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Urbanisation Is Associated With Reduced Genetic Diversity in Marine Fish Populations

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ABSTRACT

The benefits to humans of living by the ocean have led many coastal settlements to grow into large, densely populated cities. Large coastal cities have had considerable environmental effects on marine ecosystems through resource extraction, waste disposal, coastal development, and trade and travel routes. While our understanding of the ecological and evolutionary consequences of urbanisation for wildlife in terrestrial systems has received considerable recent attention, the consequences of urbanisation in marine systems are not well known. Using microsatellite datasets associated with published research on marine fish population genetics, we built a global database of genotypic data spanning 75,361 individuals sampled from 73 species at 1085 sample sites throughout the world's oceans. We found that genetic diversity and effective population sizes were significantly lower at marine fish sample sites associated with denser human populations, regardless of species and locality. The loss of genetic diversity near denser human populations indicates habitats near human settlements are less able to support large populations. Small effective population sizes, in turn, dampen the efficiency of natural selection near dense urban settlements. The loss of genetic diversity near cities is concerning for maintaining functioning marine ecosystems and sustainable fisheries. Our work highlights the need to mitigate environmental threats from human activities and focus efforts on sustainable urban planning and resource use to conserve marine biodiversity and sustain coastal fisheries and ecosystems.

1 | Introduction

Throughout history, oceans have provided humans with substantial food resources and a means for waste disposal (Berkun et al. 2005; Kite-Powell et al. 1998; O'Shea et al. 2018) and transporting goods and people (Lubchenco and Haugan 2023). This has transformed many coastal cities into regional and global centers of wealth and population growth (Li 2003). Today, more than 40% of the human population lives in densely populated cities within 100 km of the ocean (UN 2007), and 85% of marine fisheries are coastal (FAO 2024). The environmental footprint of coastal cities has grown with their economies (Li 2003), increasing oceanic habitat conversion, pollution and resource exploitation. Intact coastal regions are now globally rare—approximately 15% of coasts are considered minimally pressured by human settlement and use (Williams et al. 2022). Despite the long history of coastal settlements and the extended reach of settlements into marine environments, we know little about how urbanisation has affected evolutionary processes and biodiversity at the genetic level in oceans (Alter et al. 2021; Todd et al. 2019; Touchard et al. 2023). We hypothesised that human activities in and around coastal cities have reduced the capacity

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for marine habitats near cities to support large, intact fish populations, resulting in population declines, the loss of genetic diversity, and increased genetic differentiation.

Declines and collapses of exploited marine fish populations due to overfishing have had well-documented and significant negative ecological and socioeconomic consequences (Berkes et al. 2006; McCauley et al. 2015; FAO 2022). However, threats to marine fish biodiversity at the genetic level due to human activities are underexplored (but see Pinsky and Palumbi 2014 for the genetic consequences of fishing), particularly for species that are not commercially harvested. Genetic diversity underlies all facets of biodiversity, including population persistence (Barrett and Schluter 2008; Lande and Shannon 1996) and the capacity to adapt to environmental change (Barrett and Schluter 2008). Genetic diversity ultimately drives ecosystem stability and resilience: within-species genetic variation influences community structure and ecosystem functioning in both animal and plant species (Raffard et al. 2019). The erosion of genetic diversity is thus a significant ecological concern for maintaining functioning marine ecosystems and sustainable fisheries. However, assessments of genetic diversity are not routinely conducted as part of population monitoring and commercial harvest of marine fishes. While our understanding of the natural drivers of genetic variation in marine fishes is starting to improve (Clark and Pinsky 2024; Manel et al. 2020), we lack basic information about the threats posed to marine fish genetic diversity by human settlements.

We took advantage of the accumulation of population genetic datasets archived with individual research papers to test whether marine fish populations near big cities, in general, tend to have reduced genetic diversity at a global scale. We used nuclear microsatellite markers because they are the most common marker type in data repositories and thus give the best spatial coverage for the largest number of species. The number of loci used in microsatellite studies is most often small relative to studies that use genome-wide markers such as single nucleotide polymorphisms; however, when multiple individuals are sampled at a site, the typical number of microsatellites used in published studies are sufficient for estimating genome-wide diversity at the site-level (Mittell et al. 2015).

The specific effects of human settlements on marine environments and marine fish populations will vary substantially through space and among species. Our aim was to test whether, regardless of this variation, the effects of humans on marine fish populations were generally negative. Thus, we sought general predictors of the effects of humans on marine environments. We focused on two complementary measures of human disturbance. The first was human population density (Center for International Earth Science Information Network (CIESIN) Columbia University 2018), measured as the number of persons per square kilometre based on national censuses and population registers for the year 2010 in a 30 arc-second resolution. The second was a composite measure of cumulative human impacts (Halpern et al. 2015) derived from 19 metrics of human-caused stressors on 20 categories of global marine ecosystems. This measure includes the effects of settlements together with estimates of the effects of climate change, fishing pressure, and numerous other anthropogenic threats to the marine environment. Human population density should capture the degree of urbanisation and the associated long-term, spatially fixed effects of humans on natural environments (e.g., pollution, habitat destruction and nearshore fishing). However, the reach of humans extends further than their settlements. For example, anomalous weather patterns caused by climate change are not spatially limited, and shipping routes traverse global oceans. The composite measure of cumulative human impacts should capture these broader-scale effects of human presence. We predicted that fish population size, and thus genetic diversity, would decrease, and that populations would become increasingly fragmented and genetically differentiated with increasing exposure to urbanisation and the cumulative environmental effects of humans. We found globally consistent associations between urbanisation and reduced genetic diversity and effective population size, but not genetic differentiation, across taxa.

2 | Materials and Methods

2.1 | Data Compilation

We built a database of population genetic datasets—microsatellite allele sizes archived online with published peer-reviewed research articles—for marine fishes following protocols from previous related work (Schmidt et al. 2020; Schmidt and Garroway 2021). Dataset retention workflow and criteria can be seen in Figure S1. Briefly, we programmatically searched online public data repositories using the DataONE package (Jones et al. 2017) in R version 3.6.3 (R Core Team 2020). We searched species names (e.g., '*Petromyzon marinus*') and keywords 'microsatellite' and 'microsat*'. We focused our search on marine fishes globally, including diadromous and brackish species. Our species list (8506 species) came from the IUCN Red List database. We included diadromous species because an important portion of their lifecycle is spent in the marine environment. We arbitrarily chose 1990 as the cut-off for the earliest year of data inclusion because datasets from before this time were sparse. We used only microsatellite data defined as neutral by the original authors of publications and removed non-neutral loci where applicable. We excluded data from hatchery-bred populations, invasive species, hybrids where noted in papers and experimental data. We used microsatellite loci because they are the most commonly used and archived neutral marker type (Miles et al. 2019) and because, when sampled at the site level, they are well correlated with genome-wide diversity (~81%; Mittell et al. 2015). We based our analysis on genetic summary statistics calculated from groups that each comprised multiple individuals of a single species sampled from a single site (hereafter sample sites). We used sample site coordinates when provided in publications and georeferenced (QGIS Development Team 2021) sample sites from maps when necessary.

Our final dataset consisted of 1085 sites, 75,361 individuals and 73 species for use in subsequent analysis (Figure 1; Table S1). We imported datasets into R using the adegenet package, version 2.1.3 (Jombart 2008; Jombart and Ahmed 2011). We then estimated gene diversity, allelic richness, population-specific F_{ST} and effective population size for each sample site. The minimum number of individuals per site was set to five, which resulted in a mean of 70 individuals per site (range 5–1001 individuals);

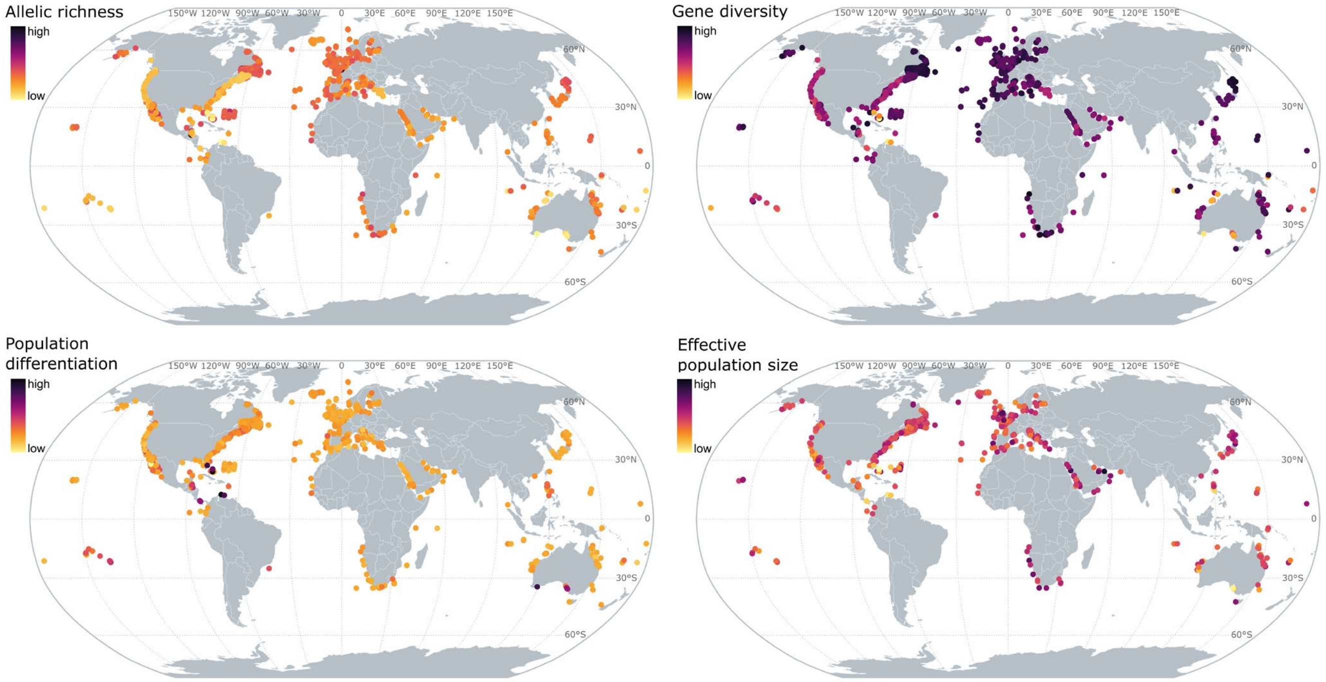

FIGURE 1 | Global maps of per population raw gene diversity, allelic richness, population differentiation (FST) and effective population size. Each point on the map is a sample site where a single species was sampled.

estimates of population parameters from the minority of our sample sites with small sample sizes may add noise (error) to the models, but they should not bias results in a particular direction.

Gene diversity is a measure of the average probability that two alleles at a given locus that are sampled from the population at random are different (Nei 1973). We estimated gene diversity with the *Hs*() function in adegenet (Jombart 2008; Jombart and Ahmed 2011). Allelic richness is an estimate of the number of alleles at a sample site corrected for sample size using rarefaction. We estimated allelic richness consistently across datasets using the *allelic.richness*() function in hierfstat with a minimum of 10 alleles, corresponding to the minimum number of 5 individuals sampled across the entire dataset (Goudet and Jombart 2015). Population-specific F_{ST} (Weir and Goudet 2017), a measure of the relative degree of divergence from a common ancestral population, was estimated using the *betas*() function in hierfstat. F_{ST} could only be estimated for species with at least two sample sites ($n = 1073$ sites). Contemporary effective population size, the estimated rate at which a population loses genetic diversity due to genetic drift, was estimated per sample site based on a linkage disequilibrium method using NeEstimator v2 with a minor allele frequency filter of 0.1 (Do et al. 2014). This conservative threshold reduces upward bias when estimating effective population size, which is more common in small sample sizes (Waples and Do 2008). Effective population size was log-transformed for use in further analysis. Estimating effective population size is difficult when sampling error overrides the signal of genetic drift, and in these cases, Ne is estimated as infinity, which we excluded from further analysis. Effective population size was estimable for 681 sample sites.

Repurposing data originally generated for different purposes adds robustness to our analyses. This is because we could estimate all population genetic parameters, measures of urbanisation, and human impacts consistently and comparably for all datasets. Additionally, because the datasets were collected for different research questions, it is unlikely that study site, system selection (e.g., selecting species or sites where effects were expected a priori), or publication bias affects our findings.

2.2 | Urbanisation and Human Impacts at Sample Sites

We used human population density as an indicator of urbanisation that should be correlated with a multitude of negative effects of human activities on associated marine ecosystems. We downloaded estimates of human population density (Center for International Earth Science Information Network (CIESIN) Columbia University 2018) (number of persons per km^2) from national censuses and population registers for the year 2010 in a 30 arc-second resolution. The density of humans in an area will not always be an indicator of exploitation and habitat degradation, as the intensity of these also depends on local environmental management and policy. However, on a global scale, we consider human population density to be an overall reliable metric of urbanisation suitable for detecting general relationships between urbanisation and the genetic composition of individuals exposed to urbanisation. To estimate the sum of human impacts on the world's oceans, we used a peer-reviewed index of cumulative human impacts that was calculated for 2013 (Halpern et al. 2015), an indicator of the influence of climate change, fishing, ocean and land-based stressors on marine ecosystems. To better understand how effects varied across spatial scales, we summarised human population density and cumulative human impact variables within buffers of 25, 50, 100 and 200-km radii around each sample site—marine fishes can be highly mobile and influenced by both their immediate and wider-scale environments. All datasets were re-projected to the Lambert Cylindrical Equal Area coordinate system to ensure their compatibility and comparability.

2.3 | Statistical Analysis

We modelled the relationships between genetic measures, urbanisation, and cumulative human impacts in separate models using Bayesian generalised linear mixed effects models fit in brms (Bürkner 2017). Predictor and response variables were scaled and centered prior to running models so that effect sizes were comparable across models. We treated species as a random effect and accounted for interspecific variation in the means of each genetic metric with random intercepts and species-specific variations in relationships with predictors by allowing slopes to vary with species. We fit hierarchical models for each measure of genetic diversity as explained by each driver. We ran all models with four chains and a minimum of 2000 iterations and a minimum of 1000 iteration warmup. In total, we ran 32 models: 4 genetic diversity measures × 2 candidate drivers × 4 buffer sizes. Models were run both with and without priors. We used a conservative normal prior of zero with a standard deviation of one for all fixed effect slope parameter estimates presented in the main text. We tested for spatial autocorrelation in our model residuals using the Moran's I test in the package spdep (Bivand and Wong 2018) and a connection network created in the package marmap (Pante and Simon-Bouhet 2013). No spatial autocorrelation was present in our model residuals. We estimated the probability of the direction of effect for each predictor using the function '*p_direction*' in bayestestR (Makowski et al. 2019). This probability measures the proportion of effect size values in the posterior distribution that have the same sign as the median effect size. Additionally, we estimated Bayesian R^2 values using the function *bayes_R2*(), the widely applicable information criterion (WAIC) using the function *waic*(), and performed posterior predictive checks using the function *pp_check* with the brms package (Bürkner 2017). We interpret models at the buffer size with the largest effect in the main text.

3 | Results

3.1 | Human Population Density Is Associated With Reduced Genetic Diversity

Allowing the relationship between the genetic composition of populations and urbanisation to vary with species, we found a globally coherent signature of the erosion of genetic diversity in marine fish populations associated with denser human populations. Populations associated with dense human settlements had reduced allelic richness, gene diversity and effective population size (Table 1; Figure 2). Human population density within a 200-km radius had the strongest effect on allelic richness and gene diversity. The strongest effect of human population density on effective population size was observed within a 100-km radius of a sample site. The consistent direction of effects suggests these relationships hold generally across taxa and sample locality. There was no detectable relationship between human population density and genetic differentiation.

Relationships between cumulative human impacts and genetic diversity and differentiation were less clear (Table 1; Figure 2). Allelic richness and gene diversity were both negatively associated with cumulative human impacts, but the relationship between cumulative human impacts and gene diversity was weaker than that between human population density and gene diversity (Table 1; Figure 2). The effects of cumulative human impacts on both allelic richness and gene diversity were strongest within a 200-km radius of a sample site. There was also little evidence for a relationship between cumulative human

TABLE 1 | Model summaries for the effects of human population density and cumulative human impacts on genetic diversity and differentiation. All model parameters had a normal prior centered on zero with a standard error of 1. The effect of human population density on gene diversity, allelic richness and FST is most evident within a 200-km radius of a sample site. The effect of human population density on effective population size is most evident within a 100-km radius. The effect of cumulative human impacts on gene diversity, allelic richness and FST is most evident within a 200-km radius. The effect of cumulative human impacts on effective population size is most evident within a 25-km radius. Mean overall effect sizes for each predictor are given with 95% credible intervals. The widely applicable information criterion (WAIC) is an indicator of relative model fit. Probability of direction (pd) is a measure of the probability an effect is positive or negative. Bayesian R^2 is the variance explained by both fixed and random effects divided by the total variance in the data. R^2 values are high because including species as a random effect, as expected, explains a large proportion of variation in the data.

	Predictor	Mean (95% CI)	Pd	Bayesian R^2	WAIC
Gene diversity	Human population density	−0.10 (−0.17, 0.01)	99%	0.83	1173.8
	Cumulative human impacts	−0.04 (−0.11, 0.03)	88%	0.81	1374.1
Allelic richness	Human population density	−0.06 (−0.15, 0.02)	95%	0.75	1587.1
	Cumulative human impacts	−0.06 (−0.13, 0.00)	97%	0.75	1661.1
Population-specific FST	Human population density	0.04 (−0.12, 0.21)	70%	0.55	2198.8
	Cumulative human impacts	0.02 (−0.08, 0.12)	66%	0.49	2408.7
Effective population size	Human population density	−0.09 (−0.23, 0.03)	94%	0.28	2412.4
	Cumulative human impacts	0.05 (−0.05, 0.17)	82%	0.32	1733.7

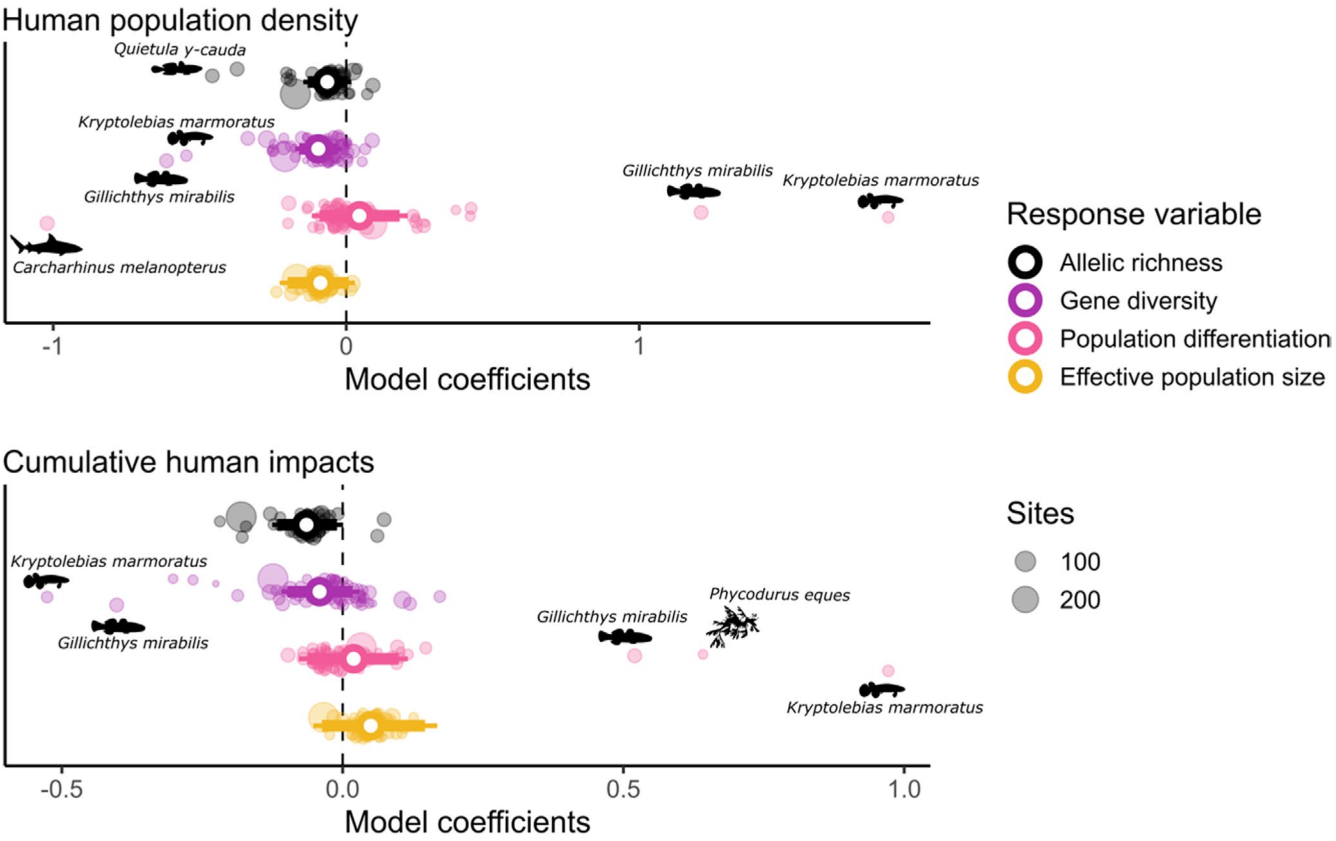

FIGURE 2 | Results of generalised linear mixed effects models for the relationship between human population density and cumulative human impacts, and allelic richness, gene diversity, population differentiation (FST) and effective population size. We allowed slopes and intercepts to vary with species. Open circles are overall parameter estimates, bold lines are 90% credible intervals and narrow lines are 95% credible intervals. Faded points are species-specific parameter estimates with outliers indicated by species name and silhouette. The effect of human population density on gene diversity, allelic richness and population differentiation (FST) is most evident within a 200-km radius. The effect of human population density on effective population size is most evident within a 100-km radius. The effect of cumulative human impacts on gene diversity, allelic richness and population differentiation is most evident within a 200-km radius. The effect of cumulative human impacts on effective population size is most evident within a 25-km radius.

impacts and population genetic differentiation. Unlike associations with human population density, we found no detectable relationship between cumulative human impacts and effective population size.

4 | Discussion

Our finding of a global pattern of reduced genetic diversity in marine fish populations associated with urban areas suggests adaptive capacity is reduced in populations near cities (e.g., Charlesworth 2009; Kardos et al. 2021). Maintaining genome-wide genetic variation prevents inbreeding depression and sustains adaptive potential (Kardos et al. 2021), and high levels of standing genetic variation could facilitate adaptation in urbanised coastal waters (e.g., Reid et al. 2016; Whitehead et al. 2017). Further, the efficiency of natural selection in a population is inversely proportional to its effective population size (Allendorf et al. 2022; Charlesworth 2009; Hartl and Clark 2007; Kimura 1983; Ohta 1992). As effective population size declines, the random process of genetic drift can increasingly overpower the more deterministic process of natural selection, with even well-adapted alleles becoming lost due to chance during Mendelian segregation. Our findings thus suggest that coastal marine fish populations and ecosystems near large cities are less resilient to future environmental change, continued exploitation and urban expansion.

The weaker associations between cumulative human impacts and the genetic composition of populations may be due to the inclusion of spatiotemporally varying factors in the composite index. For example, differences in fishing pressure and sea surface temperature anomalies vary across space and time, contrasting the more spatially fixed and persistent effects of human population densities in coastal cities, which tend to increase over time. The general lack of relationship between urbanisation and genetic differentiation for both measures of human disturbance suggests that urbanisation does not yet create sufficient barriers to dispersal and subsequent gene flow in marine fishes. Reductions in genetic diversity are due to the reduced capacity to support fish populations rather than population fragmentation.

The cumulative human impacts index we used included fishing pressure, a direct contributor to population decline, and so we had predicted it would have a detectable signature of genetic erosion. Indeed, previous meta-analytic work exploring the genetic consequences of overfishing found that fishing reduced genetic diversity (Pinsky and Palumbi 2014). We thus decided to perform a post hoc analysis to isolate the relationship between fishing pressure (hours of fishing per km^2) (Kroodsma et al. 2018) and genetic diversity and differentiation (see Data S1). We found little evidence of consistent associations between fishing pressure and genetic diversity and differentiation (Tables S4, S5, and Figure S2). The weak associations we found between the index of cumulative human impacts, fishing pressure and the genetic composition of populations do not necessarily contradict Pinsky and Palumbi (2014). Our analyses were concerned with declines in genetic diversity in populations within species, whereas Pinsky and Palumbi (2014) addressed this question across species using sister taxon comparisons between overfished species and species not known to be overfished. Taken together, these analyses suggest that fished species may lose genetic diversity on the whole (Pinsky and Palumbi 2014), with little evidence for population-level variation in the genetic consequences of fishing pressure within species. If true, genetic rescue, the movement of alleles from one population to another that increases genetic diversity, should not generally be expected to occur and may not be a viable conservation tool in exploited marine fish populations.

Outliers in our models tended to be species tied to coastal habitats with limited dispersal capabilities (Figure 2). This could make them particularly vulnerable to the coastal effects of urbanisation. For example, mangrove rivulus (*Kryptolebias marmoratus*) live in brackish waters associated with coastal mangrove forests (Tatarenkov et al. 2015); longjaw mudsuckers (*Gillichthys mirabilis*) and American shadow goby (*Quietula y-cauda*) inhabit tidal estuaries (Dolby et al. 2016, 2018); blacktip reef sharks (*Carcharhinus melanopterus*) are coastal species that inhabit shallow waters; and the leafy seadragon (*Phycodurus eques*) is a coastal species native to Australia that is threatened by habitat loss and degradation (IUCN 2016).

The effects of urbanisation on the genetic diversity of marine fish populations have received little attention (but see e.g., Alter et al. 2021; Todd et al. 2019; Touchard et al. 2023). Research to date on marine fishes has mostly been conducted across known pollution gradients (Cimmaruta et al. 2003; De Biasi et al. 2023; Maes et al. 2005; Maltagliati 2002; Marchand et al. 2010; McMillan et al. 2006; Roark et al. 2005) and salinity (Waldo et al. 2023). The small number of studies that have explored the consequences of urbanisation on marine fish populations, and the choice of environments where the negative consequences of the environment on genetic diversity are highly suspected a priori, preclude a generalisable synthesis of previous work. Our use of raw data collected across the globe for different purposes means that species and site selection should not introduce bias into our findings. Repurposing and reanalysing raw data also ensures that genetic and human activity variables of interest are comparable across species, and thus relationships can be cohesively modelled. These features of our analytical approach suggest our results should be robust and generalisable across species and localities.

We are moving toward an increasingly complete picture of the ways that urbanisation shapes neutral genetic diversity in wild populations. Human activities, in general, are now the principal driver of evolutionary change in wild species (Ålund et al. 2023; Johnson and Munshi-South 2017; Palumbi 2001). When we apply selection pressures on populations directly, such as through pest control (Heap 1997), evolutionary change is predictable—we can expect populations to evolve adaptively in response to intentionally applied selection pressures (Palumbi 2001). However, where selection pressures are more haphazardly applied, as with urbanisation, evolutionary responses can be idiosyncratic. On land, urbanisation reduces genetic diversity and increases genetic isolation in terrestrial mammals, while effects vary more strongly by species in birds (Schmidt et al. 2020). There are relatively few detectable associations between urbanisation and genetic diversity in amphibians, suggesting that the effects of urbanisation may not be generalisable for this group (Schmidt and Garroway 2021). Our findings add to this work by suggesting that there are generally negative consequences of urbanisation for marine fishes. This is important for conservation and management adhering to the precautionary principle in systems where the effects of humans on genetic diversity are unassessed—in these cases, we should assume negative consequences of urbanisation. The widespread and extensive urbanisation of coastal regions poses threats to marine fish populations, biodiversity, and ecosystems.

Human-caused biodiversity declines are concerning because they threaten both the species in question and the functioning ecosystems on which people and other species depend. Billions of people rely on the ocean for their primary food sources (FAO 2022), and approximately 260 million people rely on fisheries for at least part of their livelihood (Teh and Sumaila 2013). 85% of marine fisheries are coastal (FAO 2024), connected to coastal human communities and population centers. Relative to developed countries, fisheries play an outsized role in the economy and diet quality of developing countries (FAO 2022). The discharge of pollutants, destruction of critical habitats, spread of invasive species by the global shipping industry and unsustainable fishing practices all contribute to the degradation of marine ecosystems (Baum et al. 2016; Dafforn et al. 2015; Nunes and Leston 2022; Souissi et al. 2017). Mitigating these threats requires sustainable urban planning, improved wastewater treatment systems and the implementation of responsible fishing practices. Our results further encourage integrating genetic monitoring into conservation policy and fisheries management. By integrating conservation efforts into urban development, we will be better able to protect marine biodiversity and promote the long-term health and resilience of our oceans.

Author Contributions

Conceptualisation: E.K., C.S., M.F.D. and C.J.G.; methodology: E.K., C.S., E.d.G. and C.J.G.; analysis: E.K.; writing the first draft: E.K. and C.J.G.; revision and editing: all authors.

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Disclosure

We re-analysed publicly archived data and compiled a global genetic dataset for marine fishes, which we have made publicly available. Our synthesised dataset can be re-used to further research on genetic diversity and biodiversity conservation.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code used for this study have been deposited on GitHub under https://github.com/Karachae/urban-fish/tree/main and are publicly available. Any additional information required to reanalyse data reported in this paper is available from the authors upon request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.