



# Synthesis of Observed Field Salinity Ranges for Oyster and Seagrass Species in the U.S.

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## Abstract

Oyster and seagrass are important sessile, habitat-forming species that may be impacted by changes in salinity regimes from anthropogenic or climatic drivers. While salinity tolerance literature is focused on controlled experiments, observed field salinity ranges of species are more disparate. The salinity ranges in which organisms are observed in the field may not align exactly with their experimentally (wet lab) determined physiological salinity tolerances, since other critical factors control species occurrence. We performed a systematic review to synthesize observed practical salinity ranges for 10 oyster and 12 seagrass species in coastal waters of the United States. Of initially returned search results for oysters and seagrass, only 11.4% and 6.5% met our review inclusion criteria, respectively, corresponding to 3 oyster species and 5 seagrass species. The majority (95%) of the 57 reviewed studies were along the Atlantic and Gulf coasts, with 68% focusing on *Crassostrea virginica*. Shorter studies following episodic events were more common than long-term monitoring. Observed field salinity ranges were as follows (ppt): *Crassostrea virginica* (0.1 – 42.8, mean: 19.6), *Ostrea lurida* (1.7 – 32.5, mean: 27.8), *Thalassia testudinum* (0 – 65, mean 31.8), *Halodule wrightii* (<0.5 – 68.7, mean: 18.5), *Syringodium filiforme* (13.7 – 68.7, mean: 30.4), *Ruppia maritima* (0 – 29.4, mean: 3.8), and *Zostera marina* (19.7 – 51.2, mean: 28.9). Place-based examples highlight how reported overlapping salinity ranges for oyster and seagrass species can be used to expand existing habitat suitability models, inform restoration, and provide considerations for guiding holistic management of freshwater inflows to estuaries.

**Keywords** Habitat suitability · *Crassostrea virginica* · *Ostrea lurida* · *Thalassia testudinum* · *Halodule wrightii* · *Syringodium filiforme* · *Ruppia maritima* · *Zostera marina*

## Introduction

Estuarine and coastal ecosystems have complex biogeochemical and trophic dynamics, which provide services including shoreline stabilization and protection, nutrient cycling, water purification, carbon sequestration, and food provision (Barbier et al., 2011). Benthic habitats within coastal ecosystems are often assembled as a mosaic, which may provide diverse options for sustenance, breeding grounds, nurseries, and shelter that support coastal fisheries, and can be addressed with habitat- and ecosystem-based management approaches (Kritzer et al., 2016; Sheaves, 2009). Many habitats in estuarine and coastal ecosystems are biogenic, formed by sessile organisms through substrate-building processes, and can extend across environmental gradients (e.g., oyster reefs, shellfish beds, salt marshes, mangroves, seagrass beds, coral reefs). The spatial distribution of aquatic foundation species and habitats is dictated by many factors including salinity, substrate, depth, light, temperature, water velocity,

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tidal exposures, and connectivity among subpopulations for dispersal of seeds or larvae (Pittman et al., 2021 and references therein). Likewise, multiple factors such as tidal dynamics, wind, bathymetry, and freshwater inputs from rivers and overland flow influence habitat suitability in estuaries (Yurek et al., 2023).

While multiple factors determine spatial patterns in coastal biogenic habitats, salinity is among the most consequential because of physiological tolerances and adaptations of species to salt concentrations, and because it proxies other habitat suitability determinants. For example, in the case of *Crassostrea virginica* (eastern oyster), while biologically capable of tolerating a wide range of salinities (Galtsoff, 1964), it is observed in a narrower salinity range due to elevated pathogen, pest, and predation pressures at low and high salinities (Gunter, 1955; Jurgens et al., 2022; Paynter & Burrenson, 1991; Pollack et al., 2011; Reustle & Smee, 2020). Accordingly, in a Habitat Suitability Index developed for *C. virginica*, salinity was the index input with the greatest weight (Puckett et al., 2018; Theuerkauf et al., 2019). Salinity is a key factor in oyster habitat suitability models ranging from the Pamlico Sound in North Carolina (Puckett et al., 2018) and Northern Gulf (Linhoss et al., 2016) to the Salish Sea (Lawlor & Arellano, 2020). While salinity proxies multiple oyster stressors, it directly affects seagrass species. Salinity creates osmotic stress, and seagrasses have evolved to develop diverse physiological, ultrastructural, and morphological adaptations in response, with specific adaptations varying across species (Sandoval-Gil et al., 2023; Touchette, 2007). As with oysters, seagrass habitat suitability models account for salinity variation. For example, in a habitat suitability model used to study how changes to freshwater management impact seagrass species in Biscayne Bay, FL, salinity was a key factor in the spatial distribution of *Halodule wrightii* (shoal grass) and *Thalassia testudinum* (turtle grass), which have different salinity tolerances (Santos & Lirman, 2012).

The importance of salinity as a driver of habitat suitability is relevant given its dynamic, and sometimes extreme, responses to global and local change. Multiple mechanisms can change salinity regimes ranging from shifting precipitation patterns and sea level rise to freshwater flow management, extreme events (e.g., hurricanes, droughts), and barrier island breaches (Dessu et al., 2018; Feher et al., 2023; Ghalambor et al., 2021; Olin et al., 2020). Both acute and chronic changes can have cascading impacts on population dynamics and habitat migration. For example, harvestable subtidal oyster habitat in the Newport River estuary has been greatly reduced due to a combination of increasing salinity enhancing conditions favorable to biological degradation of subtidal reefs and a decrease in suitable bottom substrates for reef development over the past century (Tice-Lewis et al., 2022). Consequently, the combination of changing

salinity and decreasing suitable substrate is shifting oysters up estuary to intertidal reefs. Similar trends are observed in the Suwannee River estuary (Seavey et al., 2011). Brackish salinity zones, particularly oligohaline waters, are predicted to reduce in area due to interactions between decreasing freshwater inflows, rising sea levels, and in-channel barriers; the effects of this spatial compression are collectively described as “estuarine squeeze” (Little et al., 2022). For example, following a century of channelization and canal development altering natural freshwater flows, the salinity regime of Biscayne Bay has experienced a large shift towards marine conditions (Wachnicka & Wingard, 2017; Wingard et al., 2004) that are less favorable to oysters, which were once anecdotally plentiful (Smith, 1896). Conversely, benthic habitats are also affected by “freshening” events, in which freshwater surpluses are introduced to estuarine or coastal environments, creating hyposaline conditions that may prompt mass mortality events. For instance, large freshwater discharges to the Mississippi Sound in 2019, released in an effort to curb inland flooding, caused 100% mortality on multiple oyster reefs (Gledhill et al., 2020).

Because estuarine and coastal environments are highly variable, particularly in the context of local and global change, studies on species’ physiological tolerances to salinity (i.e., determined via controlled experiments) do not always reflect the salinity conditions in which species are observed. Consequently, while there is rich documentation of species salinity tolerances, determining which salinity ranges should be used to capture “observable” or practical species salinity ranges remains challenging, particularly since information on observed salinities in relation to habitat distributions is scattered throughout the literature. Thus, the purpose of this literature review is to synthesize *practical salinity ranges*, i.e., realized salinity ranges in which species occur and are observed in the field given a plethora of other confounding factors that they must endure, and identify knowledge gaps in past research for selected coastal habitat-forming species, specifically those that form seagrass and oyster bed habitats in estuarine systems of the United States. We focus on seagrasses and oysters because they are important epibenthic habitat-forming ecosystem engineers, ranking in the top 5 habitats across the temperate eastern Atlantic Coast for coastal fisheries (Kritzer et al., 2016), yet in decline globally (Beck et al., 2011; Waycott et al., 2009). Additionally, both oysters and submerged aquatic vegetation are target habitats/species for defining optimal and alternative freshwater inflow scenarios for estuarine management along the Gulf and Atlantic Coasts (Buzzelli et al., 2015; Doering et al., 2002; La Peyre et al., 2009; Mattson, 2002; Powell et al., 2002), meaning improved information on their observed salinity ranges could directly support management and restoration efforts. In addition to summarizing practical salinity ranges, we also review confounding factors that

affect interpretation and use of observed ranges (e.g., disturbances, additional environmental covariates affecting survivability, etc.). Synthesized findings from this study can be used by ecological and physical modelers and managers to identify seagrass and oyster habitats at risk of loss due to estuarine squeeze, artificial freshening, and other consequences of local and global change.

## Methods

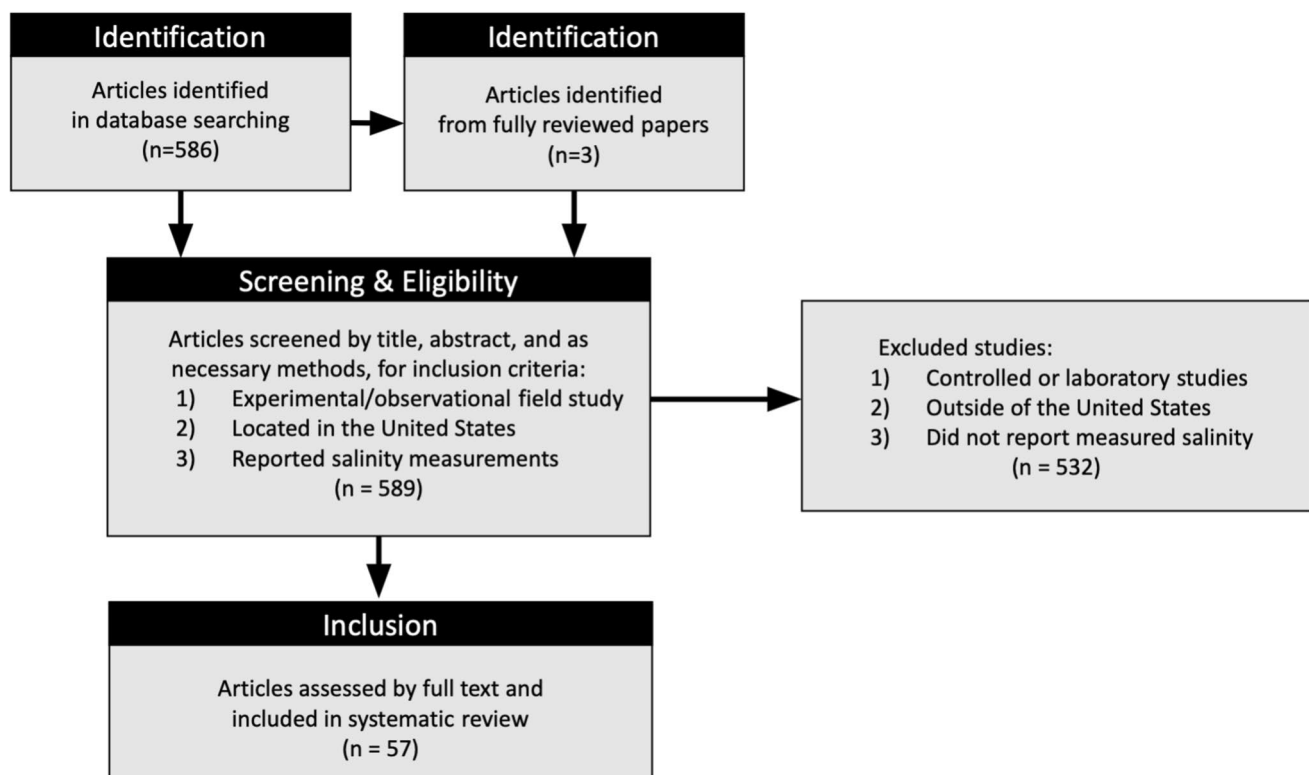
### Selection of Species

Oyster and seagrass species were selected due to their presence along the U.S. Atlantic, Gulf, and Pacific coasts, importance to coastal and estuarine ecosystems, and risk of population decline, driving conservation and management needs (Beck et al., 2001, 2011; Waycott et al., 2009). Specific species were selected by reviewing literature and reports from federal agencies. Oyster species were selected from Richardson et al.'s (2022) global review of reef-building oysters. We selected all species native ( $n=8$ ) or established ( $n=2$ ) in temperate or tropical waters surrounding the United States and its territories (Supplemental Table A). Seagrass species were selected from Short et al.'s (2007) global assessment of seagrass distribution and diversity. We selected all species

( $n=12$ ) native to North American, Caribbean, and Hawaiian coastal waters (Supplemental Table A). Two oyster species, eastern oyster (*Crassostrea virginica*) and Pacific oyster (*Crassostrea gigas/Magallana gigas*), are also listed in the U.S. National Oceanic and Atmospheric Administration's (NOAA) Estuarine Living Marine Resources (ELMR) Database (National Centers for Coastal Ocean Science, 2024), which includes 153 estuarine species with ecologic and economic value. Additionally, six of the ten oyster species from Richardson et al. (2022) and ten of twelve seagrass species from Short et al. (2007) are reported by one or more initial (2005) or revised (2015) State Wildlife Action Plans and are thus included in the National List of Species with Greatest Conservation Needs (United States Geological Survey, n.d.), demonstrating their management relevance.

### Literature Search

A systematic approach (Fig. 1) was taken to identify literature with the Web of Science search engine. On August 10–11, 2023, literature was searched for a title or author keyword match with terms for the species name (common, scientific, and synonyms; refer to Supplemental Table A) paired with terms related to salinity conditions. For example, ("Crassostrea virginica" OR "*C. virginica*" OR "eastern oyster" OR "American oyster" OR "Atlantic



**Fig. 1** Flow diagram of systematic literature review approach used in this study

oyster” OR “Virginia oyster” OR “American cupped oyster”) AND (hy\*salin\* OR salinity OR “salinity tolerance” OR fresh\*water OR flow\*). Results for individual species were combined by category (e.g., oyster, seagrass) into a single report and exported as a comma-separated file.

We screened the titles, abstracts, and, if needed, methods of each article to complete an inclusion–exclusion matrix (available in supplemental materials) to determine eligibility based on our criteria. Our study includes only peer-reviewed research or review articles reporting experimental or observational field studies located in the United States and its territories. Articles were excluded if they did not contain salinity measurements, or if measured salinity was produced from laboratory or controlled environment experiments. Excluded articles generally focused on genetics, osmotic stress mechanisms, pathology, and aquaculture system design. If salinity was measured and discussed in relative terms with no values reported, the article was excluded from results and considered for discussion (e.g., Peñalver et al., 2020). For summarization, species required a minimum of at least two papers meeting the inclusion criteria.

Three additional articles, Tice-Lewis et al. (2022), Ridge et al. (2017), and Fredley et al. (2019), which did not appear in the initial search results but were cited in fully reviewed papers, were added.

## Synthesizing Literature

A database was populated with articles identified for full review to synthesize and visualize information on field observations of potential salinity ranges. Articles were classified by organism group (oyster or seagrass), individual species, and location of study. Life-stage of species was included as a grouping category, though not all articles specified life-stage. Oyster life stages included recruits, sub-legal, and legal oysters. Although there was some variation in size ranges associated with life stages, common size thresholds were <25 mm shell height for recruits, 25–75 mm shell height for sub-legals, and >75 mm shell height for legal oysters. Life history events included spawning and settling. Study site locations were included and aggregated to estuary system, state, and marine ecoregions (Spalding et al., 2007) for mapping and investigating spatial trends. When specific latitude and longitude site locations were not explicitly stated, approximate locations were taken from site location maps. Temporal information regarding the year and duration of the studies was included and aggregated into study types (episodic, long-term). Finer resolution of temporal information was not synthesized due to challenges in applying consistent seasonal (e.g., winter, summer) or condition period (e.g., warm, cold, wet, dry) classifications across all studies due to the geographic area spanning multiple climate zones, and because studies were inconsistent in

their timing and duration. In cases of episodic studies performed in response to a disturbance, the type of disturbance was recorded (e.g., hurricane, freshwater release, freshwater diversion, observed die-off).

Salinity is commonly reported in a wide variety of units including practical salinity unit, absolute salinity unit, electrical conductivity (Siemens per area), and parts per thousand (ppt). For uniformity, all reported observed salinity values were converted to ppt. When a time series of salinity was reported, the mean, minimum, and maximum values were extracted from text, tables, or figures. If an article had multiple sites reporting observed salinity, they were entered as separate rows in the database. Reported synergies (e.g., temperature/thermal stress) and salinity-related mortality events were noted.

## Results

### Summary of Reviewed Studies

Initial searches of the publication database identified 586 unique articles on oysters and seagrass. Table 1 lists the number of articles that met our inclusion criteria for full review (Fig. 1). Of initially returned search results for oysters ( $n=385$ ) and seagrass ( $n=201$ ) only 11.4% and 6.5% met our inclusion criteria, respectively. Of the 57 fully reviewed articles, approximately three-fourths ( $n=44$ ) focused on oysters and the remaining ( $n=13$ ) focused on seagrasses. For both oyster and seagrass categories, a single species dominated the reviewed articles. For oysters, 89% of articles focused on *Crassostrea virginica* (eastern oyster) and for seagrasses, 54% of articles focused on *Thalassia testudinum* (turtle grass). Reviewed literature primarily represented species of the U.S. Atlantic and Gulf coasts; there was a dearth of articles meeting our inclusion criteria for Pacific and Caribbean oyster and seagrass species.

The spatial distribution of the study locations of synthesized literature was uneven across our study domain, with 95.5% of study sites along the eastern coastline of the contiguous United States (Fig. 2; Supplemental Table B). The marine ecoregions (Spalding et al., 2007) with the greatest literature representation are Virginian ( $n=15$  oyster, 2 seagrass), Carolinian ( $n=3$  oyster), Floridian ( $n=3$  oyster, 8 seagrass), and Northern Gulf ( $n=24$  oyster, 3 seagrass). In the Virginian marine ecoregion, studies were concentrated around the following estuarine systems: Hudson River (Gregory et al., 2023), Delaware Bay (Kraeuter et al., 2007; Munroe et al., 2013; Powell et al., 2013; Hemeon et al., 2020), Chesapeake Bay (Albright et al., 2007; Audemard et al., 2011; Calvo et al., 1999, 2001; Johnson et al., 2021; Karp et al., 2018; Kimmel et al., 2012), and Albemarle and Pamlico Sounds (Lenihan, 1999; Motes et al., 1998;

**Table 1** The number of articles returned in initial Web of Science search results that met the inclusion criteria for this study across oyster and seagrass species. Some articles reported on more than one species. Species are in their native range, unless marked (\*) indicating that they have been introduced and established. Rows are organized in descending order by the number of studies that apply to each species

| Oysters                                         | Met inclusion criteria |
|-------------------------------------------------|------------------------|
| <i>Crassostrea virginica</i>                    | 39                     |
| <i>Ostrea lurida</i>                            | 3                      |
| <i>Magallana gigas*</i>                         | 1                      |
| <i>Crassostrea rhizophorae</i>                  | 0                      |
| <i>Isognomon alatus</i>                         | 0                      |
| <i>Isognomon bicolor</i>                        | 0                      |
| <i>Dendostrea sandvichensis</i>                 | 0                      |
| <i>Pinctada margaritifera</i>                   | 0                      |
| <i>Striostrea prismatica</i>                    | 0                      |
| <i>Ostrea edulis*</i>                           | 0                      |
| <b>Seagrasses</b>                               |                        |
| <i>Thalassia testudinum</i>                     | 7                      |
| <i>Ruppia maritima</i>                          | 2                      |
| <i>Zostera marina</i>                           | 2                      |
| <i>Syringodium filiforme</i>                    | 2                      |
| <i>Halodule wrightii</i>                        | 4                      |
| <i>Halophila decipiens</i>                      | 0                      |
| <i>Halophila engelmannii</i>                    | 0                      |
| <i>Halophila hawaiiiana</i>                     | 0                      |
| <i>Halophila ovalis</i> ( <i>H. johnsonii</i> ) | 0                      |
| <i>Phyllospadix scouleri</i>                    | 0                      |
| <i>Phyllospadix serrulatus</i>                  | 0                      |
| <i>Phyllospadix torreyi</i>                     | 0                      |

Dunn et al., 2014; Ridge et al., 2017; Ferguson et al., 1993). Locations in the Carolinian, Floridian, and Northern Gulf marine ecoregions (e.g., Leonhardt et al., 2017; Marshall et al., 2020; Martinez et al., 2022; Swam et al., 2022a, b; Sehlinger et al., 2019; Wilson-Ormond et al., 1997) were more evenly dispersed along the coastline. However, there are noteworthy concentrations of oyster studies in Breton Sound/Barataria Bay and seagrass studies in Florida Bay. On the Pacific coast, there was one seagrass study in Yaquina Bay (Kentula & DeWitt, 2003) in the Oregon, Washington, Vancouver Coast and Shelf marine ecoregion, and two oyster studies (Bible & Sanford, 2016; Chang et al., 2018) in San Francisco Bay in the Northern California marine ecoregion. Most studies focused on a single water body or sampled multiple water bodies within a given ecoregion (e.g., Parker et al., 2013); however, one study spanned three ecoregions along the Atlantic and Gulf coast (Motes et al., 1998).

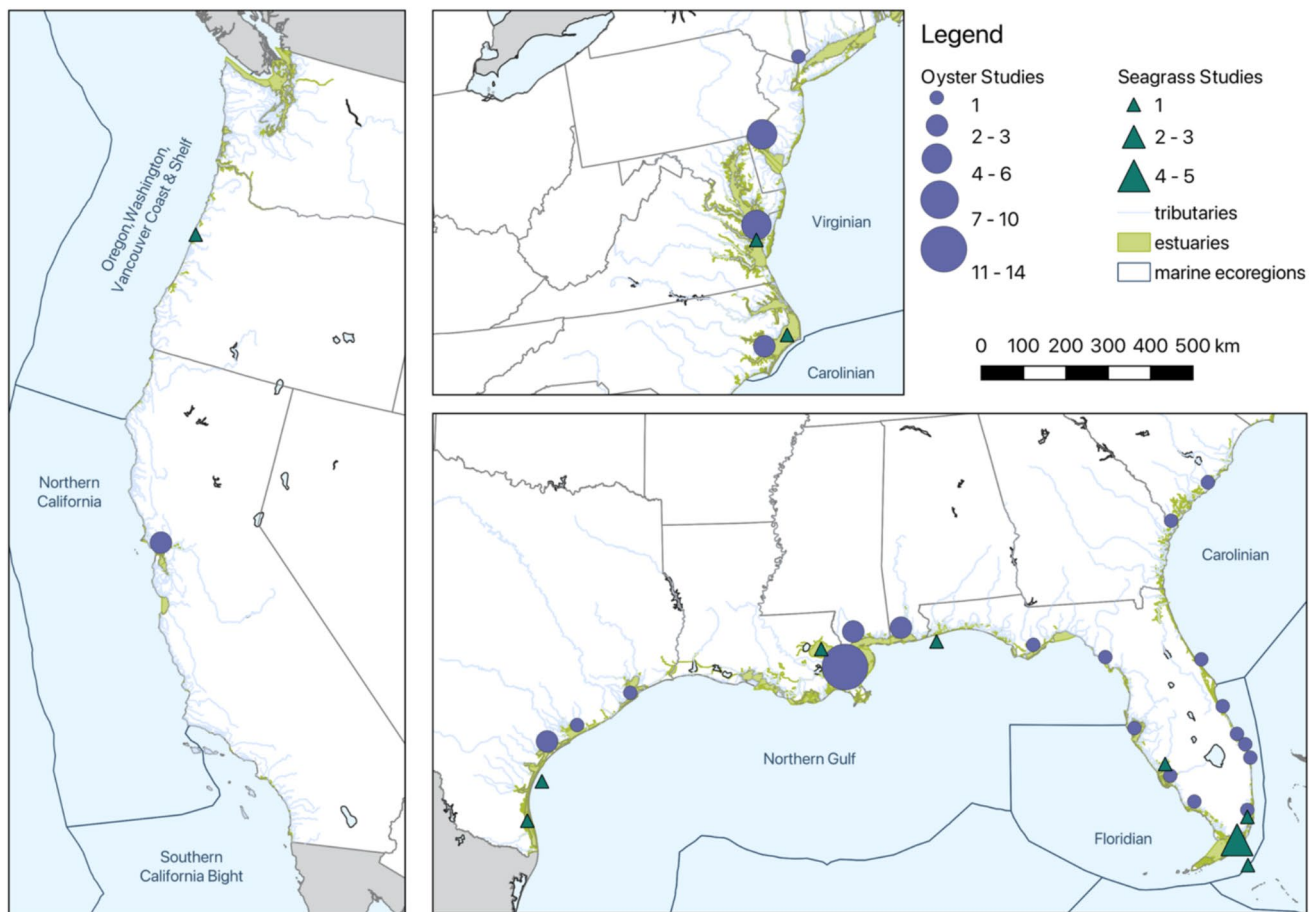
Overall, temporal distribution of observational oyster study durations ranged from 2 months to 28 years

(mean = 1.7 years, excluding two 28-year studies), with most studies representing episodic or event-driven investigations compared to long-term monitoring. The types of events motivating studies of organism response were hurricanes, releases of freshwater for flooding or oil spill management, drought, freshwater diversions, and acute mortality. Long-term studies included both monitoring efforts, such as in Louisiana (Lowe et al., 2017), and remotely sensed imagery analysis of changes in reef extent, such as in Florida (Seavey et al., 2011). A study that combined data from resampling historic reefs with long-term salinity monitoring (Tice-Lewis et al., 2022) was not included in the duration range but had discrete measurements dating as far back as 1955 and 1913. Most articles explicitly investigated anthropogenic impacts to natural flow/salinity regimes and less focused on climate causes. Eight studies focused on restored reefs, site suitability, or restoration success, but more often ( $n = 22$ ) studies discussed implications for restoration.

For seagrasses, study durations ranged from 2 months to 10 years, with a mean duration of  $3.8 \pm 3.2$  years. Two studies were performed for multiple years but only monitored seasonally. Common motivations for investigations were seagrass die-off events ( $n = 4$ ), response/recovery following disturbances or extreme weather events ( $n = 4$ ), impacts of freshwater management ( $n = 3$ ), water quality ( $n = 2$ ), and assessing restoration success ( $n = 1$ ).

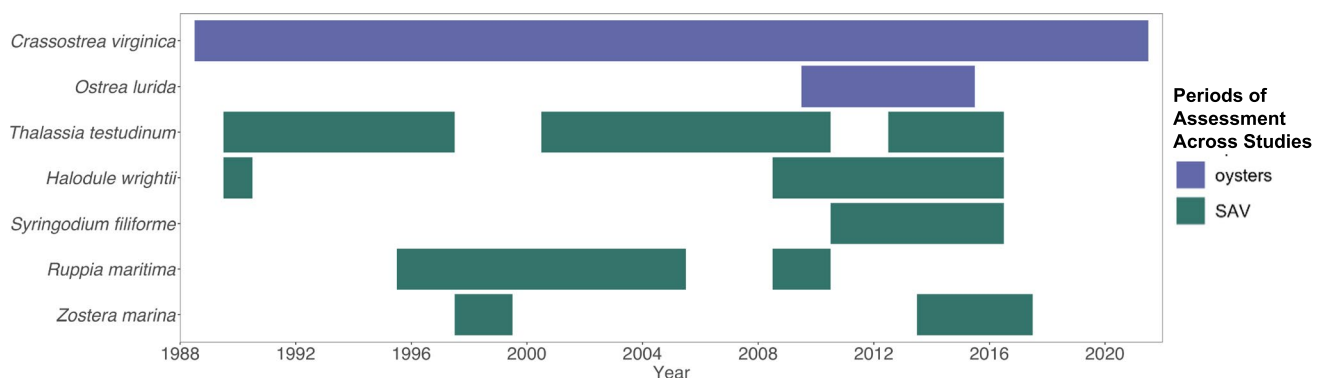
Over the past few decades, *C. virginica* had the longest overlapping period of assessment (1988–2021) of the reviewed species (Fig. 3). *T. testudinum* had the second longest assessment period (1990–2016) punctuated with two multi-year gaps. Between 2009 and 2017, there was a notable concentration of assessments across all species, including the first occurrence of assessments for *O. lurida* and *S. filiforme* in the reviewed literature. *H. wrightii* and *Z. marina* had over ten years between assessments, while *R. maritima*'s last period of assessment was over ten years ago. The start and end of observation periods do not always coincide with the beginning and end of the calendar year; there are frequent, however inconsistent, seasonal components to the timing of assessments driven by the research question.

Methodologies and reported metrics varied greatly across studies, which generally focused on species response to changing environmental conditions along gradients or following disturbances. Oyster studies measured variables such as reef extent, spawning, recruitment, growth, mortality, predation, and disease (e.g., *Vibrio vulnificus*, *Perkinsus marinus*) and seagrass studies frequently measured coverage, productivity, growth, and reproduction. Typical examples of reported metrics were the range and/or mean salinity and temperature for the study period. Some studies included additional information such as depth, tidal position, species life stage, or additional water quality parameters such as dissolved oxygen, pH, or suspended sediments.



**Fig. 2** Spatial distribution of reviewed studies with field-based oyster (purple circles) or seagrass (green triangles) salinity ranges, separated by marine ecoregions (Spalding et al., 2007). Estuary boundaries and

tributaries are from the US EPA Estuary Data Mapper virtual portal ([www.epa.gov/edmm](http://www.epa.gov/edmm); Detenbeck et al., 2009)

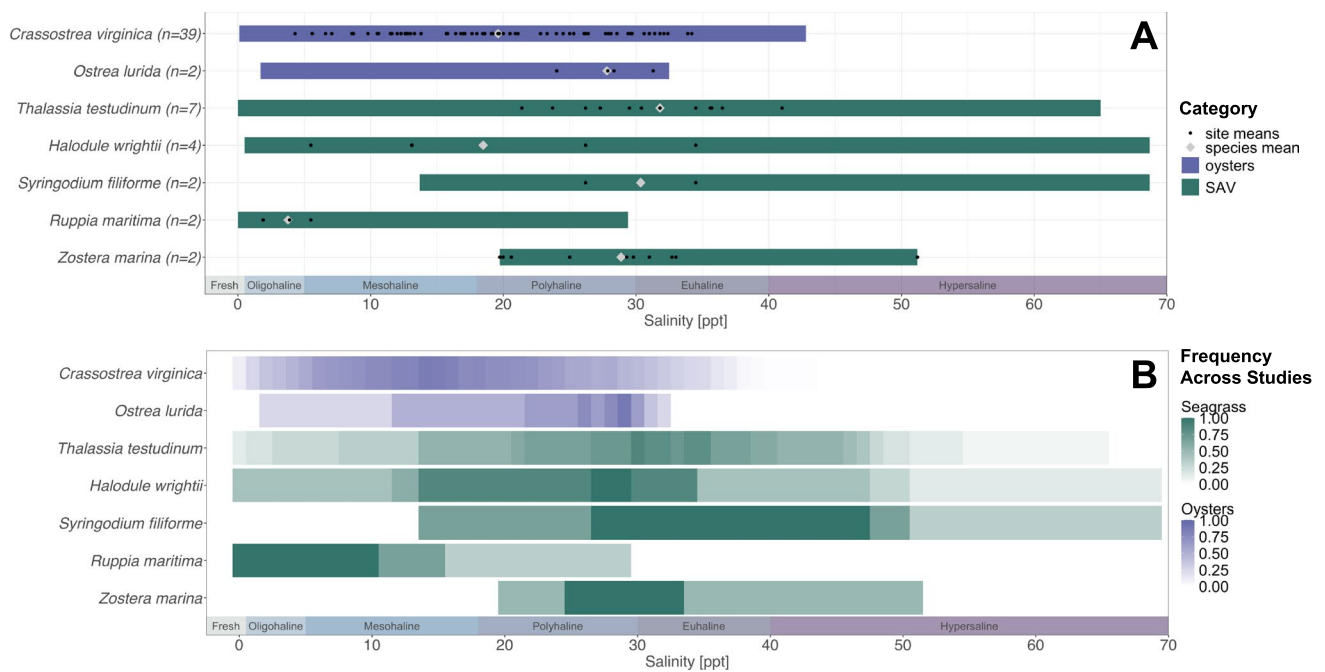


**Fig. 3** Periods of assessment across studies by species from 1988 to 2021. Years including one or more reviewed salinity studies are shaded, highlighting overlaps and gaps in species assessments. Sea-

grasses are referred to as submerged aquatic vegetation (SAV) in the legend

Differences in study duration, seasonality, and the averaging of conditions made it challenging to separate acute vs. chronic salinity change. Optimal salinity tolerance bands were rarely presented. Thus, practical salinity

ranges were summarized based on the diverse studies reviewed (Fig. 4). Additional information on species-specific findings based on representation in the literature is outlined below.



**Fig. 4** **A** Observed field salinity ranges (colored bars), site means (black points), and species means (mean salinity across all studies for a species, light gray diamonds) for selected estuarine species of oyster (purple) and seagrass (green) from reviewed studies (n) in this synthesis. **B** Frequency of observed field site salinity across study ranges selected estuarine species. Saturation of salinity range

is related to overlapping individual site ranges; deeper colors have a greater fraction of sites reporting overlapping salinity ranges. Note these observed field ranges are not necessarily the optimal ranges for species. Seagrasses are referred to as submerged aquatic vegetation (SAV) in the legend

### *Crassostrea virginica*

Across all studies of *C. virginica*, the range in observed salinity was 0.1 to 42.8 ppt, with a mean value of 19.6 ppt. Observed water temperatures ranged from 0 to 35.6 °C, with an average mean of 21.0 °C. In Louisiana, optimal salinity conditions for growth and survival were between 10.7 and 16.1 ppt paired with temperatures ranging from 20.0 to 26.3 °C (Lowe et al., 2017). Extended exposure of *C. virginica* in Louisiana to water temperatures exceeding 30 °C and salinities < 5 ppt negatively impacted oyster growth and mortality, especially in market-sized adults (Lowe et al., 2017; Rybovich et al., 2016). In Virginia, *C. virginica* growth rates and mortality were impacted by salinities < 15 ppt (Calvo et al., 1999) and in Delaware, exposure to salinities < 7 ppt for more than 20 days impacted mortality of market-sized oysters (Monroe et al., 2013).

### *Ostrea lurida*

In the two studies of *O. lurida* in the San Francisco Bay, the range in observed salinity was 1.7 to 32.5 ppt, with an average mean value of 27.8 ppt (Bible & Sanford, 2016; Chang et al., 2018). The range in observed water

temperature was 6.9 to 24.7 °C. Evidence of local adaptation to salinity and temperature variation in *O. lurida* was observed in a transplant experiment, where oysters originating from their transplant location survived better than oysters transplanted from populations adapted to different local conditions (Bible & Sanford, 2016). Optimal salinity conditions for peak recruitment of *O. lurida* in the San Francisco Bay were 25–30 ppt in combination with water temperatures > 16 °C; however, the timing of these conditions varied radically over the 6-year study period following interannual variation in climate (Chang et al., 2018). Earlier recruitment was observed during drought conditions (several months earlier); during wet years with cooler temperatures and salinity levels < 25 ppt, delayed settlement and near complete mortality of adults in upstream locations that previously were the known densest populations were observed.

### *Thalassia testudinum*

Across seven studies of *T. testudinum*, the range in observed salinity was 0.0 to 65.0 ppt, with an average mean value of 31.8 ppt. Reported water temperatures ranged from 7.6 to 38.0 °C with an average mean of 24.9 °C and reported depth

ranged 0.5 to 2.3 m. Biomass, growth, and productivity of *T. testudinum* were positively correlated with salinity (Irlandi et al., 2002; McDonald et al., 2016), water clarity (Irlandi et al., 2002; McDonald et al., 2016; Tomasko & Hall, 1999), and phosphorus availability (Herbert & Fourqurean, 2009). Lower relative growth rates of *T. testudinum* were observed in salinities < 20 or > 40 ppt (Herbert & Fourqurean, 2009) and plants growing in environments with greater fluctuations in water temperature, salinity, and turbidity tended to be smaller with shorter lifespans and exhibited earlier flowering with more instances than plants in more stable environments (McDonald et al., 2016). *T. testudinum* can acclimatize to a wide range of salinity conditions (McDonald et al., 2016), and hypersaline conditions (60–65 ppt) alone are not the sole cause of mass mortality events (Fredley et al., 2019; Hall et al., 2016; Koch et al., 2007). Prior to die-off events in the Florida Bay, *T. testudinum* proliferated in coverage as salinity increased, outcompeting *Halodule wrightii* and *Syringodium filiforme*. The presence of high-density *T. testudinum* beds compounded environmental stressors (e.g., nutrients, sediment, temperature, oxygen imbalance, pH, and sulfides) contributing to unfavorable conditions for both dominant and non-dominant seagrass species in the bay's meadows (Fredley et al., 2019; Hall et al., 2016; Koch et al., 2007).

#### *Halodule wrightii*

From the four studies of *H. wrightii*, the range in observed salinity was < 0.5 to 68.7 ppt, with a mean value of 18.5 ppt. Reported temperatures ranged from 15.8 to 33.0 °C with an average mean of 27.0 °C. Reported depths ranged from 0 to 1.72 m. Across the Everglade ecotone gradient, *H. wrightii* was observed at greater percentages (0%, 19%, and 97%) in locations with increasing salinity (11, 14, 21 ppt, respectively) and, if there are more frequent periods of salinity fluctuations in the 10–30 range, it is anticipated that the communities previously dominated by *Ruppia maritima* may shift to *H. wrightii* with climate change and sea level rise (Strazisar et al., 2015). In the Pamlico Sound, *H. wrightii* was observed flowering from May – August with salinities ranging from 12 to 34 ppt and temperatures ranging 28.5 to 30.0 °C; plants were found as low as 8 ppt but were sterile (Ferguson et al., 1993). In Florida, following circumstances where salinity was > 60 ppt for 17 days (maximum 66.3 ppt) and water temperature above 30 °C for six consecutive days (maximum 35.9 °C), and above 28 °C for 42 consecutive days, *H. wrightii* coverage decreased 50% (Fredley et al., 2019). However, in upper Laguna Madre following an extended period of salinities 50–70 ppt, *H. wrightii* replaced *S. filiforme* coverage following a four-year period (2010–2013) where salinity increased from 31.4 to 50.0 ppt and stayed above 35.0 ppt for 1023 consecutive days starting April 19, 2011 (Wilson & Dunton, 2018).

#### *Syringodium filiforme*

From the two studies of *S. filiforme*, the range in observed salinity was 13.7 to 68.7 ppt, with an average mean value of 30.4 ppt. These studies highlighted drought, hypersaline conditions, and significant die-offs. In Texas, extended conditions (13 months) of elevated salinity (50–70 ppt) were the suggested driver of *S. filiforme* mortality and shift to a community dominated by *H. wrightii* (Wilson & Dunton, 2018). In Florida, following circumstances where salinity was > 60 ppt for 17 days (maximum 66.3 ppt) and water temperature above 30 °C for six consecutive days (maximum 35.9 °C), and above 28 °C for 42 consecutive days, resulted in *S. filiforme* coverage decreasing by 50% (Fredley et al., 2019).

#### *Ruppia maritima*

In the two studies of *R. maritima*, the range in observed salinity was 0 to 29.4 ppt, with an average mean value of 3.8 ppt. Rapid fluctuations in salinity (2.5–20.0 ppt) over short periods (< 24 h) were associated with low survival rates and limited population persistence of *R. maritima* in the Everglades ecotone; however, lower magnitude (2.5–10.0 ppt) and longer-term (2 to 3 days) changes in salinity were well tolerated and positively correlated with seedling and adult survivorship (Strazisar et al., 2015). In Lake Pontchartrain, *R. maritima* became the dominant species as it outcompeted freshwater SAV recovery following disturbances that increased salinity (Poirrier et al., 2009). At this location, *R. maritima* was negatively impacted following the opening of the Bonnet Carré spillway and decreased salinity but did better during drought conditions and hurricane storm surges when salinity increased. These studies highlight the nuances in the timing and intensity of salinity changes on population dynamics of *R. maritima*.

#### *Zostera marina*

In the two studies reporting on *Z. marina*, mean observed salinity ranged from 19.7 to 51.2 ppt and temperature ranged from 10.6 to 14.6 °C, with average mean values of 28.4 ppt and 11.6 °C, respectively. In Oregon, a positive correlation was found between biomass and cover of *Z. marina* and salinity, which both decreased upriver in summer months (Kentula & DeWitt, 2003). In Virginia, the 2018 summer experienced a decrease in salinity (–3.9 ppt) and an increase in water temperature (+17.3 more days above 28 °C) compared to the average summer conditions of the previous 4 years and, in the following year, sites with the greatest variation in conditions experienced reduced adult clone survival (Johnson et al., 2021). The timing of events pushing salinities lower and temperatures higher than normal conditions

can profoundly impact the reproduction, both sexual and asexual, of *Z. marina* (Johnson et al., 2021).

## Discussion

Oysters and seagrasses are benthic habitat-forming species that are well adapted to dynamic salinities typical of estuaries, but within limits. Synthesizing results from 57 peer-reviewed articles, we found there were limited studies reporting field salinities in which oyster or seagrass were observed. Our findings highlight limited availability of field salinity observations compared to laboratory and controlled salinity tolerances. Of the studies reporting observed salinities (ppt), the ranges and mean values are summarized by species as follows: *Crassostrea virginica* (0.1–42.8, mean: 19.6), *Ostrea lurida* (1.7–32.5, mean: 27.8), *Thalassia testudinum* (0–65, mean: 31.8), *Halodule wrightii* (<0.5–68.7, mean: 18.5), *Syringodium filiforme* (13.7–68.7, mean: 30.4), *Ruppia maritima* (0–29.4, mean: 3.8), and *Zostera marina* (19.7–51.2, mean: 28.9). Though included in our literature search, there were insufficient studies from which to summarize observed field salinity ranges for eight oyster species (*Crassostrea rhizophorae*, *Isognomon alatus*, *Isognomon bicolor*, *Magallana gigas*, *Ostrea edulis*, *Dendostrea sandwichensis*, *Pinctada margaritifera*, *Striostrea prismatica*) and seven seagrass species (*Halophila decipiens*, *Halophila engelmannii*, *Halophila hawaiiiana*, *Halophila ovalis*, *Phyllospadix scouleri*, *Phyllospadix serrulatus*, *Phyllospadix torreyi*). We emphasize that the ranges reported here do not necessarily represent target optimal ranges, long-term salinity averages, or conditions that can be sustained for extended durations without experiencing stress or negative impacts to reproduction, growth, or survival. Although confounding factors influenced species presence or absence in field observations, we focused only on salinity and did not examine a suite of variables. The reported ranges provide literature-based evidence of the conditions over which species were observed, as well as some of the nuances in the timing and intensity of salinity changes on population dynamics of foundational species.

The practical salinity tolerance ranges highlight how individual oyster and seagrass species display differences in sensitivity to salinity conditions. Both oyster species were observed over a wide range of brackish to marine salinity conditions; however, *C. virginica*, while observed across a wider range, had lower average mean salinity conditions (19.6 ppt) than *O. lurida* (27.8 ppt). Optimal conditions for *O. lurida* recruitment are colder and more saline (25–30 ppt, >16 °C; Chang et al., 2018) compared to *C. virginica* (10–30 ppt, ≥25 °C; Dekshenieks et al., 1993). Though this may have also been due to differences in sample size or number of locations between the two species, only two studies

targeted *O. lurida*, and these were both from San Francisco Bay. Seagrass species were also observed over a wide range of salinity conditions. *T. testudinum*, *H. wrightii*, and *S. filiforme* appear to have a very high, or no, upper limit, based on their being observed at salinities up to 65 or 70 ppt, which aligns with Morris et al.'s (2021) study in Florida's Indian River Lagoon finding no upper salinity boundaries for these species. *R. maritima* and *Z. marina* had upper salinity thresholds of approximately 30 and 50 ppt, respectively. *S. filiforme* and *Z. marina* appear more sensitive, or less competitive, at lower salinities as they were observed in conditions above 13.7 ppt and 19.7 ppt, respectively. *R. maritima* had the overall lowest average mean observed salinity of 3.8 ppt, followed by *H. wrightii* (18.5 ppt), while other seagrass species were closer to 30 ppt. While Morris et al. (2021) found *R. maritima* constrained to salinities up to 18 ppt at one location, our findings suggested a higher maximum salinity threshold. This is supported by observations at 30 ppt near Hatteras Inlet of Pamlico Sound (Voigt & Eggleston, 2022). This extended salinity range may be due to phenotypic plasticity across populations (Bercovich et al., 2019) at a broader spatial scale than those considered by Morris et al. (2021). The practical salinity ranges we report for *C. virginica* and *T. testudinum* have relatively low uncertainty given the number of studies included in our analysis for these two species (39 and 7, respectively), while the ranges reported for other species were summarized from fewer studies (<5), making them highly uncertain.

Experimental manipulation of salinity and other factors such as temperature can provide important insights into the observed field ranges of salinity reported herein. For example, (Heilmayer, 2008) tested the main and interacting effects of temperature and salinity between 2–25 ppt and 15–30 °C on stress tolerance of *C. virginica* and found lowest Body Condition Index (BCI) values at combinations of salinities less than 5 ppt with a temperature above 25 °C. Throughout the experiment, oysters subjected to salinity treatments below 5 ppt ceased feeding, produced no feces or pseudofeces, and maintained their valves in a closed position. As salinity increased and temperature decreased, highest mean BCI occurred at salinities between 15 and 25 ppt and temperatures below 17.5 °C (Heilmayer, 2008). Similarly, Marshall et al. (2021) examined divergence in salinity tolerance of *C. virginica* collected from the northern Gulf under field and laboratory exposures. In their study, wild oysters were collected from four estuarine sites from Texas with mean annual salinity at the sites ranging from 7.4 to 35.5 ppt. The spawned progeny of oysters collected from these four sites were compared in field and laboratory studies under different salinity regimes. The results indicate that oysters adapted to high-salinity conditions exhibited rapid mortality at low salinities, and oysters acclimated to moderate salinity conditions did poorly when exposed to both extreme high

and low salinities. Thus, while the practical salinity range we report is 0.1–42.8 ppt, it is important to acknowledge that all salinities within this range are not necessarily suitable.

Similarly, variation in salinity could have negative effects on various life history stages of seagrasses, as well as their physiology, which mesocosm and laboratory experiments could reveal. For example, Kahn and Durako (2006) quantified the response of *T. testudinum* seedlings to changes in water chemistry in Florida Bay, USA, that might occur as part of the Comprehensive Everglades Restoration Plan by examining seedling survival, growth, photosynthesis, respiration, and osmolality in response to hypo- and hyper-salinity conditions using mesocosm experiments. Hyper- and hypo-saline conditions were detrimental to the fitness of *T. testudinum* seedlings. Plants at 0 and 70 ppt exhibited 100% mortality and displayed a significant decrease in survival in the range of 10, 50, and 60 ppt (Kahn & Durako, 2006). Yet, the practical salinity range from the seven studies of *T. testudinum* we reviewed was 0.0 to 65.0 ppt. Garrote-Moreno et al. (2014) examined the effects of salinity on the morphology and ion accumulation in leaves and rhizomes of *T. testudinum* and *H. wrightii* planted in a series of aquaria and exposed for 7 days to 10, 23 (control treatment), 30, 40, 50, and 70 ppt. Increasing salinity reduced the number of leaves per shoot and leaf elongation rates for *T. testudinum* and total photosynthetic surface for *H. wrightii*. The overall results suggest that *H. wrightii* possesses a better physiologic capacity to cope with salinity variations than does *T. testudinum* (Garrote-Moreno et al., 2014). Though the practical salinity range we reported for *H. wrightii* (<0.5–68.7 ppt) was slightly wider than that of *T. testudinum*, the controlled study offers more detailed insights as to when the plants are likely to experience stress.

Findings of this review generally agree with salinity ranges used in habitat suitability index (HSI) studies for oyster and seagrass species but include larger ranges than those previously used in HSI models. The larger range could be due, in part, to phenotypic plasticity and/or genetic diversity within individual species (Hornick & Plough, 2021; Pazzaglia et al., 2021) studied in the reviewed articles. Across Atlantic and Gulf coasts, *C. virginica* HSI salinity thresholds commonly range from 5 or 6 ppt up to 35–45 ppt, with optimal conditions around 10–25 ppt (Supplemental Table C). Our review found instances of eastern oysters at salinities <5 ppt, but prolonged exposure to salinity <10 ppt is associated with stressful conditions (La Peyre et al., 2013; Miller et al., 2017); we note that reported salinity stress limits are variable across the literature (Rybovich et al., 2016 (<7 ppt); La Peyre et al., 2016 (<9 or >13 ppt); Lowe et al., 2017 (<5 ppt)). HSI studies for *O. lurida* (Lawlor & Arelano, 2020; Bohlen, 2019) used salinity ranges for larva (9–39 ppt) and adults (0–32 ppt), with optimal conditions for adults being lower (16–27 ppt) than larva (30–33

ppt; Supplemental Table C); our synthesis includes a practical salinity range for *O. lurida* with essentially the same upper limit as those used in HSI studies, but our findings demonstrate that *O. lurida* has been observed at salinities below the lower limit of those used in HSIs. For seagrass species, our findings are consistent with HSI salinity ranges for *T. testudinum* (0–50) and *H. wrightii* (3.9–50.0), though we reviewed studies that documented both species at higher salinities (i.e., >50), indicating the HSI ranges used for these species could be extended.

While our summarized field salinity ranges highlight the conditions in which oyster and seagrass species of the United States are generally observed, a key theme of the reviewed studies was that salinity alone was not the only determinant of habitat suitability. Rather, salinity in combination with other factors shaped survivability, a finding that supports the need for understanding the synergistic effects of multiple stressors (Fredley et al., 2019; La Peyre et al., 2016). For example, increased infections of *Vibrio vulnificus* and *Perkinsus marinus* are associated with intermediate salinities (5–25 ppt) and warmer water temperatures (18 to >26 °C); short periods with salinities <5 ppt can be tolerated by oysters but are unfavorable to these pathogens (Motes et al., 1998; Monroe et al., 2013). In Louisiana, predation pressure from oyster drills on subtidal oyster reefs increases as salinity exceeds 15 ppt (La Peyre et al., 2009, 2013; Miller et al., 2017). Prolonged periods (weeks to months) of salinity <5 ppt coinciding with temperatures exceeding 25 or 30 °C produce conditions where *C. virginica* may be vulnerable to reduced growth, recruitment, and survival due to extended valve closures resulting in starvation or asphyxiation (La Peyre et al., 2009; Rybovich et al., 2016; Lowe et al., 2017; Powers et al., 2017; Wadsworth et al., 2019; Pruette et al., 2022). In Apalachicola Bay, Florida, oysters experiencing freshwater conditions for up to 2 weeks suffered 80–90% mortality (Edmiston et al., 2008). Additionally, freshwater pulses can impact the water quality in addition to salinity and temperature, and these changes can also affect species survivability. Water quality variables affected by changes in salinity include dissolved oxygen, turbidity, and nutrients, which can impact light penetration and primary productivity of plankton and seagrasses, as well as particulate organic matter and food sources for oysters (Marshall et al., 2019; Loh et al., 2017; Dieudonne & Carroll, 2022; Pruette et al., 2022; Fredley et al., 2019; Koch et al., 2007; Hall et al., 2016). Hurricane impacts, for example, not only can rapidly alter salinity but also drive re-suspension of estuarine sediments as well as land-based runoff that can lead to sedimentation on seagrass and oyster reefs (e.g., Livingston et al., 1999; Oprandi et al., 2020). Accordingly, when assessing habitat suitability for seagrass and oyster species, site-specific considerations are key to account for, as salinity alone will not predict species' geographic

distributions. The importance of considering covarying environmental variables underscores the utility of multifactor habitat suitability models, which provide opportunities to more holistically consider site characteristics.

Observed field salinity ranges for oyster and seagrass species were synthesized using search results gathered in a systematic literature review using a scholarly database, an approach that is limited by search terminology and the content of returned articles. Due to species-specific search terms, if a study used general or unique terms such as “seagrass”, “oyster-associated”, “oyster-reef”, or “reefs” and did not specify the associated common or scientific name, it was likely not included in the search results (e.g., Fredley et al., 2019; Ridge et al., 2017; Tice-Lewis et al., 2022). Our search terms still provided a sizable return of species-specific literature related to salinity tolerances, though a large portion were excluded from this synthesis due to being laboratory or mesocosm experiments, outside of our area of interest (United States), or not measuring/reporting observed salinity. There are comparatively fewer field-based salinity tolerance studies when compared to controlled experiments.

Literature that met our inclusion criteria was biased towards oysters in marine ecoregions along the Atlantic and Gulf coasts (95% of the 57 reviewed studies). We reviewed a larger number of oyster studies than seagrass studies related to salinity tolerance, and the eastern oyster was the most represented species. Thus, of the summarized field salinity ranges (Fig. 4), that of the eastern oyster is the most robust. Despite the presence of oyster and seagrass species in the Pacific and Caribbean, there is a lack of literature in these regions related to salinity tolerance, which could be addressed with additional field studies in these areas. One reason for the limited number of studies could be related to resources for long-term coastal salinity monitoring, which is primarily located along the Atlantic and Gulf coastlines (based on the Coastal Salinity Index database for monitoring droughts; Petkewich et al., 2019).

Reported field salinity was measured and reported in a variety of ways, which hindered our ability to draw more quantitative comparisons across the reviewed studies. In general, studies tended to report stressed conditions over optimal condition ranges. When reported, salinity measurements were most often sourced from monitoring networks (e.g., National Estuarine Research Reserve System) and sonde-based measurements collected by researchers during site visits. Several studies utilized alternative methods, including spatial kriging (Powers et al., 2017) and pre-defined salinity zones (Kimmel et al., 2012) to improve limited spatial or temporal resolution. Field salinities were commonly reported in parts-per-thousand (ppt) or practical salinity units (psu), which can be used interchangeably, although some studies had no units present for reported salinities (e.g., Le Peyre et al., 2013). Styles for reporting

salinity metrics included mean and standard deviation over the entire study period, range observed over the study period, salinities for specific increments during the study period (e.g., months, seasons) duration above or below a salinity threshold (e.g., <5), and time series figures. In narrative, hyper, high, and low salinity were frequently used terms but were relative to individual site or regional studies and often did not include a corresponding salinity range. What is described as low salinity in one study may be considered intermediate or high in another. Thus, greater standardization in reported salinities could increase opportunities for meta-analyses and syntheses like the one presented here. We found studies that reported descriptive statistics of salinities for comparable time frames (annual, seasonal, monthly—in addition to duration of study period, which varied) to be the easiest to summarize and include within the analysis. Studies that included frequency and duration above/below thresholds were insightful but could be easier to summarize with consistent thresholds or duration of events counted. Future studies could benefit from a consistent set of time series analysis metrics to be reported for salinity as a baseline, in addition to more unique data analysis pertinent to the study.

In addition to variation in reported metrics, the temporal intervals and duration at which field salinities were summarized varied greatly between reviewed studies, with the majority representing short-term, post-disturbance impact or recovery. Shorter duration and event-driven response studies were much more prevalent than those that investigated the effects of long-term and chronic salinity changes. Several multi-year studies only sampled during specific times of year, as they focused more on spawning and recruitment. Event-driven studies tend to capture responses of extreme events including hurricanes, flooding, freshwater diversions following the Deepwater Horizon oil spill, and droughts. Hydroclimate events such as droughts, floods, and freshets as well as associated freshwater management responses are drivers of salinity change that are likely to increase in frequency and duration in the face of climate change (Gledhill et al., 2020). Research studies are often funded over short grant periods and conducted by short-term research trainees (e.g., graduate students, postdoctoral researchers), which may contribute to the relative abundance of short-term studies. Greater access to long-term studies could help overcome some of the limitations of inferring habitat suitability criteria from event-driven investigations.

Estuarine species are well adapted to fluctuating brackish environments, but they are not immune to stress or mortality from changes in salinity regimes. While there are many potential mechanisms that can drive acute or chronic changes and estuarine squeeze, these impacts extend beyond a single species and may require a more holistic or ecosystem management approach. For example, freshwater management practices impacting estuarine inflows have profoundly altered

salinity regimes and impacted oyster and seagrass communities, which are the foundation of habitats that other species rely upon (La Peyre et al., 2016; Lowe et al., 2017; Parker et al., 2013; Seavey et al., 2011; Volety, 2008). For example, oyster habitats in the Big Bend region of Florida have seen a net loss in reef extent, with the greatest losses in the off-shore areas and landward migration of reefs coinciding with decreases in freshwater discharge from the Suwannee River, likely influencing recruitment and survival (Seavey et al., 2011). We acknowledge there are reviews and studies focused on restoration (e.g., Smith & Pruett, 2024; Smith & Castorani, 2023; Rezek et al., 2019; Ward & Beheshti, 2023; Gagnon et al., 2020; Buzzelli et al., 2015; Orth et al., 2020), as well as modeling approaches (e.g., Bittner et al., 2020; La Peyre et al., 2021). This literature review provides a context for multiple species with overlapping field salinity ranges, which could inform habitat suitability indices and assessments. This information could also apply to those managing aquatic nurseries, ecosystems dealing with saltwater intrusion, species migration corridors, estuarine reserve spatial expansion plans (including potential reduction in spatial extent), or coastal agricultural lands that may become inundated as estuaries migrate. The timing and duration over which high or low salinities occur are also considerations for researchers and natural resource managers considering using the ranges reported here for habitat suitability assessments or making management recommendation. For example, La Peyre et al. (2009) suggest managing freshwater inflows to decrease salinity to < 5 ppt for roughly 3 weeks in late winter/early spring to reduce *P. marinus* infections, then increasing salinities to around 9 ppt in the early summer to promote growth and recruitment in the northern Gulf.

## Conclusions

Using a systematic approach to review literature pertaining to field observations of oyster and seagrass species' salinity ranges, 57 articles were identified, and their full text was assessed for this synthesis. The eastern oyster, *Crassostrea virginica*, was the species with the greatest representation, corresponding to 68% of the 57 reviewed studies. Studies were predominantly (95%) concentrated along the Atlantic and Gulf coasts, leaving the Pacific and Caribbean coasts (and related species) underrepresented. Of the seagrasses, *Thalassia testudinum* and *Halodule wrightii* had the widest salinity ranges, *Syringodium filiforme* was observed at salinities > 13 ppt, and *Ruppia maritima* was observed at the lowest ranges (< 30 ppt). All seagrass species overlapped with oyster species salinity ranges. Observed field salinity ranges reported here generally align with the salinity ranges used in published HSI models for oyster and seagrass species, but our ranges

are wider, highlighting the potential for our findings to inform updates to existing HSI criteria. Confounding effects on organism survival in different salinity conditions were temperature, light penetration, predation, disease, nutrient/food source, and organism density. Elevated water temperatures create or exacerbate stressful conditions for both oysters (>25 °C) and seagrass (>30 °C). These reported ranges may be useful to others considering criteria for guiding freshwater management or habitat restoration or assessing potential climate change impacts to these estuarine species with overlapping observed salinity ranges. The literature on Before-After-Control-Impact studies (e.g., Stewart-Oaten & Bence, 2001) may provide a useful framework for designing studies to assess how foundational species such as seagrasses and oysters respond to various types of pulsed versus chronic changes in salinity. Understanding practical species salinity ranges is key to improving our understanding of how habitat-forming estuarine species distributions may shift as freshwater and brackish habitats are squeezed between hard anthropogenic barriers and rising sea levels, while also accompanied by changes in freshwater inflow.

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**Author Contribution** • Conceiving the ideas and design of the experiment: Charlotte Lee, Natalie Nelson, Simeon Yurek.

- Participating in the active execution of the study: Charlotte Lee
- Analyzing and interpreting the data: All authors
- Writing the manuscript: All authors

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**Data Availability** All data analyzed in this study are from published literature, with all data sources cited within the article.

## Declarations

**Ethics Approval and Consent to Participate** Not applicable.

**Consent for Publication** Not applicable.

**Competing Interests** The authors declare no competing interests.

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