Molecular Ecology

WILEY

MOLECULAR ECOLOGY

INVITED REVIEW OPEN ACCESS

Putting Structural Variants Into Practice: The Role of Chromosomal Inversions in the Management of Marine Environments

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Received: 13 August 2024 | **Revised:** 1 April 2025 | **Accepted:** 14 April 2025

Handling Editor: Michael M. Hansen

Funding: This work was supported by ARC Discovery Grant, DP240102310, DP250101690; ARC SRIEAS Grant, SR200100005; Vetenskapsrådet Research Grant, VR 2021-04191.

Keywords: adaptive capacity | conservation genomics | fisheries management | inversion | marine protected areas | structural variation

ABSTRACT

Major threats to marine species and ecosystems include overfishing, invasive species, pollution and climate change. The changing climate not only imposes direct threats through the impacts of severe marine heatwaves, cyclones and ocean acidification but also complicates fisheries and invasive species management by driving species range shifts. The dynamic nature of these threats means that the future of our oceans will depend on the ability of species to adapt. This has led to calls for genetic interventions focussed on enhancing species' adaptive capacity, including translocations, restocking and selective breeding. Assessing the benefits and risks of such approaches requires an improved understanding of the genetic architecture of adaptive variation, not only in relation to climate-resilient phenotypes but also locally adapted populations and the fitness of hybrids. Large structural genetic variants such as chromosomal inversions play an important role in local adaptation by linking multiple adaptive loci. Consequently, inversions are likely to be particularly important when managing for adaptive capacity. However, under some circumstances, they also accumulate deleterious mutations, potentially increasing the risk of inbreeding depression. Genetic management that takes account of these dual roles on fitness is likely to be more effective at ensuring population persistence. We summarise evolutionary factors influencing adaptive and deleterious variation of inversions, review inversions found in marine taxa, and provide a framework to predict the consequences of ignoring inversions in key management scenarios. We conclude by describing practical methods to bridge the gap between evolutionary theory and practical application of inversions in conservation.

1 | Introduction

Anthropogenic impact on the environment and climate is inducing an unparalleled rate of change that is causing a shift of the global environment towards a point of no return (Richardson et al. 2023). Changes to the Earth's water cycle (Allan et al. 2020) in addition to direct effects mean that marine species are faced with many challenges including global warming, ocean acidification, pollution and overfishing (Doney et al. 2012). Marine heatwaves, in particular, have already caused multiple mass coral bleaching events (Hughes et al. 2017), species range shifts (Poloczanska et al. 2013) and mass mortality of seaweeds and seagrasses, leading to large and persistent ecosystem shifts (Genin et al. 2020; Pearce and Feng 2013; Reusch et al. 2005; Wernberg et al. 2013). Consequently, a new key focus of conservation must aim to protect species' abilities to adapt. This ability includes direct adaptation to climate change impacts such as extreme temperatures, decreasing ocean pH and more frequent storms, as well as resilience to survive altered competitive landscapes resulting from species' range shifts. Preserving genetic diversity is at the heart of conservation initiatives, as reflected in Goal A of The Convention on Biological Diversity (CBD) 2050, which seeks to 'safeguard the adaptive potential' of wild and domesticated species by maintaining their genetic diversity (CBD 2023).

DNA sequencing techniques are crucial to the planning, implementation and monitoring of efforts to preserve genetic diversity and adaptive capacity, especially for marine taxa where behaviour and movement are often challenging to observe (Avise 1998) and where locally adapted populations (Akopyan et al. 2022; Grupstra et al. 2024) and cryptic species (Appeltans et al. 2012) are difficult to detect without genetic information. As genomic techniques have advanced, they have not only informed finer scale delineation of population structure based on neutral markers, but have also identified key components of adaptive variation, sometimes with significant consequences for species management (Andersson et al. 2023; Pettersson et al. 2019; Waples et al. 2020). For example, in Pacific salmon, the significance of early spawning lineages was not recognised until recently with the discovery of a single locus (GREB1/ROCK1 region) that controls early and late spawning populations (Prince et al. 2017; Waples et al. 2022). Similarly, in Atlantic herring, important adaptive differences among local stocks were not discovered until the application of genome-wide sequencing (Han et al. 2020) identified several important genomic regions (including large ~2 Mb inversions) that house genes involved in temperature tolerance, vision and spawning time (Hill et al. 2019; Martinez Barrio et al. 2016; Pettersson et al. 2019).

Examples in Pacific salmon, Atlantic herring and three-spined stickleback (Roesti et al. 2015) illustrate how structural variants with large phenotypic effects can influence conservation decision-making in the marine environment (Kardos and Shafer 2018; Waples et al. 2022). Perhaps the most obvious way that this can occur is by contributing to the delineation of management units (Waples et al. 2022) but there is a growing recognition that structural variants could influence a broad range of conservation actions and outcomes (Wold et al. 2021) because they create strong linkages between non-neutral loci and thereby impact both adaptive and deleterious variation (Berdan et al. 2023). Moreover, simulations suggest that when a trait is associated with multiple linked genes rather than independent loci, its evolutionary dynamics may be complex and non-linear (Oomen et al. 2020), which highlights the need to consider genomic architecture when managing for adaptive capacity.

Some types of structural variants such as large polymorphic inversions and chromosomal fusions are of particular interest in a conservation context because they strongly suppress recombination in heterokaryotypes. This phenomenon leads to divergence between arrangements, can alter the genetic architecture of traits, affects the strength of selection on linked loci, and the rate at which deleterious variants are purged (Berdan et al. 2021; Huang et al. 2020). In this review, we focus specifically on large, polymorphic chromosomal inversions as this is where theory and empirical evidence are best developed (Berdan et al. 2023; Faria, Johannesson, et al. 2019; Kirkpatrick 2010). We consider inversions to be large if they span multiple non-neutral loci and polymorphic if the derived arrangement is sufficiently common that it is likely to have persisted for some time. Such inversions also tend to exhibit divergence between arrangements since the derived arrangement experiences strong genetic drift early in its evolution (Berdan et al. 2023) and because differences in allelic content of arrangements contribute to divergent selection (Berdan et al. 2023; Faria, Johannesson, et al. 2019).

The potential for inversions to impact evolutionary processes, and to facilitate divergence under gene flow has long been recognised (Kirkpatrick and Barton 2006) and studied extensively in fruit flies (Beadle and Sturtevant 1935; Kapun and Flatt 2019; Ranz et al. 2007; Sturtevant and Beadle 1936). Recent rapid advances in genomic sequencing have allowed this work to be expanded across a wide range of taxa, allowing theories about the ecological and evolutionary roles of inversions to be tested (reviewed in Hoffmann and Rieseberg 2008; Kirkpatrick 2010). Large (0.2–57 Mb) chromosomal inversions have now been identified in species representing a wide variety of high level taxa including butterflies, plants, birds, mammals, fish, marine gastropods and corals (Faria, Chaube, et al. 2019; Harringmeyer and Hoekstra 2022; Huang et al. 2020; Le Moan et al. 2024; Matschiner et al. 2022; Zhang et al. 2024). In many cases, the different arrangements of these inversions are associated with a complex set of traits that segregate between ecotypes of a species and host key genes involved in local adaptation of populations (Han et al. 2020; Koch et al. 2021, 2022; Sinclair-Waters et al. 2018). Genetic signatures shared by inversions and other recombination-inhibiting structural variants can be identified using widely available methods based on genome-wide single-nucleotide polymorphism (SNP) data. Once verified, there is strong potential for the development of cost-effective methods for genotyping these large, highly divergent structural variants across populations to inform management.

It is increasingly clear that structural variants are likely to be responsible for a significant fraction of both adaptive and deleterious variation in many species (Berdan et al. 2023; Koch et al. 2021; Sirén et al. 2021; Wold et al. 2021) making them important targets for conservation genetics (Wold et al. 2021). In this review, we highlight risks associated with inversion-naïve management of marine species and how conservation efforts can benefit from recognising inversions in decision-making. We briefly describe empirical and theoretical results that demonstrate how inversions are established and maintained and discuss the implications of different selective pressures on the accumulation of adaptive and deleterious variation on inverted loci. We then review evidence that these processes are at play in marine taxa, and find that despite a relative paucity of studies so far, many describe inversions or putative inversions that have clear implications for conservation. Our

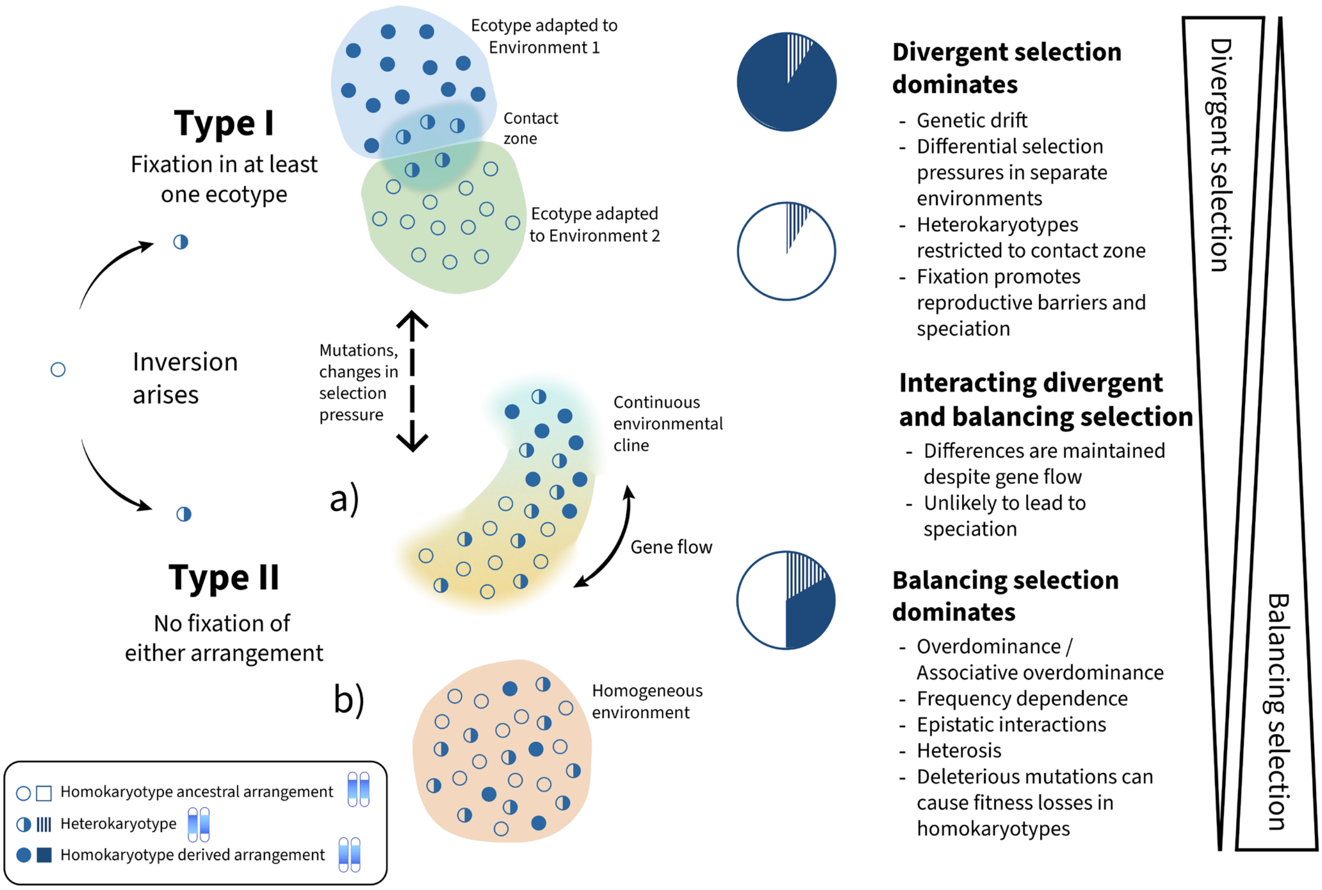


FIGURE 1 | Overview of the Type I/Type II framework for classifying an inversion polymorphism (Faria, Johannesson, et al. 2019) and understanding the role of inversions in adaptation. In the Type I scenario, the inversion facilitates local adaptation to one environment, while the alternative arrangement is maintained in another environment by divergent selection. Heterokaryotypes are only present in the contact zone. Type II is maintained by some form of balancing selection. (a) When species occupy an area that spans across an environmental cline, local adaptation can favour arrangements at different locations despite gene flow and the prevalence of heterokaryotypes. (b) In a homogeneous environment, all karyotypes are present. This scenario is most conducive to the accumulation and persistence of recessive deleterious mutations. Pie charts illustrate karyotype proportions indicative of the Type I and Type II scenarios. Type I and Type II are not fixed states, but shifts can occur through mutations or changes in selection pressures.

review concludes by describing how emerging techniques in genotyping and analysis could help to bridge the gap between evolutionary theory and practical application of inversions in conservation.

2 | Role of Inversions in Fitness and Adaptation

Inversions are a form of structural variant that has received increasing attention in population genetics, partly due to being recognised as one of the mechanisms behind the formation of 'supergenes' (Thompson and Jiggins 2014). A key feature of inversions is that they disrupt crossing-over between alternate arrangements, resulting in sharply reduced rates of recombination in heterokaryotypes (Kirkpatrick 2010). If a new inversion happens to capture two (or more) co-adaptive alleles, these will be inherited together and promote local adaptation in the face of gene flow between populations that occupy different environments (Berdan et al. 2023; Faria, Johannesson, et al. 2019; Kirkpatrick and Barton 2006; Mackintosh et al. 2024; Schaal et al. 2022). Consequently, inversion polymorphisms are often found associated with species that have evolved locally adapted ecotypes in a heterogeneous environment. Terrestrial examples include North American sunflowers that are adapted to adjacent dune versus non-dune locations (Todesco et al. 2020), ecotypes of monkey flowers living in arid and moist habitats (Twyford and Friedman 2015), host-races of stick insects associated with different plants (Lindtke et al. 2017), ecotypes of bumble bees living at different altitudes on African mountains (Wallberg et al. 2017), and many more (see Wellenreuther and Bernatchez 2018). Indeed, inversions can be relevant at large geographic scales with the same inversions being involved in parallel evolution of locally adapted ecotypes (Reeve et al. 2024; Westram et al. 2023).

Inversion polymorphisms can be classified into two types based on the predominant mode of selection leading to their establishment and maintenance (Faria, Johannesson, et al. 2019; Figure 1). Considering a pair of populations for simplicity, a Type I inversion polymorphism occurs when the inverted arrangement spreads to fixation in one population while being absent in the other, a process that is typically driven by divergent selection but may involve genetic drift (Faria, Johannesson, et al. 2019; Faria and Navarro 2010). The result is two populations (ecotypes) that are fixed for alternate arrangements with the production of heterokaryotypes restricted to zones of contact (Figure 1, Type I). An extreme example is found in the snail species *Littorina fabalis* in which locally adapted populations are fixed or nearly fixed for different arrangements in 12 large putative inversions, while hybridization leads to strong polymorphism in the contact zone (Le Moan et al. 2024). In contrast, Type II inversion polymorphisms are maintained by some form of balancing selection, which opposes fixation of the different arrangements. Importantly, in a Type II inversion polymorphism, both arrangements occur throughout the population, and heterokaryotypes can be found across the distribution (Figure 1, Type II b). Maintenance of inversion polymorphisms by balancing selection can include a range of underlying mechanisms, many of which have been observed in nature (Berdan et al. 2023; Wellenreuther and Bernatchez 2018), including frequency-dependent selection (Nassar et al. 1973), antagonistic pleiotropy (Mérot, Llaurens, et al. 2020) and associative overdominance (Jay et al. 2021). An interaction of balancing and divergent selection combined with gene flow across the species range can create inversion arrangement clines that are continuous rather than showing a sharp genetic break (Figure 1, Type II a).

The simple dichotomy between Type I and II inversion polymorphisms forms a useful framework for discussing the role of inversions in conservation because it captures differences in the occurrence of heterokaryotypes that have implications for management strategies (see Section 4; Table 2). While useful for describing key processes that maintain inversion polymorphisms, the distinction between Type I and Type II is not always clear in practice. Inversions may experience a mix of Type I and Type II processes; these can change over time, and multiple inversion types may exist within the same species (Faria, Johannesson, et al. 2019; Meyer et al. 2023). Fortunately, differences between Type I and II inversion polymorphisms, such as the distribution and frequency of heterokaryotypes, are measurable, and with the relevant environmental information, can be used to predict conservation outcomes.

Evidence from snails, sunflowers and flies suggests that over time, Type I inversion polymorphisms may accumulate stronger barriers, eventually leading to reproductive incompatibilities and potentially even speciation (Ayala et al. 2013; Faria and Navarro 2010; Johannesson et al. 2024; Le Moan et al. 2024; Todesco et al. 2020). Thus, one important consideration for Type I inversion polymorphisms is the potential for significantly reduced fitness in heterokaryotypes, which increases the risk of outbreeding depression (Frankham et al. 2011). A key practical difference between Type I and Type II inversion polymorphisms is that heterokaryotypes in Type I tend to be restricted to zones of contact between ecotypes and therefore are less abundant than in Type II. This is important because inversions only suppress recombination in heterokaryotypes, meaning that the effects of recombination suppression are more prominent in Type II inversion polymorphisms where heterokaryotypes comprise a higher proportion of the population.

Recessive deleterious variants have been found to accumulate at a faster rate within inversions than in the collinear genome (Huang et al. 2022; Jay et al. 2021; Navarro et al. 2000). This is because suppressed recombination in heterokaryotypes lowers the effective population size of individual arrangements, thereby reducing the efficiency with which deleterious variants can be purged (Berdan et al. 2021; Faria, Johannesson, et al. 2019; Keightley and Otto 2006). As predicted, and as shown by empirical data from sunflowers (Huang et al. 2022), this effect is likely to be stronger for Type II inversions where heterokaryotypes are most abundant. It is also affected by arrangement frequency since the rarer arrangement is more likely to exist in a heterokaryotypic state and will have a lower effective population size. In the most dramatic cases, accumulation of recessive deleterious variants leads to homokaryotypes that exhibit clear fitness penalties (Berdan et al. 2022; Butlin et al. 1984; Jay et al. 2021; Wasserman and Koepfer 1975; Wielstra 2020) relative to heterokaryotypes, where the effects of recessive deleterious variants are masked. Even when no clear fitness penalties in homokaryotypes are observed, genomic studies have shown that rates of deleterious variation can be higher within balanced inversion polymorphisms (Huang et al. 2022; Zhang et al. 2024). Understanding rates of recessive deleterious variant accumulation and their fitness impacts has clear consequences for conservation since it could elevate risks of inbreeding depression. However, there are gaps in our understanding of the evolutionary dynamics of inversions that make it difficult to predict when such strong fitness impacts will be present or can be overcome by other mechanisms (Berdan et al. 2021, 2022; Zhang et al. 2024).

3 | Chromosomal Inversions in Marine Species

We performed a review of articles in which genetic signatures indicative of large polymorphic inversions have been identified in marine species (Table 1). In most cases, the primary method of detection was some variant of the local principal component analysis (PCA) method (see Box 1) combined with analysis of differences in heterozygosity between clusters. Although most articles referred to these signatures as inversions or putative inversions, only 10 out of 27 studies used complementary techniques such as genome sequencing or experimental verification to confirm that an inversion was present (denoted 'Verified' in Table 1). In keeping with the majority of articles, we continue to refer to these signatures as inversions for simplicity, however, it is important to acknowledge that other types of structural variant such as chromosomal fusions can block recombination to a similar extent and generate similar signatures in local PCA. Since these other recombination-inhibiting structural variants have similar effects on linkage disequilibrium (LD) to inversions they may also have comparable conservation implications, however, efforts to definitively distinguish these different types of structural variants are important as future work may reveal differences that impact conservation outcomes.

While the focus of many early studies was on species of commercially important ray-finned fish, inversions have now been identified in diverse taxa, including ascidians, gastropod molluscs, crabs and corals. Since the adaptive role of inversions is a crucial determinant of their conservation implications (see Section 4) our review focuses on the relevant selection mechanisms that are linked with inversion establishment and maintenance (see Section 2). Furthermore, we look at

TABLE 1 | Summary of studies that report large polymorphic inversions in marine species. Inversions that have been characterised with molecular or cytogenetic support for the breakpoints are denoted as ‘Verified’. Inversions detected using genetic marker data without further validation are referred to as ‘Putative’. Where possible, selective processes contributing to spread and maintenance of the inversion polymorphism are categorised as Type I or Type II. In cases where multiple inversions of different types are present or where the selective process is not clear no classification is given.

Species	Ecotype or Environmental association	Selective process	Distribution of inversions	Verified/ Putative inversion	References
Stony corals					
Reef coral *Acropora kenti* (GBR)	None found	Balancing selection inferred (Type II)	Karyotype frequencies vary very little between locations; not entire species range covered	Verified	Zhang et al. (2024)
Reef coral *Acropora tenuis* (WA)	Lagoon/Reef slope habitats	Divergent selection; high gene flow	MAF differences; different genotype frequencies	Putative	Thomas et al. (2022)
Crustaceans					
European green crab *Carcinus maenas*	Temperature adaptation along latitudinal gradients	Balancing selection under high gene flow (Type II)	Arrangement gradients in native and invasive ranges associated with cold tolerance and latitudinal divergence	Putative	Tepolt et al. (2022), Tepolt and Palumbi (2020)
Molluscs					
Black abalone *Haliotis cracherodii*	North–South cline; potential association with resistance to withering syndrome (WS)	Not resolved	Cline corresponds to environmental gradients/ distinct regions	Verified	Wooldridge et al. (2024)
Eastern oyster *Crassostrea virginica*	Genetic break between Gulf of Mexico and Atlantic coast	Divergent selection Potentially balancing selection in aquaculture	Inversions close to fixation; Few heterokaryotypes in the wild	Putative	Puritz et al. (2022)
European flat oyster *Ostrea edulis*	Association with parasite resistance; Some geographic association (North Sea, Eastern Mediterranean Sea)	Not resolved; limited data	Potentially genetic parallelism or introgression	Putative	Lapègue et al. (2023), Sambade et al. (2022)
Marine snail *Littorina fabalis*	Dwarf and Large ecotypes adapted to different wave-exposure conditions	Divergent selection in combination with underdominance generate strong inversion arrangement clines (Type I)	Deficiency of heterokaryotypes in hybrid zone	Putative	Le Moan et al. (2024)

(Continues)

TABLE 1 | (Continued)

Species	Ecotype or Environmental association	Selective process	Distribution of inversions	Verified/ Putative inversion	References
Marine snail *Littorina saxatilis*	Adaptation over multiple intertidal environmental axes (crab predation-wave action, and high-low shore). Parallel ecotype divergence in Spain, UK/France and Sweden	Divergent selection combined with balancing selection leads to clines in arrangement frequencies but rarely fixation of arrangements (Type II)	Distinct inversion arrangements characterise the different ecotypes which diverged in parallel and under gene flow	Putative	Faria, Chaube, et al. (2019), Kess, Brachmann, et al. (2021), Koch et al. (2022), Le Moan et al. (2024), Morales et al. (2019), Westram et al. (2023)
Ascidians					
Ascidian *Ciona intestinalis* (types A and B)	Pacific, Mediterranean/ North Atlantic	Divergent selection leading to speciation (Type I)	Differentially fixed inversion arrangements between sympatric lineages; polymorphic inversions within type B lineage	Verified	Satou et al. (2021)
Ray-finned fishes					
American eel *Anguilla rostrata*	None found	Balancing selection inferred	No contribution to population structure	Putative	Ulmo-Diaz et al. (2023)
Arctic charr *Salvelinus alpinus* (anadromous)	Local adaptation to high latitude environment inferred	Unclear; recent evolution of small inversion in one region points to adaptive mechanism	Polymorphism found in only one of four populations studied	Putative	Hale et al. (2021)
Atlantic cod *Gadus morhua*	Migratory/Stationary (Offshore/Coastal)	Divergent ecotypes partial arrangement fixation in four supergenes, however balancing selection maintains alternate arrangements and heterokaryotypes in some regions	One inversion associated with migratory behaviour; clinal patterns in other inversions suggest temperature, dissolved oxygen and salinity adaptation. Inversions independently inherited	Verified	Barth et al. (2019), Berg et al. (2016, 2017), Kess et al. (2019, 2020), Kirubakaran et al. (2016), Matschiner et al. (2022), Sodeland et al. (2022, 2016)
Atlantic halibut *Hippoglossus*	None found	Not resolved	Unclear; no geographic association; Low proportion of heterokaryotypes	Putative	Kess, Einfeldt, et al. (2021)
Atlantic herring *Clupea harengus*	Seasonal reproduction/ Water temperature	Divergent selection (Type I)	North–south divide; differential fixation of alternative arrangements	Verified	Fuentes-Pardo et al. (2024), Han et al. (2020), Pettersson et al. (2019)

(Continues)

TABLE 1 | (Continued)

Species	Ecotype or Environmental association	Selective process	Distribution of inversions	Verified/ Putative inversion	References
Atlantic salmon *Salmo salar*	Unclear	Unclear; recent establishment	Multiple inversions; some environmental association; polymorphism present in all populations	Verified	Stenløkk et al. (2022)
Atlantic silversides *Menidia menidia*	North (fast growing)/ South (slow growing)	Divergent selection	Strong local adaptation along latitudinal cline; divergence in temperature-dependent gene regulation	Verified	Akopyan et al. (2022), Jacobs et al. (2024), Tigano et al. (2021)
Capelin *Mallotus villosus*	Unclear	Balancing selection (Type II)	Polymorphism across locations of one lineage, some association with spawning habitat	Putative	Cayuela et al. (2020)
European eel *Anguilla anguilla*	Unclear	Unclear	Selective sweep (high frequency) in American eel, introgressed into European eel	Putative	Enbody et al. (2021), Tengstedt et al. (2025)
European plaice *Pleuronectes platessa*	Unclear; some geographic association correlating with salinity gradient	Balancing selection inferred (Type II)	Inversions polymorphic	Putative	Le Moan et al. (2021), Weist et al. (2022)
Goldsinny wrasse *Ctenolabrus rupestris*	Sexual antagonism	Balancing selection inferred (Antagonistic selection for sex-specific growth rates) (Type II)	Similar frequencies across locations, sexes and age classes; not entire species range covered	Putative	Jansson et al. (2023)
Horse-mackerel *Trachurus trachurus*	North/South (Association with temperature and oxygen content)	Divergent selection	Frequency differences correspond to geography (North–South divide; latitudinal genetic break)	Putative	Fuentes-Pardo et al. (2023)
Lesser sandeel *Ammodytes marinus*	Some association with sea bottom temperature	Balancing selection inferred (Type II)	Some arrangement frequency differences between polymorphic populations	Putative	Jiménez-Mena et al. (2020)
Lincod *Ophiodon longatus*	North/south	Divergent selection (Type I)	Fixation of different arrangements; admixed individuals in contact zone with latitudinal cline	Putative	Longo et al. (2020)

(Continues)

TABLE 1 | (Continued)

Species	Ecotype or Environmental association	Selective process	Distribution of inversions	Verified/ Putative inversion	References
Rainbow trout *Oncorhynchus mykiss*	Sex-specific migration 'supergene'	Balancing selection (sexually antagonistic), however arrangement fixation in some regions (Type II)	Sex-dependent karyotype frequencies; some latitudinal clinal pattern observed	Verified	Hale et al. (2024), Pearse et al. (2019)
Sablefish *Anoplopoma fimbria*	None found	Balancing selection inferred	No geographic differences in karyotype frequencies; potential accumulation of deleterious variation and linkage between inversions; not entire species range covered	Putative	Timm et al. (2024)
Seahorse *Hippocampus guttulatus*	Marine/lagoon habitats	Both divergent selection and associative overdominance	Differential fixation of arrangements corresponds to ecotypes; inversions polymorphic at some locations	Verified	Meyer et al. (2023)
Threespine stickleback *Gasterosteus aculeatus*	Freshwater/saltwater	Divergent selection	Inversions and other structural variants associated with freshwater and saltwater adaptation (phenotypic differences)	Verified	Jones et al. (2012), Li et al. (2022), Reid et al. (2021), Ross and Peichel (2008)

the management recommendations given and how an understanding of genomic structure could help inform conservation practices.

Publications reviewed in Table 1 include some striking examples of Type I and Type II inversions involved in ecotype adaptation to different habitat types across diverse taxa including species of fish, ascidians, molluscs, crustaceans and hard corals (Faria, Chaube, et al. 2019; Le Moan et al. 2021, 2024; Li et al. 2022; Meyer et al. 2023; Sambade et al. 2022; Thomas et al. 2022; Wooldridge et al. 2024). There is also evidence of inversions shaping complex adaptive traits such as migratory behaviour in Atlantic cod (Kirubakaran et al. 2016; Matschiner et al. 2022), growth rates in Atlantic silversides (Akopyan et al. 2022; Tigano et al. 2021), and spawning time in Atlantic herring (Han et al. 2020; Pettersson et al. 2019). Examples of Type I inversions can be found in the marine snail species *Littorina fabalis*, seahorses, ascidians and Atlantic herring (Han et al. 2020; Le Moan et al. 2024; Meyer et al. 2023; Satou et al. 2021). Some studies found an association of inversion arrangement frequency and geographical distribution correlating with many variables where the adaptive role of the inversions remained unclear (Enbody et al. 2021; Fuentes-Pardo et al. 2023; Jiménez-Mena et al. 2020; Longo et al. 2020; Satou et al. 2021; Wooldridge et al. 2024). Nevertheless, these examples clearly demonstrate how inversions can facilitate adaptation under gene flow in marine species.

Clear examples of Type II inversion polymorphisms that are maintained by some form of balancing selection across the sample range (Figure 1 Type II b) have been identified in goldsinny wrasse (Jansson et al. 2023), the American eel (Ulmo-Diaz et al. 2023), the Capelin (Cayuela et al. 2021), and the hard coral species *Acropora kenti* (Zhang et al. 2024). Examples of Type II inversions that form a clinal pattern can be found in European green crab (Tepolt et al. 2022), European plaice (Le Moan et al. 2021), rainbow trout (Pearse et al. 2019) and the snail species *Littorina saxatilis* (Faria, Chaube, et al. 2019). As expected for inversions where heterokaryotypes are abundant (Berdan et al. 2021; Huang et al. 2022), putatively deleterious mutations were found at higher rates within inversions in the coral *Acropora kenti* than in the collinear genome (Zhang et al. 2024). In rainbow trout, maintenance of an inversion polymorphism was attributed to antagonistic selection for sex-specific migration (Pearse et al. 2019) and to sex-specific growth rates in goldsinny wrasse (Jansson et al. 2023).

To infer selection mechanisms that lead to the establishment and maintenance of an inversion polymorphism, sampling must be performed at an appropriate scale. For example, in the coral *Acropora tenuis*, genetic signatures indicative of inversions were discovered that segregate between different thermal environments (lagoon vs. slope) on the same reef separated by distances of less than a kilometre (Thomas et al. 2022), whereas, in, for example, black abalone and Atlantic silversides, sampling over much larger distances (> 500 km) was required to discover adaptive ecotypes associated with inversions (Tigano et al. 2021; Wooldridge et al. 2024). In other cases, it is unclear if the sampling failed to capture representative numbers of potential subgroups, and some studies acknowledge a need for further sampling (Fuentes-Pardo et al. 2023; Ruigrok et al. 2022).

Among the 27 reviewed studies (Table 1) many highlight the important role that inversions play in evolution and adaptive fitness, and recognise that analysis of inversions should therefore inform fisheries and conservation management interventions. Further, seven of the reviewed studies gave clear recommendations specifically to inform the partitioning of populations into ecologically significant units with relevance for translocations, assisted migration, and stock management (Enbody et al. 2021; Fuentes-Pardo et al. 2023; Jiménez-Mena et al. 2020; Johansen et al. 2020; Longo et al. 2020; Puritz et al. 2022; Ulmo-Diaz et al. 2023; Wooldridge et al. 2024). One objective that a number of studies raise is that of safeguarding local adaptation and avoiding loss of diversity (Jansson et al. 2023; Jiménez-Mena et al. 2020; Weist et al. 2022; Wooldridge et al. 2024; Zhang et al. 2024). Another concerns the delineation of stock boundaries (Fuentes-Pardo et al. 2023; Johansen et al. 2020; Longo et al. 2020; Timm et al. 2024), and finally, more targeted research efforts are suggested for many species to substantiate management recommendations (Fuentes-Pardo et al. 2023; Jansson et al. 2023; Lapègue et al. 2023; Meyer et al. 2023; Pearse et al. 2019). As a general trend, it is recommended to maintain the polymorphism and inversion arrangement frequencies to sustain standing genetic variation of populations and species until the adaptive role of the inversion is clear.

4 | Implications of Inversion Polymorphisms for Conservation and Management

Since inversions often have large effects on phenotype and fitness, it is important that they are recognised and considered in conservation decision-making. Although doing so requires some new genetic tools (see Box 1) it is now practical to use inversions for making management decisions and genetic monitoring because (once verified) they can be genotyped using a range of low-cost methods. Thus, inversions can be used to monitor important components of putative non-neutral genetic variation, select individuals that can be used as broodstock or for translocation, and help inform the delineation of management units.

Here, we discuss the implications of inversion polymorphisms for four management activities. The first three of these are conventional activities, already in widespread use and typically focussed on improving overall demographic or genetic indices of populations without targeting a specific gene or trait. For these conventional activities, we consider the risks associated with inversion-naïve management (summarised in Table 2). As a fourth management activity, we consider the use of translocations to facilitate evolutionary rescue in the face of climate change. This management activity is considered separately because it involves deliberate targeting of climate-adaptive traits, the genetic architecture of which may be affected by the presence of inversion polymorphisms.

For three widely used management activities, Table 2 highlights risks for marine conservation if a large polymorphic inversion is present, but is either unknown or ignored (an inversion-naïve approach). The first of these activities, delineation of management units, directly impacts well established and widely used practices in fisheries management and the design of protected areas. The

BOX 1 | Methods to Discover and Karyotype Inversions.

Methods for discovery and genotyping of structural variants including inversions are advancing rapidly (Ebler et al. 2022; Sirén et al. 2021) and have been the subject of several comprehensive reviews (Alkan et al. 2011; Mahmoud et al. 2019), including some with a specific focus on evolutionary and conservation applications (Mérot, Oomen, et al. 2020; Wold et al. 2021). Recent reductions in cost and increased quality of DNA sequencing data, especially long-read data, have supported the development of advanced sequence-based techniques that now permit comprehensive discovery and genotyping of structural variants in a population sample (Sirén et al. 2021). While these developments present many exciting opportunities for conservation applications (Wold et al. 2021) the genomic resources required are not yet available for most taxa of conservation concern. Fortunately, large polymorphic inversions have unique properties that allow them to be detected using techniques that are already in widespread use for non-model organisms. Here, we outline how these techniques can be used to discover and genotype large, highly polymorphic (high minor allele frequency) inversions and refer the reader to other reviews (Mahmoud et al. 2019) for more general techniques that can be applied to other structural variant types including rare or small inversions.

In a conservation context we consider discovery and genotyping of inversions as separate processes. Typically, large polymorphic inversions need only be discovered once for a population, whereas genotyping might need to be performed often and sometimes under time pressure to inform selection of individuals, for example, for breeding or translocation. We first give a brief overview of the key steps involved in inversion detection, and then discuss methods for genotyping inversions, focusing on low-cost and rapid techniques.

Detecting and Mapping Inversions

Candidate inversions that are sufficiently old, large and polymorphic can be discovered using a sliding window scan for regions with exceptionally strong population structure as implemented in the software pcadapt (Luu et al. 2017), pcangsd (Meisner et al. 2021) and lostruct (Li and Ralph 2019). This technique, which we refer to as local principal component analysis or (local PCA), relies on the fact that inverted and ancestral arrangements diverge over time, resulting in strong differences in allelic content of SNPs. This manifests as strong population structure in a PCA based on SNPs within the inverted region, and a summary statistic capturing the degree of divergence evident from PCA (Galinsky et al. 2016; Meisner et al. 2021) can be used to measure the extent to which population structure within a genomic window is higher than expected (e.g., compared with the genome-wide mean). Plotting this statistic against genomic coordinates will reveal regions with strong genetic structure as contiguous blocks with exceptionally high values. Such regions may be considered candidate inversions; however, it is important to recognise that a variety of mechanisms, including recent strong selection, introgression and other types of structural variants, can also generate strong local genetic structure.

One issue with the local PCA method is that it typically requires a highly contiguous reference genome in which scaffolds are larger than inversions themselves. Many draft genomes may not meet this high bar since the types of inversions discussed in this review are often multiple megabases in size (Wellenreuther and Bernatchez 2018). In such cases, it may still be possible to discover inversions based on SNP data using linkage disequilibrium network analysis (LDna) (Kemppainen et al. 2015). This approach identifies clusters of SNPs in LD, does not require a reference genome, and has been used to detect inversions in marine snails (Faria, Chaube, et al. 2019), herring (Petrou et al. 2021) and an invasive crab (Tepolt et al. 2022).

The core principle underlying both local PCA and LDna approaches is the expectation that LD will be especially high within inversions due to the fact that recombination is greatly reduced in heterokaryotypes. Further evidence that a region of strong LD is generated by alternate karyotypes of a structural variant can be obtained by performing a PCA using SNPs captured within the region of elevated LD. If the loci are linked to a structural variant, three separate clusters representing alternate karyotypes are expected (Figure 2b) (Mérot, Oomen, et al. 2020). Heterokaryotypes should form the middle cluster, and individuals within this cluster should display an excess of heterozygous SNPs (Figure 2c) and should therefore have a significantly lower value of F_{IS} than the other clusters. This combination of statistical signatures is expected in situations where inheritance of alternate arrangements effectively behaves as a single large biallelic locus. Although large inversions often display such signatures, other types of large structural variants that strongly inhibit recombination between karyotypes such as chromosomal fusions (Wellband et al. 2019) can generate very similar patterns.

More definitive validation that population genetic signatures are indeed due to inversions can be obtained using direct sequence-based methods (Figure 2d). These methods typically rely on expected patterns of alignment for reads that span inversion breakpoints (Hanlon et al. 2022) or direct alignment of assembled chromosomes (e.g., Satou et al. 2021). While such methods are resource intensive, requiring deep short or long-read sequencing data (Cameron et al. 2019) and a reference genome, they need not be applied to a large sample of individuals. If an inversion is present, it should be identifiable within a single heterokaryotypic individual. Breakpoint positions inferred from this analysis should approximately correspond to regions of strong local structure in the local PCA method (see for example, Zhang et al. 2024) although it should be kept in mind that LD (and hence local structure) may extend beyond the breakpoints (Li et al. 2023; Stevison et al. 2011). It should be noted that while read-based methods provide independent evidence in support of inversions, they are not without issues that can result in false positives (Cameron et al. 2019; Hanlon et al. 2022). Since inverted tandem repeats often occur at inversion breakpoints, these can cause problems with read alignment, including read orientation which is used to infer the presence of an inversion. Manual inspection of alignments and long-read sequencing data can be used to reduce false positives when inferring structural variants including inversions from short-read data (David et al. 2024).

The signatures of LD and arrangement divergence make large polymorphic inversions highly detectable from population genomic data, however, definitively verifying inversions, and characterising breakpoints remains a challenging problem. Much of the difficulty arises because inversion breakpoints are often associated with repetitive sequences (Hanlon et al. 2022; Harringmeyer and Hoekstra 2022) and they may overlap with other structural variants including other inversions. Furthermore, there is evidence from human studies that inversion breakpoints can represent regions of genetic instability leading to inversion recurrence or 'toggling' over time (Porubsky et al. 2022). It remains to be explored to what extent such complexities can influence the evolutionary dynamics of inversions and hence their population management implications.

Karyotyping Inversions

Where population genetic data have been used to identify inversions (e.g., using local PCA or LDna) the karyotypes of sampled individuals can be determined based on the cluster to which they are assigned. As described above, a local PCA within an inversion should produce three clusters, with the middle cluster corresponding to heterokaryotypes and flanking clusters to alternate homokaryotypes (Figure 2b). If equivalent data are obtained for new individuals, they can then be karyotyped by co-analysis with the original data, which should result in their placement into one of these three clusters.

Karyotyping inversions for genetic monitoring, or to inform selection of individuals for translocation or breeding demands techniques that are rapid and very low cost. Although a wide range of techniques are available (Hanlon et al. 2022), many require detailed knowledge of inversion breakpoints or specialist lab equipment. A promising general principle for karyotyping assays in non-model organisms is the fact that alternate arrangements of an inversion are often highly divergent. Exploiting this principle (Figure 2), inversions have been karyotyped based on targeted sequencing of diagnostic SNPs (see for example, Mérot 2018), and restriction fragment length polymorphism (RFLP) assays where divergent SNPs overlap with restriction enzyme binding sites (Figure 2f) (Montanez-Gonzalez et al. 2021). In cases where arrangements are less diverged, it will be necessary to infer karyotype based on genotypes at larger numbers of SNPs. If individual karyotypes are not required, Pool-seq is a promising technique for characterising arrangement frequencies for inversions (Figure 2g) across many sampling sites (e.g., across a suspected cline or a large geographic range) (Kapun et al. 2014; Westram et al. 2023), while minimising sequencing costs.

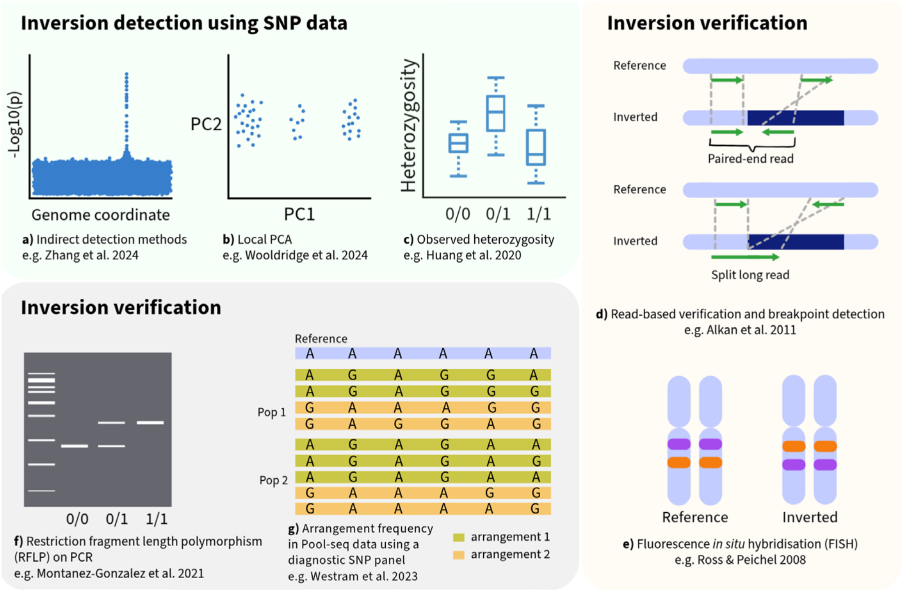
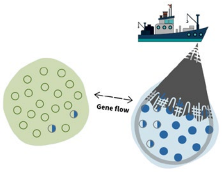
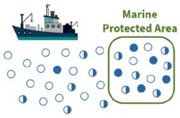
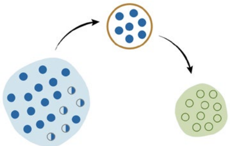
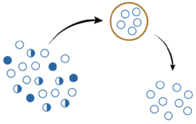
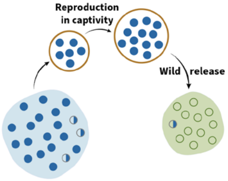
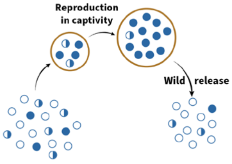


FIGURE 2 | Indirect inversion detection involves analysis of (a) sliding window genome scans for regions of high differentiation where statistically extreme values indicate putative inversions; (b) local principal component analysis within highly differentiated regions. Inversions should show three clusters where the middle cluster represents heterokaryotypes (0/1) which show (c) higher heterozygosity than either group of homokaryotypes. Inversion verification can be done with (d) read-based methods such as paired-end read and long-read approaches that consider read alignment, read direction, mapping quality and read length; or (e) experimental methods such as FISH. Inversion karyotyping can be performed using a panel of diagnostic SNPs which can be sequenced directly or (f) used as the basis for a restriction fragment length polymorphism assay. Arrangement frequencies in different populations can be determined at low cost using Pool-seq (g).

TABLE 2 | Risks of inversion-naïve implementation of conservation management activities. Each management activity is represented by two rows. Each row represents an undesirable outcome (risk), associated with ignoring either a Type I or Type II inversion polymorphism. Thus, the first row illustrates cases when barriers to gene flow are strong, inversion arrangements are almost alternately fixed between populations and where divergent selection and underdominance are more prominent (most relevant for Type I scenarios). The second row illustrates cases when balancing selection is maintaining inversions as polymorphic, and where balancing selection and rates of accumulation of deleterious recessive mutations are expected to be higher (most relevant for Type II scenarions). Risks shown are those most likely to be relevant to Type I or Type II polymorphisms respectively but are not exclusively associated with either type. Each risk is illustrated and described according to the following letter codes: (a) Near or complete arrangement loss due to overexploitation when ecotypes are not recognised as separate management units, (b) inadequate size and connectedness of protected areas, (c) translocation involving highly divergent ecotypes, (d) translocation failing to recognise a missing arrangement, (e) supportive breeding involving divergent ecotypes, (f) supportive breeding leading to distorted arrangement frequencies.

	Risks	Mitigation	Knowledge gap
Delineation of management units			
(a) Type I 	Failure to protect vulnerable genetic variation Loss of adaptive variation	Include inversion arrangements in delineation of management units Monitor inversion arrangement frequencies	Inversions remain unmapped in many species
(b) Type II 	Protecting only a small part of the population with high mutational load due to inversion polymorphism(s) with increased risk of inbreeding depression	Include elevated risks of inbreeding depression due to inversion polymorphisms in population viability analysis	Inversions remain unmapped in many species Limited understanding of the fitness consequences of recessive deleterious variation accumulated inside inversions
Translocations for genetic rescue			
(c) Type I 	Outbreeding depression	Target source populations with the same or similar arrangement frequencies if possible Established frameworks (Frankham et al. 2011) can be used to assess the risk of outbreeding depression	Inversions remain unmapped in many species
(d) Type II 	Translocated individuals may fail to include missing arrangements	Screen translocated individuals for inversion arrangements Attempt to restore historical arrangement frequency if known	Inversions remain unmapped in many species
Supportive breeding			
(e) Type I 	Swamping Outbreeding depression Loss of genetic diversity associated with inversions	Match arrangement frequencies in hatchery produced individuals with target population	Inversions remain unmapped in many species
(f) Type II 	Swamping Loss of genetic diversity associated with inversions	Match arrangement frequencies in hatchery produced individuals with target population	Inversions remain unmapped in many species

○ Homokaryotype arrangement A
◐ Heterokaryotype
● Homokaryotype arrangement B
🟩 Ecotype environment 1
🟦 Ecotype environment 2

second activity, genetic rescue, considers translocations in situations where a population is suffering from inbreeding depression or serious loss of genetic diversity due to small population size (Frankham 2015). The third activity, supportive breeding, is performed at a massive scale in the management of commercially exploited species (Laikre et al. 2010; Waples and Drake 2008) and could be an important tool for performing demographic rescue, but poses a risk to genetic diversity if used improperly (Laikre et al. 2010). Although supportive breeding sometimes also involves translocation, we consider it separately from genetic rescue because much larger numbers of individuals are involved, changing the nature of risks and mitigation strategies.

4.1 | Inversions in Delineation of Management Units and Protected Area Design

Inclusion of inversions in delineation of management units can improve conservation outcomes because inversions are expected to be strongly associated with adaptive variation (Berdan et al. 2023), a prediction which is supported by most empirical studies (see Section 2). Thus, inversion polymorphisms should be considered large-effect loci likely to be involved in population adaptation, and should be included in the delineation of evolutionarily significant units (Moritz 1994; Waples et al. 2020). ESUs are at the heart of conventional management which includes fisheries regulation and marine protected area design (Waples et al. 2008). Most frameworks for delineating ESUs incorporate two main axes of differentiation, reproductive isolation and adaptation (Hoelzel 2023; Waples 1995). Although the isolation axis can readily be measured using neutral genetic markers, adaptation is much more challenging to infer using genetic data and is therefore usually inferred based on proxies (habitat or phenotype) which have inherent limitations (Waples et al. 2022). Therefore, the presence of adaptive inversions provides a stronger case for ESU delineation on the basis of adaptation, and if inversions are ignored, important locally adapted populations may not receive adequate protection (Hoelzel 2023). This is especially important in cases where inversions delineate locally adapted populations that are experiencing gene flow and therefore would not be considered separate on the basis of isolation as measured for the neutral part of the collinear genome. Examples of populations that show strong ecotype divergence within inversions but much less so in collinear genomic regions include large and dwarf ecotypes of the marine snail *Littorina fabalis* (Le Moan et al. 2024), northern and southern populations of black abalone (Wooldridge et al. 2024), and northern and southern populations of lingcod (Longo et al. 2020).

Several theoretical and empirical studies have shown that recessive deleterious variants can accumulate at higher rates within inversions (see Section 2), especially Type II inversions where a high proportion of heterokaryotypes is maintained by balancing selection and the rate of purging is thus reduced because of the lower effective size of homokaryotypes. While this could elevate risks associated with inbreeding depression, further work is needed to determine the conditions under which this occurs. The existence of balanced lethal systems in nature (Wielstra 2020) indicates that recessive deleterious effects within inversions can be severe, even if such extreme cases may be rare (Berdan et al. 2022). In most Type II inversions, however, homokaryotypes are viable and may occur at or close to Hardy Weinberg proportions (Zhang et al. 2024) which suggests much milder fitness impacts of recessive deleterious variants. The extent to which the fitness of homokaryotypes is impacted by recessive deleterious variants in these systems, and how this might be exacerbated by inbreeding, is not yet well understood. Filling this knowledge gap could help with the planning of marine protected area networks by improving models used for population viability analysis (Pierson et al. 2015), especially if it is found that inversions have a significant impact on the risks of inbreeding depression.

4.2 | Inversions in Genetic Rescue

Translocation of individuals from a large outbred population into a smaller inbred one is a well-established technique that has been shown to improve the viability of vulnerable populations, a process known as genetic rescue (Frankham 2015; Ralls et al. 2020). Genetic rescue is rarely used in marine systems (except see Pregler et al. 2023); however, there is a growing body of evidence that it should be considered (Novak et al. 2020; van Oppen et al. 2017). Inbreeding and inbreeding depression occur in wild populations of marine species including sea lions (Acevedo-Whitehouse et al. 2003), cetaceans (Foote et al. 2021; Kardos et al. 2023) and fish (Ovenden et al. 2020). Inversions have the potential to act as a useful marker when selecting individuals for translocation as part of genetic rescue. When selecting source populations in the presence of inversions, the risk of outbreeding depression is likely to be reduced if translocated individuals are chosen to match the historical arrangement frequencies in the destination population. This is likely to be more important for Type I inversions, where heterokaryotypes are more likely to have reduced fitness (Faria, Johannesson, et al. 2019). If populations harbouring Type II inversions become very small, it is possible for one of the arrangements to be lost due to drift, a scenario that could exacerbate the chances of inbreeding depression. This is because Type II inversions are more likely to experience overdominance (higher fitness in heterokaryotypes) and there is evidence that recessive deleterious variants accumulate at faster rates in Type II inversions (Huang et al. 2022). Restoration of the lost arrangement through genetic rescue in this case could be particularly beneficial. One potential roadblock to the use of inversions in informing, for example, translocations is that local extinctions, overexploitation, and genetic drift in endangered populations can cause drastic shifts to historically established arrangement frequencies and limit options for available source populations. Therefore, in species at risk of population decline, there is an imperative to perform baseline genetic surveys and maximise protection of representative populations.

4.3 | Implications of Inversions for Supportive Breeding

Wild release of propagated individuals, also called supportive breeding, is a widespread practice in marine systems, especially for commercially harvested species where vast numbers of fish and shellfish are released with the goal of supplementing wild stocks (Hagen et al. 2021; Laikre et al. 2010). Supportive breeding is also used to boost the numbers of threatened species (demographic rescue) or restore habitats through increasing numbers of keystone species such as corals (Baums et al. 2022). The main risks associated with wild release arise from the introduction of large numbers of individuals from a potentially small gene pool (e.g., broodstock, colonies for clonal propagation). This can lead to a loss of genetic diversity over time due to reduced effective population size (Ryman and Laikre 1991), inhibit local adaptation by genetic swamping (Laikre et al. 2010), or reduce fitness via outbreeding depression (Laikre et al. 2010) if there is strong divergence between source and destination populations. One of the most important risks is that adaptive genetic diversity will be lost if the number of effective breeders in a hatchery is small. When large polymorphic inversions are present, these risks are magnified because a change in the arrangement frequency of an inversion will affect many hundreds of linked and potentially adaptive loci. Moreover, inversions are unlikely to be neutral to individual fitness, and so changes in the frequency of inversion arrangements away from original frequencies are likely to have negative impacts on population fitness. Hatchery production and wild release also increase risks associated with translocations such as outbreeding depression, especially if broodstock are taken from a population dominated by one arrangement and release is performed into a population where the alternate arrangement dominates.

4.4 | Inversions and Evolutionary Rescue

Evolutionary rescue refers to the situation where a population suffering decline due to a changing environment experiences recovery following the increase in abundance of adaptive genotypes (Carlson et al. 2014). The idea that evolutionary rescue could be facilitated through the active spread of adaptive variation, also known as assisted gene flow (Aitken and Whitlock 2013), is now being considered as a conservation action that could be beneficial in combating the negative effects of climate change (Catullo et al. 2019). Translocation for evolutionary rescue remains controversial because it is challenging to monitor in nature (Carlson et al. 2014) and because the benefits must be weighed against risks, such as outbreeding depression, swamping, spread of disease and loss of species integrity (Kovach et al. 2016). Nevertheless, evidence from natural experiments (Brauer et al. 2023; Oziolor et al. 2019) suggests that evolutionary rescue could be effective, and the severity of the climate threat to some species and ecosystems is forcing researchers to give serious consideration to this idea. In marine systems, evolutionary rescue is particularly prominently discussed in the context of coral reefs where bleaching due to marine heatwaves is considered an existential threat (Colton et al. 2022; DeFilippo et al. 2022; Hughes et al. 2017).

Large polymorphic inversions could have a major influence on the outcomes of interventions for evolutionary rescue because they can influence the genetic architecture of traits. This applies both to climate-adaptive traits targeted under an intervention (e.g., heat tolerance) as well as traits that have little effect on future climate fitness but may be adaptively important in other environmental contexts. Both are important because they influence the efficiency of rescue and the potential harms from outbreeding depression.

Here, we refer to the scenario in which adaptation to different environments is at least partially under the control of an inversion. Examples of inversions with arrangement frequencies that vary along a latitudinal cline suggest that this scenario may occur in a variety of high-level taxa including insects, fish and molluscs (Kapun et al. 2016; Longo et al. 2020; Ma et al. 2024; Wooldridge et al. 2024). Since many environmental variables often covary with latitude, these observations do not in themselves demonstrate that climate-related phenotypes are encoded by inversions; however, more convincing evidence has been found in flies where latitudinal clines in inversion frequency have been shown to shift over time (Anderson et al. 2005; Kapun et al. 2016).

The capture of climate-adaptive alleles within inversions could pose a double-edged sword for conservation. On the one hand, inversions are readily identified, allowing individuals with beneficial karyotypes to be selected for translocations, potentially enhancing the efficiency of assisted gene flow. On the other hand, suppressed recombination within inversions makes it more likely that climate-adaptive variation carried by an inversion arrangement could be tightly linked to alleles that are maladaptive for other traits in the context of the population requiring rescue. In this situation, introgression of climate-adaptive alleles into the target population could be inhibited by the presence of linked maladaptive variants. In addition, even if inversions are not associated with climate-related traits, their presence as polymorphisms within the population could increase the potential for outbreeding depression, especially for Type I inversions (Table 2). Thus, inversions have the potential to beneficially or detrimentally affect the efficacy and safety of evolutionary rescue.

We recommend thorough analysis of the role of inversions present, which includes considering risk factors of outbreeding depression and swamping. Understanding natural patterns of gene flow, divergence and selective forces should allow for informed decision-making on the effectivity and sustainability of management actions involving translocations of adaptive genotypes.

4.5 | Including Inversions in Conservation Decision Making

The Type I and Type II-based framework provided here is intended to serve as a tool to assist with genetic management of marine populations and to highlight the potential consequences if inversions are ignored. Guidelines are provided based on the extent of adaptive and deleterious variation expected for Type I and Type II inversion polymorphisms. To apply the framework, it is therefore necessary that inversions have been verified (see Box 1) and their karyotype frequencies characterised throughout the population. Even when this is given, it should be noted that the framework is a simplified model, reflecting expectations from theory and supported by a small empirical base (Table 1). Application of the framework is suggested when karyotype frequencies across a species range clearly indicate Type I or II adaptation for—example, distinct ecotypes (Figure 1; Type I), clinal adaptation (Figure 1; Type II a), or a uniform distribution of inversion arrangements (Figure 1; Type II b).

Important limitations of the Type I/Type II framework include the fact that it is not designed to account for complex structural variants, direct breakpoint effects, or inversion recurrence (see Box 1). A further issue is that multiple inversions may be present, and these may be of different Types (I or II), potentially leading to conflicting priorities. Besides this, we would like to stress the importance of understanding the selection pressures, as well as the adaptive, demographic and physiological processes involved in maintaining inversion polymorphisms. If relevant empirical evidence for the relative fitness of hetero- and homokaryotypes of a particular species is available (e.g., through analysis of hybrid zones or experimental crosses) this should override assumptions based purely on a Type I/II designation.

Even though large polymorphic inversions can capture a significant proportion of adaptive variation and act as supergenes, variation in other genomic regions should not be neglected. A recent study in marine snails, for example, found that adaptive variation encoded by at least 17 inversions was still only of a similar magnitude to that in the collinear genome (Koch et al. 2022) highlighting the importance of maintaining genetic diversity both within and outside inversions.

Contemporary conservation management is faced with increasingly complex challenges and an unforeseen level of urgency. This means we need thorough planning, realistic targets and cost-effective approaches to monitor management outcomes. When safeguarding genetic diversity, it is imperative to manage for adaptive potential. Therefore, knowledge of large-effect loci such as polymorphic inversions that shape adaptation can be hugely beneficial for species management and avoid risks associated with inversion-naïve interventions (Table 2). The evolutionary and ecological significance of inversion polymorphisms in many species suggests that these are important functional loci to be recognised in conservation genetics and general species management.

5 | Conclusions—What Is Needed to Bridge the Gap

Recent advances in whole genome sequencing have revealed large, polymorphic and adaptive chromosomal inversions in economically and ecologically important marine species (Table 1), and in many cases, these inversions can be used to inform decision-making around conventional genetic management (Table 2). However, some important gaps remain. First, despite an increasing number of papers describing highly polymorphic inversions, they remain uninvestigated in the vast majority of species. This problem should be resolved as techniques for identifying population genetic signatures of genomic structural variants from SNP data see greater application and as high-quality genomic resources, combined with improved sequencing technologies, allow these structural variants to be characterised into inversions, fusions and other large rearrangements. Second, more work is required to fully understand the evolutionary forces that allow inversions to become established and maintained. Attention should be paid to species- and population-specific conditions that influence the prevalence of inversion karyotypes. Examples from the literature illustrate the complexity of functions inversions can have in different species, but as a general rule, large polymorphic inversions are key candidates either supporting local adaptation in different habitats or enabling divergent strategies of, for example, mating, within populations (Hill et al. 2023; Veale and Russello 2017). Future work will shed light on the degree to which recessive deleterious variants accumulated on inversions contribute to mutational load in populations with different evolutionary histories, an important unknown governing the potential role of inversions in inbreeding depression. Finally, techniques that allow rapid and cost-effective karyotyping of inversions need to be further developed and more widely adopted for marine species, not least in key species of marine groups hitherto poorly investigated (e.g., seaweeds, seagrasses, corals, crustaceans and echinoderms). Such techniques will allow inversions to be used as markers for genetic monitoring and as rapid decision-making tools in a wide range of contexts.

Author Contributions

Nadja M. Schneller: conceptualisation (equal); writing – original draft (equal); writing – review and editing (equal); visualisation – figures (lead); investigation – reviewed papers (lead). **Jan M. Strugnell:** conceptualisation (equal); writing – original draft (supporting); writing – review and editing (supporting). **Matt A. Field:** conceptualisation (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Kerstin Johannesson:** conceptualisation (equal); Writing – original draft (supporting); writing – review and editing (supporting); visualisation – figures (supporting); investigation – reviewed papers (supporting). **Ira Cooke:** conceptualisation (equal); writing – original draft (equal); writing – review and editing (equal); visualisation – figures (supporting); investigation – reviewed papers (supporting). All authors approved the final version. All authors have read and agreed to the published version of the manuscript.

Acknowledgements

Many thanks to Claire Mérot and an anonymous reviewer for their very helpful suggestions in the review process. This work was supported by ARC SRIEAS Grant SR200100005 Securing Antarctica's Environmental Future, ARC Discovery Grants DP240102310 and DP250101690, and Vetenskapsrådet Research Grant VR 2021-04191. Open access publishing facilitated by James Cook University, as part of the Wiley ‐ James Cook University agreement via the Council of Australian University Librarians.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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