The stars are out: Predicting the effect of seawater freshening on the ecological impact of a sea star keystone predator

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A R T I C L E   I N F O

A B S T R A C T

Predicting the myriad effects of climate change on ecological communities is a major challenge for scientists, and to date relatively few studies have focused on the effects of sea freshening on species interactions. In particular, changes in keystone species predatory effects could be pervasive. Here, we assess the consequences of decreasing salinity on the ecological impact exerted by a keystone predatory sea star, *Asterias rubens*. We quantified sea star functional responses (FRs; *per capita* predation as a function of prey density) under decreasing salinity treatments aligned with climate change projections (18ppt, 15ppt, 12ppt). Furthermore, we combined FRs with larval recruitment estimates, i.e. ecological "Impact Potential", to act as an ecological indicator of predator population-level responses under this environmental change. Attack and maximum feeding rates of sea stars were reduced by decreasing salinities, with no instances of predation found at 12ppt. Given that decreasing salinities also reduced larval sea star recruitment, the overall Impact Potential of this keystone predator species was lessened by decreased salinity. Sea freshening projections by the end of this century could thus drive significant decreases in the effects of this keystone predator, with serious implications for the structuring and functioning of ecological communities.

1. Introduction

Climate change is a major threat to global biodiversity (Thomas et al. 2004; Harley 2011; IPBES 2019), however, predicting the extent of its role in driving biodiversity loss has proven difficult (Urban 2015), with a vast suite of biotic and abiotic consequences likely (Brook et al. 2008). While warming, ocean acidification and changing weather patterns are well documented (Harley et al. 2006), sea freshening is a neglected outcome of climate change (Bindoff & Hobbs 2013). Salinity changes occur as a result of water cycle strengthening, with warm air able to hold and distribute more water, meaning greater evaporation and greater precipitation. This has been described as a "rich get richer" mechanism (Chou et al. 2009), whereby the ocean surface in areas of net evaporation is likely to become saltier, and areas of net precipitation likely to get fresher with amplified patterns of precipitation and evaporation (Held & Soden 2006; Durack et al. 2012). Over longer time periods, further

changes will stem from a weakening of the Atlantic Meridional Overturning Circulation, hydrological cycle changes and glacier and sea ice decline (Bindoff & Hobbs 2013; Bindoff et al. 2019). The Baltic Sea is one area likely to freshen (Gräwe et al. 2013).

Keystone predators exert disproportionately large effects on community structure and function relative to their abundance (Power et al. 1996), and preferentially consume and regulate the abundance of species that might otherwise dominate ecosystems (Paine 1966, 1969). While interpretation of such classic keystone species studies have attracted some criticism (e.g. the important differences between primary and secondary "space occupiers": Lafferty & Suchanek 2016), a range of recent analyses support the idea that keystone species removal can lead to dramatic trophic cascades globally. For example, the eradication of grey wolves (*Canis lupus*) from Yellowstone National Park, USA in the mid-1920s, and their associated density-mediated and trait-mediated effects (Laundré et al. 2010), led to an elk population boom (Ripple &

Beschta 2004). In turn, overgrazing by elk led to suppression of riparian browse species, facilitating soil erosion and reduced faunal diversity (Ripple and Beschta, 2011). Another classic example surrounds the removal of the Pacific sea otter (*Enhydra lutris*) by the fur trade in the 1800s, which boosted sea urchin abundance and in turn converted biodiverse, kelp-dominated systems into urchin-dominated algal lawns (Estes & Duggins 1995). While such examples feature keystone predator removal through human persecution, the role of climate change on keystone predatory impact remains relatively understudied (however, see Szathmary et al. 2009; Harley 2011; Bonaviri et al. 2017).

Here, we therefore assess the potential of sea freshening to drive changes in the predatory impact of a well-known keystone predator, the common sea star, *Asterias rubens* (Saier 2001). Ubiquitous across the northwest Atlantic, *A. rubens* is the only sea star species in the Baltic Sea, our study system, where it survives near the lower limit of salinity tolerated by echinoderms (for extensive reviews of the echinoderm-salinity literature see Stickle & Diehl 1987; Russell 2013). Indeed, no *A. rubens* have been found east of nearby Rügen, where salinities as low as 8ppt are experienced (Casties et al. 2015). With echinoderms possessing limited capacity to regulate biologically important ions in response to osmotic stress (Russell 2013), decreasing salinity could lead to a change in the predatory capacity of *A. rubens* and, due to its keystone nature, this could lead to profound trophic cascades. Scientists, policy makers and resource managers need user-friendly tools that clearly highlight and indicate the ecological consequences of global climate change, and here we apply the Relative Impact Potential metric (Dickey et al. 2020) which combines the functional response (FR: consumer *per capita* effect: Holling 1959), with proxies for the numerical response (NR: consumer population response), to provide quantification of how keystone predator impact changes with sea freshening conditions. Specifically, we hypothesise that decreasing salinity will reduce the *per capita* feeding rates of this keystone predator and, further, by combining this *per capita* impact with a measure of sea star population change with water freshening - that of larval recruitment - we hypothesise reductions in the predicted ecological impact of the species.

2. Material and methods

2.1. Experimental procedure

Asterias rubens were collected from the Baltic Sea, specifically Kiel Fjord (54.329577, 10.148900), between the 19th and 21st February 2018, using traps consisting of 50 × 50 × 20 cm PVC pipe structures, with an entrance on one side, covered with a 1 mm mesh and filled with crushed blue mussels (*Mytilus edulis*) as bait (Nour et al. 2020). Collected sea stars were held at 16ppt salinity (i.e. Kiel Fjord level at the time of collection), followed by an acclimation period of at least three days in a laboratory at 12 °C ± 1 °C with a 12:12 light:dark regime. The collected animals were kept in a 10L plastic aquarium with constantly aerated water. Sea stars were fed *ad libitum* with blue mussels and water was changed daily. The *A. rubens* were size matched (mean arm length ± SE: 33.89 ± 0.55 mm; mean arm width ± SE: 12.75 ± 0.39 mm) and randomly separated into three salinity groups (18ppt, 15ppt 12ppt), with five individuals per group, and each group moved to 5L aquaria, again with constantly aerated water. The experimental salinities of 18ppt and 15ppt were chosen as realistic current scenarios in Kiel Fjord, while the lowest salinity treatment was based on predictions of a ~ 2ppt decrease of salinity to <13ppt by the end of the century (Gräwe et al. 2013). Note that the lowest experimental condition of 12ppt does currently occur in Kiel Fjord for short periods of time – the current salinity range in Kiel Fjord is between 10.5 and 24.7ppt (Thomsen et al. 2018) - but will be more common in the future, and thus the study predators and prey were not being subjected to unrealistic conditions (Wernberg et al. 2012). The water used for experiments was 5-µm

filtered Kiel Fjord water, with salinity adjusted by adding artificial seawater (System Instant Ocean®) or dechlorinated potable tap water, and mixed to obtain allotted salinities. Despite evidence suggesting that the rate of transfer of echinoderms to reduced salinity has little effect on their tolerance (Stickle & Diehl 1987), salinity was changed at a rate of 1ppt from 16ppt per day until the desired level was reached, with water of the same salinity added to the groups that had already reached their experimental salinity to standardise physical disturbance across all three groups and ensure trials commenced on the same day. Once each sea star group reached their allocated salinity, they were held for at least three days, and then starved for 48 h in advance of functional response trials commencing.

Trials were undertaken in three batches, with *A. rubens* individuals re-used three times to avoid over-harvesting of limited numbers of sea stars available (see also Alexander et al. 2015 for similar method of re-use). There was no rotation in and out of acclimation, and sea stars were maintained under the same experimental treatments until the third batch was completed. For each experimental trial, individual *A. rubens* were presented separately with five densities of blue mussel prey under each salinity treatment (1, 2, 4, 8 or 15; size: 8–14 mm; also held in experimental salinities prior to trials), with no individuals given the same prey density more than once. As well as their ecological significance, blue mussels were used due to their known robustness to the experimental salinities, with a minimal tolerance in the Baltic of ~ 3ppt (Riisgård et al. 2013). During experimental trials, individual sea stars were held in separate 2L aquaria with 800ml of water and continuous aeration and allowed to feed for 48 h under the corresponding salinity level. Sea stars were starved immediately post-trial for two days before the next batch under treatment salinities. Control trials were run for each salinity group and each prey density (n = 3), whereby mussels were held under experimental conditions in the absence of *A. rubens* to assess prey deaths occurring for any reason other than predation.

2.2. Data analyses

Functional responses were modelled using the R package 'frair' (Pritchard et al. 2017). The type of curve was derived from the proportion of prey consumed as a function of prey density via logistic regression. A Type II curve is categorised by a significantly negative first-order term, whereas a significantly positive first-order term and significantly negative second-order term indicates a Type III functional response (Juliano 2001). Functional responses were modelled using maximum likelihood estimation (MLE; Bolker et al. 2009) and the random predator equation (Rogers 1972), due to the prey not being replaced as they were consumed:

$$N_e = N_0(1 - \exp(a(N_e h - T)))$$ (1)

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack rate, h is the handling time and T is the total time available (i.e. 48 h). The model was fit to the data using the Lambert W function (Bolker 2008).

To assess the population-level impacts of *A. rubens* under decreasing salinity levels, we calculated the "Impact Potential" (Dick et al. 2017; Dickey et al. 2020) of the predator at each experimental salinity. This measure of ecological impact combines the functional response maximum feeding rate (1/h; Eq. (1)) and a proxy for the consumer numerical response (i.e. the population response of the consumer to prey supply: Dick et al. 2017). Here, we used larval recruitment as our numerical response proxy, taken from Casties et al. (2015), which also used a Kiel Fjord population of *A. rubens*. That study followed sea star larval development across the same experimental salinities used here, taking counts every 3–4 days. The results of the final count before settlement in that study were used as our measure of recruitment, outlined in Table 1. Impact Potential (IP) for each experimental salinity was therefore

Table 1

First-order terms calculated from logistic regression to denote functional response type across all predator treatments. The significantly negative first-order term values across both 18ppt and 15ppt indicate Type II functional responses for *A. rubens*. Attack rate (*a*), handling time (*h*) and maximum feeding rate (1/*h*) parameter estimates were derived using Rogers' random predator equation (Eq. (1)). Recruitment data are derived from Casties et al. (2015), with the final larval count before settlement used. *** p < 0.001, ** p < 0.01.

Salinity	First-order term, *P*	Attack rate, *a*	Handling time, *h*	Maximum feeding rate, 1/*h*	Recruitment (larvae per 10 ml)	Impact Potential
18ppt	−0.242***	3.250**	0.122***	8.197	2.667	21.861
15ppt	−0.131**	1.462**	0.153**	6.536	1.000	6.536
12ppt	–	N/A	N/A	0	0	0

calculated as the product of functional response maximum feeding rate and larval recruitment:

$$IP = maximum\ feeding\ rate \times recruitment \tag{2}$$

Biplots were used to compare the effects of the experimental salinities on the overall ecological impact of *A. rubens,* with impact increasing from bottom-left to top-right (Fig. 2).

3. Results

No sea stars died during the experiment and prey survival in controls was 100%, allowing mortality in experimental treatments to be attributed to *A. rubens* predation, which was also commonly observed. Type II functional responses were derived for the 18ppt and 15ppt salinity treatments, whereas no consumption by sea stars occurred at any prey density in the 12ppt treatments (Table 1; Fig. 1). This lack of consumption negated formal consideration of this group in functional response modelling. Under 18ppt conditions, attack rates were greatest, with handling times (*h*) found to be lowest and, hence, maximum feeding rates (1/*h*) highest (Table 1; Fig. 1). Attack rates decreased and handling times increased (i.e. feeding rates decreased) with decreasing experimental salinity (Table 1; Fig. 1). These FR parameter trends mirrored the larval recruitment data, with a mean of 2.67 larvae per 10 ml surviving to settlement under 18ppt conditions, a mean of 1.00 larva per 10 ml surviving under 15ppt conditions, and zero surviving at 12ppt (Table 1). Combining these data, as per the Relative Impact Potential
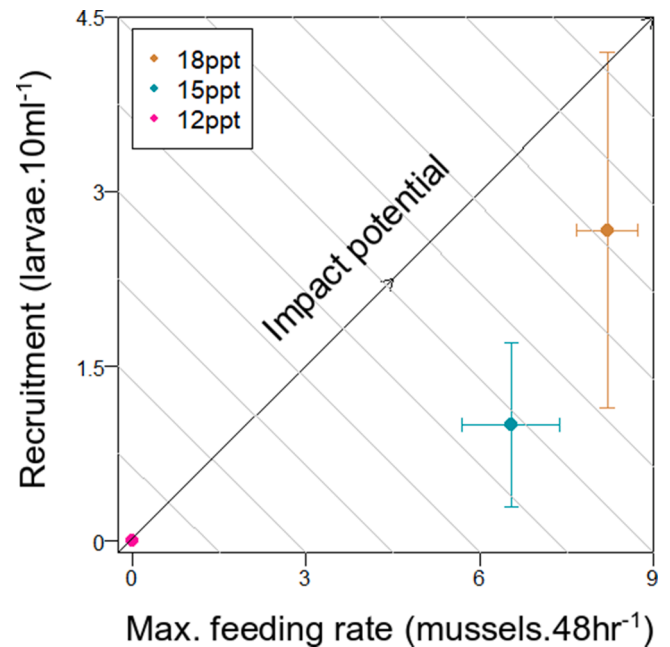

Fig. 2. Biplots displaying Relative Impact Potential based on maximum feeding rate (±standard errors) and larval recruitment (±standard errors) of *A. rubens* at three salinities: 18ppt, 15ppt and 12ppt.

biplot method (Dick et al. 2017; Dickey et al. 2020), indicates that *A. rubens* exerts the greatest predatory ecological impact at 18ppt salinity, with this decreasing to zero with decreasing salinity (Table 1; Fig. 2).

4. Discussion

Predicting the ecosystem effects of climate change is one of the greatest challenges facing ecologists, and there is a need to develop effective tools that help draw attention to the myriad consequences of climate change on ecosystems worldwide. Here, we highlight how the Relative Impact Potential metric (Dick et al. 2017; Dickey et al. 2020) can indicate the consequences of climate change-induced sea freshening on a keystone predator. While understudied, sea freshening is likely to have a wide range of impacts at species, community and ecosystem levels, across regions and time scales (Bindoff et al. 2019). Echinoderm keystone predators play vital ecosystem roles worldwide (Paine 1969; Power et al. 1996; Bonaviri et al. 2017; Hermosillo-Núñez 2020), and here, we thus quantified the effect of sea freshening on the ecological impact exerted by *A. rubens*, a keystone species living close to the lower salinity limit of any echinoderm globally (Russell 2013), in a representative area expected to see reduced average salinities by the end of the century.

Here, across three ecologically relevant salinities (18ppt, 15ppt, 12ppt), we demonstrate that decreasing salinity significantly reduces *per capita* adult sea star feeding rates on blue mussels i.e. their predatory
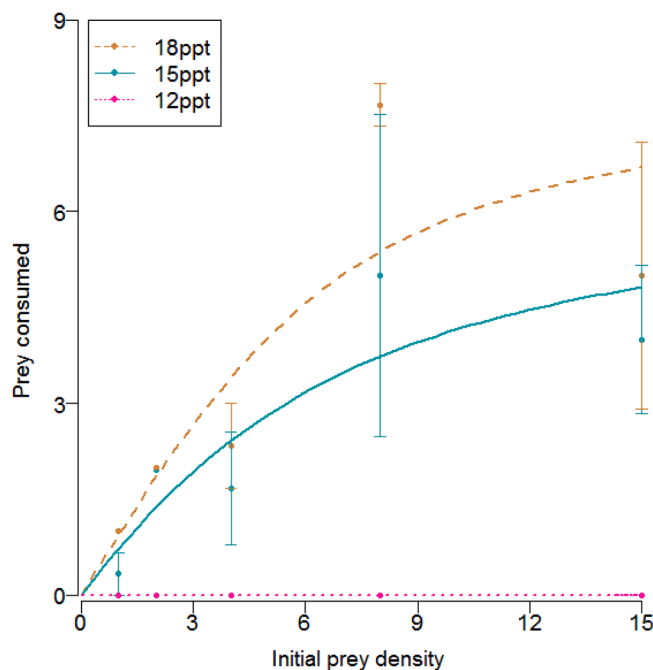

Fig. 1. Functional response curves for *A. rubens* towards *M. edulis* prey at three salinities: 18ppt, 15ppt and 12ppt. Data points are mean mussels consumed over 48 h ± standard errors.

functional reponses. There was a decrease in attack rate, and longer handling times (and hence lower feeding rates) at 15ppt relative to 18ppt, despite both being familiar salinities for *A. rubens* in the Baltic (Sarantchova 2001). At the future scenario of 12ppt, no predation occurred. Further, with Casties et al. (2015) showing that there was no larval recruitment of sea stars at the lowest salinity, the possibility of drastic reduction in overall ecological impact, i.e. Impact Potential, of this keystone species could drive wide ranging community alterations.

Our results corroborate the observation of Stickle & Diehl (1987) that, amongst echinoderms, there is strong correlation between the distribution of adults along salinity gradients and premetamorphic tolerance. The mechanisms behind these salinity effects likely centre around the inability of our study species to osmoregulate extracellularly, which causes body-fluid volume to decrease in lower salinities due to the high permeability of the outer body surface (Stickle & Diehl 1987). This has energetic costs, and decreased feeding is reported for numerous species as a response to hyposaline stress, however, whether this is due to suppressed appetite or due to insufficient activity levels required to feed upon *M. edulis* is uncertain (Held & Harley 2009). Casties et al. (2015) attributed the lack of larval development at low salinities to a lack of energy reserves for intracellular homeostasis or the ion regulatory epithelia not having fully developed, leading to intracellular homeostasis failure. While the authors of that study proposed that impacts of *A. rubens* larvae failing to develop under less saline conditions could be compensated by allochthonous supply of later-stage larvae, our results indicate that even for the larvae that can settle and reach adulthood, feeding could be severely reduced. While there are suggestions that with sufficient periods of acclimation some echinoderm species can adapt to changing salinities (Held & Harley 2009), acclimation of echinoderm adults has been shown to have little effect on embryo development or survival (Roller & Stickle 1993), and the population of *A. rubens* studied may exist close to its physiological limits (Stickle & Diehl 1987). Indeed, with great salinity-dependent interannual variation in *A. rubens* recruitment already, a lack of feeding backs up the possibility of local extinction and a westward shift in their Baltic distribution (Casties et al. 2015).

These effects of decreasing salinity on predation and larval recruitment could have significant impacts at an ecosystem level, with *A. rubens* consuming up to 77% of the annual *M. edulis* recruitment in Kiel Fjord (Nauen 1978), with a diet also including numerous other species (e.g. mudsnail, *Hydrobia ulvae*; Baltic clam, *Macoma baltica*; trumpet worm, *Pectinaria koreni*) and detritus (Anger et al. 1977). Moderation of *M. edulis* recruitment by *A. rubens* has been shown to facilitate biodiversity, with otherwise reduced and/or excluded species able to establish (Enderlein & Wahl 2004). Accordingly, major shifts in the trophic structure of ecosystems could happen under sea freshening scenarios (Mills et al. 1993). For example, a shift towards a decapod crustacean-dominated system could occur, with non-native species such as the Asian brush clawed crab (*Hemigrapsus takanoi*), the Harris mud crab (*Rhithropanopeus harrisii*) and the Chinese mitten crab (*Eriocheir sinensis*) already established elsewhere in the Baltic (Ojaveer et al. 2007; Hegele-Drywa & Normant 2014; Morón Lugo et al. 2020) and highly tolerant of a range of salinities in their adult forms (Normant & Gibowicz 2008; Shinji et al. 2009; Leignel et al. 2014; Long et al. 2017). Future studies with greater sample sizes should aim to further assess at what point between 15ppt and 12ppt the salinity stress "tipping" point occurs for *A. rubens,* and how the feeding rates of decapod crustacean predators compare at such salinities. Similarly, how feeding rates of *A. rubens* and non-native crab species are affected not only by static experimental salinities, but realistic fluctuating salinities over greater experimental timescales warrants investigation. Further, we propose that the Relative Impact Potential metric offers, from a management perspective, a readily accessible, easily understood indicator that can be applied across a wealth of abiotic contexts ensuing from global climate change, and we thus encourage further use (e.g. see Dick et al. 2017; Dickey et al. 2020, and their supplementary materials for guides to implementation).

The majority of keystone predator case studies highlight that trophic cascades ensue when species have been removed through human persecution (Estes & Duggins 1995; Ripple & Beschta 2004). Indeed, *Homo sapiens* has been recognized as a "hyperkeystone" species, i.e. one that can trigger cascades by affecting other keystone species across different habitats (Worm & Paine 2016), and climate change is proving another way in which this can occur. How climate change may reduce (Bonaviri et al. 2017) or enhance the interactions between keystone predators and their ecosystems is still understudied, and the many abiotic consequences of climate change will likely impact direct, density-mediated, predator–prey interactions (South & Dick 2017; Figueira et al. 2019; Dickey et al. 2021), the strength of trait-mediated indirect effects (Lass & Spaak 2003), and predator and prey species recruitment, breeding periods, development times, growth rates, phenology and distributional limits (Harley 2011; Bellard et al. 2012). With keystone species present across marine, freshwater and terrestrial realms (Power et al. 1996), methods that indicate the myriad consequences of climate change on their ecological impacts, and the ensuing consequences for biodiversity and ecosystem services, require urgent consideration.

Author contributions

JWED, SLM, and IC conceived the study, with JWED and SLM conducting the experiments, with assistance from GTS. JWED and RNC conducted statistical analyses, with JWED, RNC, JTAD and EB preparing the initial manuscript. All authors provided valuable input to the development of the final manuscript, and have given approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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