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Predicting the future of our oceans – evaluating genomic forecasting approaches in marine species

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Abstract:	Climate change is restructuring biodiversity on multiple scales and there is a pressing need to understand the downstream ecological and genomic consequences of this change. Recent advancements in the field of eco-evolutionary genomics have sought to include evolutionary processes in

forecasting species’ responses to climate change (e.g. genomic offset), but to date, much of this work has focused on terrestrial species. Coastal and offshore species, and the fisheries they support, may be even more vulnerable to climate change than their terrestrial counterparts, warranting a critical appraisal of these approaches in marine systems. First, we synthesize knowledge about the genomic basis of adaptation in marine species, and then we discuss the few examples where genomic forecasting has been applied in marine systems. Next, we identify the key challenges in validating genomic offset estimates in marine species, and we advocate for the inclusion of historical sampling data and hindcasting in the validation phase. Lastly, we describe a workflow to guide marine managers in incorporating these predictions into the decision-making process.

Response to Reviewers

We thank both reviewers and the Subject Editor for their helpful comments and revisionary suggestions that have significantly improved this manuscript. We provide a response to each of the reviewer's comments below, but briefly, we have strengthened our arguments and opinion throughout the text, clarified some key processes and methodologies and expanded our discussion of how best to implement these approaches in a marine management setting. New text has been detailed below in bold italicized font.

Reviewer One:

C1_1: The manuscript succinctly evaluates genomic forecasting approaches in marine species, acknowledging the pressing need to comprehend the downstream ecological and genomic consequences of climate change. However, given that the manuscript is submitted as an Opinion piece, it would benefit from a clearer statement of the specific Opinion and objective to guide readers more effectively. In the following, I provide some feedback and suggestions to the different sections. The introduction adeptly establishes the context of climate change impacts on marine ecosystems. However, as mentioned above, it could be enhanced by explicitly stating what should be done in the authors opinion and maybe provide a more detailed roadmap of the manuscript's sections to reinforce the importance of evaluating genomic forecasting in the marine context.

R1_1: We agree with the reviewer that a clear statement of our central opinion was lacking here and we have since explicitly stated our main arguments and provided a roadmap on lines 119-127 (see below).

"In this opinion piece, we review the literature on the genomic basis of climate adaptation in marine species (section 3), evaluate current examples of genomic offset estimates in marine systems (section 4), assess the potential for validation of these estimates (section 5), and finally we discuss the utility of these estimates in informing fisheries policy (section 6). ***Here, we argue that the wealth of data available from long-term monitoring programs in exploited marine species provides an unprecedented opportunity for validating offset estimates in an otherwise logistically challenging environment. We also argue that implementing offset estimates in marine management will enable a more comprehensive assessment of the impacts of climate change on exploitation.***"

C1_2: In the following section the authors provide a comprehensive overview of potential drivers of adaptation in marine species, including temperature, salinity, and other environmental factors. The authors effectively integrate recent studies to support their arguments. However, consider providing more context or examples for certain terms, e.g., "large effect" and "small effect" chromosomal rearrangements to aid readers less familiar with these concepts. Similarly, Table 1 is quite helpful in summarizing current publications. But the clarity could be enhanced by ensuring that the terminology used in the table aligns precisely with that in the main text. Also, a brief explanation of the methodologies used (e.g., redundancy analysis, generalised dissimilarity modelling) could be included for readers unfamiliar with these techniques.

R1_2: We agree with the reviewer that some concrete examples and more detailed explanation of methodologies is necessary here to improve readability- thank you for this suggestion. To address this, we have added text to lines 136-149 that reads:

“For some species with high connectivity and gene flow, like Atlantic cod (*Gadus morhua*), herring (*Clupea harengus*), horse mackerel (*Trachurus trachurus*), and northern sand lance *(Ammodytes dubius*), a few “large effect” chromosomal rearrangements seem to explain most of the climate-associated genomic variation (e.g., Barth et al. 2017; Kess et al. 2020; Fuentes-Pardo et al. 2023a). ***For example, a large 10Mb inversion on chromosome 21 discriminates northern and southern populations of horse mackerel in Europe (Fuentes-Pardo et al. 2023a).*** In other cases, a signature of local adaptation is restricted to many regions of “small effect” in the genome, requiring dense genomic data for detection, as seen in Arctic charr (*S. alpinus*), Atlantic silversides (*Menidia menidia*) and the Baltic copepod (*Eurytemora affinis*) (Wilder et al. 2020; Kess et al. 2021; Stern et al. 2022). ***Here, adaptive SNPs are dispersed across most of the genome, rather than being concentrated in one particular region, constituting a signature of polygenic adaptation.”***

We have also added text to lines 221-231 that reads:

To derive the offset estimate, allele frequencies of putatively adaptive, climate-associated loci are the response variables to environmental predictor data to model climate-associated genomic variation using any number of modelling approaches. ***The most common modelling approaches include generalized dissimilarity modelling (GDM) and gradient forest (GF)—both of which accommodate for nonlinear associations of genomic and environmental data. The former uses distance matrices to model climate-associated genomic variation while the latter employs a regression-tree approach that is especially suitable in the context of steep environmental gradients (Fitzpatrick & Keller 2015). The*** model is then used alongside environmental data from both current and future time periods and across the species’ range to predict current and future adaptive indices, respectively.

We also wanted to point out that we now define common garden experiments on lines 302-304 in response to a comment from reviewer two. “The only examples of experimental validation to date are from terrestrial species, where genomic offset estimates were compared to population performance measured in common garden settings—***where distinct populations are grown under the same environmental conditions to identify differences in fitness (***e.g. Fitzpatrick et al. 2021; Gain et al. 2023).”

C1_3: The authors further highlight the importance of validating genomic offset estimates, which is highly important, but often neglected. To strengthen this section, consider providing more details on the potential biases or limitations associated with validation methods. Additionally, discussing the implications of such biases on the reliability of genomic offset estimates would add depth to the analysis.

R1_3: We agree that while we’ve highlighted the unique opportunity for validation in marine systems, we haven’t fully addressed the shortcomings of these possible validation methods. For instance, one of the biggest challenges to common garden-based validation in marine systems is the long generation times of many exploited species (and species of conservation concern). To address this concern, we’ve added the following text in section 5:

Lines 315-324: “Although very informative and likely the gold standard, the potential for experimental validation of offset estimates through either reciprocal transplant or common garden experiments in marine species are limited by comparison with terrestrial plants or animals. This is largely due to the added complexity of these experiments in the marine environment, but some exceptions exist. For instance, Jacobs et al. (2022) reared fertilized eggs of Atlantic silversides (*Menidia menidia*) in temperature-controlled water baths and compared growth rates amongst treatments. ***However, long generation times in many exploited marine species (e.g. 20 years in deepwater redfish, Sebastes mentella, COSEWIC 2010) means that the short timescales with which common garden experiments are typically performed will provide only a snapshot of response."***

Lines 336-339: ***"These approaches to validation, although powerful, are biased toward exploited species whose stocks are already depleted from fishing and thereby teasing apart the relative impacts of climate change and exploitation will be critical in these cases."***

C1_4: The last section effectively outlines the steps required to integrate genomic offset estimates into marine management. Maybe a more explicit discussion of potential challenges or limitations that marine managers may encounter in implementing these predictions would enhance the practicality of the proposed workflow? Finally, the conclusion summarizes the main findings and emphasizes the potential of genomic offset in marine species. To enhance this section, consider reiterating the identified gaps or uncertainties in the field and suggesting potential directions for future research.

R1_4: We agree with the reviewer that a more detailed discussion of challenges and limitations is needed here in order for these methods to be implemented in a management setting. To address this, we have added the following text to section 6:

Lines 344-348: ***"Validating offset estimates in the marine environment will continue to be an important avenue for future work, but the integration of these estimates in marine management is even more vital. This is because existing management approaches typically rely on SDMs, which although informative, are best used to compliment methods that explicitly consider adaptation."***

Lines 366-373: ***"Although straightforward in theory, this proposed workflow can be challenging to implement in practice given constraints on budget and time. For instance, generating dense genomic datasets for many individuals and populations can be expensive and thus targeting a smaller subset of climate-associated loci might be a feasible alternative. Additionally, sampling from all known populations across a species range can be logistically challenging and thus selecting a subset of populations that best represent variation (both genomic and environmental) in the system could be an alternative approach."***

We have also significantly revised the second paragraph of the Conclusions section to emphasize directions for future work, and we conclude with a much stronger statement. Lines 399-409 now read:

"Here, we argue that future work should focus on leveraging the wealth of long-term population data available for many economically and ecologically vital marine species to validate offset estimates when more traditional approaches are logistically challenging. A particularly exciting avenue for future work is the potential for generating models of past climate-associated variation with historical samples. Beyond validation, there is even greater uncertainty on how to apply offset estimates in real-world fisheries management and marine conservation scenarios. ***To this end, we provide a 'standard operating procedure' for marine managers, outlining how to generate offset estimates and modify workflows in the face of budgetary and time constraints. Genomic offset has the potential to transform***

marine management and is highly complementary to other genetic and non-genetic approaches to conserving vital marine resources."

C1_5: As a general comment, I suggest being a bit more consistent in terminology throughout the manuscript, particularly regarding the use of terms such as "genomic offset" and "genomic vulnerability." Also, it would be helpful for the reader to incorporate more explicit connections between sections to improve the overall flow and coherence of the manuscript. In summary, the manuscript provides a valuable exploration of genomic forecasting in marine species. Addressing the suggested refinements will contribute to the clarity and impact of the manuscript, making it a more accessible and influential contribution to the field.

R1_5: We agree with the reviewer that consistency in terminology is key to readability here. The term 'genomic vulnerability' now only appears once in section 2 where we mention that Bay et al. (2018) used this term before 'genomic offset' became ubiquitous. Throughout the rest of the manuscript, we use 'genomic offset' to avoid confusion. We still use the term 'vulnerability' at points in the manuscript, but this does not refer to the genomic offset approach but rather species' response or vulnerability to climate change more generally.

Reviewer Two:

In the manuscript ' Predicting the future of our oceans – evaluating genomic forecasting approaches in marine species' Layton et al. present an overview of the emerging field of genomic forecasting and highlight several studies from marine systems that have employed genomic forecasting approaches such as the calculation of genomic offset. They then discuss several challenges pertaining to the validation of such approaches and present a clear and feasible roadmap for researchers to validate such approaches going forward, particularly utilising experimental evidence and linking to historical population or distribution data and hindcasting models. This is a very timely paper and was clear and easy to read. I thoroughly enjoyed it. many of the points that the authors make are not well known amongst the marine science community and I believe it will be particularly useful in this context.

I have only a few minor comments:

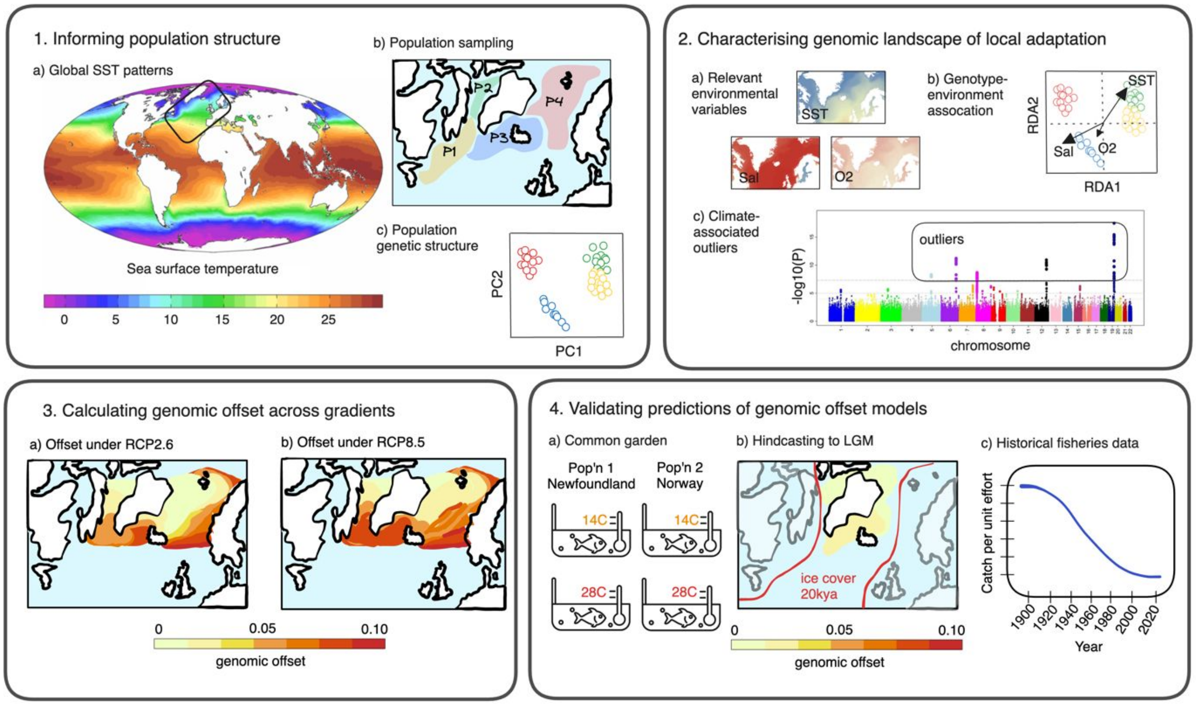
C2_1: L127: Vranken et al only show genomic evidence for putative adaptation (which is later acknowledged in Table 1). I suggest the authors re-word the section that says this is 'clear evidence for adaptation' - this also goes against their main point that GEA analyses are correlative only and require validation.

R2_1: We agree with the reviewer that 'clear evidence' should be revised. The text on 134-135 now reads:

"…recent studies employing genome-wide data have ***provided strong evidence*** for climate-associated adaptation in several marine taxa (e.g. Drinan et al. 2018; Vranken et al. 2021)."

C2_2: Figure 1. The font is slightly hard to read and seems quite informal here. I like the infographic style but suggest changing to a more standard font style. I also suggest changing the location 'Labrador' to somewhere recognisable globally for readers not familiar with the location. I also suggest the authors either define what a common garden experiment is for readers, as it seems as though the target audience are not necessarily going to be familiar with these and insert relevant examples or references either in the Figure legend or main text.

R2_2: We thank the reviewer for these helpful revisionary suggestions. We have since changed the font to improve readability and we have changed the location to Newfoundland, which we believe is a more globally recognizable location. See revised figure here:



We have also addressed the comment about common garden experiments and have added new text to lines 300-307 that reads:

"The only examples of experimental validation to date are from terrestrial species, where genomic offset estimates were compared to population performance measured in common garden settings—***where distinct populations are grown under the same environmental conditions to identify differences in fitness (e.g. Fitzpatrick et al. 2021; Gain et al. 2023***). For instance, Fitzpatrick et al. (2021) reported a negative relationship between genomic offset and common garden performance consistent with significant power of offset estimates to predict population response to climate change, exceeding that of climate differences alone."

Predicting the future of our oceans – evaluating genomic forecasting approaches in marine species

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1. Abstract

Climate change is restructuring biodiversity on multiple scales and there is a pressing need to understand the downstream ecological and genomic consequences of this change. Recent advancements in the field of eco-evolutionary genomics have sought to include evolutionary processes in forecasting species' responses to climate change (e.g. genomic offset), but to date, much of this work has focused on terrestrial species. Coastal and offshore species, and the fisheries they support, may be even more vulnerable to climate change than their terrestrial counterparts, warranting a critical appraisal of these approaches in marine systems. First, we synthesize knowledge about the genomic basis of adaptation in marine species, and then we discuss the few examples where genomic forecasting has been applied in marine systems. Next, we identify the key challenges in validating genomic offset estimates in marine species, and we advocate for the inclusion of historical sampling data and hindcasting in the validation phase. Lastly, we describe a workflow to guide marine managers in incorporating these predictions into the decision-making process.

2. Introduction

Climate change results in severe environmental change, with recent years being the warmest on record throughout the industrial period (Cheng et al. 2023). The global increase in average temperature is accompanied by a suite of environmental changes including increases in the frequency and intensity of extreme weather events, regional temperatures, atmospheric water vapour, and ocean heat, as well as decreases in pH, dissolved oxygen, and land and sea ice cover. For marine ecosystems, increased glacial runoff and rising sea temperatures pose significant challenges (He & Sillman 2019). The consequences of these impacts are evidenced by distributional shifts in many taxa (e.g., Poloczanska et al. 2013), with populations at the trailing edge declining and populations at the leading edge shifting poleward or into deeper waters (Polyakov et al. 2020; Pinsky et al. 2020). In fact, marine species and the fisheries they sustain appear to be more vulnerable to climate change than their terrestrial counterparts (Pinsky 2021). Given the global reliance on marine resources, these changes will undoubtedly impact food security and economic stability (Payne et al. 2021). Consequently, there is a need to 'future-proof' marine ecosystems and conservation areas through proactive management based on a sound understanding of the ecological and genetic impacts of climate change (Tittensor et al. 2019).

There is a pressing necessity to predict climate change impacts in marine species and ecosystems to inform conservation planning and strategies. These predictions are particularly relevant to global fisheries and aquaculture, which provide a major source of nutrition to developed and developing countries (Bene et al. 2016). For instance, ocean warming has been linked to significant decreases in production capacity and shifts in the distribution of fisheries-targeted species (e.g., tuna, Monllor-Hurtado et al. 2017). Predicting range shifts in marine taxa remains a significant challenge and ultimately requires information on existing ranges, predictions of future environments, capacity for adaptive and plastic responses to environmental change, dispersal potential, and ecosystem structure and function. Marine species' ranges largely conform to their thermal limits (Sunday et al. 2012) and therefore even small changes in the thermal profile of a given marine region can have measurable consequences on population survival and subsequent extirpation.

A growing body of research has focused on developing tools to predict the impacts of climate change on wild populations. Ecological niche modelling - akin to species distribution modelling (SDM) - has been used in the last 20 years to map the probability of occurrence of a species across a landscape (Kearney & Porter 2009). However, traditional SDMs do not consider adaptive responses of populations to environmental change, for instance through multigenerational selection of advantageous genomic variants (e.g., standing genetic variation), or through the expression of epigenetic variants leading to acclimation via phenotypic plasticity. More recently, genomic offset - also termed genomic vulnerability (Bay et al. 2018) - has been applied to both terrestrial and marine taxa to predict potential future maladaptation driven by climate change (e.g., Fitzpatrick & Keller 2015; Laruson et al. 2022; Layton and Bradbury 2021). This approach maps the contemporary spatial turnover of adaptive alleles onto current environmental conditions and then calculates the offset between present and future climate-associated genomic composition as a measure of maladaptation to climate change. In other words, genomic offset is an estimate of the change in genomic composition that would be required to track predicted climate change. Despite some limitations and challenges, including validation and management buy-in (Rellstab et al. 2021), the approach seems to accurately estimate climate change vulnerability when compared to experimental predictions (e.g., Fitzpatrick et al. 2021). Bernatchez et al. (2023) provide a comprehensive overview of this method, among others, in their recent review of genomics-based monitoring approaches, but to date, no study has assessed these methods in specific ecological contexts. Given the potential of genomic offset estimates to inform climate change predictions, and the observation that marine species are already being impacted by climate change, an evaluation of the method’s applicability to marine species is warranted.

There are several reasons why estimating genomic offset can be useful for managing and conserving marine ecosystems and species. The poikilothermic nature of most marine fish, invertebrates, and macrophytes means that temperature is often a dominant selective pressure driving adaptive genetic diversity across populations. The low genetic structure and generally large effective population sizes (Ne) often observed within marine species (Bradbury et al. 2008) means that the influence of genetic drift is typically minimal compared with that of natural selection. Moreover, many marine species occupy large latitudinal ranges and genomic approaches have repeatedly demonstrated putative adaptation across these variable environments. Taken together, our ability to resolve the genomic basis of climate-associated adaptation may be elevated in the marine environment compared with terrestrial, which can translate into improved power to predict population-level responses or vulnerability in these systems.

In this opinion piece, we review the literature on the genomic basis of climate adaptation in marine species (section 3), evaluate current examples of genomic offset estimates in marine systems (section 4), assess the potential for validation of these estimates (section 5), and finally we discuss the utility of these estimates in informing fisheries policy (section 6). Here, we argue that the wealth of data available from long-term monitoring programs in exploited marine species provides an unprecedented opportunity for validating offset estimates in an otherwise logistically challenging environment. We also argue that implementing offset estimates in marine management will enable a more comprehensive assessment of the impacts of climate change on exploitation.

3. Genomic basis of adaptation in marine species

Accurate prediction of potential maladaptation requires an understanding of how species are adapted to their environments. The number of potential drivers of adaptation in the marine environment is broad and includes numerous environmental variables such as temperature, salinity, dissolved oxygen, pH, and depth. Although theory would predict that extensive gene flow facilitated by long pelagic larval durations in marine species would erode and prevent local adaptation, recent studies employing genome-wide data have provided strong evidence for climate-associated adaptation in several marine taxa (e.g. Drinan et al. 2018; Vranken et al. 2021). For some species with high connectivity and gene flow, like Atlantic cod (*Gadus morhua*), herring (*Clupea harengus*), horse mackerel (*Trachurus trachurus*), and northern sand lance (*Ammodytes dubius*), a few “large effect” chromosomal rearrangements seem to explain most of the climate-associated genomic variation (e.g., Barth et al. 2017; Kess et al. 2020; Fuentes-Pardo et al. 2023a). For example, a large 10Mb inversion on chromosome 21 discriminates northern and southern populations of horse mackerel in Europe (Fuentes-Pardo et al. 2023a). In other cases, a signature of local adaptation is restricted to many regions of “small effect” in the genome, requiring dense genomic data for detection, as seen in Arctic charr (*S. alpinus*), Atlantic silversides (*Menidia menidia*) and the Baltic copepod (*Eurytemora affinis*) (Wilder et al. 2020; Kess et al. 2021; Stern et al. 2022). Here, adaptive SNPs are dispersed across most of the genome, rather than being concentrated in one particular region, constituting a signature of polygenic adaptation. The genomic underpinnings of local adaptation can vary not only across species but also across environmental gradients, and this is especially complex in marine systems where species are distributed across both geographic and bathymetric clines.

Genomic signatures of thermal adaptation have repeatedly been reported and appear to be more prevalent in marine systems than in terrestrial or freshwater systems (Sasaki et al. 2022). For example, temperature-driven structure has been observed in sea scallop (*Placopecten magellanicus*) (Van Wyngaarden et al. 2017), northern shrimp (*Pandalus borealis*) (Stanley et al. 2018), capelin (*Mallotus villosus*) (Cayuela et al 2021), and Atlantic herring (*Clupea harengus*) (Fuentes-Pardo et al 2023b). Extreme thermal events can also result in a reshuffling of genetic clusters leading to local adaptation. For example, Coleman et al. (2020) demonstrated that an extreme marine heatwave caused a significant poleward shift in populations of kelp forests along the coast of western Australia, whereby ‘cool water’ alleles were replaced by ‘warm water’ alleles, resulting in a genetic tropicalisation of the populations. While within a species the same adaptive alleles can be selected multiple times in distinct geographic areas, resulting in parallel evolution of thermal adaptation (Bradbury et al. 2010), the universality of the molecular processes involved in thermal adaptation is largely unknown in marine systems, partly due to the lack of genomic resources and functional validation of the markers under selection in published studies.

Climate change projections not only indicate a rapid increase in ocean temperature in the next century but also lower salinity in relation to glacier melting and higher precipitation in some regions, like the northern hemisphere (Luo et al. 2016). Additionally, many marine species use a variety of habitats throughout their life cycle, some spanning freshwater and estuarine environments and thereby experiencing steep salinity clines. A significant body of work supports salinity adaptation in marine organisms (Johannesson et al. 2020), particularly in the Baltic Sea. For instance, whole genome sequencing revealed hundreds of regions across the genome of Atlantic herring (*C. harengus*) that showed significant differentiation between Baltic and Atlantic populations (Han et al. 2020). Equivalent comparisons of Baltic and Atlantic populations have yielded similar results in other species such as Atlantic cod (*G. morhua*) (Berg et al. 2015), sand goby (*Pomatoschistus minutus*) (Leder et al. 2021), and European plaice (*Pleuronectes platessa*) (Le Moan et al. 2021), indicating adaptation to low salinity levels. Within the Baltic, different species of mussels have also shown salinity-related adaptation between western and eastern regions (Knöbel et al. 2021). Recently, Stern et al. (2022) showed experimental and genomic evidence of Baltic copepod (*E. affinis)* rapidly adapting to decreasing salinity. Similar to thermal adaptation, species can adapt to salinity changes through either parallel or convergent evolution (Le Moan et al. 2021), involving either few genetic variants of large effect or many loci of small effect (e.g., Berg et al. 2015; Le Moan, et al. 2021).

Additionally, it is increasingly clear that the basis of local adaptation in marine taxa extends beyond SNPs to large-scale chromosomal rearrangements, copy number variants (CNVs), and epigenetic variation. For instance, environmental adaptation in American lobster (*Homarus americanus*) was driven almost entirely by CNVs with little to no signal in SNP data (Dorant et al. 2020). In contrast, Layton et al. (2021) reported similar spatial trends in genomic offset calculated from CNV and SNP datasets in Arctic Charr populations from eastern Canada. In three-spined stickleback, differentially methylated regions (DMRs) were more significantly associated with environmental variation (salinity) than outlier SNPs (Ruiz-Arenas et al. 2017). Given these findings, Layton and Bradbury (2022) suggest a revised offset approach incorporating normalized read counts and methylation scores alongside allele frequencies which might better reflect overall (genetic + epigenetic) adaptive processes, thereby improving prediction accuracy. Despite a complex landscape of adaptive genomic variation in marine species, only a few studies have leveraged this information for estimating genomic offset in the marine environment.

4. Prediction of climate change impacts using genomic tools in marine taxa

As discussed above, local adaptation to ocean climate is widespread (at least at regional scales) across marine species in various taxonomic groups and ecological contexts. However, climate change is expected to disrupt local adaptation in the coming years, resulting in potential maladaptation as the speed of change outpaces natural selection in many species and populations (Razgour et al. 2019). The ability to resolve the genomic basis of adaptation, in conjunction with fine-scale climate projections, presents an opportunity to leverage these datasets to forecast future climate-associated genomic composition and maladaptation. Genomic offset, defined as the difference between current genomic composition and the predicted future composition required to maintain adaptation, was first introduced by Fitzpatrick and Keller (2015) and later by Bay et al. (2018) and has been used to identify populations most vulnerable to future climate change. Additionally, the genomic offset approach can be employed across historical timescales, for instance by calculating the difference between current genomic composition and past genomic composition hindcasted at the last glacial maximum.

In the past few years, this method has been increasingly employed across various terrestrial systems (e.g., Capblancq et al. 2020), with more recent work focussing on *in situ* validation of these offset estimates (Fitzpatrick et al. 2021). To derive the offset estimate, allele frequencies of putatively adaptive, climate-associated loci are the response variables to environmental predictor data to model climate-associated genomic variation using any number of modelling approaches. The most common modelling approaches include generalized dissimilarity modelling (GDM) and gradient forest (GF)—both of which accommodate for nonlinear associations of genomic and environmental data. The former uses distance matrices to model climate-associated genomic variation while the latter employs a regression-tree approach that is especially suitable in the context of steep environmental gradients (Fitzpatrick & Keller 2015). The model is then used alongside environmental data from both current and future time periods and across the species' range to predict current and future adaptive indices, respectively. The difference between these values represents offset, with larger values indicating that a population is more likely to be maladapted to future climate. This method has typically been used in species with strong population structure distributed across well-defined environmental gradients, but its utility and downstream interpretation in marine species has been understudied. However, recent work has begun to address this gap, demonstrating its potential utility in eleven species of fish, invertebrates and marine plants (Table 1).

Table 1: List of current publications employing genomic offset estimates in marine species. The statistical method used to generate offset estimates, and the environmental predictors used, is also listed (RDA=redundancy analysis; GDM= generalised dissimilarity modelling; GF=gradient forest).

Organism	**Region**	**Method**	**Included Climate Variables**	**Validated**	**Reference**

Macrophytes					
Eelgrass (*Zostera marina*)	Coastal North America	RDA	Seasonal, annual bottom & surface temperature, salinity	No	Jeffery et al. (2024)
Seaweed (*Phyllospora comosa*)	Southeastern Australia	GDM	Sea surface temperature	No	Wood et al. (2021)
Kelp (*Ecklonia radiata)*	Western Australia	GF	Dissolved oxygen, sea surface salinity, sea surface nitrate, seawater velocity, attenuation	No	Vranken et al. (2021)
Vertebrates					
Arctic Charr (*Salvelinus alpinus*)	Newfoundland/Labrador	GF	Precipitation, air temperature	No	Layton et al. (2021)
Sockeye salmon (*Oncorhynchus nerka*)	British Columbia & Yukon	GF	Precipitation, air temperature	No	Tigano et al. (2024)
Invertebrates					
Multi-species: Urchin (*Parechinus angulosus*), crab (*Cyclograpsus punctatus*) & limpet (*Scutellastra granularis*)	South Africa	GF	Sea surface temperature, sea surface salinity & air temperature	No	Nielsen et al. (2021)
Coral (*Acropora digitifera*)	Western Australia	GF & GDM	Sea surface temperature	No	Adam et al. (2022)
Tubeworms (*Galeolaria caespitosa* & *G.gemineoa*)	Southeast Australia	GF	Sea surface temperature	No	Gallegos et al. (2023)

Most of these studies have focused on generating offset estimates in single species across a variety of spatial scales, with variable patterns across taxonomic groups and geographic areas. For instance, in eastern Canada, offset estimates were highest in southern populations of Arctic charr (*S. alpinus*) (Layton et al. 2021), indicative of a scenario of contraction of the southern range limit of this Arctic species. Alternatively, genomic offset values were higher in northern (subarctic) populations of a widely distributed seagrass species (*Z. marina*) across a similar area (Jeffery et al. 2024). Estimates of future offset in *Acropora digitifera* in western Australia are more spatially complex, but populations living at the upper thermal limits (i.e. at lower latitudes) were predicted to require less of an adaptive shift than mid-latitude reefs (Adam et al. 2022). Similarly, Wood et al. (2021) shows a spatially complex pattern of future offsets in a forest-forming seaweed (*P. comosa)* in Australia, demonstrating that offset estimates do not follow a simple latitudinal cline and rather vary with standing genetic diversity and predicted rates of climate change. Finally, Nielsen et al. (2021) in a comparative study of three marine invertebrates, explore genomic offset values and reveal a strong correlation among temperature and genomic variation in some species but not others and that species-specific patterns were better predictors of required adaptive shifts than environmental data alone. These findings suggest that broad generalizations of climate change vulnerability in marine species, even among closely related taxa or within similar geographic regions, might be challenging. However, they clearly indicate that additional investigations of genomic offset in marine organisms are necessary. This is especially true when considering validation, as no studies to date have attempted to validate genomic offset estimates in marine species.

Generating and validating genomic offset estimates in marine environments

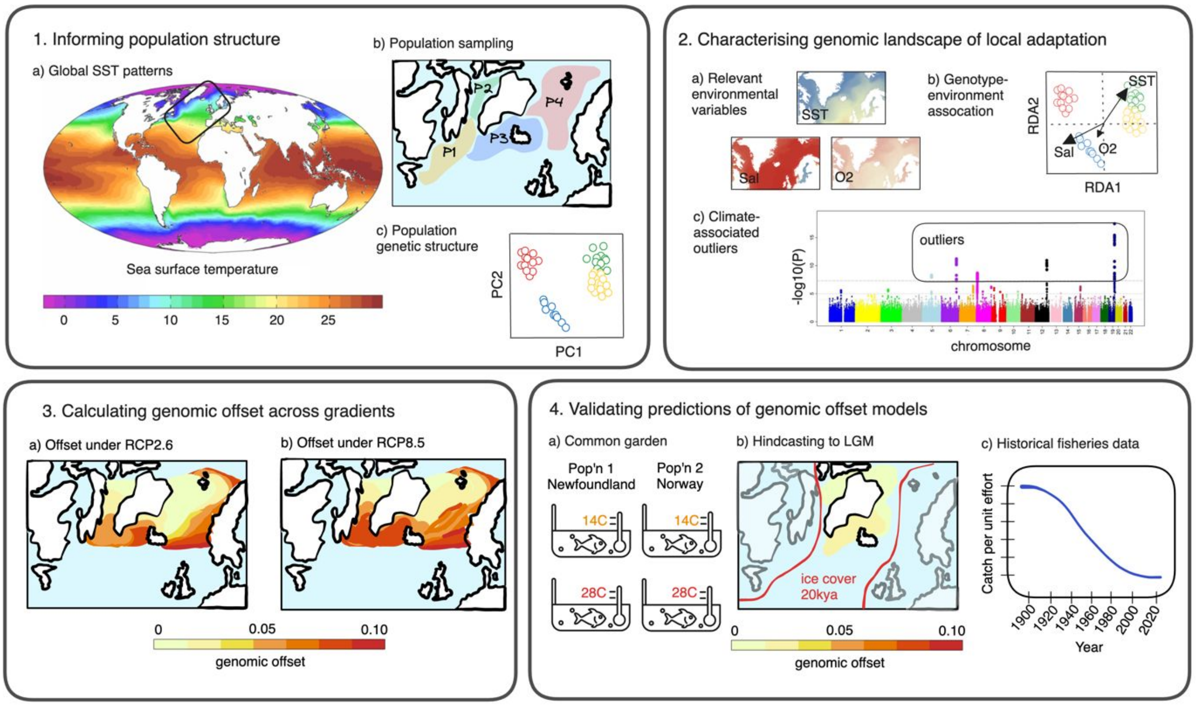

Figure 1: The first step in calculating genomic offset estimates in the marine environment is to sample populations from across the range, ideally from steep environmental gradients, to inform population structure in the species of interest (1a,b,c). Next, allele frequencies/read counts/methylation scores (response) and environmental (predictor) data are used for genotype-environment association (GEA) analyses to identify climate-associated outlier variants (see Bernatchez et al. (2023) for a detailed overview of GEA approaches) (2a,b,c). Allele frequencies/read counts/methylation scores from outlier variants are used alongside current and projected future environmental data in a modelling framework to generate genomic offset estimates (3a,b). Lastly, multiple methods can be employed to validate these model-based offset estimates, including assessing the fitness of constituent populations in common garden experiments (4a), generating historical offset estimates using publicly available climate data (e.g. BioOracle) (4b), and comparing historical offset estimates with recent/historical demographic patterns uncovered through long-term fisheries data (4c). Abbreviations: SST, sea surface temperature; Sal, salinity; O_2, dissolved oxygen.

5. Validating genomic offset in marine systems

Predictions of climate change vulnerability via genomic offset are correlative in nature and as such, these models can be prone to misinterpretation or errors when the underlying genomic data, climate projections, or their associations are of low resolution or inaccurate. Moreover, these models largely ignore much of the underlying complexity of real-world evolutionary scenarios including effective population size, rates of mutation and recombination (Rellstab et al. 2021). The approach assumes that there will be a non-negligible mismatch between current and future optima and that the current genotype-environment association accurately reflects spatial patterns in local adaptation, assumptions that can be impacted by demographic patterns and genetic drift (Rellstab et al. 2021; Laruson et al. 2022). For instance, spatial changes in allele frequencies may reflect neutral drift rather than selection, and this is especially likely when population size varies along environmental gradients. Laruson et al. (2022) employ simulations to demonstrate that although genomic offset is broadly correlated with population mean fitness, it could be confounded by demography, drift, genomic architecture, and the nature of the offset-fitness relationship.

Beyond the recent simulation study, few studies to date have attempted to validate the assumptions inherent to, or the projected vulnerabilities associated with, genomic offset calculations. In theory, validation may come from experimental studies, or comparison of predictions with existing demographic or ecological data. The only examples of experimental validation to date are from terrestrial species, where genomic offset estimates were compared to population performance measured in common garden settings—where distinct populations are grown under the same environmental conditions to identify differences in fitness (e.g. Fitzpatrick et al. 2021; Gain et al. 2023). For instance, Fitzpatrick et al. (2021) reported a negative relationship between genomic offset and common garden performance consistent with significant power of offset estimates to predict population response to climate change, exceeding that of climate differences alone. In contrast, Bay et al. (2018) used genomic offset to identify vulnerable populations of the yellow warbler (*Setophaga petechia*) and compared offset estimates to historical trends in abundance. Although they report a correlation between offset projections and demographic decline, this approach assumes that historical population trends are indicative of future trends, and it can be biased by non-selective / demographic influences on the offset prediction (Laruson et al. 2022). Interestingly, no direct attempts to validate genomic offset predictions in marine species have been published to date.

Although very informative and likely the gold standard, the potential for experimental validation of offset estimates through either reciprocal transplant or common garden experiments in marine species are limited by comparison with terrestrial plants or animals. This is largely due to the added complexity of these experiments in the marine environment, but some exceptions exist. For instance, Jacobs et al. (2022) reared fertilized eggs of Atlantic silversides (*Menidia menidia*) in temperature-controlled water baths and compared growth rates amongst treatments. However, long generation times in many exploited marine species (e.g. 20 years in deepwater redfish, *Sebastes mentella*, COSEWIC 2010) means that the short timescales with which common garden experiments are typically performed will provide only a snapshot of response. Alternatively, marine species, particularly exploited ones, often have extensive stock assessment and long-term monitoring programs with decades of time series data that can be used for validation in the absence of common garden experiments. Rather than comparing future estimates of climate change impact with past demographic data, time series data allows direct comparison of past demographic trends with predictions of past climate-induced maladaptation (i.e. offset). This approach, although not perfect, offers a means for validation when offset calculations are hindcast to the period over which population monitoring has occurred. Furthermore, sampling programs spanning decades present the opportunity to retrospectively test for temporal changes in allele frequencies in response to climate change. Here, we can pair historical DNA (e.g. from scales or otoliths) with environmental data from the same time to estimate past climate-associated variation (e.g. Atmore et al. 2022). This dataset can then serve as the base model for computing genomic offset, both for contemporary and future scenarios. These approaches to validation, although powerful, are biased toward exploited species whose stocks are already depleted from fishing and thereby teasing apart the relative impacts of climate change and exploitation will be critical in these cases. Nonetheless, we argue that the availability of extensive population data and historical samples for many economically and ecologically relevant marine species creates an unprecedented opportunity for retrospective indirect validation in marine systems.

6. Implementing genomic offset in marine management

Validating offset estimates in the marine environment will continue to be an important avenue for future work, but the integration of these estimates in marine management is even more vital. This is because existing management approaches typically rely on SDMs, which although informative, are best used to compliment methods that explicitly consider adaptation. To first generate and integrate genomic offset estimates into marine management decisions, the following steps should be taken. First, comprehensive sampling across the range of the species of interest is needed (i.e. covering all known populations, latitudes, conservation areas, spawning areas, temperature regimes, etc.). Next, suitable genomic sampling is required to inform population structure and to produce accurate and robust allele frequencies (i.e. minimum 30 individuals per sampling location, and genomic variants through high resolution whole genome sequencing, including pool-seq, or methylation sequencing at depths >2-10X). Then, high resolution long-term climate data is needed for the study region, covering biologically relevant environmental variables and preferably validated with *in situ* measurements accounting for depth and seasonal variation. To complement this, future climate change scenario models of the same resolution as contemporary climate data are required, which often show a trade-off of model resolution and geographic scale. Selection of future emissions scenarios should be justified, aligning with relevant management priorities in a region (e.g., RCP 4.5 versus 8.5). The resulting offset estimates offer valuable insights, particularly for identifying populations or areas expected to be hotspots of future maladaptation, thereby serving as focal points for proactive management. In such cases, we recommend applying genomic offset estimates in the real-world through 'assisted evolution' or restoration through transplantation, enhancing resilience to a changing climate (e.g., Wood et al. 2021). Although straightforward in theory, this proposed workflow can be challenging to implement in practice given constraints on budget and time. For instance, generating dense genomic datasets for many individuals and populations can be expensive and thus targeting a smaller subset of climate-associated loci might be a feasible alternative. Additionally, sampling from all known populations across a species range can be logistically challenging and thus selecting a subset of populations that best represent variation (both genomic and environmental) in the system could be an alternative approach.

As genomic offset models are refined and applied to other taxa of conservation interest, there will be a need to integrate predictions into management and decision making. While validating genomic offset models, through experiments or observations over time, should foster trust in the method, there are consequences to inaction as well (Salafsky and Redford 2013). The standards of proof for a model or prediction can vary depending on the potential consequences of action versus inaction, and whether management or mitigation strategies are reversible. When inaction might result in long-term ecological consequences and when there is some certainty regarding a positive outcome for a population or species, a relatively low standard of proof may suffice (Salafsky and Redford 2013). In a management context, a plain-language report that states the results of the study, the caveats of the genomic offset estimates, and potential consequences of action versus inaction is vital for informing decision-making processes.

7. Conclusions

Climate change is restructuring marine ecosystems, diminishing biodiversity and compromising ecosystem function. The global reliance on marine resources means that these changes will undoubtedly have clear repercussions on food security, economic stability, and human health (Payne et al. 2021). Our ability to mitigate these changes and “future-proof" management decisions and conservation actions through placing them in the larger context of climate change impacts could be a powerful tool. However, achieving this will depend on a thorough understanding of the basis of biological adaptation to climate and accurate predictions of the impacts of climate change on marine species.

Here, we reveal a growing wealth of examples of climate-associated adaptation in marine taxa, whose demonstration is only now possible with high-depth genomic sequencing and high-resolution marine climate data. Yet, there remains a general lack of application and validation of genomic offset estimates, heightening the uncertainty of these predictions. Here, we argue that future work should focus on leveraging the wealth of long-term population data available for many economically and ecologically vital marine species to validate offset estimates when more traditional approaches are logistically challenging. A particularly exciting avenue for future work is the potential for generating models of past climate-associated variation with historical samples. Beyond validation, there is even greater uncertainty on how to apply offset estimates in real-world fisheries management and marine conservation scenarios. To this end, we provide a ‘standard operating procedure’ for marine managers, outlining how to generate offset estimates and modify workflows in the face of budgetary and time constraints. Genomic offset has the potential to transform marine management and is highly complementary to other genetic and non-genetic approaches to conserving vital marine resources.

Conflict of Interest Statement

The authors declare that they have no conflicts of interest.

Data Availability

Data sharing not applicable – no new data generated in this manuscript.

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Predicting the future of our oceans – evaluating genomic forecasting approaches in marine species

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1. Abstract

Climate change is restructuring biodiversity on multiple scales and there is a pressing need to understand the downstream ecological and genomic consequences of this change. Recent advancements in the field of eco-evolutionary genomics have sought to include evolutionary processes in forecasting species' responses to climate change (e.g. genomic offset), but to date, much of this work has focused on terrestrial species. Coastal and offshore species, and the fisheries they support, may be even more vulnerable to climate change than their terrestrial counterparts, warranting a critical appraisal of these approaches in marine systems. First, we synthesize knowledge about the genomic basis of adaptation in marine species, and then we discuss the few examples where genomic forecasting has been applied in marine systems. Next, we identify the key challenges in validating genomic offset estimates in marine species, and we advocate for the inclusion of historical sampling data and hindcasting in the validation phase. Lastly, we describe a workflow to guide marine managers in incorporating these predictions into the decision-making process.

2. Introduction

Climate change results in severe environmental change, with recent years being the warmest on record throughout the industrial period (Cheng et al. 2023). The global increase in average temperature is accompanied by a suite of environmental changes including increases in the frequency and intensity of extreme weather events, regional temperatures, atmospheric water vapour, and ocean heat, as well as decreases in pH, dissolved oxygen, and land and sea ice cover. For marine ecosystems, increased glacial runoff and rising sea temperatures pose significant challenges (He & Sillman 2019). The consequences of these impacts are evidenced by distributional shifts in many taxa (e.g., Poloczanska et al. 2013), with populations at the trailing edge declining and populations at the leading edge shifting poleward or into deeper waters (Polyakov et al. 2020; Pinsky et al. 2020). In fact, marine species and the fisheries they sustain appear to be more vulnerable to climate change than their terrestrial counterparts (Pinsky 2021). Given the global reliance on marine resources, these changes will undoubtedly impact food security and economic stability (Payne et al. 2021). Consequently, there is a need to 'future-proof' marine ecosystems and conservation areas through proactive management based on a sound understanding of the ecological and genetic impacts of climate change (Tittensor et al. 2019).

There is a pressing necessity to predict climate change impacts in marine species and ecosystems to inform conservation planning and strategies. These predictions are particularly relevant to global fisheries and aquaculture, which provide a major source of nutrition to developed and developing countries (Bene et al. 2016). For instance, ocean warming has been linked to significant decreases in production capacity and shifts in the distribution of fisheries-targeted species (e.g., tuna, Monllor-Hurtado et al. 2017). Predicting range shifts in marine taxa remains a significant challenge and ultimately requires information on existing ranges, predictions of future environments, capacity for adaptive and plastic responses to environmental change, dispersal potential, and ecosystem structure and function. Marine species' ranges largely conform to their thermal limits (Sunday et al. 2012) and therefore even small changes in the thermal profile of a given marine region can have measurable consequences on population survival and subsequent extirpation.

A growing body of research has focused on developing tools to predict the impacts of climate change on wild populations. Ecological niche modelling - akin to species distribution modelling (SDM) - has been used in the last 20 years to map the probability of occurrence of a species across a landscape (Kearney & Porter 2009). However, traditional SDMs do not consider adaptive responses of populations to environmental change, for instance through multigenerational selection of advantageous genomic variants (e.g., standing genetic variation), or through the expression of epigenetic variants leading to acclimation via phenotypic plasticity. More recently, genomic offset - also termed genomic vulnerability (Bay et al. 2018) - has been applied to both terrestrial and marine taxa to predict potential future maladaptation driven by climate change (e.g., Fitzpatrick & Keller 2015; Laruson et al. 2022; Layton and Bradbury 2021). This approach maps the contemporary spatial turnover of adaptive alleles onto current environmental conditions and then calculates the offset between present and future climate-associated genomic composition as a measure of maladaptation to climate change. In other words, genomic offset is an estimate of the change in genomic composition that would be required to track predicted climate change. Despite some limitations and challenges, including validation and management buy-in (Rellstab et al. 2021), the approach seems to accurately estimate climate change vulnerability when compared to experimental predictions (e.g., Fitzpatrick et al. 2021). Bernatchez et al. (2023) provide a comprehensive overview of this method, among others, in their recent review of genomics-based monitoring approaches, but to date, no study has assessed these methods in specific ecological contexts. Given the potential of genomic offset estimates to inform climate change predictions, and the observation that marine species are already being impacted by climate change, an evaluation of the method's applicability to marine species is warranted.

There are several reasons why estimating genomic offset can be useful for managing and conserving marine ecosystems and species. The poikilothermic nature of most marine fish, invertebrates, and macrophytes means that temperature is often a dominant selective pressure driving adaptive genetic diversity across populations. The low genetic structure and generally large effective population sizes (Ne) often observed within marine species (Bradbury et al. 2008) means that the influence of genetic drift is typically minimal compared with that of natural selection. Moreover, many marine species occupy large latitudinal ranges and genomic approaches have repeatedly demonstrated putative adaptation across these variable environments. Taken together, our ability to resolve the genomic basis of climate-associated adaptation may be elevated in the marine environment compared with terrestrial, which can translate into improved power to predict population-level responses or vulnerability in these systems.

In this opinion piece, we review the literature on the genomic basis of climate adaptation in marine species (section 3), evaluate current examples of genomic offset estimates in marine systems (section 4), assess the potential for validation of these estimates (section 5), and finally we discuss the utility of these estimates in informing fisheries policy (section 6). Here, we argue that the wealth of data available from long-term monitoring programs in exploited marine species provides an unprecedented opportunity for validating offset estimates in an otherwise logistically challenging environment. We also argue that implementing offset estimates in marine management will enable a more comprehensive assessment of the impacts of climate change on exploitation.

3. Genomic basis of adaptation in marine species

Accurate prediction of potential maladaptation requires an understanding of how species are adapted to their environments. The number of potential drivers of adaptation in the marine environment is broad and includes numerous environmental variables such as temperature, salinity, dissolved oxygen, pH, and depth. Although theory would predict that extensive gene flow facilitated by long pelagic larval durations in marine species would erode and prevent local adaptation, recent studies employing genome-wide data have provided strong evidence for climate-associated adaptation in several marine taxa (e.g. Drinan et al. 2018; Vranken et al. 2021). For some species with high connectivity and gene flow, like Atlantic cod (*Gadus morhua*), herring (*Clupea harengus*), horse mackerel (*Trachurus trachurus*), and northern sand lance (*Ammodytes dubius*), a few "large effect" chromosomal rearrangements seem to explain most of the climate-associated genomic variation (e.g., Barth et al. 2017; Kess et al. 2020; Fuentes-Pardo et al. 2023a). For example, a large 10Mb inversion on chromosome 21 discriminates northern and southern populations of horse mackerel in Europe (Fuentes-Pardo et al. 2023a). In other cases, a signature of local adaptation is restricted to many regions of "small effect" in the genome, requiring dense genomic data for detection, as seen in Arctic charr (*S. alpinus*), Atlantic silversides (*Menidia menidia*) and the Baltic copepod (*Eurytemora affinis*) (Wilder et al. 2020; Kess et al. 2021; Stern et al. 2022). Here, adaptive SNPs are dispersed across most of the genome, rather than being concentrated in one particular region, constituting a signature of polygenic adaptation. The genomic underpinnings of local adaptation can vary not only across species but also across environmental gradients, and this is especially complex in marine systems where species are distributed across both geographic and bathymetric clines.

Genomic signatures of thermal adaptation have repeatedly been reported and appear to be more prevalent in marine systems than in terrestrial or freshwater systems (Sasaki et al. 2022). For example, temperature-driven structure has been observed in sea scallop (*Placopecten magellanicus*) (Van Wyngaarden et al. 2017), northern shrimp (*Pandalus borealis*) (Stanley et al. 2018), capelin (*Mallotus villosus*) (Cayuela et al 2021), and Atlantic herring (*Clupea harengus*) (Fuentes-Pardo et al 2023b). Extreme thermal events can also result in a reshuffling of genetic clusters leading to local adaptation. For example, Coleman et al. (2020) demonstrated that an extreme marine heatwave caused a significant poleward shift in populations of kelp forests along the coast of western Australia, whereby 'cool water' alleles were replaced by 'warm water' alleles, resulting in a genetic tropicalisation of the populations. While within a species the same adaptive alleles can be selected multiple times in distinct geographic areas, resulting in parallel evolution of thermal adaptation (Bradbury et al. 2010), the universality of the molecular processes involved in thermal adaptation is largely unknown in marine systems, partly due to the lack of genomic resources and functional validation of the markers under selection in published studies.

Climate change projections not only indicate a rapid increase in ocean temperature in the next century but also lower salinity in relation to glacier melting and higher precipitation in some regions, like the northern hemisphere (Luo et al. 2016). Additionally, many marine species use a variety of habitats throughout their life cycle, some spanning freshwater and estuarine environments and thereby experiencing steep salinity clines. A significant body of work supports salinity adaptation in marine organisms (Johannesson et al. 2020), particularly in the Baltic Sea. For instance, whole genome sequencing revealed hundreds of regions across the genome of Atlantic herring (*C. harengus*) that showed significant differentiation between Baltic and Atlantic populations (Han et al. 2020). Equivalent comparisons of Baltic and Atlantic populations have yielded similar results in other species such as Atlantic cod (*G. morhua*) (Berg et al. 2015), sand goby (*Pomatoschistus minutus*) (Leder et al. 2021), and European plaice (*Pleuronectes platessa*) (Le Moan et al. 2021), indicating adaptation to low salinity levels. Within the Baltic, different species of mussels have also shown salinity-related adaptation between western and eastern regions (Knöbel et al. 2021). Recently, Stern et al. (2022) showed experimental and genomic evidence of Baltic copepod (*E. affinis)* rapidly adapting to decreasing salinity. Similar to thermal adaptation, species can adapt to salinity changes through either parallel or convergent evolution (Le Moan et al. 2021), involving either few genetic variants of large effect or many loci of small effect (e.g., Berg et al. 2015; Le Moan, et al. 2021).

Additionally, it is increasingly clear that the basis of local adaptation in marine taxa extends beyond SNPs to large-scale chromosomal rearrangements, copy number variants (CNVs), and epigenetic variation. For instance, environmental adaptation in American lobster (*Homarus americanus*) was driven almost entirely by CNVs with little to no signal in SNP data (Dorant et al. 2020). In contrast, Layton et al. (2021) reported similar spatial trends in genomic offset calculated from CNV and SNP datasets in Arctic Charr populations from eastern Canada. In three-spined stickleback, differentially methylated regions (DMRs) were more significantly associated with environmental variation (salinity) than outlier SNPs (Ruiz-Arenas et al. 2017). Given these findings, Layton and Bradbury (2022) suggest a revised offset approach incorporating normalized read counts and methylation scores alongside allele frequencies which might better reflect overall (genetic + epigenetic) adaptive processes, thereby improving prediction accuracy. Despite a complex landscape of adaptive genomic variation in marine species, only a few studies have leveraged this information for estimating genomic offset in the marine environment.

4. Prediction of climate change impacts using genomic tools in marine taxa

As discussed above, local adaptation to ocean climate is widespread (at least at regional scales) across marine species in various taxonomic groups and ecological contexts. However, climate change is expected to disrupt local adaptation in the coming years, resulting in potential maladaptation as the speed of change outpaces natural selection in many species and populations (Razgour et al. 2019). The ability to resolve the genomic basis of adaptation, in conjunction with fine-scale climate projections, presents an opportunity to leverage these datasets to forecast future climate-associated genomic composition and maladaptation. Genomic offset, defined as the difference between current genomic composition and the predicted future composition required to maintain adaptation, was first introduced by Fitzpatrick and Keller (2015) and later by Bay et al. (2018) and has been used to identify populations most vulnerable to future climate change. Additionally, the genomic offset approach can be employed across historical timescales, for instance by calculating the difference between current genomic composition and past genomic composition hindcasted at the last glacial maximum.

In the past few years, this method has been increasingly employed across various terrestrial systems (e.g., Capblancq et al. 2020), with more recent work focussing on *in situ* validation of these offset estimates (Fitzpatrick et al. 2021). To derive the offset estimate, allele frequencies of putatively adaptive, climate-associated loci are the response variables to environmental predictor data to model climate-associated genomic variation using any number of modelling approaches. The most common modelling approaches include generalized dissimilarity modelling (GDM) and gradient forest (GF)—both of which accommodate for nonlinear associations of genomic and environmental data. The former uses distance matrices to model climate-associated genomic variation while the latter employs a regression-tree approach that is especially suitable in the context of steep environmental gradients (Fitzpatrick & Keller 2015). The model is then used alongside environmental data from both current and future time periods and across the species' range to predict current and future adaptive indices, respectively. The difference between these values represents offset, with larger values indicating that a population is more likely to be maladapted to future climate. This method has typically been used in species with strong population structure distributed across well-defined environmental gradients, but its utility and downstream interpretation in marine species has been understudied. However, recent work has begun to address this gap, demonstrating its potential utility in eleven species of fish, invertebrates and marine plants (Table 1).

Table 1: List of current publications employing genomic offset estimates in marine species. The statistical method used to generate offset estimates, and the environmental predictors used, is also listed (RDA=redundancy analysis; GDM= generalised dissimilarity modelling; GF=gradient forest).

Organism	Region	Method	Included Climate Variables	Validated	Reference

Macrophytes					
Eelgrass (*Zostera marina*)	Coastal North America	RDA	Seasonal, annual bottom & surface temperature, salinity	No	Jeffery et al. (2024)
Seaweed (*Phyllospora comosa*)	Southeastern Australia	GDM	Sea surface temperature	No	Wood et al. (2021)
Kelp (*Ecklonia radiata)*	Western Australia	GF	Dissolved oxygen, sea surface salinity, sea surface nitrate, seawater velocity, attenuation	No	Vranken et al. (2021)
Vertebrates					
Arctic Charr (*Salvelinus alpinus*)	Newfoundland/Labrador	GF	Precipitation, air temperature	No	Layton et al. (2021)
Sockeye salmon (*Oncorhynchus nerka*)	British Columbia & Yukon	GF	Precipitation, air temperature	No	Tigano et al. (2024)
Invertebrates					
Multi-species: Urchin (*Parechinus angulosus*), crab (*Cyclograpsus punctatus*) & limpet (*Scutellastra granularis*)	South Africa	GF	Sea surface temperature, sea surface salinity & air temperature	No	Nielsen et al. (2021)
Coral (*Acropora digitifera*)	Western Australia	GF & GDM	Sea surface temperature	No	Adam et al. (2022)
Tubeworms (*Galeolaria caespitosa* & *G.gemineoa*)	Southeast Australia	GF	Sea surface temperature	No	Gallegos et al. (2023)

Most of these studies have focused on generating offset estimates in single species across a variety of spatial scales, with variable patterns across taxonomic groups and geographic areas. For instance, in eastern Canada, offset estimates were highest in southern populations of Arctic charr (*S. alpinus*) (Layton et al. 2021), indicative of a scenario of contraction of the southern range limit of this Arctic species. Alternatively, genomic offset values were higher in northern (subarctic) populations of a widely distributed seagrass species (*Z. marina*) across a similar area (Jeffery et al. 2024). Estimates of future offset in *Acropora digitifera* in western Australia are more spatially complex, but populations living at the upper thermal limits (i.e. at lower latitudes) were predicted to require less of an adaptive shift than mid-latitude reefs (Adam et al. 2022). Similarly, Wood et al. (2021) shows a spatially complex pattern of future offsets in a forest-forming seaweed (*P. comosa)* in Australia, demonstrating that offset estimates do not follow a simple latitudinal cline and rather vary with standing genetic diversity and predicted rates of climate change. Finally, Nielsen et al. (2021) in a comparative study of three marine invertebrates, explore genomic offset values and reveal a strong correlation among temperature and genomic variation in some species but not others and that species-specific patterns were better predictors of required adaptive shifts than environmental data alone. These findings suggest that broad generalizations of climate change vulnerability in marine species, even among closely related taxa or within similar geographic regions, might be challenging. However, they clearly indicate that additional investigations of genomic offset in marine organisms are necessary. This is especially true when considering validation, as no studies to date have attempted to validate genomic offset estimates in marine species.

Generating and validating genomic offset estimates in marine environments

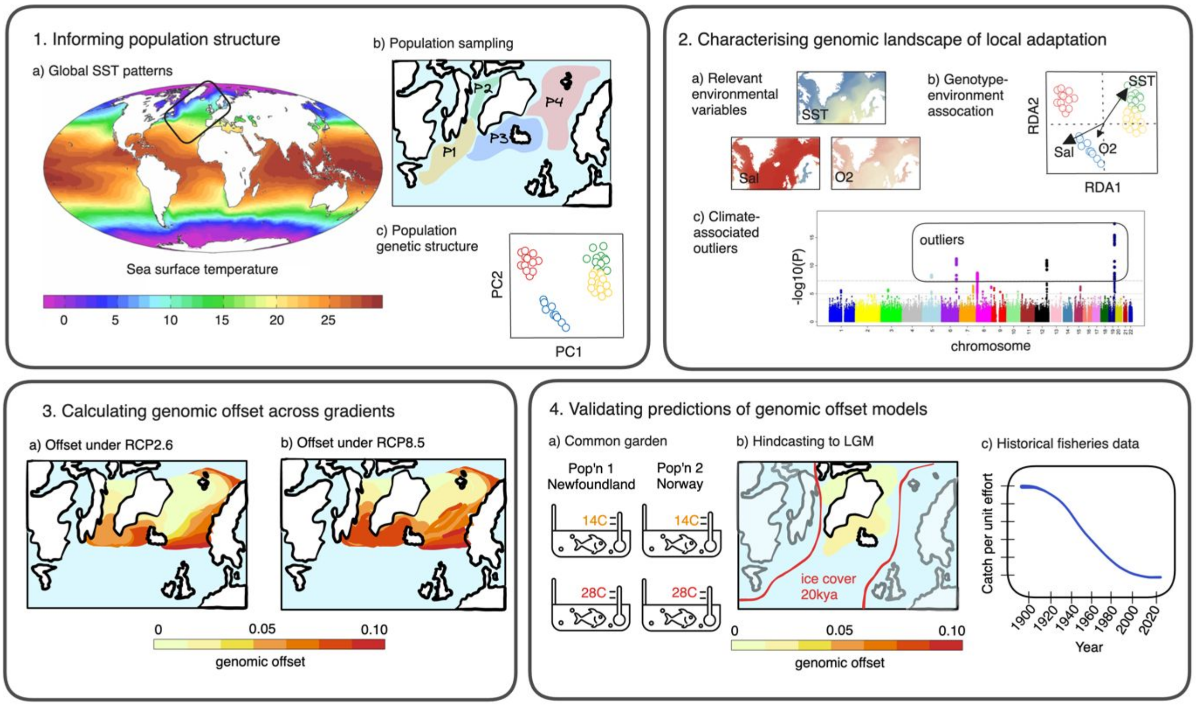

Figure 1: The first step in calculating genomic offset estimates in the marine environment is to sample populations from across the range, ideally from steep environmental gradients, to inform population structure in the species of interest (1a,b,c). Next, allele frequencies/read counts/methylation scores (response) and environmental (predictor) data are used for genotype-environment association (GEA) analyses to identify climate-associated outlier variants (see Bernatchez et al. (2023) for a detailed overview of GEA approaches) (2a,b,c). Allele frequencies/read counts/methylation scores from outlier variants are used alongside current and projected future environmental data in a modelling framework to generate genomic offset estimates (3a,b). Lastly, multiple methods can be employed to validate these model-based offset estimates, including assessing the fitness of constituent populations in common garden experiments (4a), generating historical offset estimates using publicly available climate data (e.g. BioOracle) (4b), and comparing historical offset estimates with recent/historical demographic patterns uncovered through long-term fisheries data (4c). Abbreviations: SST, sea surface temperature; Sal, salinity; O_2, dissolved oxygen.

5. Validating genomic offset in marine systems

Predictions of climate change vulnerability via genomic offset are correlative in nature and as such, these models can be prone to misinterpretation or errors when the underlying genomic data, climate projections, or their associations are of low resolution or inaccurate. Moreover, these models largely ignore much of the underlying complexity of real-world evolutionary scenarios including effective population size, rates of mutation and recombination (Rellstab et al. 2021). The approach assumes that there will be a non-negligible mismatch between current and future optima and that the current genotype-environment association accurately reflects spatial patterns in local adaptation, assumptions that can be impacted by demographic patterns and genetic drift (Rellstab et al. 2021; Laruson et al. 2022). For instance, spatial changes in allele frequencies may reflect neutral drift rather than selection, and this is especially likely when population size varies along environmental gradients. Laruson et al. (2022) employ simulations to demonstrate that although genomic offset is broadly correlated with population mean fitness, it could be confounded by demography, drift, genomic architecture, and the nature of the offset-fitness relationship.

Beyond the recent simulation study, few studies to date have attempted to validate the assumptions inherent to, or the projected vulnerabilities associated with, genomic offset calculations. In theory, validation may come from experimental studies, or comparison of predictions with existing demographic or ecological data. The only examples of experimental validation to date are from terrestrial species, where genomic offset estimates were compared to population performance measured in common garden settings—where distinct populations are grown under the same environmental conditions to identify differences in fitness (e.g. Fitzpatrick et al. 2021; Gain et al. 2023). For instance, Fitzpatrick et al. (2021) reported a negative relationship between genomic offset and common garden performance consistent with significant power of offset estimates to predict population response to climate change, exceeding that of climate differences alone. In contrast, Bay et al. (2018) used genomic offset to identify vulnerable populations of the yellow warbler (*Setophaga petechia*) and compared offset estimates to historical trends in abundance. Although they report a correlation between offset projections and demographic decline, this approach assumes that historical population trends are indicative of future trends, and it can be biased by non-selective / demographic influences on the offset prediction (Laruson et al. 2022). Interestingly, no direct attempts to validate genomic offset predictions in marine species have been published to date.

Although very informative and likely the gold standard, the potential for experimental validation of offset estimates through either reciprocal transplant or common garden experiments in marine species are limited by comparison with terrestrial plants or animals. This is largely due to the added complexity of these experiments in the marine environment, but some exceptions exist. For instance, Jacobs et al. (2022) reared fertilized eggs of Atlantic silversides (*Menidia menidia*) in temperature-controlled water baths and compared growth rates amongst treatments. However, long generation times in many exploited marine species (e.g. 20 years in deepwater redfish, *Sebastes mentella*, COSEWIC 2010) means that the short timescales with which common garden experiments are typically performed will provide only a snapshot of response. Alternatively, marine species, particularly exploited ones, often have extensive stock assessment and long-term monitoring programs with decades of time series data that can be used for validation in the absence of common garden experiments. Rather than comparing future estimates of climate change impact with past demographic data, time series data allows direct comparison of past demographic trends with predictions of past climate-induced maladaptation (i.e. offset). This approach, although not perfect, offers a means for validation when offset calculations are hindcast to the period over which population monitoring has occurred. Furthermore, sampling programs spanning decades present the opportunity to retrospectively test for temporal changes in allele frequencies in response to climate change. Here, we can pair historical DNA (e.g. from scales or otoliths) with environmental data from the same time to estimate past climate-associated variation (e.g. Atmore et al. 2022). This dataset can then serve as the base model for computing genomic offset, both for contemporary and future scenarios. These approaches to validation, although powerful, are biased toward exploited species whose stocks are already depleted from fishing and thereby teasing apart the relative impacts of climate change and exploitation will be critical in these cases. Nonetheless, we argue that the availability of extensive population data and historical samples for many economically and ecologically relevant marine species creates an unprecedented opportunity for retrospective indirect validation in marine systems.

6. Implementing genomic offset in marine management

Validating offset estimates in the marine environment will continue to be an important avenue for future work, but the integration of these estimates in marine management is even more vital. This is because existing management approaches typically rely on SDMs, which although informative, are best used to compliment methods that explicitly consider adaptation. To first generate and integrate genomic offset estimates into marine management decisions, the following steps should be taken. First, comprehensive sampling across the range of the species of interest is needed (i.e. covering all known populations, latitudes, conservation areas, spawning areas, temperature regimes, etc.). Next, suitable genomic sampling is required to inform population structure and to produce accurate and robust allele frequencies (i.e. minimum 30 individuals per sampling location, and genomic variants through high resolution whole genome sequencing, including pool-seq, or methylation sequencing at depths >2-10X). Then, high resolution long-term climate data is needed for the study region, covering biologically relevant environmental variables and preferably validated with *in situ* measurements accounting for depth and seasonal variation. To complement this, future climate change scenario models of the same resolution as contemporary climate data are required, which often show a trade-off of model resolution and geographic scale. Selection of future emissions scenarios should be justified, aligning with relevant management priorities in a region (e.g., RCP 4.5 versus 8.5). The resulting offset estimates offer valuable insights, particularly for identifying populations or areas expected to be hotspots of future maladaptation, thereby serving as focal points for proactive management. In such cases, we recommend applying genomic offset estimates in the real-world through 'assisted evolution' or restoration through transplantation, enhancing resilience to a changing climate (e.g., Wood et al. 2021). Although straightforward in theory, this proposed workflow can be challenging to implement in practice given constraints on budget and time. For instance, generating dense genomic datasets for many individuals and populations can be expensive and thus targeting a smaller subset of climate-associated loci might be a feasible alternative. Additionally, sampling from all known populations across a species range can be logistically challenging and thus selecting a subset of populations that best represent variation (both genomic and environmental) in the system could be an alternative approach.

As genomic offset models are refined and applied to other taxa of conservation interest, there will be a need to integrate predictions into management and decision making. While validating genomic offset models, through experiments or observations over time, should foster trust in the method, there are consequences to inaction as well (Salafsky and Redford 2013). The standards of proof for a model or prediction can vary depending on the potential consequences of action versus inaction, and whether management or mitigation strategies are reversible. When inaction might result in long-term ecological consequences and when there is some certainty regarding a positive outcome for a population or species, a relatively low standard of proof may suffice (Salafsky and Redford 2013). In a management context, a plain-language report that states the results of the study, the caveats of the genomic offset estimates, and potential consequences of action versus inaction is vital for informing decision-making processes.

7. Conclusions

Climate change is restructuring marine ecosystems, diminishing biodiversity and compromising ecosystem function. The global reliance on marine resources means that these changes will undoubtedly have clear repercussions on food security, economic stability, and human health (Payne et al. 2021). Our ability to mitigate these changes and “future-proof" management decisions and conservation actions through placing them in the larger context of climate change impacts could be a powerful tool. However, achieving this will depend on a thorough understanding of the basis of biological adaptation to climate and accurate predictions of the impacts of climate change on marine species.

Here, we reveal a growing wealth of examples of climate-associated adaptation in marine taxa, whose demonstration is only now possible with high-depth genomic sequencing and high-resolution marine climate data. Yet, there remains a general lack of application and validation of genomic offset estimates, heightening the uncertainty of these predictions. Here, we argue that future work should focus on leveraging the wealth of long-term population data available for many economically and ecologically vital marine species to validate offset estimates when more traditional approaches are logistically challenging. A particularly exciting avenue for future work is the potential for generating models of past climate-associated variation with historical samples. Beyond validation, there is even greater uncertainty on how to apply offset estimates in real-world fisheries management and marine conservation scenarios. To this end, we provide a ‘standard operating procedure’ for marine managers, outlining how to generate offset estimates and modify workflows in the face of budgetary and time constraints. Genomic offset has the potential to transform marine management and is highly complementary to other genetic and non-genetic approaches to conserving vital marine resources.

Conflict of Interest Statement

The authors declare that they have no conflicts of interest.

Data Availability

Data sharing not applicable – no new data generated in this manuscript.

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