





SYMPOSIUM

Recognizing Salinity Threats in the Climate Crisis

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Synopsis Climate change is causing habitat salinity to transform at unprecedented rates across the globe. While much of the research on climate change has focused on rapid shifts in temperature, far less attention has focused on the effects of changes in environmental salinity. Consequently, predictive studies on the physiological, evolutionary, and migratory responses of organisms and populations to the threats of salinity change are relatively lacking. This omission represents a major oversight, given that salinity is among the most important factors that define biogeographic boundaries in aquatic habitats. In this perspective, we briefly touch on responses of organisms and populations to rapid changes in salinity occurring on contemporary time scales. We then discuss factors that might confer resilience to certain taxa, enabling them to survive rapid salinity shifts. Next, we consider approaches for predicting how geographic distributions will shift in response to salinity change. Finally, we identify additional data that are needed to make better predictions in the future. Future studies on climate change should account for the multiple environmental factors that are rapidly changing, especially habitat salinity.

Introduction: Rapid salinity transformations across the globe

The Earth’s ecosystems are transforming at alarming rates due to human-induced habitat destruction, biological invasions, pollution, and climate change. As a result, our ecosphere is now undergoing the 6th Mass Extinction, with current extinction rates far surpassing pre-human background rates of extinction (Barnosky et al. 2011; Ceballos et al. 2015; Ceballos et al. 2020). Among the many variables affected by global change, habitat salinity stands out as a rapidly shifting variable that requires more attention.

Environmental salinity demarcates major biogeographic boundaries that most taxa are unable to penetrate, structuring bacterial, plant, algal, and animal communities (Hutchinson 1957; Lee and Bell 1999;

Lozupone and Knight 2007; Pavlouli et al. 2017). Saline and freshwater organisms are typically separated by a biogeographic boundary (of ~5 PSU ≈ 5 parts per thousand salinity ≈ 150 mOsm/kg), across which most species are physiologically unable to penetrate (Remane and Schlieper 1971; Khlebovich and Abramova 2000). As a consequence, rapid changes in salinity could have devastating impacts on many populations and communities worldwide.

In high-latitude coastal regions, increases in precipitation and ice melt are causing salinity declines on unprecedented rapid time scales (Fig. 1) (Rabe et al. 2011; Durack et al. 2012; Bintanja and Selten 2014; Durack 2015; Loder et al. 2015; Long and Perrie 2015; McCrystall et al. 2021). Recent models indicate that drastic changes in the global water cycle are as seri-

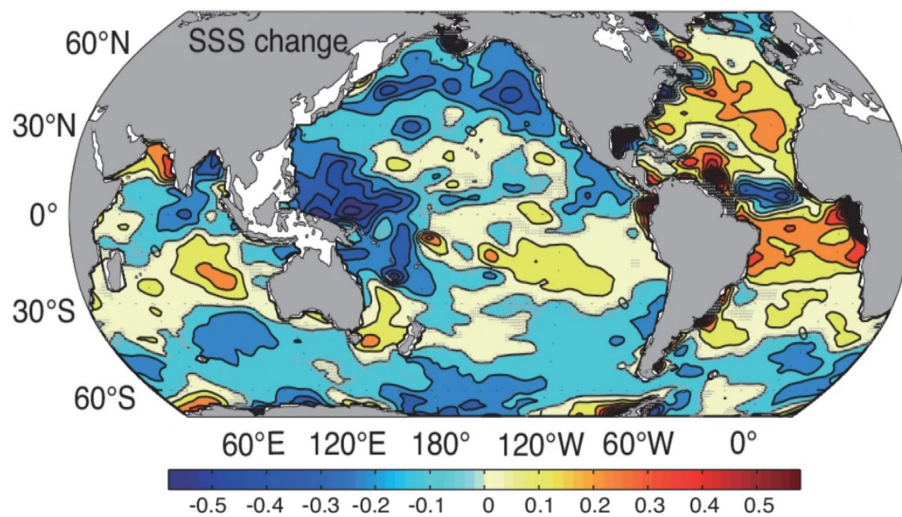


Fig. 1 Global depiction of sea surface salinity (SSS) change over a 58-year period (1950 to 2008) with salinity increases shown in red and salinity declines in blue. White areas indicate regions where the calculations were not performed (Adapted from Rhein et al. 2014).

ous as the direct effects of rising temperature, resulting in large-scale changes in global precipitation patterns (Durack et al. 2012; Bintanja and Selten 2014; Durack 2015; Loder et al. 2015; Long and Perrie 2015; Siepielski et al. 2017). In addition, massive volumes of ice melt are exacerbating the freshening trend on a multi-decadal time scale (Rabe et al. 2011). These factors are causing “Great Salinity Anomalies” along the coasts of Greenland and Labrador, contributing to significant freshening of the Arctic and Northwest Atlantic oceans (Belkin et al. 1998; Wadley and Bigg 2006; Dukhovskoy et al. 2019).

Likewise, the salinity structure of the Baltic Sea is being heavily impacted by climate change. Several studies had projected that much of the Baltic Sea could become close to completely fresh by 2100, with detrimental impacts on its communities currently adapted to brackish-water conditions (Janssen et al. 1999; Meier et al. 2006; Kniebusch et al. 2019). For instance, a 2 PSU salinity decline was predicted to result in a 3-fold reduction in biomass of the commercially important Baltic Sea cod fishery (Thøgersen et al. 2015). However, a more recent study casts doubt on earlier model projections, predicting increased vertical salinity gradients and stratification in the Baltic Sea, rather than an overall precipitous salinity decline (Meier et al. 2021). The degree of uncertainty among different model projections emphasizes the need for studies that incorporate more information on critical factors that might influence salinity change (see section: *Can we predict how geographic distributions will shift in response to salinity change?*), with intensive time series sampling and finer scale salinity measurements covering broader geographic regions.

In contrast to high latitude regions, many lower latitude areas are experiencing increased sea surface salinities due to evaporation and reduced riverine flow (Schroeder et al. 2017). For instance, the Mediterranean Sea is a semi-enclosed marginal sea where rates of change in salinity and temperature are projected to be far greater than in the open seas (Schroeder et al. 2016; Schroeder et al. 2017). Already an evaporation-dominated system, some areas of the Mediterranean are projected to experience salinity increases of 2–4 PSU within 7 years, due to decreases in precipitation and reduced riverine flow from damming (Schroeder et al. 2017). The increases in salinity and temperature are expected to have profound negative impacts on the productivity of estuaries and lagoons of the Mediterranean Sea (Coll et al. 2010; Schroeder et al. 2016; Piroddi et al. 2017).

In addition to coastal shoreline habitats and bays, more inland estuaries, rivers, and lakes are also projected to experience profound changes in habitat salinity. The extent and direction of salinity change could depend on multiple factors, as well as complex feedbacks among them, including changes in precipitation patterns and riverine flow, human water and land usage, sea-level rise, and frequency and intensity of extreme weather events (e.g., storms) (Herbert et al. 2015; Alcérrecas-Huerta et al. 2019; Mulamba et al. 2019; Tweedley et al. 2019; Ghalambor et al. 2021; Leal Filho et al. 2022). For instance, sea-level rise and the diversion of rivers for agricultural irrigation are important factors contributing to estuarine and wetland salinization (DeLaune et al. 1987; Herbert et al. 2015; Ghalambor et al. 2021). Additionally, many high latitude inland waters are becoming increasingly saline due to anthropogenic

inputs of salt (Herbert et al. 2015; Dugan et al. 2017). For example, a survey of 371 Midwest and Northeast lakes in North America found that thousands of lakes in these regions are at risk of long-term salinization (Dugan et al. 2017).

Sea level rise is already of serious concern in many low-lying areas, such as Bangladesh (Bhuiyan and Dutta 2012; Chen and Mueller 2018; Anwar et al. 2022). The resulting soil inundation and salinization is expected to cause intense human migration and crop losses (Chen and Mueller 2018). Saltwater intrusion causes salinization of both ground and surface waters in coastal areas; for instance, a rise of ~60 cm may cause an increase in salinity of ~1 PSU many kilometers upstream of riverine estuaries (Bhuiyan and Dutta 2012). While such small increases in salinity may seem harmless, strictly freshwater fauna are particularly sensitive to subtle increases in water conductivity and salinity, such as the stenohaline insects Ephemeroptera, Plecoptera, and Trichoptera (Cañedo-Argüelles et al. 2012; Kefford 2019). Salinization of approximately 3 PSU can detrimentally impact freshwater communities, resulting in decreased taxon richness and diversity (Cañedo-Argüelles et al. 2012).

Many populations that are invading or colonizing novel habitats are also experiencing drastic changes in salinity. Among aquatic invaders, populations that originate from more saline habitats currently dominate as contemporary invaders in freshwater habitats (Lee 1999; Lee and Gelembiuk 2008; Lee 2010; Casties et al. 2016) (see section: *Resilience to rapid changes in habitat salinity: which taxa will survive?*). These invasions, particularly by brackishwater populations, are occurring at rates much higher than expected based on abundance and transport opportunity (Casties et al. 2016). As a consequence, many formerly brackishwater species are now some of the most destructive invaders in freshwater habitats (e.g., zebra and quagga mussels, many amphipods, and sea lamprey) (Marsden et al. 1995; Marsden et al. 1996; Cristescu et al. 2001; Gelembiuk et al. 2006; May et al. 2006), despite being inefficient osmoregulators under freshwater conditions (Dietz et al. 1996; Lee et al. 2013).

In this perspective, we briefly discuss responses of organisms and populations to rapid changes in habitat salinity occurring on contemporary time scales and identify gaps in research that need to be addressed. While many studies on climate change have focused on rapid changes in temperature, far fewer have focused on the effects of rapidly changing environmental salinity. Consequently, predictive studies on physiological, evolutionary, and migratory responses of organisms and populations to rapid salinity change are relatively rare. For instance, a plethora of studies have performed niche

modeling (Box 1) to predict future distributions in response to temperature change, but not in response to rapidly changing habitat salinity. This omission is a major oversight, given that salinity is among the most important factors that defines biogeographic boundaries in aquatic habitats (Hutchinson 1957; Lozupone and Knight 2007; Pavlouidi et al. 2017). Future studies on climate change in aquatic habitats should account for the multiple factors that are rapidly changing, particularly habitat salinity.

How do organisms and populations respond to rapid salinity change?

When confronting the rapid salinity changes outlined above, organisms and populations will need to respond in one of three ways to avoid extinction, that is, to tolerate the rapid change, evolve, or migrate. Below are a few examples, which are not comprehensive, that illustrate a range of organismal and population responses to rapid salinity change, while highlighting the clear gaps in our understanding.

In the face of salinity fluctuations, organisms rely on physiological compensatory mechanisms to regulate water and ion fluxes to maintain homeostasis (ionic and osmotic regulation, Box 1), depending on the ionic and osmotic gradients with the environment (Schultz and McCormick 2013; Evans and Kültz 2020). Acclimation (Box 1) to salinity change prompts well-established, predictable responses across a wide range of fish and invertebrate species known to have evolved osmoregulatory strategies (e.g., bony fishes and invertebrates, such as copepods, isopods, amphipods, and decapods; Goolish and Burton 1989; Zanotto and Wheatly 2006; Evans 2009; Henry et al. 2012; Schultz and McCormick 2013; Lee 2016). In euryhaline organisms (Box 1), crossing salinity boundaries activates a suite of mechanisms to achieve necessary shifts between absorbing ions in dilute freshwater environments *versus* secreting ions in concentrated saline conditions (Evans 2009). These mechanisms include altering drinking and urination rates, regulating permeability of membranes to water, cell and tissue remodeling, and increasing the expression and activity of ion transporters (Box 1) in osmoregulatory organs (Evans 2009; Kültz 2015; Rivera-Ingraham and Lignot 2017).

Patterns and predictability of acclimatory responses to salinity change have been intensely evaluated for a few select ion transporters in many different taxa. For example, the ion transporter Na^+/K^+ -ATPase consistently shows increased activity or expression in the gills of killifish, alewife, sturgeon, salmon, and herring, as well as in copepod legs, during acclimation to seawater (Scott et al. 2004; Bystriansky et al. 2006;

Box 1: Definitions of Concepts and Terms

Acclimation: Changes in phenotype of an individual, resulting from phenotypic plasticity. This term includes both developmental acclimation (occurring during development and generally irreversible, e.g., human height) and short-term acclimation (typically reversible, such as a suntan).

Adaptation: The process by which organisms become better suited to their environment as a result of Natural Selection. Thus, adaptation occurs across multiple generations at the population level. Consequently, the frequency of beneficial alleles increases in the population, causing a shift in genetic composition of a population across generations. Thus, adaptation requires genetic variation at the critical trait, upon which natural selection could act.

Natural selection: The differential survival and reproduction of individuals that vary in a heritable trait, leading to proportional changes of the alleles that encode the trait in the population.

Allele: A version of a gene resulting from mutation. For a diploid organism, there are two alleles at each locus (e.g., gene).

Gene: DNA sequence in the genome that encodes a function or phenotype.

Pleiotropic constraint: Pleiotropy occurs when a single gene influences more than one trait. Pleiotropic constraint on selection occurs when selection favoring a beneficial trait is impeded because it will simultaneously result in a negative effect on another trait encoded (or influenced) by the same gene(s).

Genome architecture: The arrangements of genetic elements (genes, regulatory regions, noncoding DNA) in a genome. Features of genome architecture include number of genes, gene order, nucleotide composition (e.g., GC content), genome size, amount of coding *versus* noncoding DNA, amount of transposons and repetitive DNA (e.g., microsatellites), mean number and size of introns within genes, number of chromosomes, and ploidy levels.

Ion transporter: A protein that moves ions (or other small molecules) across a biological membrane to accomplish many different biological functions, such as ionic regulation, osmotic regulation, acid/base regulation, neuronal signaling, cellular communication, and energy production.

Ionic regulation: The regulation of the type and concentration of ions between the cell, body fluids (hemolymph), and environment. Typically, an ionic gradient is maintained across the cell membrane. This regulation is achieved in part through the action of ion transporters.

Osmotic regulation: The regulation of osmotic pressure between the cell and body fluids. The osmotic pressure typically needs to be the same between the cell and extracellular fluids. This regulation is achieved through the production and destruction of osmolytes and the action of ion transporters.

Stenohaline: Able to tolerate only a narrow range of salinity, or unable to tolerate fluctuations in salinity. Most freshwater and marine species are considered stenohaline.

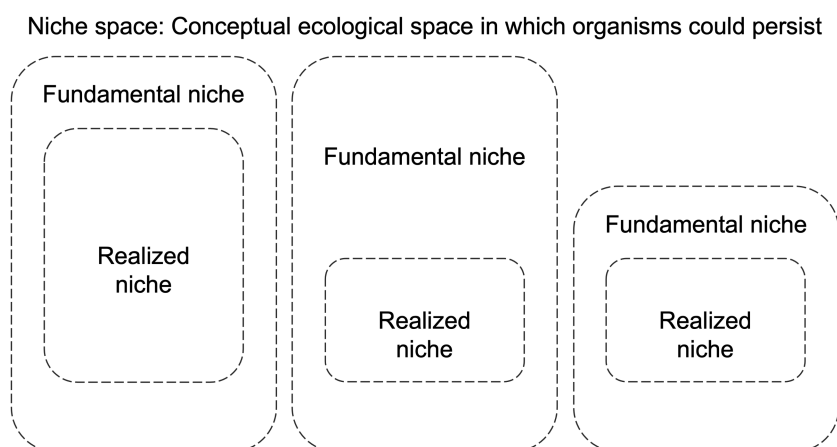
Euryhaline: Organisms or populations that are able to tolerate, live in, or acclimate to a wide range of salinities. This term is typically assigned to taxa with broad salinity ranges, without consideration of mechanism, whether it be broad tolerance, phenotypic plasticity, or evolutionary potential. Thus, this term has been applied both to taxa that show physiological broad tolerance or plasticity at the individual level and also to those that exhibit broad geographic range, containing populations that vary in their physiological tolerances. For example, the copepod *Eurytemora affinis* complex is considered a “euryhaline” copepod, but is composed of physiologically distinct populations that cannot span the salinity range of the species complex. When using this term, it is important to clearly indicate what is meant by this term, whether it is being applied to individual organisms that are known to have broad tolerance or plasticity, or whether a species spans a broad geographic range.

Conductivity: Degree to which a material conducts electricity, heavily impacted by ion content in water. This measurement is used to measure ionic concentrations at very low salinities.

Fundamental and Realized Niches (see Figure below): The fundamental niche is the full range of environmental conditions or potential habitat space in which a species is viable (able to survive and reproduce), as determined in laboratory and/or field experimental studies. In contrast, the realized niche is the actual environmental conditions or habitat space occupied by a species; the realized niche is in theory the same size or smaller than the fundamental niche.

The relationships between fundamental and realized niches for generalist and specialist organisms are illustrated below. Generalists (left) have relatively large realized niches because generalist strategies allow the exploitation of diverse resources. Specialists have small realized niches compared to generalists because they are specialized at exploiting a small proportion of resources with high efficacy. The realized niche of Specialist A (center) is constrained mostly by competition and not by physiological thresholds, such that its realized niche is much smaller than its fundamental niche. Specialist B (right) is physiologically limited to a small range of ecological conditions, possessing a

smaller fundamental niche than the physiological generalists (Generalist and Specialist A), and has a smaller realized than fundamental niche due to competition.



Niche Modeling: In the conventional approach, niche modeling is a type of species distribution modeling that can use actual occurrence data, as well as predictions based on trait data in conjunction with environmental data, to make a correlative model of the environmental conditions that meet a species' ecological requirements and predict the relative suitability of habitat. Species distribution modeling approaches can also be more mechanistic (see section: *Can we predict how geographic distributions will shift in response to salinity change?*).

SNP: single nucleotide polymorphism, which is variation in nucleotide at a position in DNA (such as A versus T at a nucleotide position). SNPs are common genetic markers used in genome-wide studies to determine genetic polymorphism within and between populations. SNP frequency shifts between populations are often used as signatures of natural selection.

Allen et al. 2009; McCormick et al. 2009; Christensen et al. 2012; Velotta et al. 2015; Gerber et al. 2016; Velotta et al. 2017; Posavi et al. 2020). Increased salinity also induces the synthesis of osmolytes to maintain constant osmotic pressure across the cell membrane (Yancey et al. 1982; Willett and Burton 2002). In some marine/estuarine decapod crabs, reduced salinity prompts increases in Na^+/K^+ -ATPase activity to maintain internal fluid concentrations above brackishwater levels (see reviews in Evans 2009; Henry et al. 2012). In freshwater habitats, the proton pump *V-type* H^+ -ATPase drives ion uptake from dilute media for many taxa, including crustaceans and fishes (Evans 2009; Lee et al. 2011; Henry et al. 2012; Kültz 2015; Lee 2021). Additional ion transporters are critical for ion uptake or excretion in aquatic habitats (Towle and Weihrauch 2001; Charmantier et al. 2009; Evans and Clairborne 2009; Dymowska et al. 2012; McNamara and Faria, 2012); but for many, their specific functions have been less well studied.

Acclimatory responses, such as transient increases in ion transporter activity, are often induced by changes in gene expression. For instance, a genome-wide expression analysis of populations of the killifish *Fundulus*

heteroclitus exposed to short term salinity transfers (32 to 0.1 PSU and 0.2 to 15 PSU) revealed changes in expression of genes involved in ion transport, intracellular calcium, energetic processes, and cellular remodeling (Brennan et al. 2015). The ion transport genes that showed differential expression in response to the salinity challenges included *NKA*, *NKCC*, and subunits of *V-type* H^+ ATPase (*VHA*) (Brennan et al. 2015). Another genome-wide gene expression analysis found gene expression changes due to developmental acclimation at different rearing salinities (0 and 15 PSU) in populations of the copepod *Eurytemora affinis* complex for a set of key ion transporters, such as Na^+/H^+ -antiporter (*NHA*), Na^+/K^+ -ATPase (*NKA*), and $\text{Na}^+, \text{K}^+, 2\text{Cl}^-$ co-transporter (*NKCC*) (Posavi et al. 2020). Short term acclimation studies in the threespine stickleback, *Gasterosteus aculeatus*, revealed a rapid plastic response to changes in salinity through DNA methylation (Artemov et al. 2017), which is an important mechanism for altering gene expression. Marine stickleback fish kept in freshwater conditions for four days exhibited shifts in methylation status of genes involved in ion transport, skeletal ossification, and gene regulation (Artemov et al. 2017).

While most studies focus on responses to single environmental variables, it is important to recognize that salinity change will interact with other environmental factors (e.g., temperature, hypoxia, and acidification) that are also becoming altered with climate change (Madeira et al. 2014; Przeslawski et al. 2015; Lefevre 2016). Responses to salinity and temperature shifts have been studied separately, but relatively few studies have examined the joint effects of multiple factors that will become altered with climate change. Most studies examining the simultaneous effects of salinity and temperature change find that their joint effects are negatively synergistic and detrimental to organisms (Devreker et al. 2009; Przeslawski et al. 2015; Kelly et al. 2016; Souissi et al. 2016), whereas a few reveal that their joint effects could be beneficial (Mak and Chan 2018; Torres et al. 2021).

For many organisms, higher temperatures will result in reduced ability to acclimate or adapt to salinity changes. In the copepod *E. affinis*, decreasing temperature coupled with ideal salinity conditions led to lower fecundity and lower growth rates upon hatching (Devreker et al. 2009). Another study found that while *E. affinis* could maintain good fitness at 20°C in both optimal and stressful salinities, an additional increase in temperature of 4°C resulted in loss of size and fecundity, especially at the stressful salinity (Souissi et al. 2016). In the tidepool copepod *Tigriopus californicus*, five generations of selection under simultaneous heat and low-salinity stress led to decreased heat tolerance, implying physiological trade-offs between adaptation to the two stressors (Kelly et al. 2016).

On the other hand, increasing temperatures might expand the salinity ranges of certain taxa. For instance, the green crab *Carcinus maenas* may experience the ability to expand its habitat range under increasing temperatures and salinities (Torres et al. 2021). At warmer temperatures, larval stage *C. maenas* showed a 3-fold higher ability to osmoregulate, which led to faster development times. Therefore, the green crab might gain fitness benefits from future increases in temperature and salinity, and could, consequently, experience range expansions going forward. In the purple urchin *Heliocidaris crassispina*, the impact of temperature-salinity interaction was negative at the urchin's larval stage, but not at its post-larval stages (Mak and Chan 2018). At the larval stage, temperature increase and salinity decline led to lower rates of survivorship. However, once the urchins reached the post-larval stage, warmer temperatures helped reduce the negative impact of lower salinity on fitness (Mak and Chan 2018).

As illustrated in the few examples above, the interactions between multiple factors can amplify or mitigate the negative effects of each factor. Thus, it is important

to conduct more studies assessing the combined impacts of environmental variables and their complex interactions for a wide variety of organisms. Understanding which organisms are able to acclimate and adapt to these changes will provide further insights into how organisms and populations will respond to multiple factors in our changing world.

When environmental change exceeds the physiological tolerances of individuals, populations that are unable to migrate will need to evolve in order to avoid extinction. Despite the profound negative impacts of rapid salinity change in aquatic habitats, evolutionary responses have been insufficiently investigated. The endeavor of exploring evolutionary responses to salinity is different from elucidating particular mechanisms of physiological tolerance or performance, such as osmotic or ionic regulation. For example, certain ion transporters might be important for ion uptake, but they might not be the specific transporters that are evolving in response to salinity change. In particular, certain traits that are important for salinity tolerance or phenotypic plasticity might not have the capacity to evolve. That is, even if a physiological trait shows an acclimatory response, that trait cannot evolve if genetic variation underlying that trait (upon which natural selection could act, Box 1) is lacking in the population. In addition, genes (Box 1) that encode a physiological trait might be unable to evolve due to pleiotropic constraint (Box 1) or linkage to a maladaptive allele (Box 1).

Investigating whether phenotypic evolution has occurred in wild populations requires controlled experiments to distinguish between the effects of acclimation *versus* adaptation (Box 1). In one type of approach, the “common garden” experiment involves rearing different populations under the same conditions for two or more generations and then comparing the heritable differences among populations. Rearing at the common condition removes acclimatory differences between the populations, such as developmental acclimation to native salinities that could significantly influence the physiological tolerances and traits of adults (Lee and Petersen 2003). Then, following common garden rearing, the phenotypic differences that remain between the populations represent heritable, genetically based differences. Such experimental approaches are limited to species with shorter generation times that can be reared under controlled conditions. Numerous common garden experiments performed on populations of the copepod *E. affinis* complex have revealed rapid evolution of a myriad of physiological traits following recent saline to freshwater invasions. In the past several decades, saline estuarine and salt marsh populations of this copepod have invaded freshwater lakes and reservoirs multiple times independently (Lee 1999; Lee 2016). Compar-

tive functional assays performed in common garden on ancestral saline freshwater and invasive freshwater populations have revealed evolutionary shifts in salinity tolerance and life history traits (Lee and Petersen 2002; 2003; Lee et al. 2003), starvation resistance (Lee et al. 2013), hemolymph osmolality (Lee et al. 2012), and ion transporter activity and expression (Lee et al. 2011; Posavi et al. 2020).

In addition, laboratory and field natural selection experiments serve as valuable tools that enable us to directly observe rapid evolutionary responses to salinity change. For instance, laboratory selection in response to declining salinity (15 to 0 PSU) for 6–10 generations in the copepod *E. affinis* complex revealed rapid evolution of increased low salinity tolerance (Lee et al. 2007), evolutionary shifts in ion transport activity (Lee et al. 2011), and genome-wide signatures of selection, especially at ion transport related genes (Stern et al. 2022). In terms of evolutionary responses to elevated salinity, the freshwater water flea *Daphnia pulex* reared at elevated salinities for 5–10 generations in mesocosms displayed rapid evolution of tolerance of increased salinity (Coldsnow et al. 2017). In particular, *D. pulex* treatments that experienced selection at high salinities were subsequently able to survive higher salinities ($1300 \text{ mg Cl}^- \text{ L}^{-1} \approx 2.3$ PSU salinity) relative to control treatments reared at their natural low salinity conditions ($15 \text{ mg Cl}^- \text{ L}^{-1} \approx 0$ PSU salinity). In a field experiment, anadromous threespine stickleback (*G. aculeatus*) were released into two lakes, with starting populations of about 3000 each (Bell et al. 2016; Divino et al. 2016). After 4–6 years of selection, 20% of the fish exhibited a highly heritable freshwater phenotype (Bell et al. 2016), with increases in freshwater tolerance (Divino et al. 2016) and shifts in life history traits (Kurz et al. 2016).

Understanding the genetic loci that are under natural selection during habitat shifts could help reveal which traits are limiting evolutionary adaptation to novel environments. While several genome-wide studies have examined evolutionary responses to salinity change on longer time scales (e.g., during Pleistocene colonizations) (Hohenlohe et al. 2010; Kozak et al. 2014; Brennan et al. 2018; Reid et al. 2021), few have examined adaptive responses to salinity change on contemporary time scales of several decades (Posavi et al. 2020; Stern and Lee 2020). For the copepod *E. affinis* complex, which has invaded freshwater habitats in the past several decades, multiple studies have found that natural selection during rapid salinity change tends to occur at genes related to ion transport, energy production, gene regulation, and stress response. The dominant functional categories under selection are related to ion transport, including putatively cooperating ion transport related proteins. These loci under selection

include gene paralogs and/or subunits of *NHA*, *NKA*, *VHA*, *NKCC*, *carbonic anhydrase*, *sodium bicarbonate transporters* (*AE*, *NBC*, *NDAE*), and *Rh Protein* (Posavi et al. 2020; Stern and Lee 2020; Lee 2021; Stern et al. 2022). Most notably, the same SNPs (Box 1) at these loci repeatedly show signatures of natural selection (SNP frequency shifts) across multiple independent saline to freshwater transitions (Stern and Lee 2020). This pattern of parallel evolution suggests that the evolutionary pathways for salinity adaptation are relatively constrained (Stern et al. 2022). Interestingly, some of these same ion transporter genes also exhibit signatures of selection during more ancient freshwater colonizations (e.g., Pleistocene) by stickleback and killifish (Hohenlohe et al. 2010; Kozak et al. 2014; Brennan et al. 2018).

In contrast to the relatively consistent responses to salinity change, evolutionary responses to temperature shifts tend to be far less predictable, typically exhibiting nonparallel evolution among replicate events (Barghi et al. 2019). This pattern arises because a wide and complex suite of metabolic and biochemical processes depend directly or indirectly on environmental temperature (Guderley 2004). Given the broadscale physiological impacts of temperature, it is not surprising that temperature adaptation and acclimation are highly polygenic, controlled by very many interacting genes, making it especially challenging to predict evolutionary responses and pathways (Barghi et al. 2019; Barghi et al. 2020; Otte et al. 2021). Additionally, teasing out temperature-related effects on organisms often yields confounded experimental results due to the inherent effect of temperature on rates of metabolic reactions throughout the organism, especially in ectotherms (Guderley 2004; Logan and Buckley 2015). As the physiological and evolutionary responses to salinity change tend to be relatively more predictable, we have greater capacity to identify the specific physiological and genetic targets of natural selection and predict future range expansions and probability of extinction in response to salinity change (Anciaux et al. 2018).

If populations cannot tolerate or evolve in response to salinity change, then they must migrate to avoid extinction. Climate change will result in altered migratory patterns for many species (Cohen et al. 2018; Tomotani et al. 2018). Altering migration patterns may allow organisms to avoid abiotic stressors (Magoulick and Kobza 2003; Nye et al. 2009; Pinsky et al. 2013), gain access to food sources (Clairbaux et al. 2019; Horton et al. 2020), and avoid predation or disease (Shaw et al. 2019). However, most of the current research on migration patterns focuses on the impacts of temperature changes (Crozier et al. 2008; Fullerton et al. 2018; Thorstad et al. 2021), with a dearth of research exploring the effects of salin-

ity. Salinity preferences have been found to be important in initiating migratory behavior (Baggerman 1960; McInerney 1964) and navigation (Edeline et al. 2009). Consequently, it is likely that changing salinity will impact migratory behaviors, as well. At present, research on migratory responses to salinity tends to focus on bird migration (Haig et al. 2019; Orellana Macías et al. 2020). For example, declines in salinity resulted in increases in macroinvertebrate abundance in the winter at Gökçeada Salt Lake, North Aegean Sea, leading to increased numbers of migratory birds (Aslan et al. 2021). Given that salinity change is likely to impact migratory behaviors for a wide range of organisms, there is a pressing need for more research on this topic.

Furthermore, salinity changes could alter temporal structuring and seasonal succession in aquatic communities. For instance, estuaries typically experience seasonal oscillations in salinity, which are being altered by climate change (Robins et al. 2016; Costa et al. 2018). Seasonal changes in salinity can drive the temporal succession of aquatic community structure, including phytoplankton community composition (Masmoudi et al. 2015; Devlin et al. 2019). Over decadal time scales, progressive increases in salinity caused by declines in seasonal patterns of freshwater runoff resulted in reduced numbers of phytoplankton taxa in Kuwait Bay (Al-Said et al. 2017). Such impacts of salinity change on phytoplankton community composition could have reverberating impacts on zooplankton and fish abundance, given that phytoplankton availability can have bottom-up impacts within ecosystems (Boldt et al. 2019).

On another note, it is important to consider that taxa are not responding to salinity changes alone, but as holobionts, with both host and symbionts responding and migrating to novel or changing habitats. Although often overlooked, parasites can have pronounced and varied impacts on their host's response to salinity changes. Increases in abiotic stress, such as salinity changes, have been documented to weaken host immune systems (Birrer et al. 2012; Chen et al. 2018), increasing host susceptibility to infection and resulting in population declines (Patz et al. 2000; Marsland et al. 2002; Milotic et al. 2017; Hall et al. 2020). Similarly, changes in salinity can also result in increases in parasite transmission. This outcome can occur when altered salinity conditions benefit a transmission stage of the parasite, e.g., by increasing fecundity or growth (Southgate 1997). For example, the 2002 population crash of the blue crab *Callinectes sapidus* in Georgia was attributed to an outbreak of the parasitic dinoflagellate *Hematodinium* sp., which can only be transmitted at higher salinities (>15 PSU) (GAEPD 2003; Lee and Frischer 2004; Gandy et al. 2011; Coffey et al. 2012).

Parasite transmission can also decrease as a result of changing salinity due to the fact that the fundamental salinity niches (Box 1) are often larger in the host species than in their parasites. Parasite life cycles that contain free-living stages may be vulnerable to abiotic stress (Lei and Poulin 2011). Blakeslee et al. (2021) found that the free-living larval stage of a parasite of the estuarine white-fingered mud crab (*Rhithropanopeus harrisi*) was unable to tolerate low salinities. Therefore, there exists a trade-off for the mud crabs between low salinity tolerance and parasite exposure, whereby "parasite escape" may be achieved by occupying less favorable, lower salinity environments (Rogowski and Stockwell 2006). Taking advantage of this situation, handling procedures in aquaculture can employ "salt baths" to remove ectoparasites from freshwater fishes (Selosse and Rowland 1990; Tavares-Dias 2022). These baths are adjusted in duration and salinity to avoid excessive stress on the host fish, while simultaneously providing sufficient stress for the ectoparasites to detach from their host (Selosse and Rowland 1990; Souza-Bastos and Freire 2009; Garcia et al. 2014; Tavares-Dias 2022). As it is possible that changing salinities will enable taxa to escape their parasites, there is a clear need to consider how this phenomenon might impact host populations and ecosystem dynamics (Byers 2020).

The examples we have briefly outlined here illustrate various responses to rapid salinity change, including physiological acclimation at the organismal level and evolutionary genomic responses of populations. In the future, it is essential that we conduct multifactorial analyses that account for the variety of possible responses in order to predict the holistic impact of salinity change on organismal and population survival.

Resilience to rapid changes in habitat salinity: which taxa will survive?

Certain types of taxa are more likely to survive rapid salinity transformations. The ability to tolerate or evolve in response to changes in salinity could depend on several key factors including, 1) the evolutionary history of a lineage, 2) the current halohabitat, and 3) any existing behavioral and physiological/molecular mechanisms (Freire et al. 2008; Schultz and McCormick 2013; Larsen et al. 2014; Lee and Gelembiuk 2008). For instance, recent evolutionary history of salinity transitions could greatly influence a population's ability to survive future salinity change (James et al. 2003; Alverson et al. 2007; Logares et al. 2009). In addition, current environmental conditions (such as environmental fluctuations), and the selection regimes they impose on populations, could affect propensity to endure or evolve in response to environmental change (Lee and Gelembiuk 2008). Taxa

that are likely to stand out as successful include invasive populations, populations from disturbed habitats, and brackishwater species. Often these properties of populations and species coincide and overlap (e.g., many invasive populations are also from disturbed and brackishwater habitats).

Aquatic taxa vary greatly in their ability to tolerate changes in salinity. Tolerance of salinity change may be achieved through a combination of acclimatory mechanisms that contribute to the maintenance of cellular volume and ionic gradients across the cell membrane and/or stability of the extracellular medium (Freire et al. 2008; Larsen et al. 2014). Physiological threshold limits of organisms would be represented by the boundaries of their fundamental salinity niche (Box 1), which include the range that could be acquired through acclimation. Thus, vulnerability to salinity change would be expected to most negatively affect taxa that possess limited capacity for acclimation, namely strictly stenohaline freshwater fauna, much more so than euryhaline species (Box 1) (Little et al. 2017). For example, the stenohaline ostarionphysian freshwater fishes, such as the siluriform *Clarias gariepinus* and the cypriniform *Carassius auratus*, essentially do not acclimate, as their salinity tolerance limit is only in the range 11–16 PSU upon direct transfer and then 11–22 PSU upon gradual acclimation (Schultz and McCormick 2013). On the other hand, Nile tilapia *Oreochromis niloticus* has a broader range, and can extend its halotolerance from 14–20 PSU to up to 46 PSU when gradually submitted to salinity increase (Schultz and McCormick 2013). The broadest salinity ranges could be achieved by euryhaline species, such as the killifish genus *Fundulus*. Species of this genus can already tolerate an upper range of 43–44 PSU upon direct transfer from fresh water, but show extended tolerance to 55–80 PSU upon gradual acclimation (Schultz and McCormick 2013). Species with even broader salinity tolerance ranges include the tidepool copepod *Tigriopus californicus*, which has a salinity tolerance range of ~5–120 PSU, depending on latitude (Leong et al. 2018; DeBiasse et al. 2018), and the brine shrimp genus *Artemia*, which includes populations that can reproduce at salinities as high as ~150–200 PSU (Dana and Lenz 1986; Browne and Wanigasekera 2000; Baxevanis et al. 2004).

Organisms and populations with a more recent history of habitat transitions are expected to possess a greater potential for surviving novel transitions, increasing their resilience to climate-change-induced habitat disturbances. For example, most microbial lineages are limited in their salinity ranges, having established their natal salinity several hundred million years ago, much earlier in geological history than fishes (Logares et al. 2009). Early lineage specialization to narrow salinity ranges is reflected in the very low per-

meability of salinity boundaries in most archaea, bacteria, unicellular eukaryotes, and viruses despite their large population sizes, fast reproductive rates, and potential to disperse long distances (i.e., population characteristics expected to increase rates of salinity transitions; Logares et al. 2009). For fishes, salinity transitions into freshwater and marine environments have occurred multiple times in deep and shallow evolutionary time, beginning 350 million years ago to as recent as a few hundred years ago (Schultz and McCormick, 2013). In fishes with relatively recent freshwater colonizations, the likelihood of retained salinity tolerance is much higher than for those with more ancient freshwater transitions (James et al. 2003). For example, alewife (*Alosa pseudoharengus*) and the threespine stickleback (*G. aculeatus*) are two species with high likelihood of resilience to salinity disturbance, given their migratory life histories and repeated instances of freshwater colonizations as recently as 300 and 33 years ago, respectively (Bell and Foster 1994; Palkovacs et al. 2007; Terekhanova et al. 2014; Roberts Kingman et al. 2021).

Current or recent conditions of disturbance or temporal environmental fluctuations could greatly influence the ability to transition to novel habitats (Lee and Gelembiuk 2008). These environmental conditions could lead to the evolution of increased tolerance/plasticity in response to salinity change or greater evolutionary potential, depending on the period of fluctuations relative to generation time (Lee and Gelembiuk 2008). In particular, for organisms with short generation times, temporally fluctuating salinity could lead to the maintenance of genetic variation for salinity tolerance within populations (i.e., through the action of balancing selection). Such genetic variation for critical traits (salinity tolerance) in their native ranges would provide the genetic substrate on which natural selection could act, enabling rapid evolution during habitat transitions into novel salinities (Lee and Gelembiuk 2008; Posavi et al. 2014; Stern and Lee 2020). An evolutionary history in disturbed or fluctuating conditions could lead to the evolution of life history traits that promote survival under environmental change (Grabowski et al. 2007; Lee and Gelembiuk 2008). Such life history characteristics include high fecundity, rapid larval development, higher growth rate, and shorter time to reproduction, as observed in invasive species of amphipods (Grabowski et al. 2007). However, it is important to note that the traits that enable rapid colonization of a novel habitat salinity might not be the same as those that promote long-term persistence of the population. We currently lack sufficient information to determine which factors and characteristics will promote the persistence of taxa following salinity change over longer time scales.

Brackishwater invaders typically originate from temporally fluctuating habitats, where selection would favor either greater evolutionary potential or greater individual tolerance/plasticity to better cope with rapid environmental change (see previous paragraph) (Lee and Gelembiuk 2008). Many freshwater invading populations with brackishwater origins are typically physiologically maladapted to freshwater conditions but are, nevertheless, successful as invaders into freshwater habitats (Dietz et al. 1996; McMahon 1996; Lee and Gelembiuk 2008). For instance, North American Great Lakes populations of the zebra mussel *Dreissena polymorpha*, which originated from the brackish Black Caspian Sea (Ponto-Caspian) region (Gelembiuk et al. 2006; May et al. 2006), have high ion efflux and are inefficient osmoregulators under freshwater conditions (Dietz et al. 1996). Likewise, freshwater invading populations of the amphipod *Corophium curvispinum*, also of brackish Ponto-Caspian origin, exhibit high sodium influx and efflux rates relative to freshwater amphipods (Taylor and Harris 1986). Additionally, estuarine and saltmarsh populations of the *E. affinis* species complex exhibit very low freshwater tolerance, with extremely high mortality at the larval (naupliar) stages following introduction into freshwater conditions (Lee and Petersen 2003; Lee et al. 2003; Lee et al. 2007). Such freshwater invasions often entail higher energetic costs and the need for higher food consumption in freshwater habitats (Lauringson et al. 2007; Lee et al. 2013).

Despite the physiological challenges faced by formerly brackishwater populations, they often outcompete native freshwater species in freshwater habitats. Likely as an outcome of evolution under fluctuating conditions, brackishwater species tend to have much higher reproduction rates, which enable them to numerically overwhelm freshwater species (Mackie 1991; Peterson 2001). For instance, brackishwater gammarid amphipods have greater numbers of broods, lifetime potential fecundity, and reproductive potential than freshwater and marine species (Sainte-Marie 1991). Moreover, brackish species have a relative advantage when invading anthropogenically disturbed habitats where native species are absent or in decline, especially reservoirs and polluted lakes (Havel et al. 2005; Hufbauer et al. 2012).

As in the examples above, high allocation of energetic resources into growth and reproduction likely increases the probability of success in changing salinity environments. According to the conventional theory of osmoregulation, energy allocated toward osmoregulation should be minimized when possible, and allocated instead toward reproduction (Kefford 2019). On the other hand, environmental change to maladaptive salinities can be energetically costly, leaving less energy for growth and survival. For example, populations of *E. affi-*

nis complex that have recently invaded freshwater habitats exhibit retarded larval development (Lee et al. 2003; Lee et al. 2007) and require higher food intake following adaptation to lower salinities (Lee et al. 2013). Likewise, in the invasive mosquitofish *Gambusia holbrooki*, reproductive output (gonadal mass, oocyte mass, and embryo mass) declines with decreasing conductivity (proxy for salinity; Box 1) (Alcaraz and Garcia-Berthou 2007). Further studies into the links between habitat salinity and fitness (survival and reproduction) will provide insights into which taxa will likely survive, migrate, or go extinct in the face of salinity change.

In addition to the time scale of salinity change (e.g., fluctuations, see above), the spatial scale and distribution of salinity variation could also affect the ability of organisms to respond. Salinity distribution or stratification can provide halo-refugia and shape community structures and species competition. The spatial scale or “graininess” of climatic effects (e.g., changes in temperature, salinity, acidity or oxygen levels) relative to the size of the organism is important in determining their responses. The size of animals affects how they perceive their environment, such that habitats will be much more “fine-grained” for large fish or crabs but much more “coarse-grained” for small larvae or worms (Levins 1968). Thus, small-sized animals will be more readily able to explore and exploit microhabitats, which may serve as refugia from unsuitable conditions (Willmer et al. 2005; Helmuth 2009). For instance, while multiple invasive (originally brackish) amphipod species have colonized high conductivity river sections in the Polish Baltic basin, some native freshwater species have found refugia and have remained dominant in small, low conductivity affluents (Grabowski et al. 2009).

This section briefly touches on a few factors that could influence the capacity of individuals or populations to survive future changes in environmental salinity. At this point, the information we have is far from comprehensive. We especially need more information on factors that affect short term survival in response to salinity change *versus* longer-term persistence in a novel salinity habitat. As we learn more about these factors, it would be helpful to incorporate this information into predictive models to assess future distributions and range expansions of populations in response to rapid salinity change (see next section).

Can we predict how geographic distributions will shift in response to salinity change?

Current predictive models consist of two main approaches: mechanistic, which combine trait observations with environmental data, and correlative, which predict organism distributions based on environmen-

tal factors (Fig. 2) (Elith et al. 2006; Kearney and Porter 2009). Mechanistic species distribution models (SDMs) explicitly account for range-limiting factors and can incorporate multiple complex parameters, such as behavior and physiology, to predict distributions of well-studied populations (Kearney et al. 2021). In contrast, correlational SDMs (e.g., conventional niche models, Box 1), require only a location data point for each recorded organism and are, therefore, especially useful for poorly studied taxa. Optimal species distribution prediction under future salinity conditions will require the use of both types of approaches, depending on data limitations.

While correlative niche modeling approaches are commonly used to predict how environmental changes will affect present and future animal distributions (Madeira et al. 2014), a combined mechanistic and correlative analysis would be more powerful for predicting future species distributions (Kearney and Porter 2020; Kearney et al. 2021). Models examining the impacts of temperature change are abundant in the literature, with plenty of discussion on the pros and cons of utilizing correlative *versus* physiologically/mechanistically based models (Kearney and Porter 2009; Kearney et al. 2010; Buckley et al. 2011; Martínez et al. 2014; Kearney and Porter 2020). Niche modeling studies that account for salinity change, however, are rare (Martínez et al. 2014). In one example, Zimmer et al. (2021) combined correlational and mechanistic approaches to analyze the current distribution of freshwater fishes in the Northern Hemisphere. They then compared the realized and fundamental niches (Box 1) of these freshwater fishes to identify species and populations that may be under threat of extinction due to water acidification or salinity change. Similar to how Zimmer et al. (2021) used realized and fundamental niches to predict which populations and species that would be at risk, this combined analysis of niches could also be used to predict, or “map,” future species distributions.

To successfully map species distributions in response to salinity change, we must have access to accurate measurements of future salinity predictions. While numerous predictive maps are available for global temperature estimates forecasting as far as 100 years into the future on the NASA website and in published research (Kearney and Porter 2009; Hazeleger et al. 2013), very little is available on a global scale for ocean salinity predictions. This dearth of data is problematic, given that predictions of future salinity change are arguably of equal importance for understanding the future impacts of climate change (see Introduction, above). There is also a notable sparsity of validated salinity measurements for some of the most critical parts of the world's oceans, particularly the Arctic and coastal regions, with

fewer data points relative to the open ocean (Fig. 1). The lack of sampling in some regions is problematic, given that the extent and impacts of salinity change will be uneven in distribution (Fig. 1). Sampling records in the World Ocean Database (WOD), the largest bank of long-term ocean data (Boyer et al. 2018), reveal that many high-risk areas have only 1–5 data points, whereas open-ocean locations have > 20 (see WOD data distribution plot: <https://www.ncei.noaa.gov/access/world-ocean-database-select/bin/dbextract.pl>). This problem is evident in the white portions of the map in Fig. 1, which indicate areas where comparative calculations were not performed, emphasizing the deficit of global salinity data.

Additionally, surface satellite measurements do not account for water column depth and the spatial resolution is too low to accurately measure salinity distributions in habitats that are likely to experience drastic salinity changes in the future, such as Arctic and coastal habitats (e.g., estuaries, salt marshes, and coastal rivers) (Geiger et al. 2013; Tang et al. 2018). Salinity data can be and have been collected at finer spatial scales for such locations using buoy sampling, colored dissolved organic material assessments, remote operated drone measurements, and many of the techniques already employed by Argo and WOD (Geiger et al. 2013; Chen and Hu 2017; Vazquez-Cuervo et al. 2019). These finer scale measurements could then be used in covariance models to estimate subsurface salinities that reach below the depth provided by drifting floats (Smith and Murphy 2007). In order to improve salinity predictions for highly variable locations, one or all of these techniques must be implemented repeatedly to establish accurate salinity distributions. The inclusion of these validated data in the WOD would vastly increase the power of global salinity forecasts.

In contrast to the deficit of Arctic and coastal salinity data mentioned above, a plethora of salinity data are available for the larger open-ocean regions in several public databases. The WOD hosts ocean measurements of varying quality and spatial resolution ranging from the 1960s to the present day. It includes over 1 million total data points of temperature, depth, and conductivity measurements collected world-wide. The international Argo program continues to add to this extensive database via 3,000 drifting profile floats that are able to descend as deep as 2000 m, providing roughly 100,000 temperature and salinity readings annually. NASA's Aquarius and SMAP missions and the European Space Agency SMOS mission (Reul et al. 2020) provide satellite validation of the WOD data using sea surface salinity. However, data estimated from satellite measurements alone do not account for the microclimate factors which impact these habitats, skewing any

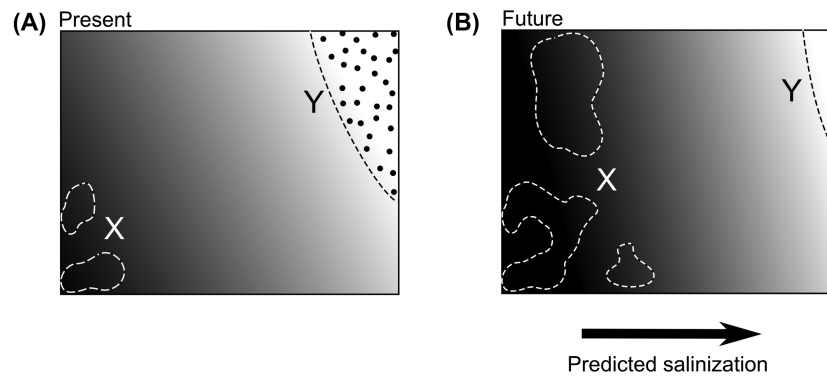


Fig. 2 Simplified application of mechanistic (species X) and correlative (species Y) modeling to predict impacts of anticipated salinity change on species distributions. **(A) Current Distribution:** Using present data, the fundamental niche (dotted white lines) of species X is determined using mechanistic modeling of behavior, physiology, and environmental data. In contrast, for species Y, locations of individuals within a population of species Y are identified based on sampling data (black dots). Then, environmental data (e.g., salinity measurements) are correlated with the sampled locations of species Y and characteristics of its niche are identified (dotted line). **(B) Future Distribution:** Using maps of predicted future conditions (salinity, depth, pH, temperature, etc.), regions matching the fundamental (species X) and correlational (species Y) niches are identified. These represent the predicted future distributions of each species. The greyscale represents a hypothetical environmental salinity gradient.

predictions derived from the data (Faye et al. 2014). The combined float and satellite sampling methods allow scientists to avoid this pitfall, which has been a serious problem that has been noted in the soil temperature field.

While further sampling at finer spatial scales is necessary for the most accurate predictive models, efforts can be made to establish salinity maps using existing salinity data from varying depths. Among the more common methods for short-term prediction of salinity changes are autoregression and neural networking (Box 1), both of which use existing time series data to calculate predictive models (Bowden et al. 2005; Qiu and Wan 2013; Rath et al. 2017; Song et al. 2020; Ye et al. 2020). To date, the most accurate regression-based predictive model required roughly 20 years of time series data for calibration (Qiu and Wan 2013). Song et al. (2020) developed a model that predicted 2-week future salinity variation in the South China Sea with 97% accuracy, but the model has yet to be validated with long-term forecasting and was not designed to account for ocean currents. Ye et al. (2020) developed a neural network machine-learning model capable of predicting long-term salinity variations in the Pearl River Estuary in China using only a few years of river runoff, tide, and time series salinity data from different depths as input. Though less accurate than the previous two examples, this model required substantially less time for data collection and was computationally less intensive. These machine-learning models are designed to include multiple interacting variables such as precipitation, runoff, and many others that impact future salinity estimates. Over time, models such as these could be employed to produce predictive maps with gradually increasing levels of accuracy as more data are collected.

As discussed here, there is a long way to go before predictions of species distributions under changing salinity are as informed and as common as temperature and climate-related distribution studies. Ensuring that global maps include salinities at varying depths will allow for prediction of possible refugia in deeper waters. Finer-scale measurements of salinity at multiple depths, especially in coastal and Arctic regions, are currently lacking, yet are vital to understanding organism distributions in these areas of great projected salinity change. With improved salinity data, better models of future salinity can be produced. Then, salinity data and predictions, including both aquatic and soil salinity measures, can be used to predict species distributions under anticipated climate and salinity conditions using the framework of existing models. Model type selection and efforts to optimize the information included in these models, e.g., by determining the fundamental niche of a species based on the improved salinity predictions, are also necessary to best understand and anticipate species distributions following salinity changes.

What information or tools are needed for better predictions in the future?

Physiological thresholds & modifiers

Continued study of physiological thresholds of organisms and drivers of physiological change is critical to improving predictive models of responses to our changing environment. Models based purely on correlative relationships are limited in their capacity to predict changing species distributions (Kearney and Porter 2020; Kearney et al. 2021). The integration of observed physiology and performance in mechanistic models is an information rich and critical approach to predict-

ing survival, resilience, and distribution of populations moving forward (Reist et al. 2006; Kearney et al. 2008; Miller 2011; Madeira et al. 2014; Martínez et al. 2014). Salinity tolerance thresholds (i.e., fundamental salinity niche) should be given especially close attention, and concerted efforts should be made to address physiological properties and thresholds at all life history stages (Kearney et al. 2008). Physiological constraints at larval and juvenile stages of aquatic organisms are often understudied compared to adult life-stages, particularly for species that perform salinity-transition migrations (Kearney et al. 2008; Meretsky et al. 2011). To fully understand whether organisms and populations could survive salinity changes, it would be critical to determine which specific life history stages are vulnerable or resilient to salinity change. For instance, salinities that are tolerated by adults are often lethal to larval stages (Lee et al. 2003). Moreover, it would be important to determine the extent to which different life history stages could acclimate or evolve in response to salinity change. Additionally, the dynamic role that biotic interactions play in altering physiological constraints is largely overlooked. For example, parasites play an important role in regulating populations and some parasites will be more heavily impacted by climate change than their hosts, while others might become more virulent (Scott and Dobson, 1989; Altizer et al. 2013; Cizauskas et al. 2017).

Genome architecture & evolution

Genome-wide evolutionary studies have the potential to reveal the genetic and physiological targets of natural selection during salinity change in a comprehensive manner and also provide insights into the future demography of populations under selection (Chevin et al. 2010; Anciaux et al. 2018). For developing predictions on evolutionary responses to future salinity change, we specifically require information on the evolutionary potential of critical traits that limit or enable evolutionary adaptation to novel environments. This information would include the genome architecture (Box 1) underlying the traits under selection, including allelic variation of the traits under selection and selection coefficients of the beneficial alleles favored by selection (i.e., how much allele frequencies will change with selection). We would also need to know how these beneficial alleles impact the fitness (survival and reproduction) of populations when confronted with salinity change. With this information, we could determine the extent to which natural selection in response to salinity change will cause the rise in frequency of beneficial alleles in a population. We would then be able to predict how this increase in allele frequency will impact the fitness and demography of populations experiencing salinity change. This information would provide us with insights into whether

populations are likely to survive or go extinct in the face of salinity change.

However, the full potential of genomic approaches in explicating physiological targets of acclimation or selection has been far from realized. In many genomic studies, a large portion of the genetic targets consist of genes that are “unknown” or “unidentified” or not clearly known (e.g., Stern and Lee 2020; Stern et al. 2022; Brennan et al. 2018; Maynard et al. 2018). In some cases, automated annotation pipelines identify genes incorrectly, especially for invertebrate and non-model systems. For example, manual annotation was required to correctly identify *NHA* paralogs in the genomes of the copepod *E. affinis* complex and the amphipod *Hyalella azteca*, as *NHA* was initially identified as its sister clade *NHE* using automated pipelines created for insects (Eyun et al. 2017; Poynton et al. 2018). Some genomic studies do not provide full lists of gene names showing signatures of acclimation or adaptation in response to salinity (e.g., DeBiasse et al. 2018). In many instances, the functions of key genetic targets of acclimation or selection in response to salinity change are poorly characterized. For example, studies on the ion transporter *NHA* in animals have yielded divergent and inconclusive results regarding the functions of gene products of different *NHA* paralogs in different taxa, indicating that we cannot assume functional uniformity among the paralogs (Day et al. 2008; Xiang et al. 2012; Chintapalli et al. 2015). For the related families of bicarbonate transporters, *AE*, *NBC*, and *NDAE*, the stoichiometry and mechanisms of ion transport remain unresolved and controversial (Liu et al. 2015). More interdisciplinary studies are needed, where genomicists and evolutionary biologists collaborate with physiologists to understand the particular functions of the genetic loci that show acclimatory or evolutionary responses during environmental change.

Environmental monitoring

Improved integration of physiological and genomic data are only part of the battle and must be accompanied by greater environmental monitoring to produce especially accurate and robust models for future projections. Considerable preliminary work must be conducted to determine the most informative variables (e.g., runoff, precipitation, evaporation, sea-level rise) to include in forecast models for different locales. Increasing availability of high quality data for sea surface and subsurface salinities are especially important in coastal and shallow water areas that experience high variability (Klemas 2011). Special attention should also be paid to those regions that are particularly data-poor, such as the Arctic and coastal regions (Fig. 1). Estimates of future species distributions based on niche modeling would be greatly

improved by including environmental factors such as those we discussed above (Helmuth 2009; Martínez et al. 2012; Oomen and Hutchings 2017). An interdisciplinary approach to data acquisition and modeling will be necessary to meet the recommendations above as they span multiple fields of study. Above all else, effectively predicting and responding to the ramifications of climate change, even just those posed by salinity changes, requires a team effort. In this perspective, we brought attention to the data and models required to fully comprehend the future impacts of global salinity change in our current climate crisis.

The next and most challenging step is creating an informed response. To succeed in this effort, it is vital that we as scientists exchange and share data and continue an open dialogue of diverse viewpoints and ideas. The integrative and interdisciplinary approaches outlined in this perspective would provide us with tools to predict future distributions of populations, as well as a deeper understanding of the factors that govern which populations are likely to survive the ongoing climate crisis.

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