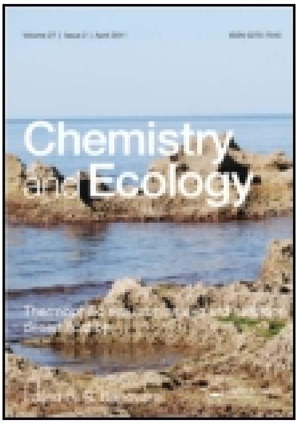

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Climate change and population genetic structure of marine species

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Climate change and population genetic structure of marine species

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Climate change influences populations by reducing or extirpating local populations, by disrupting patterns of migration and by shifting geographical distributions. These events can affect genetic population structure in several ways. Molecular markers have been used in numerous population genetic and phylogeographical studies of marine species and have detected population responses to climate change in the last few decades, such as range expansions, adaptative shifts and declines or increases in abundance. Little is known, however, about the molecular and physiological basis of adaptive responses to climate change in marine Mediterranean species. The Mediterranean Sea ecosystem is a 'living laboratory' with native species that are challenged by environmental change and by invasive species and a 'gene-climate' approach should be adopted as a way of focusing on the relationship between climate warming and genetic diversity.

Keywords: climate change; population genetics; phylogeography; Mediterranean Sea

1. Introduction

Concentrations of atmospheric greenhouse gases have increased significantly since the start of the industrial era. This anthropogenic gas loading has altered the radiative forcing of the atmosphere and has changed the Earth's climate, producing an increase in average surface temperatures across the globe in the twentieth century [1]. In the marine realm, climatic changes have shifted the chemical and biological properties of many marine systems on macro-geographical scales. However, the processes linking large-scale climate changes and local population responses on small spatial scales are poorly understood.

Strong interactions occur between the atmosphere, land and sea, but the coarse resolution of variables in climate models hinders progress in understanding the effects of climate variables on populations in some topographically complex regions, such as Southern Europe [2]. The Mediterranean Sea represents a relatively simple system that is more amenable to analysis than complex terrestrial landscapes or large ocean basins. The Mediterranean is a semi-enclosed sea with a complex system of currents that is shaped by wind patterns, straits and passages, large islands and complex archipelagos [3]. Hence, the various provinces in the Mediterranean are hydrologically

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heterogeneous, and this produces a complex biogeography of species' distributions [3–6]. This sea basin is, therefore, ideal for understanding how a variety of marine species respond to climate warming.

Global warming is now recognised as the prominent threat to biodiversity in many parts of the world. Even populations in protected habitats, such as 'marine protected areas' (MPA), are susceptible to climate changes, because of the pervasive effects of temperature shifts. Habitat protection alone may not be enough to ensure the persistence of a population, thus the conservation and harvest management of species requires the development of objective criteria to assess species' vulnerability to global climate change [7]. Current criteria for evaluating the actual and potential effects of climate change on species assume that populations respond rapidly to environmental changes and, hence, these criteria are largely based on assessing ecological variables [5]. Already, the distributions of several warm-water invertebrates have expanded northward in the Mediterranean [8–10], and local populations of cold-water species have disappeared during unusual periods of warm weather [11,12].

Currently, the methods used to evaluate the effects of climate warming on biodiversity are largely ecological (e.g. population abundance and range) and tend to ignore differences among species in physiological optima and tolerances that influence ecological and adaptive potentials. However, researchers are increasingly using molecular techniques and quantitative models to measure genetic diversity and to investigate the dynamics of climatically influenced populations [13,14]. Thus, population genetics surveys, quantitative genetic assessments and phylogenetics play important roles in understanding the responses of species to climate warming. These approaches complement ecological methods for identifying populations at risk of depletion or extinction. Although ecologists have long appreciated the conclusion that intrinsic physiological differences among individuals have a large genetic component, surprisingly few quantitative data support this relationship, especially for marine species.

2. The link between genetic traits and climate

Understanding the genetic structure of natural populations is a foundation for managing fishery resources [15] and for formulating evolutionary hypotheses [16]. The early use of genetic data to assess population structure was based on the premise that population variables affected loci in the same way. However, successive results clearly showed that the factors influencing allelic distributions can differ from locus to locus because of different regimes of natural selection [17,18]. Hence, an indispensable requirement in designing a study is to match the temporal and spatial scopes of the research objectives with appropriate molecular markers.

The use of genetic markers to better understand the effects of climate warming on populations has to be based on the recognition that the genetic profiles of present-day populations were shaped by historical events. Observed genetic diversities, therefore, provide a view largely into the past; nevertheless, high-resolution DNA markers can be used to make inferences about relatively recent events [19]. The use of neutral molecular markers – those unaffected by natural selection – is important, because these makers can provide insights into factors influencing population structure (e.g. reproductive isolation), historical demography and levels of genetic diversity. These markers include some allozyme loci and DNA-based markers such as single nucleotide polymorphisms (SNPs), mitochondrial DNA (mtDNA) and microsatellite DNA [20].

Three simple models capture the major features of population structure for most organisms in the Mediterranean Sea [21]. High gene flow species, which are common in marine environments, are expected to follow the 'single panmictic unit' model, in which individuals in a population potentially mate with any other individual in the population (Figure 1(a)). Some species with

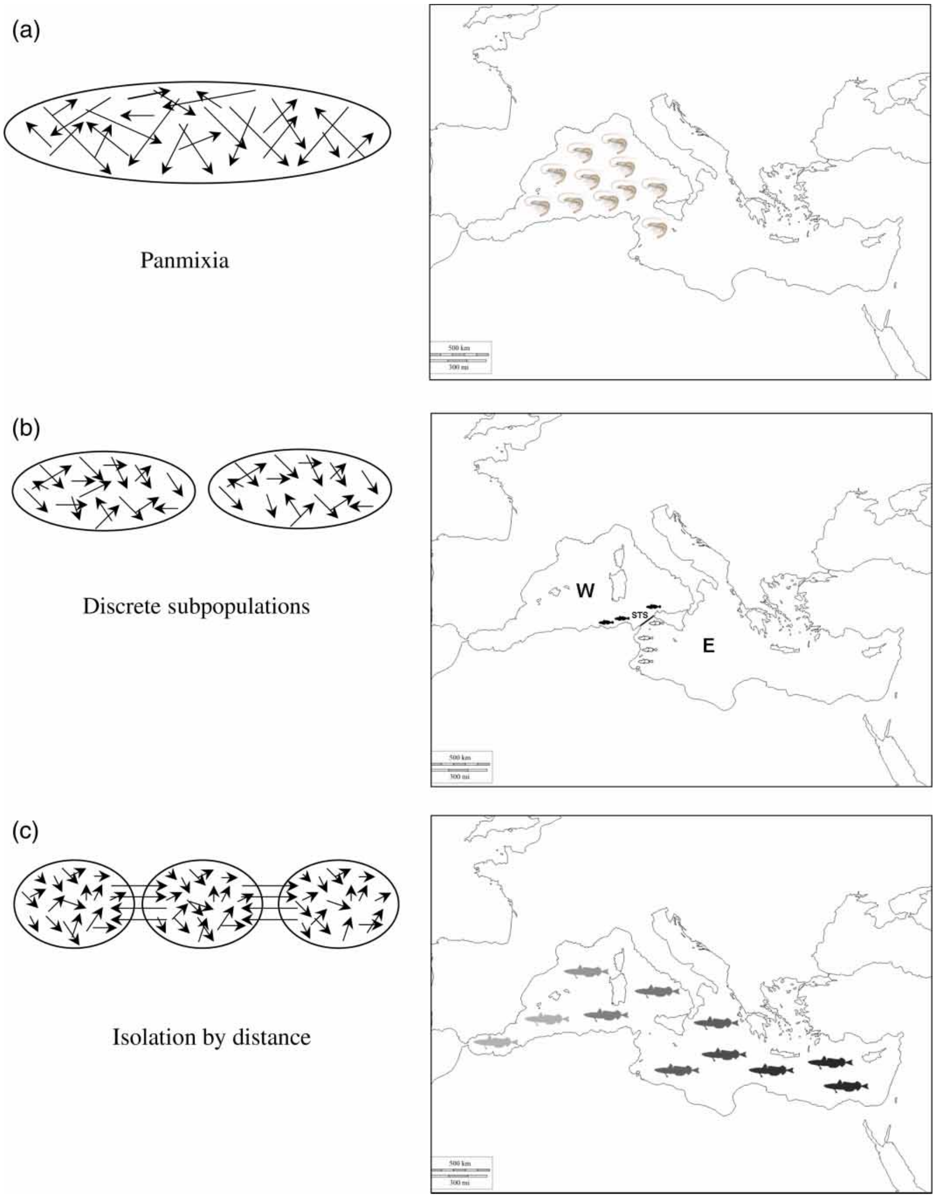

Figure 1. (Left) Diagrammatic representation of the essential differences between the three models of population structure: (a) Panmixia, free interchange; (b) discrete subpopulation, no interchange between subpopulations: free interchange within subpopulations; (c) isolation by distance, local interchange only. Arrows indicate the direction of movement by individuals for breeding and reproduction, i.e. gene exchange [21]. (Right) Examples of the respective models in Mediterranean species. (a) Panmixia: blue-red shrimp *Aristeus antennatus* sampled in the western and central Mediterranean Sea showed an absence of population structure as evidenced by the distribution of the mitochondrial haplotypes [79]. (b) Discrete subpopulations: the gobid *Pomatoschistus tortonesei* showed a strong genetic partition between the western (W) and eastern Mediterranean (E) sub-basin, revealing the Siculo-Tunisian Strait (STS) as a hydrographic barrier to gene flow [30]. (c) Isolation by distance: allele frequencies at the gene *Gapdh* in the European hake *Merluccius merluccius* varied gradually along the cline of the salinity values at the surface layers within the Mediterranean Sea [36].

high levels of migration, or with restricted geographical distributions, may consist of a single panmictic population. Genetic samples within the distribution of a panmictic population would not be expected to show significant allele-frequency differences. A second 'discrete subpopulation' model assumes that subpopulations are separated from one another by physical, environmental or behavioural barriers that limit migration (i.e. gene flow) between areas (Figure 1(b)). A third 'isolation by distance' model assumes limited migration in a physically homogeneous environment so that neighbouring populations show higher levels of genetic connectivity than more distant populations (Figure 1(c)). A correlation between genetic and geographical distances between populations is a signature of this model. The appearance of allele-frequency clines may also indicate isolation-by-distance population structure.

The results from a population genetic study represent a 'snapshot' of not only the accumulated effects of historical events, but also equilibrium processes such as random drift and gene flow. However, the apparent lack of genetic differences between areas should not be mistaken for a lack of information about population structure in a species. For example, results indicating panmixia (e.g. *Aristeus antennatus* see below) can yield insights for evaluating possible influences of global warming.

Because present-day genetic profiles reflect past events, the analysis of genetic variability, especially DNA sequences, can be used to reconstruct past demographical histories of a species [19]. Historical population events can also be inferred through direct analysis of ancient tissues from which DNA can be extracted and analysed, as in the case of the recent study by Riccioni et al. [22]. These authors compared microsatellite DNA in Atlantic bluefin tuna samples, *Thunnus thynnus*, from the Mediterranean that had been collected almost a century apart, 1911–1926 and 1999–2007 [22] and unexpectedly found heterogeneous genetic population structures in both time strata without signs of a declining population. Many oceanographic changes show decadal cycles [1,23], and these cycles must be accounted for in detecting the effects of climate warming on genetic structure. For example, introduced populations of the Mediterranean mussel, *Mytilus galloprovincialis*, expanded rapidly along the west coast of North America and hybridised with indigenous blue mussels, *M. trossulus* [24]. The hybrid zone and the distribution of the warm-adapted population of *M. galloprovincialis* were expected to move northward with climate warming, but a resampling of the population a decade later showed that both its distribution and the hybrid zone had moved southward in response to a cooling trend in the Pacific Decadal Oscillation [25].

In the phylogeographic approach to understanding population structure, the dispersal histories of populations can often be deduced by overlying gene genealogies on population landscapes (or seascapes) [26]. This approach complements traditional population genetics in understanding the historical processes influencing population demographics that have sculpted contemporary populations [26]. In addition to random drift and gene flow, natural selection can also influence the distributions of molecular markers within and among natural populations [18,27]. On long time scales, phylogeography converges with biogeography, and together these disciplines shed light on past dispersal and vicariance events and, possibly, predict future population expansions or contractions prompted by climate change.

At higher taxonomic levels, researchers can use neutral molecular markers to test biogeographical models, to delineate phylogenetic relationships among taxa and to detect cryptic species. For example, mtDNA resolved the phylogenetic relationships among European spider crabs in the genus *Maja* and provided insights into the biogeographical origins of species in the eastern Atlantic and Mediterranean [28]. Further, mtDNA sequences confirmed the taxonomic standings of three European species, *M. brachydactyla*, *M. squinado* and *M. crispate*, which are often combined in catch statistics [29].

Bianchi [5] noted the importance of defining biogeographical provinces in the Mediterranean basin as a means of recognising changes from climate warming. The boundaries separating different biota are not necessarily the same as those representing barriers to gene flow within a species. Nevertheless, the detection of biogeographical barriers can serve as a starting point for predicting future micro-evolutionary expansions or dispersal routes of marine species. Within the Mediterranean, some barriers to gene flow coincide with a biogeographical transition, such as the Siculo-Tunisian Strait (STS). A genetic transition detected in a molecular study of the goby *Pomatoschistus tortonesei* occurs at hydrographic breaks in the STS [30], and phylogenetic analysis and significant allele-frequency differences revealed a significant division between populations in the western and eastern Mediterranean sub-basins [30].

The complex hydrography of the STS exerts a strong influence on the water masses flowing through the strait [31] and appears to limit the dispersal of individuals in several species across it. This barrier to dispersal has led to genetic differentiation between populations of several species ([30] and references therein). However, Bianchi [5] suggested that the Strait of Sicily is more of a physiological than a physical barrier to dispersal. In this case, sea temperature gradients play an important role in defining the boundary between biota in the eastern and western Mediterranean. A shift in these temperature gradients from climate warming is predicted to also result in a biogeographical shift [5]. Both range expansions and local adaptation may be responses to climate warming and can often be detected with genetic analysis, which can also be used to test competing hypotheses.

3. The 'gene-climate' approach

Several environmental variables in the Mediterranean Sea are expected to shift with climate warming and directly, or indirectly, influence population abundances. Temperature is an important variable that directly influences the physiology of an organism. However, shifts in salinity from altered patterns of precipitation during climate warming can also bring about changes in the Mediterranean, and these changes may be useful, not only for detecting climate change itself, but also for anticipating the effects of climate change on populations.

The immediate benefit of a 'gene-climate' approach is the possibility to correlate changes in these environmental variables with population dynamics, with recent dispersals or with novel adaptations [17]. Marine species can respond to challenges from temperature shifts in several ways. One is a plastic response mediated by 'all-purpose' genotypes or by changes in gene expression, without changes in the structural genes themselves. Short-term protection from temperature increases may be conferred by heat-shock proteins that protect metabolic enzymes and other biologically important proteins [32,33]. A plastic response, however, may be difficult to distinguish from some kinds of selection, for example, heterozygote advantage, in which heterozygous individuals may thrive in a wider range of temperatures than homozygous individuals. Heterozygous advantage might be detected with departures from Hardy–Weinberg genotypic proportions, but only if selection is strong. This form of selection is unlikely to produce a shift in gene frequencies that could be detected with a search for outlier molecular markers or candidate genes.

A second adaptive response to climate change is an increase in the frequencies of genes that provide an adaptive advantage to an individual. The search for genes that confer production advantages has been a major research effort in agriculture and mariculture, and many of the same methods can be applied to the study of natural populations. If ecological differences between natural populations are due to genetically based functional differences, then it may be possible to make predictions not only about potential range-shifts in the Mediterranean, but also about the fate of a species during climate warming.

The search for correlations between molecular markers and environmental variables is an important first step, but only detailed studies of behaviour or physiology can lead to a more robust understanding of the adaptive responses to climate change. For example, Bernardo et al. [34] explored the utility of using interspecies physiological variation to track the effects of climate warming by relating physiological phenotypes in salamanders to patterns of genetic exchange. The basal metabolic rate (BMR) differed significantly among species, with the largest BMRs in species with the largest ranges, and smaller BMRs in species with smaller ranges, a pattern not associated with body size. The authors concluded that, if physiological properties influenced vagility, physiological differences might initially be detected as limited dispersal using genetic markers. Eurythermal generalists exhibited little to no phylogeographic structure, whereas high altitude, montane specialists showed moderate to extreme levels of genetic differentiation over small spatial scales. In accordance with a previous hypothesis [35], the authors concluded that metabolic stress arising from low intrinsic BMR of montane stenotherms limited genetic exchange and dispersal, leading to restricted ranges. By contrast, the high BMR of widespread eurytherms permitted exploitation of a wider range of thermal environments, conferring greater vagility, and facilitating range expansion and substantial genetic exchange [34].

3.1. *Analysis of individual genes*

Geographical clines may be a good starting point for detecting the effects of natural selection. Shifts in ocean salinity are indirect, but potentially sensitive, indicators of changes in precipitation, evaporation, river run-off and ice melt [1]. Patterns of salinity change have been correlated with gene diversity among Mediterranean populations of the demersal fish, European hake *Merluccius merluccius*. In a study of several allozyme loci, Cimmaruta et al. [36] demonstrated that two loci, *Gapdh* and *Gpi-2*, were characterised by allele-frequency clines, most evident in *Gapdh*, which were congruent with a Mediterranean salinity gradient. This pattern was consistent with the ‘Isolation by Distance’ model, in which genetic distances between populations were correlated with geographical distances. In this case, geographical distances were associated with a gradient in salinity. Again, genetic clines for several microsatellite loci in Atlantic cod, *Gadus morhua*, in Scandinavia were correlated with temperature and salinity gradients [37]. These two environmental variables are likely linked to climate changes in marine waters.

Adaptive ‘seascapes’ can be examined with molecular markers in several ways. One focuses on genes that respond to environmental variability over space and time. Temperature may exert a primary influence on some metabolic loci through the regulation of enzyme kinetics [38] and, hence, may exert a large influence on population abundance and distributions in warmer climates. Numerous studies of inidividual genes, particularly of metabolic genes, have demonstrated the effects of selection on shaping frequency distributions. For example, a latitudinal cline appears in the frequencies of lactate dehydrogenase B alleles among populations of the killifish, *Fundulus heteroclitus*, along the east coast of North America. A laboratory analysis of the kinetic properties of the LDH-B alleles showed that the genotype LDH-B^bB^b had greater catalytic activity at lower temperatures than genotypes of the alternate allele, and this was consistent with frequency shifts in the alleles along the coast [39]. Another well-studied example of selection is the Pantophysin gene in species of cod, which appears to respond to selection on small geographical scales [40,41].

The analysis of orthogonal gene sequences may give clues to the extent and nature of selection by comparing the rates of non-synonymous (d_N) and synonymous (d_S) nucleotide substitutions among species or adaptive morphs within a species [42]. Functional divergence of a gene between taxa can be identified by an increase over neutral expectations in the number of non-synonymous nucleotide substitutions that result in an amino acid replacement in the corresponding protein. Purifying selection tends to produce fewer non-synonymous substitutions than neutral substitutions ($d_N < d_S$), but positive selection is expected to elevate the number of non-synonymous substitutions relative to synonymous substitutions ($d_N > d_S$) because of the adaptive benefits of the the corresponding amino acid replacements [43]. Among related mammalian species, d_N/d_S falls within the range 0.10–0.25 [44], indicating that a substantial part of the mammalian genome is under positive selection. Most examples of positive selection among marine populations involve genes conferring pathogen resistance [45], self-recognition genes [46] or genes coding for reproductive proteins [47].

3.2. *Analysis of quantitative trait loci (QTLs)*

Although the study of single genes can be informative about some kinds of adaptive variability, most phenotypic or behavioural traits susceptible to environmental selection are controlled by the small effects of several genes, which collectively are called quantitative trait loci (QTLs) [48,49]. A current focus is on mapping these genes with linked molecular markers, such as microsatellites or SNPs, to understand adaptive variability in wild populations [50,51]. Most of these studies have been aimed at terrestrial species, or at aquatic species under culture, for which experimental crosses between parents of known genotypes can be used to map QTLs in the genome.

QTLs are more difficult to study than individual loci, because the associations among alleles at different loci produced by natural selection lead to gametic and linkage disequilibria that are weakened over time by independent assortment of chromosomes and by recombination. The effects of some QTLs on adaptive variation have been studied directly. For example, the Ectodysplasin (EDS) QTL has a major effect on lateral plate number in threespine sticklebacks [52]. A geographical survey of EDS alleles grouped populations by plate morphology differed from geographical groupings based on neutral markers [53]. However, the spatial distribution of closely associated microsatellite markers, which assorted with plate number in experimental matings, did not differ from neutral microsatellite markers.

The study of QTLs in wild populations requires the mapping of the molecular markers in controlled breeding experiments to detect linkages a QTL. This requirement limits the usefulness of linked markers for eliciting the adaptive responses to climate change in wild populations. Hence, an initial research approach might be to survey QTLs in species that include captive populations or are artificially cultured. A few studies of wild populations have used this approach, but most of these studies have been on terrestrial species of mammals [54,55] or on freshwater fishes [56].

3.3. *Genomic scans*

Footprints of selection on individual loci can often be detected by contrasts in the amount of geographical differentiation relative to differentiation observed in neutral molecular markers. One approach to detecting QTLs, or areas in the genome under selection, is to survey a large number of molecular markers throughout the genome (a genomic scan) and to test for non-neutral patterns of differentiation. Molecular markers showing a greater amount of differentiation among populations than expected from the effects of random drift and migration may be linked to ‘candidate’ genes that are under positive selection in different environments. Researchers have used several classes of molecular markers in genomic scans, including SNPs [57,58], amplified fragment length polymorphisms (AFLPs) [59], or microsatellites linked to coding genes identified by express sequence tags (ESTs) [60,61]. Large databases for EST sequences are available for many species (see [51] for fishes). High densities of genomic markers developed with sequenced restriction-site associated DNA (RAD) tags [62] have been used to study parallel evolution of marine sticklebacks in freshwater [63].

Several studies of marine organisms have identified ‘candidate’ loci that may be under selection. Many of these studies have sampled different morphs in a species as a head-start to finding the molecular basis of previously established adaptive differences. For example, a survey of two ecotypes of eelgrass in the northeastern Atlantic with SNPs, EST microsatellites and anonymous microsatellites identified outlier loci that appeared to reflect habitat-specific selection [61,64]. A similar pattern of divergence at replicate locations for markers linked to a cell membrane gene mediating osmotic stress indicated parallel adaptations. Other studies used AFLPs and microsatellite markers to survey variability in two sympatric morphs of an intertidal whelk and found that $\sim$5% of the markers were outliers, showing a greater degree of divergence than the degree expected under neutrality [65–67]. Genomic scans have been used to survey variation in lake whitefish [56], oysters [68], sticklebacks [69] and Atlantic eels [70] with variable success in identifying candidate loci under positive selection.

4. Which species to study?

The Mediterranean Sea supports a great variety of species in nearly all phyla [71]. These species include taxa at all trophic levels, ranging from heterotrophic bacteria, to photosynthetic algae and higher plants, to lower trophic level consumers, and to higher trophic level fishes and mammals. This assemblage represents a large variety of adaptations to ecological niches extending from the deep sea to surface waters and from warm temperate waters in the western Mediterranean to nearly tropical in the eastern Mediterranean. As Mediterranean climates change, the physiologies of many species will be challenged because of altered metabolic rates and trophic relationships; the distributions of many species will shift, and some local populations will become extinct [72,73]. How species react to climate change will depend on numerous variables, including body size, generation time and trophic level.

Species consisting of small individuals have shorter generation times and their richness and abundance are more affected by short-term climate variability than are the richness and abundance of large-bodied marine species. Thus, an organism's size should be considered when choosing a species to detect the link between population structure and climate changes. For example, smaller zooplankton, such as copepods, which represent the major portion of marine zooplankton, may be more informative than larger, longer-lived invertebrates. Unfortunately, a very limited literature reports genetic data on small invertebrates, but new data are emerging. Examples are studies of the freshwater copepods that inhabit temporary water bodies [74].

In addition to life-history type, a consideration of habitat could be important for selecting species for study, especially in the light of the sensitivity of European natural environments to climate change [75]. Variability in the abundances of species inhabiting deep-sea regions can also be linked to oceanic variables that are influenced by climate change. Large- and meso-scale ocean currents transport water masses from the surface into the depths, and vice versa. These pathways are important for detecting anomalies caused by changes in the surface conditions [3,6,76]. Changes in the abundances of key ecological species can influence an entire marine community [77,78]; however, the genetic population structures of deep-sea organisms are still poorly studied for the Mediterranean Sea.

A recent study of a deep-sea crustacean decapod in the western Mediterranean Sea [79] revealed a homogeneous pattern among samples, in an area characterised by turbulent mixing. This area is characterised by vertical fluxes, especially in the Tyrrhenian basin, and cascading flows of denser upper-layer waters that enrich deep waters with organic matter [3,6,76]. The blue-red shrimp, *A. antennatus*, is characterised by extensive gene flow among subpopulations, which are organised into a large panmictic unit [79]. Additionally, this species has an excess of rare haplotypes that produced high values of haplotypic diversity but low values of nucleotidic diversity, a combination that is generally associated with a recent population expansion [80]. Indeed, these results describe a scenario in which a species shows little geographical structure but is characterised by unstable population dynamics [79]. Recently, Company et al. [80] and Maynou [76] found evidence of long-term fluctuations in populations of *A. antennatus* after climate shifts affected the oceanography of the deep sea. Apparently, strong deep currents of cold and turbid water acted as a physical disturbance, causing individuals to migrate to greater depths and thereby leading to the disappearance of this species from upper levels. This zooplankton migration produced a temporary population collapse of fishes that fed on these shrimp. These results were consistent with genetic results, in which a single Mediterranean panmictic population displayed evidence of growth and decline. Researchers supposed that cohorts of *A. antennatus* migrated to greater depths searching for food, particularly after physical disturbances caused by shifting climatic conditions to the hydrological parameters of water, salinity and temperature [76,81]. Thus, evidence of vertical and horizontal displacements, promoting gene flow between populations, appeared to be consistent with the deep-water circulation pattern of the western Mediterranean. The spatial–temporal variations in the population abundance of the blue-red shrimp appeared to be linked to climatic conditions.

The Mediterranean is also a changing sea. Invasive marine species have had large ecological impacts in several places around the globe [82,83] and are particularly problematic in the Mediterranean [84,85] because this sea encompasses a large number of ecozones. Colonisations by alien species have largely been facilitated by humans through inadvertent and intentional introductions, but also 'naturally' through the Suez Canal and Strait of Gilbaltar [5,16,86]. Colonisations from eastern areas have a well-dated starting point, estimated to be about 1970 [5], after the opening of the Suez Canal. These invasives are tropical species, called Lèssepsian species, and have opportunistically migrated from the Red Sea into the Mediterranean Sea.

Being several species of recent origin, the search for climate change effects on these 'young Mediterranean species' may be particularly informative. These colonising propagules are establishing new populations in the Mediterranean, which will reorganise and develop unique genetic architectures [16,86] in response to the climate changes in progress. Genetic monitoring of these species could provide useful insights into the short-term genetic changes in response to rapid environmental shifts from climate change. However, most studies have focused little attention on the mechanisms leading to local adaptation, which should be a pre-requisite to a better understanding of range expansion models for invasive alien species (IAS), which are often used as indicators of climate warming [5].

5. Prospects

Species in the Mediterranean Sea are likely to experience unprecedented levels of disturbance from the effects of coastal development, climate change and invasive species. Researchers can use molecular markers in a variety of ways to monitor the effects of these influences on marine life. Neutral molecular markers can be used to assess possible shifts in genetic architectures due to demographic changes in abundance and connectivity between populations. Most molecular studies of Mediterranean species have focused on estimating population genetic parameters such as genetic diversity, gene flow and effective population size, which are indirectly influenced by climate variability. However, many markers can be used to study the effects of natural selection, either indirectly as markers linked to quantitative trait loci, or directly on genes under selection. Equally important are the QTLs themselves, which form the basis of adaptation, but which may not always reflect the same patterns of genetic diversity detected with neutral molecular markers [87].

Attempts to find candidate genes that respond to climate change have been limited by a 'needle-in-a-haystack' application of linked molecular markers. AFLP methods provide a large number of markers across a genome, but the developments of SNPs and microsatellite markers for genomic scans are more time-consuming. These markers must be closely linked to candidate genes to be effective in the search for adaptive variation. However, a new generation of high-throughput sequencing methods can sequence substantial portions of a genome in a short time [88,89]. Sequences provide direct access to candidate genes for statistical analysis in wild populations without having to first map linkage groups and can be used to develop assays, such as microarrays, for rapid assessments of environmental effects.

Studies of expanding invasive populations, or of declining native populations, can provide insights into evolutionary mechanisms that shape genetic diversity and can provide valuable information for the management and conservation of Mediterranean marine biodiversity.

Assuming that colonisations through the Suez Canal and the Strait of Gibraltar are correlated with temperature changes, future observations could strengthen the correlation between invasive alien species and the increase of sea surface temperature. The Mediterranean Sea is an example of a ‘living laboratory’ for studying biological processes induced by climate change, because of its location and because of its biological diversity.

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