactions. *Behav Process* **148**: 20–26.

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