Genomic analyses indicate resilience of a commercially and culturally important marine gastropod snail to climate change

Matt J. Nimbs [Corresp., 1, 2], **Curtis Champion** [1, 2], **Simon E. Lobos** [3, 4], **Hamish A Malcolm** [5], **Adam D. Miller** [3, 4], **Kate Seinor** [1], **Stephen D. A. Smith** [1, 6], **Nathan Knott** [7], **David Wheeler** [8], **Melinda A Coleman** [1, 2]

[1] National Marine Science Centre, 2 Bay Drive, Southern Cross University, Coffs Harbour, New South Wales, Australia

[2] National Marine Science Centre, 2 Bay Drive, New South Wales Fisheries, Coffs Harbour, NSW, Australia

[3] School of Life and Environmental Sciences,, Deakin University, Warrnambool, Vic, Australia

[4] Deakin Genomics Centre, Deakin University, Geelong, Vic, Australia

[5] NSW Department of Primary Industries, Fisheries Research, Coffs Harbour, NSW, Australia

[6] Aquamarine Australia, Mullaway, NSW, Australia

[7] NSW Department of Primary Industries, Fisheries Research, Huskisson, NSW, Australia

[8] NSW Department of Primary Industries, Orange, NSW, Australia

Corresponding Author: Matt J. Nimbs
Email address: matthew.nimbs@dpi.nsw.gov.au

Genomic vulnerability analyses are being increasingly used to assess the adaptability of species to climate change and provide an opportunity for proactive management of harvested marine species in changing oceans. Southeastern Australia is a climate change hotspot where many marine species are shifting poleward. The turban snail, *Turbo militaris* is a commercially and culturally harvested marine gastropod snail from eastern Australia. The species has exhibited a climate-driven poleward range shift over the last two decades presenting an ongoing challenge for sustainable fisheries management. We investigate the impact of future climate change on *T. militaris* using genotype-by-sequencing to project patterns of gene flow and local adaptation across its range under climate change scenarios. A single admixed, and potentially panmictic, demographic unit was revealed with no evidence of genetic subdivision across the species range. Significant genotype associations with heterogeneous habitat features were observed, including associations with sea surface temperature, ocean currents, and nutrients, indicating possible adaptive genetic differentiation. These findings suggest that standing genetic variation may be available for selection to counter future environmental change, assisted by widespread gene flow, high fecundity and short generation time in this species. We discuss the findings of this study in the content of future fisheries management and conservation.

Genomic analyses indicate resilience of a commercially and culturally important marine gastropod snail to climate change

Matt J. Nimbs [1,2], Curtis Champion [1,2], Simon Lobos [4,5], Hamish A. Malcolm [3], Adam D. Miller [4,5], Kate Seinor [2], Stephen D. A. Smith [2,6], Nathan A. Knott [7], David Wheeler [8], Melinda A. Coleman [1,2-]

[1] Fisheries Research, NSW Department of Primary Industries, National Marine Science Centre, 2 Bay Drive, Coffs Harbour, NSW, 2450, Australia
[2] National Marine Science Centre, Southern Cross University, 2 Bay Drive, Coffs Harbour, NSW, Australia
[3] Fisheries Research, NSW Department of Primary Industries, Coffs Harbour, NSW, Australia
[4] School of Life and Environmental Sciences, Deakin University, Warrnambool Victoria, Australia
[5] Deakin Genomics Centre, Deakin University, Geelong Victoria, Australia
[6] Aquamarine Australia, Mullaway, NSW, Australia
[7] Fisheries Research, NSW Department of Primary Industries, Huskisson, NSW, Australia
[8] NSW Department of Primary Industries, Orange, NSW, Australia

Corresponding Author:
Matt J. Nimbs[1]
New South Wales Fisheries, National Marine Science Centre, 2 Bay Drive, Coffs Harbour, NSW, 2450, Australia
Email address: matthew.nimbs@dpi.nsw.gov.au

Abstract

Genomic vulnerability analyses are being increasingly used to assess the adaptability of species to climate change and provide an opportunity for proactive management of harvested marine species in changing oceans. Southeastern Australia is a climate change hotspot where many marine species are shifting poleward. The turban snail, *Turbo militaris* is a commercially and culturally harvested marine gastropod snail from eastern Australia. The species has exhibited a climate-driven poleward range shift over the last two decades presenting an ongoing challenge for sustainable fisheries management. We investigate the impact of future climate change on *T. militaris* using genotype-by-sequencing to project patterns of gene flow and local adaptation

across its range under climate change scenarios. A single admixed, and potentially panmictic, demographic unit was revealed with no evidence of genetic subdivision across the species range. Significant genotype associations with heterogeneous habitat features were observed, including associations with sea surface temperature, ocean currents, and nutrients, indicating possible adaptive genetic differentiation. These findings suggest that standing genetic variation may be available for selection to counter future environmental change, assisted by widespread gene flow, high fecundity and short generation time in this species. We discuss the findings of this study in the content of future fisheries management and conservation.

Introduction

Rapid climate change is impacting the physical state of the world's oceans and directly threatening the structure and function of marine ecosystems. In particular, ocean warming and marine heatwave events, ocean acidification and deoxygenation, changes to ocean currents, and sea-level rise are already impacting many marine ecosystems and associated socioeconomic and cultural values at a global scale (Brierley and Kingsford 2009; Doney et al. 2011; Orr et al. 2005; Poloczanska et al. 2013, 2016; Scavia et al. 2002). Shifts in the physical ocean climate pose a direct threat to many of the world's commercial fisheries, causing changes in species distributions and abundances, altering habitats, decoupling critical trophic interactions, and pushing species beyond their physiological limits (Holland et al. 2021; Hollowed et al. 2013; Roessig et al. 2004; Sumaila et al. 2011). These effects are expected to reduce harvestable biomass in many fisheries (Brander 2013), with studies predicting reductions in catch of up to 40% for tropical fisheries alone under the RCP8.5 scenario (Lam et al. 2020). Projections suggest that climate change will continue to be an ongoing challenge for sustainable fisheries management into the future (Cheung et al. 2010), highlighting the importance of research aimed at understanding the resilience of individual fisheries to climate change effects, and identifying interventions capable of 'climate-proofing' vulnerable fisheries (Fankhauser and Schmidt-Traub 2011; Harte et al. 2019).

Evidence suggests the ability of many marine species to track their thermal niche via migration is likely to be outpaced by rapid climate change (Hiddink et al. 2012; Vranken et al. 2021). This typically applies to less vagile organisms whose persistence will depend more on their ability to

adapt to new thermal environments, either through plasticity or genetic evolution (Donelson et al. 2019; Munday et al. 2013; Somero 2010). Species with wide latitudinal ranges often show genetically based clines across thermal gradients (Berger et al. 2013; Jenkins et al. 2019; Pereira, Sasaki, and Burton 2017), suggesting standing genetic variation in quantitative traits might be available for adaptation to new environments (Barrett and Schluter 2008; Sasaki et al. 2022). Yet it is anticipated that selection itself may fail to keep pace with rapid climate change, particularly in long-lived organisms (Vranken et al. 2021; Wood et al. 2021). In such cases, gene flow is likely to play a critical role in the adaptation process, particularly when strong biological connections among locally adapted populations from thermal environments are present (Miller et al. 2019; Sork et al. 2010). Consequently, species with high connectivity among locally adapted populations may be deemed less at risk than those species with limited gene flow and poor dispersal capabilities (Ayre and Hughes 2004; Coleman 2015). In such cases, strategic intervention measures may be needed to maximise the adaptive capacity of threatened fish stocks, such as augmentation activities that include deliberately introducing genotypes from warm adapted populations to those at risks of maladaptation (Aitken and Whitlock 2013; Hagedorn et al. 2018; Layton et al. 2020; Hoffmann, Miller, and Weeks 2021). Consequently, the challenge for fisheries managers is understanding when interventions of this nature will be necessary in order to mitigate the risks of climate change.

Population genetics has played a key role in characterising structure and patterns of gene flow among populations, especially in commercially important marine species over the last few decades (Miller et al. 2019; Smith, Francis, and McVeagh 1991; Ward 2000; van Oppen and Coleman 2022). This field of research has been revolutionised by modern DNA sequencing technologies that now allows for genome wide estimates of genetic variation, providing unprecedented power for resolving fine scale patterns of genetic structure (Cheng et al. 2021; Milano et al. 2014; Sağlam et al. 2021) and signatures of adaptive genetic differentiation among fishing stocks spanning environmental gradients (Quigley, Bay, and van Oppen 2020; Riquet et al. 2013). Combined, this information can greatly assist fisheries management by providing insights into the availability of standing variation for adaptation to future environmental challenges, and the potential role of gene flow in assisting the adaptation process (Mason et al. 2022; Papa et al. 2020; Valenzuela-Quiñonez 2016). Importantly, this information can help to identify fish stocks most at risk of maladaptation, and to guide stock augmentation programs

aimed at introducing novel genotypes for selection to act upon to help combat future environmental challenges (Bernatchez et al. 2017; Reiss et al. 2009; Waples and Naish 2009).

Marine gastropod snails support many commercial and recreational fisheries around the world (Dolorosa et al. 2010; Foale and Day 1997; Leiva and Castilla 2002), many of which are expected to be susceptible to climate change effects (Ortíz, Arcos-Ortega, and Navarro 2022; Valles-Regino et al. 2022). Specifically, evidence suggests that ocean warming has the potential to suppress larval development, delay gonad maturation, reduce fecundity, stunt growth, and increase susceptibility to disease in many species, while increased ocean acidification is expected to compromise shell production in others (Holland et al. 2021; Leung, Russell, and Connell 2020; Zacherl, Gaines, and Lonhart 2003). However, some marine gastropods have broad latitudinal distributions and show genetically determined clines across thermal gradients, and strong biological connections over vast geographic distances due to long pelagic larval dispersal stages (Kelly and Palumbi 2010; Miller et al. 2016; Neethling et al. 2008; Villamor, Costantini, and Abbiati 2014). These findings suggest that some species might possess heritable genetic variation for adaptation to future thermal environments, which maybe assisted by extensive gene flow across thermal gradients (Johansson 2015; Sanford and Kelly 2010; Zardi et al. 2011). However, information for some marine gastropod groups is still lacking and is urgently needed to inform future management.

Benthic marine gastropods represent approximately 2% of the global marine mollusc fishery (Department 1997, 2012), with some species having high economic value being targeted in small-scale artisanal fisheries (i.e *Haliotis* spp., *Strombus* spp., *Busycon* spp, and *Concholepas* spp.). In recent decades commercial landings have grown with wild-stock catch increasing from 75k metric tonnes (mt) in 1979 to 103k mt in 1996 (Department 1997), however, some gastropod fisheries have been identified as being significantly threatened by climate change (Carranza and Arim 2023; Ramos et al. 2022). Unfortunately, information of the genetic structure and resilience of many commercially important gastropods is lacking, including trochid snails. To date, only a handful of studies have investigated patterns of population genetic structure among trochoid fisheries (Berry et al. 2019; Díaz-Ferguson et al. 2010; Nikula, Spencer, and Waters 2011), and, to our knowledge, no study has investigated patterns of adaptive genetic variation across the entire range of any trochid species using a dataset that includes thousands of genome-wide variants. *Turbo militaris* Reeve, 1848, is a large intertidal and shallow subtidal turbinid (Family

Turbinidae) from south-eastern Australian coast that is traditionally and recreationally harvested for human consumption (Yearsley, Last, and Ward 1999) and supports a 6.6 tonne turban snail commercial fishery in New South Wales (NSW) (DPI NSW 2019). Like many trochids, *T. militaris* is showing signs of climate stress, with evidence of a poleward range shift since the turn of the century (ALA 2018; GBIF 2016, Benkendorff & Przeslawski 2008). Given that range shifts in commercially important marine species can have socio-economic and management implications (Madin et al. 2012; Bonebrake et al. 2018), it is prudent to explore the capability of *T. militaris* to adapt to ongoing environmental change in order to maintain extant populations.

In this study we investigated patterns of population genetic structure in *T. militaris* using genotype-by-sequencing and a sampling regime encompassing the species' entire distribution spanning seven degrees of latitude and a difference of 3.9°C in mean annual sea surface temperature. We explore patterns of gene flow and population connectivity across the sampling distribution and integrate genomic and geospatial data to tests for genotype-environmental associations (GEAs) indicative of adaptive genetic differentiation between populations. Findings from this study provide valuable insights into the spatial scales of gene flow and the availability of standing genetic variation for adaptation to future environmental conditions. We discuss the findings of this study in the context of future fisheries management.

Materials & Methods

Sampling

Eight rocky shore locations (0 to 5m depth) were selected for sampling (Table 1) spanning the known range of *T. militaris* from Hastings Point (northern NSW) to Jervis Bay (southern NSW) (Fig. 1), representing a seven-degree latitudinal and a 3.9°C annual mean sea surface temperature gradient. Additionally, to sample a known cross-shelf gradient of temperature (less confounded by distance and unconfounded by latitude), three locations at varying distances from shore and under different temperature regimes were selected: Nambucca Heads (mainland), Split Solitary Island (3 km from the mainland) and South Solitary Island (7 km from the mainland). These represent inshore, mid-shelf, and offshore positions, respectively, with an annual mean sea temperature varying by about 1^{o}C from inshore to offshore (Malcolm, Jordan, and Smith 2010). Notably, South and Split Solitary islands are remote from shore and are also likely to have very low to no harvesting pressure. Between 25 and 30 *T. militaris* individuals were collected from

each location (Table 1). As internal foot muscle tissue was found to yield clean, high molecular-weight DNA, it was necessary to narcotise specimens. Field collections were carried out under a scientific collection permit granted by the NSW DPI Fisheries under section 37 of the NSW Fisheries Management Act 1994 (#P01/0059(A)-4.0).

DNA extraction and genotyping

Approximately 25 mg of foot muscle tissue was sampled from each specimen using sterilised scalpel and forceps, avoiding the inclusion of mucous-rich epidermal tissue. Tissue samples were immediately placed in 2.0mL Eppendorf snap-lock microcentrifuge tubes containing 500µL of hexadecyltrimethylammonium bromide (CTAB) lysis buffer (100mM TrisHCl, 20mM EDTA, CTAB 2% w/v, NaCl 1.5M) and refrigerated at 4°C for two weeks. Proteinase K (30 µL at 20mg/mL) was added to the samples which were incubated in a Allsheng shaking incubator at 60ºC, 200 rpm overnight. Samples were cooled to room temperature and purified by addition of an equal volume of 24:1 chloroform isoamyl. After centrifugation, the aqueous phase was retained and DNA was precipitated by the addition of 800 µL of dilute CTAB buffer (100mM TrisHCl, 20mM EDTA, CTAB 2% w/v) to each tube which were incubated in an Aosheng MSC-100 shaking incubator at 60ºC at 400 rpm until DNA/CTAB complexes were visible. After centrifugation, the DNA formed a pellet which was twice cleaned with 70% ethanol by repetitive inversion. The DNA pellet was air-dried to remove residual ethanol and subsequently resuspended in sterile lab-grade water. Extracted DNA was quality checked using NanoDrop, Qubit assay and gel electrophoresis.

For single nucleotide polymorphism (SNP) genotyping, 20 µL of extracted DNA was sent to Diversity Arrays Technology Pty Ltd (Canberra, Australia) (DArT). The DArT organisation provides a process pipeline of whole-genome profiling, without the need for a reference genome (Jaccoud et al. 2001). High-throughput DArTseq technology was used to genotype *Turbo militaris* DNA. Here, the PstI-based complexity reduction method (Wenzl et al. 2004) was applied for the enrichment of genomic representation with single copy sequences. This method involved the digestion of DNA samples with a cutting enzyme PstI, paired with a set of secondary frequently cutting restriction endonucleases, ligation with site-specific adapters, and amplification of adapter-ligated fragments. Post digestion with a restriction enzyme pair, a PstI-overhang-compatible oligonucleotide adapter was ligated, and the adapter-ligated fragments

were amplified in adherence to standard protocol (Wenzl et al, 2004). To develop SNPs, the DArTseq technology was optimized using two PstI-compatible adapters corresponding to two different restriction enzyme overhangs. The genomic representations were generated following the procedures described by Kilian et al. (2012). Next-generation sequencing technology was implemented using HiSeq2000 (Illumina, USA) to detect SNP markers. Sequence data was analysed using DarTsoft14 and DArTdb (Killian et al. 2012).

SNP calling

In total, 208 individual *T. militaris* were initially genotyped with the DArTseq™ platform yielding a total of 19,837 SNP loci with a mean read depth of 15.31 and 10.73% missing data. To improve SNP quality, while optimising the number of loci available for population genomic analyses, quality control filters, based on the descriptive statistics from the DArTseq™ pipeline, were applied to data using the R package dartR v.2.7.2 (Gruber et al. 2019; Mijangos et al. 2022). Prior to SNP quality control, we checked for the presence of genetically related individuals, as their inclusion can lead to biased genetic estimations of downstream analyses. We calculated a similarity genetic distance matrix for individuals on the proportion of shared alleles per pairs of individuals with the function *gl.propShared* in *dartR*. Two individuals, one from Nambucca Heads (NAM07) and one from South Solitary Island (SSI16) were characterised as closely related and were removed from downstream analyses.

Two SNP datasets were generated for analyses: dataset ‘1’ for the analysis of overall genetic structure, and dataset ‘2’ for tests of GEAs and the identification of candidate loci. Both datasets were generated by retaining a single SNP per tag, removing secondaries, applying a locus and individual call rate of 80%, reproducibility threshold of 80%, and a Hamming distance threshold of 0.2 to control for the influence of linkage disequilibrium between loci. SNPs were called for dataset ‘1’ by applying a minor allele frequency (MAF) threshold of 0.03 and removing all loci departing from Hardy–Weinberg expectations. In contrast, SNPs were called for dataset ‘2’ by setting MAF to 0.01, and not filtering out SNP loci deviating from by Hardy–Weinberg expectations (all loci included). Finally, we also used *poppr* (Kamvar, Tabima, and Grunwald 2014) in the R package to calculate the number of private alleles found in each population, and remove these SNPs using *gl.drop.loc* in package *dartR*. After filtering, a total of 3,527 and 6,852 SNP loci for 206 individuals (Table 2) were retained for data sets ‘1’ and ‘2’, respectively.

Tests for population differentiation

Several estimates of genetic diversity were generated using the *poppr* package in R, including observed (HO) and expected (HE) heterozygosity and allelic richness (AR) (Joop Ouborg, Angeloni, and Vergeer 2010). For AR, allele counts were rarefied by the minimum number of individuals genotyped using the *allelic.richness* command in the R package *hierfsta*t (Weir and Goudet 2017). Statistical differences in genetic diversity measures among sites was estimated using the *Hs.test* function in the R package *adegenet* (Jombart 2008). Departures from random mating were calculated using F_{IS} (inbreeding coefficient) for the overall dataset and for each sample location using the *basic.stats* function in *hierfstat.*

Tests for population genetic structure were subsequently performed, by calculating global population differentiation (F_{ST}) with 95% confidence limits (Weir & Cockerham, 1984), and population pairwise measures of F_{ST} with significance determined using permutation (999) in the *dartR*. Multiple testing effects were corrected for using the Benjamini–Hochberg FDR procedure (Benjamini and Hochberg 1995). An analysis of molecular variation (AMOVA) was performed in the R package *poppr* (Kamvar, Tabima, Everhart et al, 2014), using a model that partitioned variation among sample sites and within sample sites, with significance based on a randomization test with 999 permutations. A mantel test of isolation by distance (IBD) was carried out using the *gl.ibd* (Rousset 1997) function in the R package *dartR* (Gruber et al. 2019) with results visualised in a scatterplot. A discriminant analysis of principal components (DAPC) was performed using *adegenet* package in R (Jombart 2008). The *find.clusters* function was used to detect the number of clusters in the population. The best number of subpopulations has the lowest associated Bayesian Information Criterion (BIC). A cross validation function (Xval.dapc) was used to confirm the correct number of PCs to be retained. Finally, we used sparse non-negative matrix factorisation (sNMF) implemented in the R package *LEA* (Frichot and François 2015) in R. This algorithm estimates the genetic ancestry components for each sample. For this study, 15 runs were performed with $\alpha = 100$ for each K value (one to eight). The selection of the best number of putative ancestral populations was guided by the cross-entropy criterion (wherein, for K, a plot of the cross-entropy curve formed a ‘knee’) and the results from the best run were visualised using the *barplots* function.

Environmental variables

Physical oceanographic data were downloaded from the Copernicus Marine Environment Monitoring Service (https://marine.copernicus.eu), using a 20-year historical time-series encompassing 2001–2020 (daily temporal resolution) matched to each sampling location. These variables included temperature, water flow and productivity: sea surface temperature (SST) at 0.05º spatial resolution; remotely-sensed eddy kinetic energy (EKE) at 0.25º spatial resolution; and remotely-sensed chlorophyll a concentration (CHLa) at 0.04º spatial resolution (Table 2). The native spatial resolutions of oceanographic variables were used when matching daily data to sampling locations. Mean values were calculated for each variable by averaging the daily data. In addition, the lowest and highest SST for each location was extracted, and an absolute temperature range variable (temp.range) was calculated by subtracting the minimum from the maximum. A *pairs.panels* scatter plot of matrices was generated in the *R* package *psych* to confirm a lack of (Pearson's) correlation between variables ($r^2 \leq 0.8$), which were subsequently used in GEA analyses (described below).

Genome–environment association (GEA) analyses

To detect putative genomic signatures of selection, tests for GEAs were conducted using two complementary models: latent factor mixed models (LFMM2) (Caye et al. 2019), and the Bayesian method available in BayPass V1.01 (Gautier 2015). BayPass and LFMM accounted for potentially confounding allele frequency differences due to population structure in a mixed linear model framework, but in different ways: LFMM estimates GEAs when simultaneously correcting for population structure with latent factors, while BayPass uses a neutral covariance matrix constructed from population allele frequencies. The subset of environmental variables described above were used as predictor variables for both analyses.

Genotype-environment associations were explored with Baypass V1.01 (Gautier 2015) under the auxiliary (AUX) covariate model (-covmcmc and - auxmode flags). The first core model (without the environmental data) was run to estimate a covariance matrix (Ω) of population allele frequencies, which is an approximation of genomic differentiation between populations caused by demographic history. In order to reach convergence and reproducibility of the MCMC estimates, five independent runs, each with a randomly chosen seed were performed using default parameters, except for: pilot runs length of 1000

iterations, number of sampled parameter values of 1000, and a burn-in period length of 2500 iterations. Secondly, the average of the five covariance matrixes was used as input for the auxiliary covariate model to detect evidence of an association corrected for population structure. Environmental variables were scaled using the "-scalecov" option and the same running parameters as the core model were applied. Finally, the strength of association between genotype and the covariates was assessed by calculating the average of the log-transformed Bayes Factor (BF) in deciban units (dB) for each locus and environmental predictor. Significance was determined following Jeffrey's criterion for decisive associations ($BF_{IS} \geq 20$) (Jeffreys 1939).

Latent factor mixed models (LFMM2) tested for linear relationships between environmental variables and genetic variants with random latent factors using a least-square method. Population structure was inferred by estimating individual ancestry coefficients based on sparse non-negative matrix factorisation (SNMF) method implemented in the *snmf* function in the *R* package *LEA* v3.10.2 (Frichot and François 2015). Ancestry coefficients were determined for 1–8 ancestral populations (*K*) by generating an entropy criterion that evaluates the fit of the statistical model to the data using a cross-validation technique (Frichot and François 2015). The *K* with the lowest cross-entropy value using 100 repetitions for each *K* value was selected. Subsequently, the optimal factor, K=1, was used to inform the LFMM to identify whether allele frequencies were correlated with any of the environmental variables. To increase the statistical power of associations, missing genotype data were imputed via the '*impute'* function in the *LEA* package, using the most common allele frequency observed in each *K* with the method '*mode*'. Next, we used the function *lfmm_ridge* to compute a regularised least-squares estimate using a ridge penalty. Individual associations between each SNP frequency and each environmental variable were assessed using statistics test calibrated using genomic inflation factor (function *lfmm_test*). Corrections for multiple comparisons were applied with the Benjamini-Hochberg algorithm with a false discovery rate (FDR) threshold of 5% (Benjamini and Hochberg 1995). Significance associations were determined using a threshold of 0.001, since the probability of finding a false positive result increases with lower thresholds (Ahrens, Byrne, and Rymer 2019).

The gradient forest (GF) algorithm was subsequently used to describe the strength of the

associations of spatial, environmental variables and candidate loci and to map spatial patterns of allelic turnover in climate space (Ellis, Smith, and Pitcher 2012; Fitzpatrick and Keller 2015). Gradient forest is a machine learning method initially developed to model the turnover of ecological community assemblages in relation to environmental gradients (Ellis et al. 2012). Recently, this method has been adapted as a landscape genomics toolbox, substituting allele frequencies at genetic loci for species to model allelic turnover in climatic space (Fitzpatrick and Keller 2015). The turnover functions in gradient forest allow for inference of the environmental predictors driving observed changes in allele frequency (Fitzpatrick and Keller 2015). Analyses were implemented in the *R* package *gradientForest* (Ellis et al. 2012), using a regression tree-based approach to fit a model of responses between genomic data and environmental variables (Capblancq et al. 2020). Specifically, adaptive genetic variation turnover were modelled on the seascape using the candidate SNPs (derived from LFMM, and BayPass) set as the response variables. The machine learning algorithm partitioned allele frequencies at numerous splits values along each environmental gradient and calculated the change in allele frequencies for each split. The split importance (i.e., the amount of genomic variation explained by each split value) was cumulatively summed along the environmental gradient and aggregated across alleles to build a non-linear turnover function to identify loci that are significantly influenced by the predictor variable (Ellis et al. 2012). The analysis was run over 500 regression trees for each of the four environmental variables with all other parameters at default settings. The cumulative goodness-of-fit among SNPs was represented as an R^2 value indicating how well a predictor explained changes in allele frequency and which predictors were most important in predicting genomic changes. The resulting multidimensional genomic patterns were summarised using principal component analysis (PCA), allowing the relative importance of predictor variables on allelic turnover to be visualised. Finally, using the top gradient forest model, we interpolated genetic composition and allelic turnover across the sampling range of eastern Australia.

Results

Overall population genetic structure

Patterns of genetic diversity did not differ greatly across the eight sample locations (H_O = 0.186 – 0.212; AR = 1.630 – 1.640; Table 3). Most sites showed a weak excess of heterozygotes (F_{IS} = 0.048 – 0.118), however these estimates did not differ significantly from zero ($p > 0.01$; Table 3). Overall genetic differentiation was found to be significant, but weak and close to zero (global F_{ST} = 0.002, $p < 0.001$) indicating a lack of genetic structure among sampling locations (Table 3). These findings are further supported by weak, yet significant, estimates of genetic differentiation among all pairs of sampling locations (F_{ST} = 0.000 – 0.004, Table 4). AMOVA also indicated a lack of overall genetic structure indicating genetic variance attributed to differences among sites to be non-significant (0.212, $p > 0.05$) while the majority of variance was explained by genetic variation between individuals within sites (99.86, $p > 0.05$). Similarly, DAPC and LEA analyses indicated a lack of genetic structure, both identifying a single population cluster (K = 1). Finally, Mantel tests revealed no significant relationship between genetic differentiation and distance between sampled locations (R2 = 0.03356, p = 0.278) providing further evidence of panmixia.

Genotype x environment associations

BayPass and LFMM each identified a number of candidate SNP loci exhibiting significant genotype-by-environment associations for each of the environmental predictors tested (Fig. 2. BayPass detected between 0 and 2 SNPs with significant correlations (log10(BF) > 20) for each of the environmental predictors, with zero overlap in candidates between predictors. In contrast, LFMM detected between 5 and 12 SNPs that were significantly correlated with each of the environmental predictors (Fig. 2), but with only 2 loci overlapping between the EKE and SST predictor variables. Concordance of candidate SNP loci between methods was low (3 loci only; Figure 2) but expected given these methods have varying sensitivities to detecting loci under selection, use different methods for controlling for demography, and adopt different association algorithms. Given that *T. militaris* exhibits panmixia, its lack of population structure was likely to influence the inference of omega matrix and K clusters on BayPass and LFMM respectively. Furthermore, LFMM tests for relationships between individual-based allele frequencies whereas BayPass is at population level. Additionally, sampling design is likely to have had an influence, wherein a strategic sampling design accommodated to environmental heterogeneity and spatial variation on a landscape is essential to potentially identify and validate patterns of local adaptations across natural populations. Overall, GEAs indicated that a larger proportion of SNPs

were significantly associated with temp range (13) and CHLa (11), followed by EKE (7) and SST (5).

Gradient Forest modelling used the unique candidate adaptive loci detected by both LFMM and BayPass (Lu et al. 2021), with 39 in total, 4 in BayPass and 35 in LFMM, but three were shared between both analyses and one was shared within LFMM (variables EKE and SST) (thus 39 - 3 - 1 = 35 unique candidate loci). Gradient forest analyses showed 14 of the 35 candidate SNP loci to be significantly correlated with environment (R^2 values > 0; mean = 0.08, range 0.003 – 0.3). Overall, EKE, CHLa and SST were found to be the most important predictors of genomic variation, while temp range had less of an effect (Figure 3). Turnover functions from the GF model show the weighted cumulative importance values and sharp turnovers for all environmental predictors, but again with temp range having lower importance relative to all other predictors (Figure 3a). Biplots based on the first two principal components captured approximately 99% of the total variation and point to EKE and SST as the most prominent drivers of genomic variation (Figure 3b). A spatial depiction of genomic composition in multi-dimensional climatic space based on PCA is provided in the allelic turnover map (Figure 3c). The map indicates that the turnover of putatively adaptive allelic variation tracks closely with latitude, with the genomic composition of northern and southern most sampling locations being distinct from those from geographically intermediate locations (Fig. 3d).

Discussion

Understanding spatial patterns of gene flow and local adaptation can help predict species responses to climate change and to identify populations most at risk of maladaptation (Hoffmann and Sgrò 2011; Sexton et al. 2009). Such information is critically important for assisting with the adaptive management of commercially important marine species, many of which are already showing signs of climate stress (Cheung et al. 2013; Pinsky et al. 2018; Sunday et al. 2015). This study represents the first population genomic analysis of *T. militaris*, a commercially and culturally important trochid marine gastropod from the east coast of Australia, with the purpose of informing fisheries managers about vulnerability of this species to future climate change. Analyses of SNP genotypes across the species' entire distribution spanning seven degrees of latitude and 3.9°C in mean annual sea surface temperature indicate the presence of a single admixed, and potentially panmictic, demographic unit with no evidence of genetic subdivision

along the entirety of its range. Furthermore, significant genotype associations with heterogeneous habitat features were observed at regional spatial scales, including associations with sea surface temperature, ocean currents, and nutrients, indicating possible adaptive genetic differentiation among sample locations. Combined, these findings provide insights into the potential resilience of *T. militaris* to changing marine climates and the potential influence of gene flow and selection on future adaptive responses.

Evidence of panmixia

Our analyses point to a lack of genetic structure across the entire distribution of *T. militaris* indicating widespread gene flow along the eastern seaboard of Australia. Such genetic patterns are also found amongst other trochoid taxa with long pelagic larval phases which are expected to facilitate long distance dispersal (Berry et al. 2019; Díaz-Ferguson et al. 2010; Nikula et al. 2011; Silliman, Grosholz, and Bertness 2009). Several other eastern Australian marine invertebrates also exhibit high gene flow facilitated by larval traits including the Crown-of-thorns sea star (*Acanthaster* spp.) (Pratchett et al. 2015), the surf bivalve *Donax deltoides* Lamarck, 1818 (Murray-Jones and Ayre 1997; Miller et al. 2013) and the black sea-cucumber *Holothuria* (*Mertensiothuria*) *leucospilota* (Brandt, 1835) (Chieu et al. 2023). Here gene flow and population structure has been linked to the long-distance dispersal of pelagic larvae facilitated by a fast-flowing east Australian current (EAC). While knowledge of the reproductive biology or larval competency of *T. militaris* is poor, our results suggest that the species may also generate long-lived, planktotrophic larvae contributing to high levels of biological connectivity across its distribution (Cowen and Sponaugle 2009). Overall, these findings are consistent with previous genetic studies on trochoid taxa indicating population admixture over vast geographical areas. In this case we have provided evidence of gene flow among potentially locally adapted populations spanning major environmental gradients.

Evidence of local adaptation

Despite a lack of overall genetic structure across the sampling distribution, significant genotype associations with heterogeneous habitat features were observed across the sampling distribution, including associations with annual mean sea surface temperature, sea surface temperature range, EKE and productivity (CHLa). Drift processes leading to neutral genetic structure are often suppressed in broadcast spawning marine organisms with large population sizes (Gélin et al.

2017; Palumbi 2003; Pinsky and Palumbi 2014), but numerous studies have shown that adaptive genetic divergences can still be established and maintained under strong selection pressure (Hendry 2017; Nosil 2012; Schluter 2000). In fact, many studies have demonstrated that adaptive variation can be maintained despite high levels of gene flow specifically in marine invertebrates, including gastropod snails (Miller et al. 2019; Sandoval-Castillo et al. 2018). However, these findings are based on correlative tests only and should be interpreted with caution, as controlled mechanistic experiments are needed to validate these patterns and drivers of putative adaptive differentiation (Savolainen, Lascoux and Merilä 2013; Stinchcombe and Hoekstra 2008). Also, while our sampling regime was designed to correct for geographical distance, we cannot rule out the possible influence of artefactual associations (i.e., false positives) and SNP associations with other environmental factors varying with latitude (such as light intensity, dissolved oxygen levels and rainfall-driven variation in salinity). Nevertheless, our findings are consistent with many studies of marine species which demonstrated genetically determined clines related to climatic variables in Australia and overseas (Poloczanska et al. 2013, 2016; Wernberg et al. 2016).

Resilience to future climatic challenges

The coastal waters of south-eastern Australia are a recognised climate change hotspot with warming occurring above the global average with changes enhanced by strengthening of the EAC (Cresswell, Peterson, and Pender 2016; Malcolm et al. 2011; Oliver et al. 2017). Predictions anticipate warming to continue to increase, generating deteriorating marine conditions for sessile taxa that are already at their thermal limits (e.g. Davis et al. 2021). Within the EAC, the effect of warming and changes to circulation may also counter one another, with warming enhancing larval survival, but a strengthened current reducing larval supply to the coast by restricting cross-current larval dispersal (e.g. in lobster, Cetina-Heredia et al, 2015). Our findings suggest that *T. militaris* may have the capacity to adapt to future climatic challenges, assisted by both widespread gene flow across environmental gradients and the availability of standing genomic variation for selection to act upon. Findings of putative adaptive genetic differentiation associated with temperature, nutrients and ocean currents is a particularly important finding, suggesting that standing genetic variation may be available for selection to act on to counter future environmental change, assisted by widespread gene flow, high fecundity (Romolo and Trijoko 2021) and highly probable short generation time in this species (Kimani 1996; Romolo and Trijoko 2021).

While our findings suggest that *T. militaris* is likely to be generally resilient to shifts in the physical ocean climate, aggregations in some areas may still be vulnerable to risks of maladaptation. Those most at risk are likely to include locally adapted populations, where projected local changes in climate are high, and connections to non-local aggregations are relatively weak (Hoffmann and Sgro 2011). Recent climate projections indicate that many low energy embayment habitats are likely to experience greater increases in SST than open coastal habitats (Guyondet et al. 2015; Scanes, Scanes, and Ross 2020; Vila-Concejo et al. 2007); Also, biophysical models suggest that the biological connections between low energy embayment and high energy open coastal habitats can be weak in some marine invertebrates from south-eastern Australia (Riginos et al. 2016; Treml et al. 2015). Consequently, it is possible that locally adapted aggregations from low energy embayment habitats may be most vulnerable to climate change effects, where gene flow is unlikely to assist local aggregations in adapting to warming sea surface temperatures via the migration of thermally adapted genotypes. In such cases adaptive management strategies might be needed, including the assisted migration of thermally adapted genotypes to populations showing signs of climate stress. Such approaches are being widely advocated as a tool for "climate proofing" threatened marine and terrestrial animal and plant communities (Aitken & Whitlock, 2013; Prober et al., 2015; Layton et al., 2020; Hoffmann, Miller and Weeks 2021). Although the northernmost Hastings Point population is not genetically isolated, its position at the northern trailing edge may render it vulnerable to stochastic events, such as heatwaves (Ab Lah et al, 2018; Mamo et al, 2019). Vulnerability in trailing edge populations can be amplified by genetic impoverishment through loss of individuals, without replenishment through immigration (gene-flow), consequently exposing these populations to the risk of localised extinction (Clark et al. 2020; Coleman et al. 2020). Indeed, this species has undergone prior range shifts indicating that the trailing (warm) edge is likely to be vulnerable to ongoing warming.

Implications for fisheries management

Sustainable fisheries management requires information on factors that influence the resilience of individual fishing stocks to fishing pressure and environmental disturbance (Astles et al. 2006; Kenny et al. 2018). This includes understanding the geographic boundaries of biological populations and the recruitment potential of individual stocks persisting within and across these populations (Binks et al. 2019; Roughgarden, Iwasa, and Baxter 1985) and how this might be

altered under climate change. In the case of *T. militaris*, the presence of a single panmictic population unit across its distributional range, generally means that the opportunity for recolonisation following depletion events (overharvesting or environmental disturbance) are enhanced for central and southern sub-populations. However, for the northern trailing edge, the opportunity for repopulation with genotypes from pools of genetic diversity further south may be hampered by the dominant poleward flow of the EAC. Furthermore, increasing human population and harvesting pressure may reduce local abundance (Cooling and Smith 2015) and the opportunity for thermal adaption and repopulation.

Conclusions

Knowledge of population genomics, particularly adaptive structure, is important for fisheries management and can be used to estimate vulnerability and adaptability of stocks under climate change. This study revealed that the harvested gastropod, *T. militaris*, is panmictic across its distributional range with little variation in genetic diversity and can be considered as a single stock. As such, it has the genetic capacity to survive and proliferate within its environmental niche and is likely to continue to track ocean temperatures by shifting its entire distribution poleward. Genomic studies can improve management of harvested species under climate change by providing insights into adaptive capacity and help identify opportunities for strategic adaptive management (van Oppen & Coleman 2022).

Acknowledgements

We acknowledge the assistance of Matthew Hammond for field collection at Jervis Bay, NSW.

SNP data available from Dryad and may be accessed using the DOI link - https://doi.org/10.5061/dryad.79cnp5j27. Data processing R scripts are available in Supplementary Information.

References

Ab Lah, R., Kelaher, B. P., Bucher, D., & Benkendorff, K. 2018. Ocean warming and acidification affect the nutritional quality of the commercially-harvested turbinid snail Turbo militaris. *Marine environmental research*, *141*, 100-108.

https://doi.org/10.1016/j.marenvres.2018.08.009

Ahrens, C. W., Byrne, M., & Rymer, P. D. (2019). Standing genomic variation within coding and regulatory regions contributes to the adaptive capacity to climate in a foundation tree species. *Molecular Ecology*, *28*(10), 2502–2516. https://doi.org/https://doi.org/10.1111/mec.15092

Aitken, S. N., & Whitlock, M. C. (2013). Assisted Gene Flow to Facilitate Local Adaptation to Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, *44*(1), 367–388. https://doi.org/10.1146/annurev-ecolsys-110512-135747

ALA. (2018). *Atlas of Living Australia*. Atlas of Living Australia; CSIRO. http://www.ala.org.au.

Astles, K. L., Holloway, M. G., Steffe, A., Green, M., Ganassin, C., & Gibbs, P. J. (2006). An ecological method for qualitative risk assessment and its use in the management of fisheries in New South Wales, Australia. *Fisheries Research*, *82*(1–3), 290–303.

Ayre, D. J., & Hughes, T. P. (2004). Climate change, genotypic diversity and gene flow in reef-building corals. *Ecology Letters*, *7*(4), 273–278.

Barrett, Rowan D. H., and Dolph Schluter. 2008. "Adaptation from Standing Genetic Variation." *Trends in Ecology & Evolution* 23(1):38–44. doi: https://doi.org/10.1016/j.tree.2007.09.008.

Benjamini, Yoav, and Yosef Hochberg. 1995. "Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing." *Journal of the Royal Statistical Society: Series B (Methodological)* 57(1):289–300.

Benkendorff, K., and R. Przeslawski, R. 2008. Multiple measures are necessary to assess rarity in macro-molluscs: a case study from southeastern Australia. *Biodiversity and Conservation* 17, 2455-2478.

Berger, D, Postma, E, Blanckenhorn, W. U., and Walters, R. J. 2013. Quantitative genetic divergence and standing genetic (co)variance in thermal reaction norms along latitude. *Evolution* 67(8):2385–99. doi: 10.1111/evo.12138.

Bernatchez, Louis, Maren Wellenreuther, Cristián Araneda, David T. Ashton, Julia M. I. Barth,

548 Terry D. Beacham, Gregory E. Maes, Jann T. Martinsohn, Kristina M. Miller, and Kerry A.
549 Naish. 2017. “Harnessing the Power of Genomics to Secure the Future of Seafood.” *Trends in*
550 *Ecology & Evolution* 32(9):665–80.

551 Berry, Oliver, Zoe Richards, Glenn Moore, Udhi Hernawan, Mike Travers, and Bernd Gruber.
552 2019. “Oceanic and Coastal Populations of a Harvested Macroinvertebrate Rochia Nilotica in
553 North-Western Australia Are Isolated and May Be Locally Adapted.” *Marine and Freshwater*
554 *Research* 71(7):782–93.

555 Binks, Rachel M., Margaret Byrne, Kathryn McMahon, Georgina Pitt, Kathy Murray, and
556 Richard D. Evans. 2019. “Habitat Discontinuities Form Strong Barriers to Gene Flow among
557 Mangrove Populations, despite the Capacity for Long-distance Dispersal.” *Diversity and*
558 *Distributions* 25(2):298–309.

559 Bonebrake, T.C., Brown, C.J., Bell, J.D., Blanchard, J.L., Chauvenet, A., Champion, C., Chen,
560 I.C., Clark, T.D., Colwell, R.K., Danielsen, F. and Dell, A.I. 2018. Managing consequences of
561 climate-driven species redistribution requires integration of ecology, conservation and social
562 science. *Biological Reviews*, *93*(1), pp.284-305.

563 Brander, Keith. 2013. “Climate and Current Anthropogenic Impacts on Fisheries.” *Climatic*
564 *Change* 119(1):9–21.

565 Brierley, Andrew S., and Michael J. Kingsford. 2009. “Impacts of Climate Change on Marine
566 Organisms and Ecosystems.” *Current Biology* 19(14):R602–14. doi:
567 https://doi.org/10.1016/j.cub.2009.05.046.

568 Capblancq, Thibaut, Matthew C. Fitzpatrick, Rachael A. Bay, Moises Exposito-Alonso, and
569 Stephen R. Keller. 2020. “Genomic Prediction of (Mal)Adaptation Across Current and Future
570 Climatic Landscapes.” *Annual Review of Ecology, Evolution, and Systematics* 51(1):245–69. doi:
571 10.1146/annurev-ecolsys-020720-042553.

572 Carranza, Alvar, and Matías Arim. 2023. “Assessing the Ecological Vulnerability of Western
573 Atlantic Marine Benthic Gastropods.” *Marine and Fishery Sciences (MAFIS)* 36(2):165–78.

574 Caye, Kevin, Basile Jumentier, Johanna Lepeule, and Olivier François. 2019. “LFMM 2: Fast
575 and Accurate Inference of Gene-Environment Associations in Genome-Wide Studies.”

576 *Molecular Biology and Evolution* 36(4):852–60. doi: 10.1093/molbev/msz008.

577 Cetina-Heredia, P., Roughan, M., van Sebille, E., Feng, M., & Coleman, M. A. (2015).
578 "Strengthened currents override the effect of warming on lobster larval dispersal and survival."
579 *Global Change Biology*,21(12), 4377-4386.

580 Cheng, Samantha H., Mark Gold, Nichole Rodriguez, and Paul H. Barber. 2021. "Genome-Wide
581 SNPs Reveal Complex Fine Scale Population Structure in the California Market Squid Fishery
582 (Doryteuthis Opalescens)." *Conservation Genetics* 22(1):97–110. doi: 10.1007/s10592-020-
583 01321-2.

584 Cheung, W. L., V. W. Y. Lam, J. L. Sarmiento, K. Kearney, R. E. G. Watson, D. Zeller, and D.
585 Pauly. 2010. "Large-Scale Redistribution of Maximum Fisheries Catch Potential in the Global
586 Ocean under Climate Change." *Global Change Biology* 16(1):24–35. doi:
587 https://doi.org/10.1111/j.1365-2486.2009.01995.x.

588 Cheung, William W. L., Jorge L. Sarmiento, John Dunne, Thomas L. Frölicher, Vicky W. Y.
589 Lam, M. L. Deng Palomares, Reg Watson, and Daniel Pauly. 2013. "Shrinking of Fishes
590 Exacerbates Impacts of Global Ocean Changes on Marine Ecosystems." *Nature Climate Change*
591 3(3):254–58.

592 Chieu, Hoang Dinh, H. K. A. Premachandra, Daniel Powell, and Wayne Knibb. 2023. "Genome-
593 Wide SNP Analyses Reveal a Substantial Gene Flow and Isolated-Genetic Structure of Sea
594 Cucumber Holothuria Leucospilota Populations in Western Central Pacific." *Fisheries Research*
595 264:106718.

596 Clark, Jennifer S., Alistair G. B. Poore, Melinda A. Coleman, and Martina A. Doblin. 2020.
597 "Local Scale Thermal Environment and Limited Gene Flow Indicates Vulnerability of Warm
598 Edge Populations in a Habitat Forming Macroalga." *Frontiers in Marine Science* 7:711.

599 Coleman, Melinda A., Antoine J. P. Minne, Sofie Vranken, and Thomas Wernberg. 2020.
600 "Genetic Tropicalisation Following a Marine Heatwave." *Scientific Reports* 10(1):12726. doi:
601 10.1038/s41598-020-69665-w.

602 Coleman, Neville. 2015. *Nudibranchs Encyclopedia - Catalogue of Asia/Indo Pacific Sea Slugs,*
603 *Second Edition*. New. Springwood, Qld.: Neville Coleman's Underwater Geographic.

Cowen, Robert K., and Su Sponaugle. 2009. “Larval Dispersal and Marine Population Connectivity.” *Annual Review of Marine Science* 1:443–66.

Cresswell, G. R., J. L. Peterson, and L. F. Pender. 2016. “The East Australian Current, Upwellings and Downwellings off Eastern-Most Australia in Summer.” *Marine and Freshwater Research* 68(7):1208–23.

Davis, T.R., Champion, C. and Coleman, M.A., 2021. Climate refugia for kelp within an ocean warming hotspot revealed by stacked species distribution modelling. *Marine Environmental Research*, 166, 105267.

Department, Food and Agriculture Organization of the United Nations. Fisheries. 1997. *The State of World Fisheries and Aquaculture 1996*. Food and Agriculture Organization of the United Nations.

Department, Food and Agriculture Organization of the United Nations. Fisheries. 2012. “The State of World Fisheries and Aquaculture.” *Opportunities and Challenges. Food and Agriculture Organization of the United Nations*.

Díaz-Ferguson, Edgardo, Robert Haney, John Wares, and Brian Silliman. 2010. “Population Genetics of a Trochid Gastropod Broadens Picture of Caribbean Sea Connectivity.” *PloS One* 5(9):e12675.

Dolorosa, Roger G., Angelique M. Songco, Victor Calderon, Roy Magbanua, and Jaysee A. Matillano. 2010. “Population Structure and Abundance of Trochus Niloticusin Tubbataha Reefs Natural Park, Palawan, Philippines with Notes on Poaching Effects.” *SPC Trochus Information Bulletin*.

Donelson, Jennifer M., Jennifer M. Sunday, Will F. Figueira, Juan Diego Gaitán-Espitia, Alistair J. Hobday, Craig R. Johnson, Jeffrey M. Leis, Scott D. Ling, Dustin Marshall, John M. Pandolfi, Gretta Pecl, Giverny G. Rodgers, David J. Booth, and Philip L. Munday. 2019. “Understanding Interactions between Plasticity, Adaptation and Range Shifts in Response to Marine Environmental Change.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 374(1768):20180186. doi: 10.1098/rstb.2018.0186.

Doney, Scott C., Mary Ruckelshaus, J. Emmett Duffy, James P. Barry, Francis Chan, Chad A.

English, Heather M. Galindo, Jacqueline M. Grebmeier, Anne B. Hollowed, Nancy Knowlton, Jeffrey Polovina, Nancy N. Rabalais, William J. Sydeman, and Lynne D. Talley. 2011. "Climate Change Impacts on Marine Ecosystems." *Annual Review of Marine Science* 4(1):11–37. doi: 10.1146/annurev-marine-041911-111611.

DPI NSW. 2019. *Assessment of the NSW Sea Urchin and Turban Shell Fishery*.

Edet, Offiong U., Yasir S. A. Gorafi, Shuhei Nasuda, and Hisashi Tsujimoto. 2018. "DArTseq-Based Analysis of Genomic Relationships among Species of Tribe Triticeae." *Scientific Reports* 8(1):1–11.

Ellis, Nick, Stephen J. Smith, and C. Roland Pitcher. 2012. "Gradient Forests: Calculating Importance Gradients on Physical Predictors." *Ecology* 93(1):156–68.

Fankhauser, Samuel, and Guido Schmidt-Traub. 2011. "From Adaptation to Climate-Resilient Development: The Costs of Climate-Proofing the Millennium Development Goals in Africa." *Climate and Development* 3(2):94–113. doi: 10.1080/17565529.2011.582267.

Fitzpatrick, Matthew C., and Stephen R. Keller. 2015. "Ecological Genomics Meets Community-level Modelling of Biodiversity: Mapping the Genomic Landscape of Current and Future Environmental Adaptation." *Ecology Letters* 18(1):1–16.

Foale, Simon, and Rob Day. 1997. "Stock Assessment of Trochus (Trochus Niloticus)(Gastropoda: Trochidae) Fisheries at West Nggela, Solomon Islands." *Fisheries Research* 33(1–3):1–16.

Frichot, Eric, and Olivier François. 2015. "LEA: An R Package for Landscape and Ecological Association Studies." *Methods in Ecology and Evolution* 6(8):925–29.

Gautier, Mathieu. 2015. "Genome-Wide Scan for Adaptive Divergence and Association with Population-Specific Covariates." *Genetics* 201(4):1555–79. doi: 10.1534/genetics.115.181453.

GBIF. 2016. "Global Biodiversity Information Facility." 28 January. Retrieved (http://www.gbif.org).

Gélin, Pauline, Cécile Fauvelot, Vincent Mehn, Sophie Bureau, Héloïse Rouzé, and Hélène Magalon. 2017. "Superclone Expansion, Long-Distance Clonal Dispersal and Local Genetic

659 Structuring in the Coral Pocillopora Damicornis Type β in Reunion Island, South Western Indian
660 Ocean." *PloS One* 12(1):e0169692.

661 Gruber, Bernd, Peter Unmack, Oliver Berry, and Arthur Georges. 2019. "Introduction to DartR."

662 Guyondet, T., L. A. Comeau, Cedric Bacher, J. Grant, R. Rosland, R. Sonier, and R. Filgueira.
663 2015. "Climate Change Influences Carrying Capacity in a Coastal Embayment Dedicated to
664 Shellfish Aquaculture." *Estuaries and Coasts* 38:1593–1618.

665 Hagedorn, Mary, Christopher A. Page, Keri O'Neil, Daisy M. Flores, Lucas Tichy, Valérie F.
666 Chamberland, Claire Lager, Nikolas Zuchowicz, Kathryn Lohr, Harvey Blackburn, Tali Vardi,
667 Jennifer Moore, Tom Moore, Mark J. A. Vermeij, and Kristen L. Marhaver. 2018. "Successful
668 Demonstration of Assisted Gene Flow in the Threatened Coral <Em>Acropora
669 Palmata</Em> Across Genetically-Isolated Caribbean Populations Using Cryopreserved
670 Sperm." *BioRxiv* 492447. doi: 10.1101/492447.

671 Harte, Michael, Rachel Tiller, George Kailis, and Merrick Burden. 2019. "Countering a Climate
672 of Instability: The Future of Relative Stability under the Common Fisheries Policy." *ICES*
673 *Journal of Marine Science* 76(7):1951–58. doi: 10.1093/icesjms/fsz109.

674 Hendry, Andrew P. 2017. *Eco-Evolutionary Dynamics*. Princeton university press.

675 Hiddink, J. G., F. Ben Rais Lasram, J. Cantrill, and A. J. Davies. 2012. "Keeping Pace with
676 Climate Change: What Can We Learn from the Spread of Lessepsian Migrants?" *Global Change*
677 *Biology* 18(7):2161–72. doi: https://doi.org/10.1111/j.1365-2486.2012.02698.x.

678 Hoffmann, Ary A., Adam D. Miller, and Andrew R. Weeks. 2021. "Genetic Mixing for
679 Population Management: From Genetic Rescue to Provenancing." *Evolutionary Applications*
680 14(3):634–52. doi: https://doi.org/10.1111/eva.13154.

681 Hoffmann, Ary A., and Carla M. Sgrò. 2011. "Climate Change and Evolutionary Adaptation."
682 *Nature* 470(7335):479–85.

683 Holland, Owen J., Mary A. Young, Craig D. H. Sherman, Mun Hua Tan, Harry Gorfine, Ty
684 Matthews, and Adam D. Miller. 2021. "Ocean Warming Threatens Key Trophic Interactions
685 Supporting a Commercial Fishery in a Climate Change Hotspot." *Global Change Biology*
686 27(24):6498–6511. doi: https://doi.org/10.1111/gcb.15889.

687 Hollowed, Anne B., Manuel Barange, Richard J. Beamish, Keith Brander, Kevern Cochrane,
688 Kenneth Drinkwater, Michael G. G. Foreman, Jonathan A. Hare, Jason Holt, Shin-ichi Ito, Suam
689 Kim, Jacquelynne R. King, Harald Loeng, Brian R. MacKenzie, Franz J. Mueter, Thomas A.
690 Okey, Myron A. Peck, Vladimir I. Radchenko, Jake C. Rice, Michael J. Schirripa, Akihiko
691 Yatsu, and Yasuhiro Yamanaka. 2013. "Projected Impacts of Climate Change on Marine Fish
692 and Fisheries." *ICES Journal of Marine Science* 70(5):1023–37. doi: 10.1093/icesjms/fst081.

693 Jaccoud, Damian, Kaiman Peng, David Feinstein, and Andrzej Kilian. 2001. "Diversity Arrays:
694 A Solid State Technology for Sequence Information Independent Genotyping." *Nucleic Acids*
695 *Research* 29(4):e25–e25.

696 Jeffreys, H. 1939. *Theory of Probability*. Oxford UK: Oxford University Press.

697 Jenkins, Tom L., Charlie D. Ellis, Alexandros Triantafyllidis, and Jamie R. Stevens. 2019.
698 "Single Nucleotide Polymorphisms Reveal a Genetic Cline across the North-East Atlantic and
699 Enable Powerful Population Assignment in the European Lobster." *Evolutionary Applications*
700 12(10):1881–99. doi: https://doi.org/10.1111/eva.12849.

701 Johansson, Magnus. 2015. "Adjusting to the Extreme: Thermal Adaptation in a Freshwater
702 Gastropod."

703 Jombart, Thibaut. 2008. "Adegenet: A R Package for the Multivariate Analysis of Genetic
704 Markers." *Bioinformatics* 24(11):1403–5.

705 Joop Ouborg, N., Francesco Angeloni, and Philippine Vergeer. 2010. "An Essay on the
706 Necessity and Feasibility of Conservation Genomics." *Conservation Genetics* 11(2):643.

707 Kamvar, Z. N., J. F. Tabima, and N. J. Grunwald. 2014. "Poppr: An R Package for Genetic
708 Analysis of Populations with Clonal, Partially Clonal, and/or Sexual Reproduction. PeerJ 2013:
709 1–14."

710 Kelly, Ryan P., and Stephen R. Palumbi. 2010. "Genetic Structure Among 50 Species of the
711 Northeastern Pacific Rocky Intertidal Community." *PLOS ONE* 5(1):e8594.

712 Kenny, Andrew J., Neil Campbell, Mariano Koen-Alonso, Pierre Pepin, and Daniela Diz. 2018.
713 "Delivering Sustainable Fisheries through Adoption of a Risk-Based Framework as Part of an
714 Ecosystem Approach to Fisheries Management." *Marine Policy* 93:232–40.

715 Kilian, A., Wenzl, P., Huttner, E., Carling, J., Xia, L., Blois, H., and V. Caig. 2012. “Diversity
716 Arrays Technology: A Generic Genome Profiling Technology on Open Platforms.” Pp. 67–89 in
717 *Data Production and Analysis in Population Genomics. Methods in Molecular Biology (Methods*
718 *and Protocols)*. Totowa, New Jersey, USA: Humana Press.

719 Kimani, Edward Ndirui. 1996. “The Larval Development and Juvenile Growth of the
720 Silvermouth Turban, Turbo Argyrostomus L. 1758 (Mollusca: Prosobranchia).” *Asian Mar. Biol*
721 13:105–16.

722 Lam, Vicky W. Y., Edward H. Allison, Johann D. Bell, Jessica L. Blythe, William W. L.
723 Cheung, Thomas L. Frölicher, Maria A. Gasalla, and U. Rashid Sumaila. 2020. “Climate
724 Change, Tropical Fisheries and Prospects for Sustainable Development.” *Nature Reviews Earth*
725 *\& Environment* 1:440–54.

726 Layton, C., Coleman, M.A., Marzinelli, E.M., Steinberg, P.D., Swearer, S.E., Vergés, A.,
727 Wernberg, T. and Johnson, C.R., 2020. Kelp forest restoration in Australia. *Frontiers in Marine*
728 *Science*, 7, 74.Leiva, Germán E., and Juan C. Castilla. 2002. “A Review of the World Marine
729 Gastropod Fishery: Evolution of Catches, Management and the Chilean Experience.” *Reviews in*
730 *Fish Biology and Fisheries* 11(4):283–300.

731 Leung, Jonathan Y. S., Bayden D. Russell, and Sean D. Connell. 2020. “Linking Energy Budget
732 to Physiological Adaptation: How a Calcifying Gastropod Adjusts or Succumbs to Ocean
733 Acidification and Warming.” *The Science of the Total Environment* 715:136939.

734 Luo, L., Tang, Z. Z., Schoville, S. D., & Zhu, J. (2021). A comprehensive analysis comparing
735 linear and generalized linear models in detecting adaptive SNPs. *Molecular Ecology Resources*,
736 21(3), 733-744.

737 Madin, Elizabeth M. P., Natalie C. Ban, Zoë A. Doubleday, Thomas H. Holmes, Gretta T. Pecl,
738 and Franz Smith. 2012. “Socio-Economic and Management Implications of Range-Shifting
739 Species in Marine Systems.” *Global Environmental Change* 22(1):137–46. doi:
740 https://doi.org/10.1016/j.gloenvcha.2011.10.008.

741 Malcolm, Hamish A., Peter L. Davies, Alan Jordan, and Stephen D. A. Smith. 2011. “Variation
742 in Sea Temperature and the East Australian Current in the Solitary Islands Region between

2001–2008.” *Deep Sea Research Part II: Topical Studies in Oceanography* 58(5):616–27.

Malcolm, Hamish A., Alan Jordan, and Stephen D. A. Smith. 2010. “Biogeographical and Cross-Shelf Patterns of Reef Fish Assemblages in a Transition Zone.” *Marine Biodiversity* 40(3):181–93.

Mamo, L. T., Benkendorff, K., Butcherine, P., Coleman, M. A., Ewere, E. E., Miranda, R. J., ... & Kelaher, B. P. 2019. Resilience of a harvested gastropod, Turbo militaris, to marine heatwaves. *Marine environmental research*, *151*, 104769.Mason, Julia G., Jacob G. Eurich, Jacqueline D. Lau, Willow Battista, Christopher M. Free, Katherine E. Mills, Kanae Tokunaga, Lily Z. Zhao, Mark Dickey-Collas, and Mireia Valle. 2022. “Attributes of Climate Resilience in Fisheries: From Theory to Practice.” *Fish and Fisheries* 23(3):522–44.

Mijangos, Jose Luis, Bernd Gruber, Oliver Berry, Carlo Pacioni, and Arthur Georges. 2022. “DartR v2: An Accessible Genetic Analysis Platform for Conservation, Ecology and Agriculture.” *Methods in Ecology and Evolution* 13(10):2150–58. doi: https://doi.org/10.1111/2041-210X.13918.

Milano, Ilaria, Massimiliano Babbucci, Alessia Cariani, Miroslava Atanassova, Dorte Bekkevold, Gary R. Carvalho, Montserrat Espiñeira, Fabio Fiorentino, Germana Garofalo, Audrey J. Geffen, Jakob. H. Hansen, Sarah J. Helyar, Einar E. Nielsen, Rob Ogden, Tomaso Patarnello, Marco Stagioni, FishPopTrace Consortium, Fausto Tinti, and Luca Bargelloni. 2014. “Outlier SNP Markers Reveal Fine-Scale Genetic Structuring across European Hake Populations (Merluccius Merluccius).” *Molecular Ecology* 23(1):118–35. doi: https://doi.org/10.1111/mec.12568.

Miller, A. D., A. Van Rooyen, G. Rašić, D. A. Ierodiaconou, H. K. Gorfine, R. Day, C. Wong, A. A. Hoffmann, and A. R. Weeks. 2016. “Contrasting Patterns of Population Connectivity between Regions in a Commercially Important Mollusc Haliotis Rubra: Integrating Population Genetics, Genomics and Marine LiDAR Data.” *Molecular Ecology* 25(16):3845–64.

Miller, Adam D., Ary A. Hoffmann, Mun Hua Tan, Mary Young, Collin Ahrens, Michael Cocomazzo, Alex Rattray, Daniel A. Ierodiaconou, Eric Treml, and Craig D. H. Sherman. 2019. “Local and Regional Scale Habitat Heterogeneity Contribute to Genetic Adaptation in a Commercially Important Marine Mollusc (Haliotis Rubra) from Southeastern Australia.”

772 *Molecular Ecology* 28(12):3053–72.

773 Munday, Philip L., Robert R. Warner, Keyne Monro, John M. Pandolfi, and Dustin J. Marshall.
774 2013. "Predicting Evolutionary Responses to Climate Change in the Sea." *Ecology Letters*
775 16(12):1488–1500. doi: https://doi.org/10.1111/ele.12185.

776 Murray-Jones, S. E., and D. J. Ayre. 1997. "High Levels of Gene Flow in the Surf Bivalve
777 Donax Deltoides (Bivalvia: Donacidae) on the East Coast of Australia." *Marine Biology* 128:83–
778 89.

779 Neethling, Marlene, Conrad A. Matthee, Rauri C. K. Bowie, and Sophie von der Heyden. 2008.
780 "Evidence for Panmixia despite Barriers to Gene Flow in the Southern African Endemic,
781 Caffrogobius Caffer (Teleostei: Gobiidae)." *BMC Evolutionary Biology* 8(1):325. doi:
782 10.1186/1471-2148-8-325.

783 Nikula, Raisa, Hamish G. Spencer, and Jonathan M. Waters. 2011. "Comparison of
784 Population-genetic Structuring in Congeneric Kelp-versus Rock-associated Snails: A Test of a
785 Dispersal-by-rafting Hypothesis." *Ecology and Evolution* 1(2):169–80.

786 Nosil, Patrik. 2012. *Ecological Speciation*. Oxford University Press.

787 Oksanen, Jari, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R. Minchin, R. B.
788 O'hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, and Helene Wagner. 2013.
789 "Package 'Vegan.'" *Community Ecology Package, Version* 2(9):1–295.

790 Oliver, Eric C. J., Jessica A. Benthuysen, Nathaniel L. Bindoff, Alistair J. Hobday, Neil J.
791 Holbrook, Craig N. Mundy, and Sarah E. Perkins-Kirkpatrick. 2017. "The Unprecedented
792 2015/16 Tasman Sea Marine Heatwave." *Nature Communications* 8(1):16101. doi:
793 10.1038/ncomms16101.

794 Orr, James C., Victoria J. Fabry, Olivier Aumont, Laurent Bopp, Scott C. Doney, Richard A.
795 Feely, Anand Gnanadesikan, Nicolas Gruber, Akio Ishida, and Fortunat Joos. 2005.
796 "Anthropogenic Ocean Acidification over the Twenty-First Century and Its Impact on Calcifying
797 Organisms." *Nature* 437(7059):681–86.

798 Ortíz, Alejandro, Fabiola G. Arcos-Ortega, and Jorge M. Navarro. 2022. "Effects of Temperature
799 and Salinity on the Sub-Antarctic Snail Xymenopsis Muriciformis (King and Broderip, 1832):

800 Medium-Term Exposure to Different Climate Change Scenarios." *Journal of Experimental*
801 *Marine Biology and Ecology*.

802 Palumbi, Stephen R. 2003. "Population Genetics, Demographic Connectivity, and the Design of
803 Marine Reserves." *Ecological Applications* 13(sp1):146–58.

804 Papa, Yvan, Tom Oosting, Noemie Valenza-Troubat, Maren Wellenreuther, and Peter A.
805 Ritchie. 2020. "Genetic Stock Structure of New Zealand Fish and the Use of Genomics in
806 Fisheries Management: An Overview and Outlook." *New Zealand Journal of Zoology* 48:1–31.

807 Pereira, Ricardo J., Matthew C. Sasaki, and Ronald S. Burton. 2017. "Adaptation to a Latitudinal
808 Thermal Gradient within a Widespread Copepod Species: The Contributions of Genetic
809 Divergence and Phenotypic Plasticity." *Proceedings of the Royal Society B: Biological Sciences*
810 284(1853):20170236. doi: 10.1098/rspb.2017.0236.

811 Pinsky, Malin L., and Stephen R. Palumbi. 2014. "Meta-analysis Reveals Lower Genetic
812 Diversity in Overfished Populations." *Molecular Ecology* 23(1):29–39.

813 Pinsky, Malin L., Gabriel Reygondeau, Richard Caddell, Juliano Palacios-Abrantes, Jessica
814 Spijkers, and William W. L. Cheung. 2018. "Preparing Ocean Governance for Species on the
815 Move." *Science* 360(6394):1189–91.

816 Poloczanska, Elvira S., Christopher J. Brown, William J. Sydeman, Wolfgang Kiessling, David
817 S. Schoeman, Pippa J. Moore, Keith Brander, John F. Bruno, Lauren B. Buckley, Michael T.
818 Burrows, Carlos M. Duarte, Benjamin S. Halpern, Johnna Holding, Carrie V Kappel, Mary I.
819 O'Connor, John M. Pandolfi, Camille Parmesan, Franklin Schwing, Sarah Ann Thompson, and
820 Anthony J. Richardson. 2013. "Global Imprint of Climate Change on Marine Life." *Nature*
821 *Climate Change* 3(10):919–25. doi: 10.1038/nclimate1958.

822 Poloczanska, Elvira S., Michael T. Burrows, Christopher J. Brown, Jorge García Molinos,
823 Benjamin S. Halpern, Ove Hoegh-Guldberg, Carrie V Kappel, Pippa J. Moore, Anthony J.
824 Richardson, and David S. Schoeman. 2016. "Responses of Marine Organisms to Climate Change
825 across Oceans." *Frontiers in Marine Science* 62.

826 Pratchett, Morgan S., Kristen D. Anderson, Mia O. Hoogenboom, Elizabeth Widman, Andrew
827 H. Baird, John M. Pandolfi, Peter J. Edmunds, and Janice M. Lough. 2015. "Spatial, Temporal

828 and Taxonomic Variation in Coral Growth—Implications for the Structure and Function of Coral
829 Reef Ecosystems." *Oceanography and Marine Biology: An Annual Review* 53:215–95.

830 Quigley, Kate M., Line K. Bay, and Madeleine J. H. van Oppen. 2020. "Genome-Wide SNP
831 Analysis Reveals an Increase in Adaptive Genetic Variation through Selective Breeding of
832 Coral." *Molecular Ecology* 29(12):2176–88. doi: https://doi.org/10.1111/mec.15482.

833 Ramos, Jorge E., Jorge Tam, Víctor Aramayo, Felipe A. Briceño, Ricardo Bandin, Betsy
834 Buitron, Antonio Cuba, Ernesto Fernandez, Jorge Flores-Valiente, Emperatriz Gomez, Hans J.
835 Jara, Miguel Ñiquen, Jesús Rujel, Carlos M. Salazar, Maria Sanjinez, Rafael I. León, Mark
836 Nelson, Dimitri Gutiérrez, and Gretta T. Pecl. 2022. "Climate Vulnerability Assessment of Key
837 Fishery Resources in the Northern Humboldt Current System." *Scientific Reports* 12(1):4800.
838 doi: 10.1038/s41598-022-08818-5.

839 Reiss, Henning, Galice Hoarau, Mark Dickey-Collas, and Wim J. Wolff. 2009. "Genetic
840 Population Structure of Marine Fish: Mismatch between Biological and Fisheries Management
841 Units." *Fish and Fisheries* 10(4):361–95.

842 Riginos, Cynthia, Eric D. Crandall, Libby Liggins, Pim Bongaerts, and Eric A. Treml. 2016.
843 "Navigating the Currents of Seascape Genomics: How Spatial Analyses Can Augment
844 Population Genomic Studies." *Current Zoology* 62(6):581–601. doi: 10.1093/cz/zow067.

845 Riquet, Florentine, Claire Daguin-Thiébaut, Marion Ballenghien, Nicolas Bierne, and Frédérique
846 Viard. 2013. "Contrasting Patterns of Genome-Wide Polymorphism in the Native and Invasive
847 Range of the Marine Mollusc Crepidula Fornicata." *Molecular Ecology* 22(4):1003–18. doi:
848 https://doi.org/10.1111/mec.12161.

849 Roessig, Julie M., Christa M. Woodley, Joseph J. Cech, and Lara J. Hansen. 2004. "Effects of
850 Global Climate Change on Marine and Estuarine Fishes and Fisheries." *Reviews in Fish Biology*
851 *and Fisheries* 14(2):251–75. doi: 10.1007/s11160-004-6749-0.

852 Romolo, Rijal, and Trijoko Trijoko. 2021. "Food Preference, Fecundity, Proximate Analysis on
853 Eggs and Meat of Turbo Crassus (W. Wood 1828) and Turbo Setosus (Gmelin 1791) in
854 Sepanjang Beach, Gunungkidul, Special Region of Yogyakarta." *Journal of Tropical*
855 *Biodiversity and Biotechnology* 6(2):61873.

Roughgarden, Jonathan, Y. O. H. Iwasa, and Charles Baxter. 1985. "Demographic Theory for an Open Marine Population with Space-limited Recruitment." *Ecology* 66(1):54–67.

Rousset, François. 1997. "Genetic Differentiation and Estimation of Gene Flow from F-Statistics under Isolation by Distance." *Genetics* 145(4):1219–28.

Sağlam, İsmail K., James Hobbs, Randall Baxter, Levi S. Lewis, Alyssa Benjamin, and Amanda J. Finger. 2021. "Genome-Wide Analysis Reveals Regional Patterns of Drift, Structure, and Gene Flow in Longfin Smelt (Spirinchus Thaleichthys) in the Northeastern Pacific." *Canadian Journal of Fisheries and Aquatic Sciences* 78(12):1793–1804. doi: 10.1139/cjfas-2021-0005.

Sandoval-Castillo, Jonathan, Nick A. Robinson, Anthony M. Hart, Lachlan W. S. Strain, and Luciano B. Beheregaray. 2018. "Seascape Genomics Reveals Adaptive Divergence in a Connected and Commercially Important Mollusc, the Greenlip Abalone (Haliotis Laevigata), along a Longitudinal Environmental Gradient." *Molecular Ecology* 27(7):1603–20.

Sanford, Eric, and Morgan W. Kelly. 2010. "Local Adaptation in Marine Invertebrates." *Annual Review of Marine Science* 3(1):509–35. doi: 10.1146/annurev-marine-120709-142756.

Sansaloni, Carolina, Cesar Petroli, Damian Jaccoud, Jason Carling, Frank Detering, Dario Grattapaglia, and Andrzej Kilian. 2011. "Diversity Arrays Technology (DArT) and next-Generation Sequencing Combined: Genome-Wide, High Throughput, Highly Informative Genotyping for Molecular Breeding of Eucalyptus." Pp. 1–2 in *BMC proceedings*. Vol. 5. BioMed Central.

Sasaki, Matthew, Jordanna M. Barley, Sarah Gignoux-Wolfsohn, Cynthia G. Hays, Morgan W. Kelly, Alysha B. Putnam, Seema N. Sheth, Andrew R. Villeneuve, and Brian S. Cheng. 2022. "Greater Evolutionary Divergence of Thermal Limits within Marine than Terrestrial Species." *Nature Climate Change* 12(12):1175–80. doi: 10.1038/s41558-022-01534-y.

Savolainen, Outi, Martin Lascoux, and Juha Merilä. 2013. "Ecological Genomics of Local Adaptation." *Nature Reviews Genetics* 14(11):807–20. doi: 10.1038/nrg3522.

Scanes, Elliot, Peter R. Scanes, and Pauline M. Ross. 2020. "Climate Change Rapidly Warms and Acidifies Australian Estuaries." *Nature Communications* 11(1):1803.

Scavia, Donald, John C. Field, Donald F. Boesch, Robert W. Buddemeier, Virginia Burkett,

884 Daniel R. Cayan, Michael Fogarty, Mark A. Harwell, Robert W. Howarth, Curt Mason, Denise J.
885 Reed, Thomas C. Royer, Asbury H. Sallenger, and James G. Titus. 2002. “Climate Change
886 Impacts on U.S. Coastal and Marine Ecosystems.” *Estuaries* 25(2):149–64. doi:
887 10.1007/BF02691304.

888 Schluter, Dolph. 2000. *The Ecology of Adaptive Radiation*. OUP Oxford.

889 Sexton, Jason P., Patrick J. McIntyre, Amy L. Angert, and Kevin J. Rice. 2009. “Evolution and
890 Ecology of Species Range Limits.”

891 Silliman, Brian R., Edwin Grosholz, and Mark D. Bertness. 2009. *Human Impacts on Salt*
892 *Marshes : A Global Perspective*. Berkeley: University of California Press.

893 Smith, P. J., R. I. C. C. Francis, and M. McVeagh. 1991. “Loss of Genetic Diversity Due to
894 Fishing Pressure.” *Fisheries Research* 10(3):309–16. doi: https://doi.org/10.1016/0165-
895 7836(91)90082-Q.

896 Somero, G. N. 2010. “The Physiology of Climate Change: How Potentials for Acclimatization
897 and Genetic Adaptation Will Determine ‘Winners’ and ‘Losers.’” *Journal of Experimental*
898 *Biology* 213(6):912–20.

899 Sork, Victoria L., Frank W. Davis, R. Westfall, A. Flint, M. Ikegamie, and D. Wang, HGrivet.
900 2010. “Gene Movement and Genetic Association with Regional Climate Gradients in California
901 Valley Oak (Quercus Lobata Née) in the Face of Climate Change.” *Molecular Ecology*
902 19(17):3806–23. doi: https://doi.org/10.1111/j.1365-294X.2010.04726.x.

903 Stinchcombe, John R., and Hopi E. Hoekstra. 2008. “Combining Population Genomics and
904 Quantitative Genetics: Finding the Genes Underlying Ecologically Important Traits.” *Heredity*
905 100(2):158–70.

906 Sumaila, U. Rashid, William W. L. Cheung, Vicky W. Y. Lam, Daniel Pauly, and Samuel
907 Herrick. 2011. “Climate Change Impacts on the Biophysics and Economics of World Fisheries.”
908 *Nature Climate Change* 1(9):449–56. doi: 10.1038/nclimate1301.

909 Sunday, Jennifer M., Gretta T. Pecl, Stewart Frusher, Alistair J. Hobday, Nicole Hill, Neil J.
910 Holbrook, Graham J. Edgar, Rick Stuart-Smith, Neville Barrett, and Thomas Wernberg. 2015.
911 “Species Traits and Climate Velocity Explain Geographic Range Shifts in an Ocean-warming

912 Hotspot." *Ecology Letters* 18(9):944–53.

913 Treml, Eric A., John R. Ford, Kerry P. Black, and Stephen E. Swearer. 2015. "Identifying the
914 Key Biophysical Drivers, Connectivity Outcomes, and Metapopulation Consequences of Larval
915 Dispersal in the Sea." *Movement Ecology* 3(1):17. doi: 10.1186/s40462-015-0045-6.

916 Valenzuela-Quiñonez, Fausto. 2016. "How Fisheries Management Can Benefit from
917 Genomics?" *Briefings in Functional Genomics* 15(5):352–57.

918 Valles-Regino, Roselyn, Peter Mouatt, Lachlan H. Yee, and Kirsten Benkendorff. 2022. "Ocean
919 Warming and Heat Stress Impact Molecules of Keystone Significance in a Predatory Marine
920 Gastropod." in *Frontiers in Marine Science*.

921 van Oppen, M.J. and Coleman, M.A., 2022. Advancing the protection of marine life through
922 genomics. *PLoS Biology*, 20, e3001801.

923 Vila-Concejo, Ana, Andrew D. Short, Michael G. Hughes, and Roshanka Ranasinghe. 2007.
924 "Shoreline Implications of Flood-Tide Delta Morphodynamics. The Case of Port Stephens (SE
925 Australia)." *Proceedings of the Sixth International Symposium on Coastal Engineering and*
926 *Science of Coastal Sediment Process* 1417–30.

927 Villamor, Adriana, Federica Costantini, and Marco Abbiati. 2014. "Genetic Structuring across
928 Marine Biogeographic Boundaries in Rocky Shore Invertebrates." *PLOS ONE* 9(7):e101135.

929 Vranken, Sofie, Thomas Wernberg, Armin Scheben, Anita Severn-Ellis, Jacqueline Batley,
930 Bayer Emanuel Philipp, David Edwards, David Wheeler, and Melinda Ann Coleman. 2021.
931 "Genotype-environment Mismatch of Kelp Forests under Climate Change." *Molecular Ecology*.

932 Waples, Robin S., and Kerry A. Naish. 2009. "Genetic and Evolutionary Considerations in
933 Fishery Management: Research Needs for the Future." Pp. 427–51 in *The future of fisheries*
934 *science in North America*. Springer.

935 Ward, Robert D. 2000. "Genetics in Fisheries Management." *Hydrobiologia* 420(1):191–201.

936 Weir, Bruce S., and Jérôme Goudet. 2017. "A Unified Characterization of Population Structure
937 and Relatedness." *Genetics* 206(4):2085–2103.

938 Wenzl P, Carling J, Kudrna D, Jaccoud D, Huttner E, and Kleinhofs A 2004. Diversity Arrays

939 Technology (DArT) for whole-genome profiling of barley. Proceedings of the National Academy
940 of Sciences of the United States of America. 101(26):9915–20.

941 Wernberg, Thomas, Scott Bennett, Russell C. Babcock, Thibaut De Bettignies, Katherine Cure,
942 Martial Depczynski, Francois Dufois, Jane Fromont, Christopher J. Fulton, and Renae K. Hovey.
943 2016. "Climate-Driven Regime Shift of a Temperate Marine Ecosystem." *Science*
944 353(6295):169–72.

945 Wood, Georgina, Ezequiel M. Marzinelli, Alexandra H. Campbell, Peter D. Steinberg, Adriana
946 Vergés, and Melinda A. Coleman. 2021. "Genomic Vulnerability of a Dominant Seaweed Points
947 to Future-proofing Pathways for Australia's Underwater Forests." *Global Change Biology*
948 27(10):2200–2212.

949 Yearsley, G. K., Peter Robert Last, and Robert D. Ward. 1999. *Australian Seafood Handbook:*
950 *An Identification Guide to Domestic Species*. [Hobart], Tas., CSIRO Div. of Marine Research.

951 Zacherl, Danielle C., Steven D. Gaines, and Steve I. Lonhart. 2003. "The Limits to
952 Biogeographical Distributions: Insights from the Northward Range Extension of the Marine
953 Snail, Kelletia Kelletii (Forbes, 1852)." *Journal of Biogeography* 30.

954 Zardi, Gerardo I., Katy R. Nicastro, Fernando Canovas, Joana Ferreira Costa, Ester A. Serrao,
955 and Gareth A. Pearson. 2011. "Adaptive Traits Are Maintained on Steep Selective Gradients
956 despite Gene Flow and Hybridization in the Intertidal Zone." *PloS One* 6(6):e19402.

Table 1(on next page)

Predictor variables sourced from Copernicus Marine Environment Monitoring Service used in genotype by environmental association analyses.

Table 1. Details of samples, sampling location and location based environmental covariables for *Turbo militaris* in New South Wales. (*N*=number, SST = mean sea surface temperature, Temp range = total temperature variance, EKE = mean kinetic energy, CHL*a* = mean chlorophyll *a*).

Location	**Latitude**	**Longitude**	**Date collected**	***N* samples**	**SST (°C)**	**Temp range (°C)**	**EKE**	**CHL*a***
Hastings Point	28° 21' 38.09" S	153° 34 '44.21"E	30 Mar 2021	25	23.35	8.91	0.1391	2.1094
Woody Head	29° 21 '47.70" S	153° 22' 25.96"E	08 Apr 2021	25	22.34	9.52	0.0632	3.8472
South Solitary Island	30° 12' 19.31" S	153° 16' 01.24 "E	12 May 2021	25	22.42	10.17	0.1204	0.9517
Split Solitary Island	30° 14' 24.07"S	153° 10' 50.71"E	12 May 2021	30	22.37	10.14	0.0741	2.0323
Nambucca Heads	30°38'47.49"S	153°01'15.10"E	26 Mar 2021	23	22.23	10.23	0.1223	2.0319
Crowdy Head	31° 50' 16.91"S	152° 45 '04.54"E	28 Apr 2021	22	21.34	9.94	0.0820	2.7083
Newcastle	32° 57' 31.70"S	151° 45' 02.72"E	12 Apr 2021	31	20.39	9.12	0.0178	2.2840
Jervis Bay (Plantation Pt)	35° 06 '16.15"S	150°41'53.70"E	20 Aug 2021	25	19.46	10.24	0.0311	2.9248
Total				**206**				

Table 2(on next page)

Details of samples

Table . Details of samples, sampling location and location based environmental covariables for Turbo militaris in New South Wales. (N=number, ẊSST = mean sea surface temperature, temp range = total temperature variance, ẊEKE = mean kinetic energy, ẊCHLa mean chlorophyll a).

1 **Table 2.** Predictor variables sourced from Copernicus Marine Environment Monitoring Service used in genotype by
2 environmental association analyses.

Predictor	Description	Spatial Resolution	Units
SST	Daily global sea surface temperature reprocessed (level 4) from Operational SST and Ice Analysis system downloaded from CMEMS (product #010_011).	0.05º	°C
CHLa	8-day composite mass concentration of chlorophyll *a* in seawater (level 4) from Globcolour downloaded from CMEMS (product #009_082).	4 km	mg m^{-2}
EKE	Daily eddy kinetic energy computed from zonal and meridional velocity components from the Sea Level Thematic Assembly Centre downloaded from CMEMS (product #008_047).	0.25º	m^2s^{-2}
Year	Calendar year (incorporated as a random intercept term in mixed models).	-	-

3

Table 3(on next page)

Summary of descriptive statistics

Table . Summary of descriptive statistics. Sample size (n), mean allelic richness (AR), and genetic diversity indices including expected (HE) and observed (HO) heterozygosity, and inbreeding coefficients (FIS) at each site, based on the complete filtered dataset (n = 207 individuals).

Table 3. Summary of descriptive statistics. Sample size (n), mean allelic richness (A_R), and genetic diversity indices including expected (H_E) and observed (H_O) heterozygosity, and inbreeding coefficients (F_{IS}) at each site, based on the complete filtered dataset (n = 207 individuals).

Location	n	A_R	H_E	H_O	F_{IS}
Hastings Point	25	1.635	0.218	0.190	0.110
Woody Head	25	1.633	0.216	0.189	0.107
Split Solitary Is	30	1.632	0.217	0.189	0.111
South Solitary Is	25	1.638	0.219	0.202	0.076
Nambucca Heads	23	1.640	0.221	0.212	0.048
Crowdy Head	22	1.633	0.217	0.188	0.111
Newcastle	31	1.630	0.215	0.186	0.118
Jervis Bay	25	1.630	0.217	0.194	0.096

Table 4(on next page)

Pairwise estimates of pairwise F_{ST} among sample locations. Bolded F_{ST} values were found to be significant after multiple corrections ($p < 0.05$).

Table 4. Pairwise estimates of F_{ST} among sample locations. Bolded F_{ST} values were found to be significant after multiple corrections ($p < 0.05$). Numbers in lower diagonal are p values

	Nambucca Heads	Woody Head	Newcastle	Hastings Point	South Solitary Is	Crowdy Head	Split Solitary Is	Jervis Bay
Nambucca Heads		**0.0037**	**0.0037**	**0.0031**	**0.0033**	**0.0028**	**0.0028**	**0.0043**
Woody Head	0.00		**0.0022**	**0.0019**	**0.0034**	**0.0029**	**0.0027**	**0.0038**
Newcastle	0.00	0.00		**0.0017**	**0.0024**	**0.0016**	**0.0014**	**0.0021**
Hastings Point	0.00	0.00	0.01		**0.0018**	0.0007	**0.0014**	**0.0017**
South Solitary Is.	0.00	0.00	0.00	0.00		**0.0016**	**0.0020**	**0.0031**
Crowdy Head	0.00	0.00	0.00	0.11	0.00		-0.0002	**0.0016**
Split Solitary Is	0.00	0.00	0.00	0.00	0.00	0.69		**0.0020**
Jervis Bay	0.00	0.00	0.00	0.01	0.00	0.00	0.00	

Figure 1

Map of *Turbo militaris* collection sites from the eastern seaboard of Australia

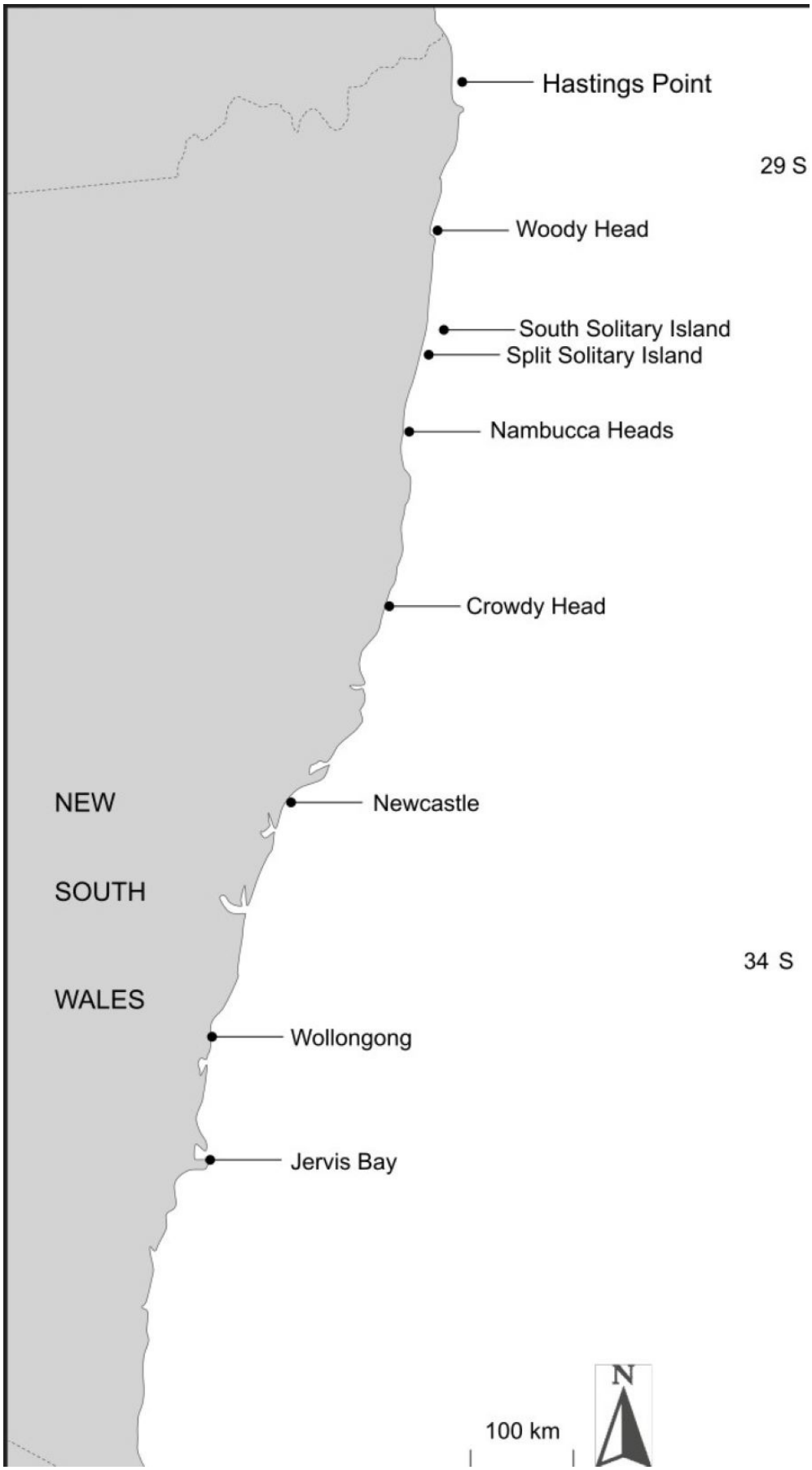

Hastings Point
29 S
Woody Head
South Solitary Island
Split Solitary Island
Nambucca Heads
Crowdy Head
NEW
SOUTH
WALES
Newcastle
34 S
Wollongong
Jervis Bay
100 km
N

Figure 2

Results of genotype x environment association analyses show the strength of associations between individual loci and environmental variables identified by BayPass and LFMM2

Bar plots show the number of putative candidate loci associated with each environmental variable.

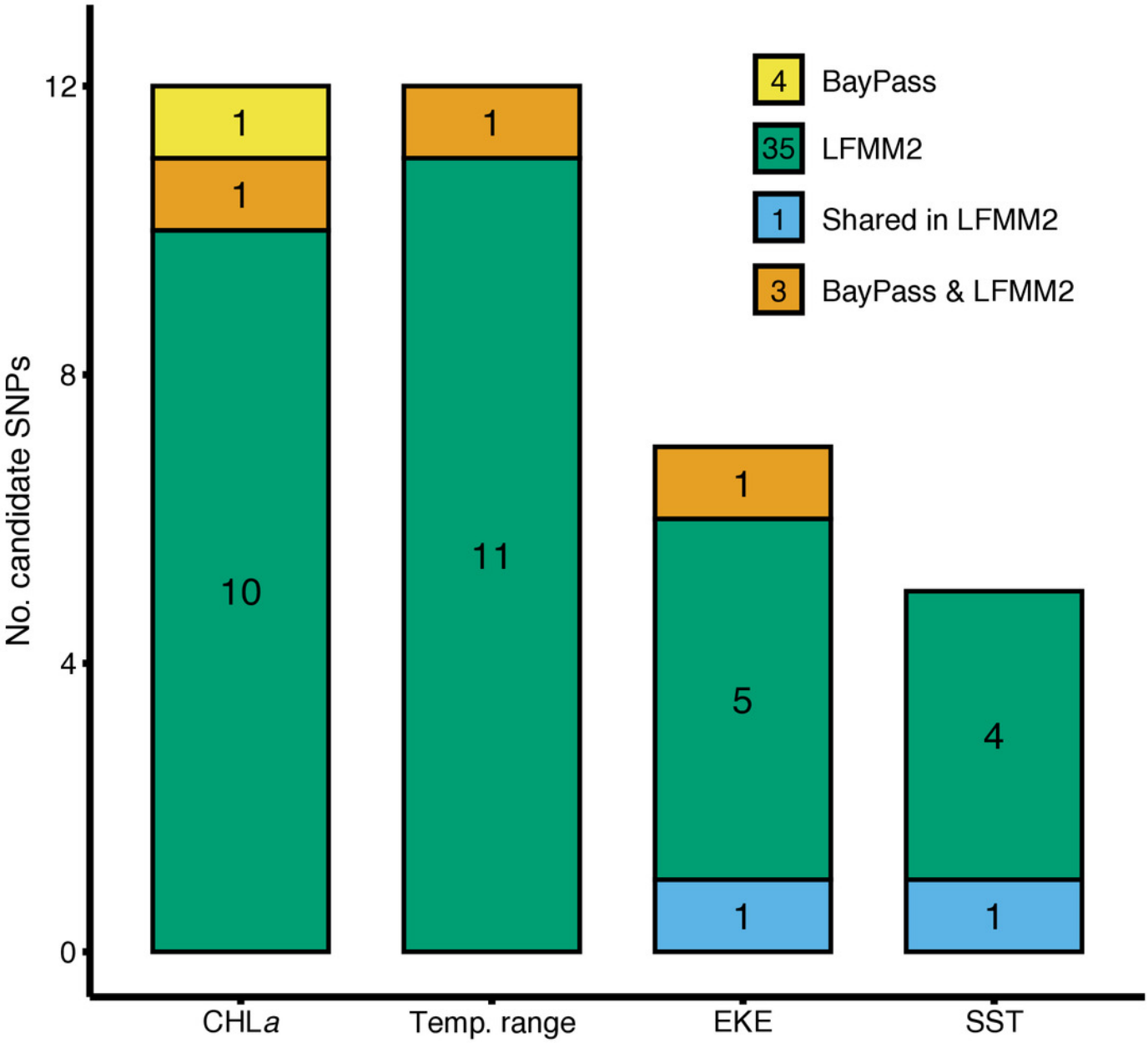
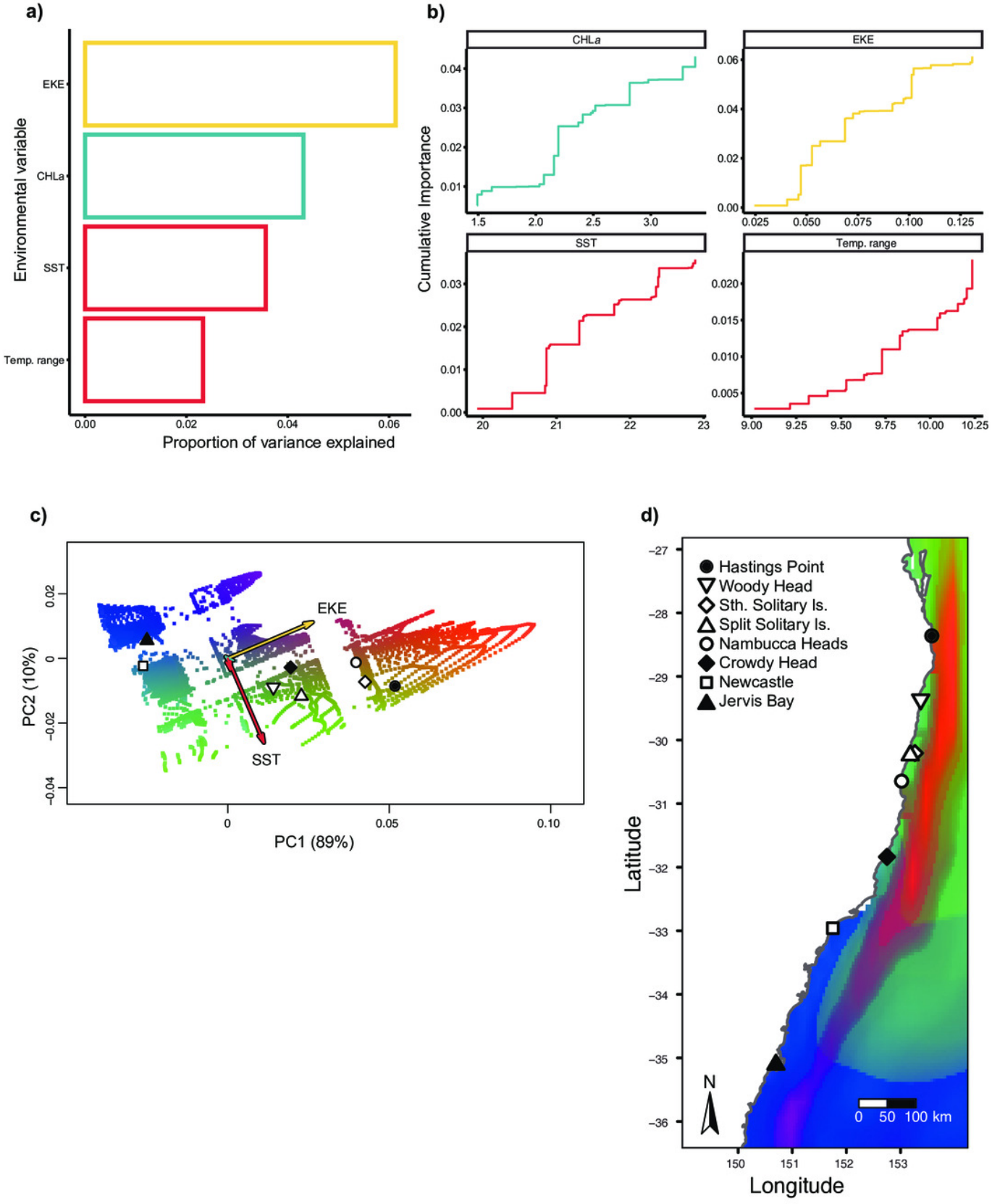

No. candidate SNPs
12
8
4
0
CHLa
Temp. range
EKE
SST
1
1
10
1
11
1
5
1
4
1
4 BayPass
35 LFMM2
1 Shared in LFMM2
3 BayPass & LFMM2

Figure 3

Gradient Forest outputs

(a) Overall relative importance for each environmental variable describing the turnover in allele frequencies from the Gradient Forest model; **(b)** cumulative importance curves showing overall pattern of genomic compositional change (R2, y-axis) for each environmental gradient (x-axis). Turnover functions for each curve are aggregated across all candidate loci. The curve shape indicates the rate of change in allele frequencies along the environmental gradient, and the maximum height indicates the total turnover in allele frequencies. Predictor variables shown here include: chlorophyll *a* concentration (CHLa), eddy kinetic energy (EKE), sea surface temperature (SST) and sea surface temperature range (temp.range); **(c)** Influence of environmental variation on candidate SNP allele frequencies inferred from Gradient Forest analyses as aPCA plot illustrating the influence of environmental variation on allele frequencies for candidate loci. Background colours denotes environmental space, whereas black dots represent the principal component (PC) scores associated with the sampling locations**; (d)** Predicted spatial turnover in allele frequencies interpolated across the study area, with black dots as labelled sampling locations. Similar colours indicated areas expected to have similar genetic composition, while divergent colours indicate divergent putatively adaptive genotypes. Colours are based on the first three principal components of transformed environmental variables.


a)
EKE
CHLa
SST
Temp. range
Environmental variable
0.00
0.02
0.04
0.06
Proportion of variance explained
b)
CHLa
EKE
SST
Temp. range
Cumulative Importance
c)
EKE
SST
PC2 (10%)
PC1 (89%)
d)
Hastings Point
Woody Head
Sth. Solitary Is.
Split Solitary Is.
Nambucca Heads
Crowdy Head
Newcastle
Jervis Bay
Latitude
Longitude
N
0 50 100 km