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The International Union for Conservation of Nature Red List does not account for intraspecific diversity

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Abstract

The International Union for Conservation of Nature (IUCN) Red List identifies threatened and endangered species and is a key instrument in global biodiversity conservation efforts. Our understanding of the structure and value of genetic biodiversity below the species level is rapidly increasing. Nonetheless, the IUCN assessment criteria overlook genetic variation within species. Here, we address this blind spot and discuss the principles of species conservation status classification relative to intraspecific biodiversity. We focus on coastal species, which thrive in heterogeneous environments known to drive genetic differentiation. The focal example species, Atlantic cod and sugar kelp, have contrasting life histories, are ecologically and economically important constituents of the coastal ecosystem, and are currently not classified as threatened in Norway and Canada. We expose important variation in population structure, the presence of ecotypes and genetic-environment covariation, as well as loss of ecotypes that threatens the conservation of these species. Because the genetic makeup of species directly influences their resilience, omitting this information from conservation status assessments can result in loss of adaptive capacity to future stressors, such as climate change. Consequently, recognizing and preserving intraspecific variation emerges as vital for species' abilities to adapt to and survive in future ocean conditions.

Keywords: biodiversity crisis; gadus morhua; intraspecific diversity; IUCN Red List; *Saccharina latissima*; species conservation

Introduction

The unprecedented pace of human-induced alterations to nature has led to a historical moment where one million in eight million identified species are regarded endangered (IPBES 2019). The global biodiversity crisis is recognized through the Convention of Biological Diversity (CBD, www.cbd.int). The urgency of addressing the crisis is eminent and streamlining of processes to account for new knowledge is vital (Costello and Kelly 2022). The CBD recognizes biodiversity at three levels; diversity within species, diversity between species and diversity of ecosystems. Although previously neglected, preparations for a post-2020 global biodiversity framework acknowledge the need to include goals for preserving genetic diversity, addressing diversity within species (Hoban *et al*. 2023).

The International Union for Conservation of Nature (IUCN) Red List is a sobering testament to the accelerating loss of biodiversity in every environment (IUCN 2023). The list offers a universally recognized standard with which to track the conservation status of species over time and serves as the foundation for conservation actions worldwide. By a set of criteria the risk of a species going extinct is assessed country by country or globally by the IUCN Species Survival Commission (SSC). Unfortunately, the current approach overlooks intraspecific diversity, a critical element in the evolutionary framework that enables species to adapt swiftly and evade

extinction (Darwin 1859; Hoffman and Sgro 2011, Gallego-García et al. 2023).

Since the onset of human related species extinctions 10 000–100 000 years ago, terrestrial species have been hardest (McCauley et al. 2015). Consequently, the IUCN criteria for assessing extinction risk exhibit a pronounced terrestrial bias, focusing on single species' ranges, population sizes, and habitats. To date, the assessment has covered 157 000 species globally with >44 000 (28%) of these classified as being threatened (IUCN 2023). However, marine species are underrepresented, comprising <15% of the species assessed, and consequently IUCN formed The Marine Biodiversity Unit (MBU) to increase the representation of marine species on the Red List. Despite fewer species experiencing complete extinction in oceans compared to on land, marine fish, seabirds and mammals have nonetheless suffered cryptic, local, ecological and commercial extinctions by range contractions, functional loss, and reductions below commercially harvestable abundances (McCauley et al. 2015). In the Anthropocene era, the amplification of threats related to climate change is increasing and poses an escalating concern for marine species. Rising temperatures, marine heatwaves, storms, as well as other stressors such as habitat loss, pollution, and reduced water clarity have emerged as significant factors (Cooley et al. 2022). While threats to some historically overharvested marine species, such as marine mammals with large ranges and frequent dispersal,

are captured by current criteria, threats to many others remain insufficiently addressed. For instance, of 25 582 bony-fish species assessed, 3359 are considered threatened and as many as 4902 could not be evaluated due to data deficiency. Only 18 species of brown algae (Phaeophyceae) are evaluated (0.4% of described species). Of these, 6 are regarded threatened, and the remaining 12 could not be evaluated due to data deficiency. To account for intraspecific diversity, particular priority should be given to semi-enclosed environments wherein biogeographic barriers and opportunities for adaptations across multiple spatial scales arise.

In this study, we highlight the importance of intraspecific variation in two coastal species, Atlantic cod (*Gadus morhua*, a bonyfish, Actinopterygii) and sugar kelp (*Saccharina latissima*, a brown alga, Phaeophyceae). We illustrate how the loss of intraspecific variation may go unnoticed using the current IUCN criteria. Cod and sugar kelp are well-studied, are ecologically and economically important, widely distributed in heterogenous coastal environments and have strong population structures (genetically distinct populations). They are not classified as endangered in the red lists in two countries, Canada and Norway, with the longest coastlines along the North Atlantic (COSEWIC 2010, Norwegian biodiversity information Centre 2021). We also discuss the most urgent knowledge gaps and recommend adjustments to the IUCN assessment criteria to better account for within-species diversity.

The IUCN Red List criteria

The IUCN describes the Red List as "a critical indicator of the health of the world's biodiversity. Far more than a list of species and their status, it is a powerful tool to inform and catalyze action for biodiversity conservation and policy change, critical to protecting the natural resources we need to survive" (www.iucnredlist.org). This biodiversity health indicator is aimed at identifying risk factors for all types of species independent of life history and designed for global assessments of extinction risk (IUCN 2022). Based on a set of quantitative criteria, risk can be assessed, and threat category allocated. Extinction is defined as population size reaching zero, if only one gender prevails, or can be justified for example by Allee effects. For species which are not extinct today, the Red List distinguishes between threatened species, i.e. species categorized as "critically endangered," "endangered," or "vulnerable (VU)" and nonthreatened or abundant species categorized as "least concern (LC)" (IUCN 2012). Taxa that are close to being classified as VU and with significant degree of uncertainty, or the anticipated correct category includes both LC and VU, are classified as near threatened (NT). The Red List also includes "Data-Deficient" taxa with too little available information. In cases where no assessment has been made, not evaluated (NE) can be applied.

Criterion A relates to the reduction in population size of a taxon, and the extent to which a reduction is reversible or not, if causes are understood and have ceased and if reductions are expected in the future. Population is by IUCN defined as the total number of individuals of a taxon (species or the taxonomic level assessed). The Guideline (IUCN 2022) mention fish stocks and fishery specifically:

"It is important to note that criterion A measures declines over the last three generations, not from the original, unexploited stock. Thus, a well-managed stock should trigger the IUCN Criterion A thresholds only during the first three gen-

erations after the commencement of exploitation. Indeed, a species that is sustainably fished to achieve, for example, maximum sustainable yield (which could be at a biomass that is ~90% of the original biomass for a shark through to ~30% of the original biomass for a highly productive tuna) should have a current decline rate of zero."

Criterion B designates populations restricted to small or fragmented areas or present at few locations, which are also in decline or experience large fluctuations. The requirements for using criterion B are strict, and must meet two of three options: severely fragmented or occurring at few locations, in continuous decline or exhibit extreme fluctuations. Criterion C is aimed specifically for taxa with small populations. In order to qualify for criterion C, taxa must also be in decline or expected to decrease in the future. In addition, this criterion is also intended to capture extinction risk linked to being divided into many subpopulations (severely fragmented) or the opposite, risk connected to having all individuals in one or a few subpopulations. Criterion D applies to small or restricted populations with few mature individuals or restricted distributions. They may not be in decline, but because of their small size the risk of going extinct is substantial. Criterion E can be regarded as a safety fuse for situations with substantial extinction risk for other reasons than mentioned above, with focus on life history, habitat requirements and management.

In combination with the other criteria, the larger the decline rate the more severe Red list category applies. The minimal requirement for being allocated to one of the threatened categories is 30% reduction in abundance in three generations (criterion A, 10–100 years), limited distribution range ($<20\,000$ km^2) or distribution area (criterion B, <2000 km^2), limited and declining population size (criterion C, $<10\,000$ reproductive individuals), few reproductive individuals in total (criterion D, <1000 reproductive individuals, limited distributional range <20 km^2 or <5 localities) or substantial risk of going extinct in 10, 20, or 100 years (criterion E). In addition to the requirements for categorization, the guideline describes requirements for data, uncertainty and analysis. The guidelines can in principle be applied to populations, but application on a small geographical scale is not encouraged to avoid unreliable assessments, and genetic diversity is not reflected well in red list status (Schmidt et al. 2023). The need for further development of the criteria and their use to focus more on conservation of genetic diversity at all levels has been acknowledged and set forth in the CBD 2050 goals addressing connectivity and integrity of ecosystems including population level of all species, quantitative goal of maintaining 90% of the genetic diversity of all species, as well as the 2030 management target to recover and conserve genetic diversity (CBD 2021). As demonstrated by Frankham (2022), allowing a 10% loss of genetic diversity over consecutive reporting intervals of 8 years amounts to a 73% loss of genetic variation over a 100-year period, and >90% reduction in population fitness. Consequently, more stringent targets are needed to ensure retention of long-term evolutionary potential and persistence of species.

The emerging understanding of intraspecific genetic diversity

The use of genetic variation to describe populations of plants and animals goes back to the early years of the previous century (Wright 1978). However, the turning point arrived in

Figure 1. Cod (*G. morhua*) and sugar kelp (*S. latissima*) (photos: E Svensen/IMR).

the 1960s with the advent of efficient screening methods for molecular polymorphisms, igniting an exponential trajectory (Utter 1991). Introduction of molecular methods gave rise to increasingly richer data sources that have changed our understanding of marine ecology in general, and marine intraspecific diversity specifically (Hauser and Carvalho 2008).

Availability of high-density genomic data has further enhanced our awareness of biological complexity, allowing more accurate characterizations of intraspecific diversity (Theissinger et al. 2023). Several marine species that were historically considered as unstructured (panmictic) have now been shown to have more complex population structure, with genetically distinct local populations, gradual genetic clines along environmental gradients, abrupt breaks at environmental transition zones, or ecological and genetic distinct forms or ecotypes. In essence, the adoption of these refined genomic techniques has elevated our ability to discern and appreciate the complexity inherent in marine populations, transforming our understanding of their dynamics. While genomic insights have the potential to drastically progress biodiversity conservation and monitoring, widespread implementation in management is unfortunately still lacking (van Oppen and Coleman 2022).

Population structure of two coastal species

The coastal zones of Canada and Norway encompass extensive, irregular coastlines that are physically structured by water masses with different temperatures and salinities, as well as geographical features in archipelagos, bays and fjords. During recent decades, strong genetic structuring has been revealed in many coastal species, including Atlantic cod and sugar kelp (Figure 1).

Throughout their North Atlantic range, cod consists of multiple groups or populations that are genetically and ecologically differentiated (Knutsen et al. 2018, Svedäng et al. 2019, Johansen et al. 2020). Atlantic cod has dispersive, pelagic egg and larval stages followed by a more restricted benthic juvenile stage on nursery grounds and adult dispersal phenotypes ranging from tens of kilometers for stationary forms to thousands of kilometres for migrating forms (Robichaud and Rose 2004). Cod mature at 2–7 years, with an increasing trend in age at maturation from south to north (Olsen et al. 2008). Intraspecific variations often take the form of genetic clines reflecting e.g. temperature adaptations

(Bradbury et al. 2010) or isolation by distance (Dahle et al. 2018, Jorde et al. 2021, Breistein et al. 2022), as well as ecotypes of genetically distinct behavioral and/or ecological units. Whereas some of the cod groups show noticeable differentiation at the genome-wide level, genomic regions harboring large chromosome inversions play a key role in the within-species divergence of cod (Berg et al. 2016, Sodeland et al. 2016, Matschiner et al. 2022). On both sides of the North Atlantic, genetic differentiation has been observed between inshore and offshore populations (Ruzzante et al. 1996, Sodeland et al. 2016, Knutsen et al. 2018).

In Canada, The Committee on the Status of Endangered Wildlife (COSEWIC) provides guidelines for assigning a status below the species level. Genetic information on strong genetic isolation within cod led to the split of the species into six distinct "designatable units" (DUs) (COSEWIC 2010), including the populations of Newfoundland and Labrador, Laurentian North, Laurentian South, Southern (the Bay of Fundy and off the South Shore of Nova Scotia), Arctic Lakes and Arctic Marine (COSEWIC 2010). These units are defined by geographic clusters of Northwest Atlantic Fisheries Organization areas (COSEWIC 2010), which are species agnostic.

In Norway, Atlantic cod is split into five arbitrary populations for the purpose of stock assessment. The North Sea cod is jointly managed with the EU and known to harbor cryptic population structure (Henriksson et al. 2023), and at least two distinct coexisting ecotypes (Knutsen et al. 2018). The wide-ranging population complex includes Norwegian coastal cod south of 62°N (not subject to ICES advice), southern Norwegian coastal cod 62–67°N, Norwegian coastal cod 67–70°N (ICES 2023a,b), and the migratory Northeast Arctic cod (NEAC) jointly managed with Russia (Johansen et al. 2020). Behavioral differences regarding migratory or resident lifestyles among and within sympatric ecotypes have recently been demonstrated (Kristensen et al. 2021, Strøm et al. 2023). Population dynamics involving formation and persistence of behavioral units are likely (e.g. Svedäng et al. 2006). Regardless of stock-separating mechanisms, poor spatial resolution of past management is considered the root cause for commercial extinction of once productive local populations in Skagerrak and Kattegat (Cardinale et al. 2017).

Recent molecular analyses have uncovered substantial genetic diversity within sugar kelp, with many European populations being virtually unconnected (Luttikhuizen et al. 2018). The populations in the southern USA are distinct from the

north, with genetic evidence of geographical barrier between Gulf of Maine and Southern New England (Mao et al. 2020). The distribution of genetic diversity in the sugar kelp appears to be structured on regional scales, along biogeographical borders (Mao et al. 2020), or at finer scales (Breton et al. 2018, Evankow et al. 2019, Grant & Chenoweth 2021; Ribeiro et al. 2022). Variants of *S. latissima* are sometimes elevated to the level of subspecies (e.g. *S. latissima angustissima*: Augyte et al. 2017). Strong population structure in *S. latissima* can be explained by life history traits and limited dispersal capacity. Kelps has a haplo-diplontic (haploid–diploid) heteromorphic life cycle and a generation time of 1–2 years. Its mobile stages are spores and gametes and it depend on ocean currents for dispersal (Wernberg et al. 2019, Ribeiro et al. 2022).

Loss of *G. morhua* and *S. latissima*

On a global scale, the historical distributions of the species are likely to have remained unchanged, and the IUCN thus lists cod as VU due to reduced population size, while sugar kelp has not been assessed. In Norway, cod and sugar kelp are both assessed and listed as LC. The Canadian cod populations are currently being assessed for inclusion in the Species at Risk Act (SARA) public registry (consistent with IUCN), while sugar kelp has not been assessed. For both cod and sugar kelp, decline leading to loss of ecological function and loss of ecotypes have been observed locally but also on large spatial scales. Cod populations have been significantly impacted by overharvesting, reducing them to levels below those economically viable for commercial extraction (Cardinale et al. 2017).

Overfishing of fish stocks and subsequent loss of predatory function have transformed coastal ecosystems globally after centuries of fishing (Jackson et al. 2001). Intensifying fishing of coastal fish stocks, including cod in the NE Atlantic kelp forests led to predator release and blooms of grazers in the 1970s (Norderhaug et al. 2021). Cod persists at low population levels and barren grounds remain in most of this area more than five decades after the urchin bloom took place. In the North Sea and Skagerrak, the coastal and offshore population complex seem to have been heavily depleted prior to the onset of modern fishing methods based on interpretation of likely effective historical population sizes (N_e) inferred from genomic data (Sodeland et al. 2022). During the period known as the "gadoid outburst," fishing mortality soared and remained excessive throughout the 1970–1990s (Horwood et al. 2006). Any rebuilding of the population complex is unlikely under the present management regime (Sköld et al. 2022). The lacking consideration of intraspecific diversity in the IUCN Red List framework mirrors the failure to implement management measures that recognize and consider the well-known local structuring of coastal fish populations, including those of Atlantic cod in the Skagerrak, which has been described as "the easy restriction syndrome" in management (Cardinale et al. 2017). In Canada, one common Red List status was initially considered throughout the species' range, and cod was assigned a case of Special Concern in 1998. COSEWIC has later assessed status classifications, ranging from the endangered Newfoundland, Labrador, Southern, Laurentian North and Laurentian South populations, to the special concern and data deficient Arctic lakes and marine populations (COSEWIC 2010). A matter of particular concern revolves around the endangered populations of cod in the offshore waters of Labrador and northeastern Newfound-

land, which has suffered a staggering decline of >90% since the early 1960s, with minimal signs of recovery. As per the criteria for "designatable units" (a unit below the level of a recognized taxonomic species, DU), losing these units would be irreversible, as they cannot be reconstituted from other populations. This implies that these units could face extirpation in Canada or global extinction, depending on whether the population range extends outside of Canada's borders (COSEWIC 2018). The endangered status of these populations and the imminent threat of loss of these discrete and evolutionarily significant units (COSEWIC 2018) are not reflected in the IUCN designation, as none of the COSEWIC listed populations have led to listing in the Species at Risk Act (SARA).

Saccharina latissima, a foundation species in the coastal ecosystem, has experienced extensive declines in range-edge populations globally in the last few decades, and with substantial loss in the North Atlantic (Smale et al. 2013, Krumhansl et al. 2016, Wernberg et al. 2019). It is therefore put on the OSPAR list of threatened and declining habitats (de Bettignes et al. 2021). *Saccharina latissima* provides important ecosystem services including habitats and food for commercial fish stocks, nutrient cycling as well as being a carbon sink (Eger et al. 2023). In the Skagerrak and Rhode Island large declines have been attributed to warming temperatures and heatwaves, with effectively complete loss in Rhode Island and losses of over 80% in the Norwegian Skagerrak over 10–20 generations (Moy and Christie 2012, Filbee-Dexter et al. 2020, Feehan et al. 2021). Loss of kelp forests due to sea urchin overgrazing affects large areas globally (Filbee-Dexter and Scheibling 2014). Blooms of *Strongylocentrotus droebachiensis* along the coasts of Nova Scotia and North Norway starting in the 1970s have caused loss of kelp forests on the scale of 100–1000s kilometers of coastline (Scheibling et al. 1999, Norderhaug and Christie 2009). In Norway high urchin densities has to date persisted for five decades and thus 25–50 generations of *L. latissima* (Norderhaug et al. 2021).

Correlations between genetic and environmental variation

Environmental conditions have an important role in driving intraspecific differences between populations of coastal species. Several studies, including Addison and Heart, (2004), Berg et al. (2016), Norderhaug et al. (2016), Gavery and Roberts (2017), Kelly et al. (2020), Ribeiro et al. (2022) and Breisten et al. (2022), provide evidence of population-level variations in response to environmental factors for various marine species. Particularly, Berg et al. (2016) showed how different populations of cod exhibited divergent genomic responses to variations in salinity, highlighting the genetic basis of adaptation to environmental stressors. Several other genomic studies have identified genes that are correlated with environmental factors such as temperature and pH, providing further evidence of the complex interplay between genetics and the environment in shaping intraspecific variation (e.g. Gavery and Roberts 2017, Kelly et al. 2020, Vranken et al. 2021, Guzinksi et al. 2020).

While less is known on the genetic basis for adaptations in *S. latissima*, there is some evidence for local adaptations to for example brackish waters (Møller Nielsen et al. 2016) and temperature (Guzinski et al. 2020). *S. latissima* also shows differentiation into ecotypes (spatial differences in traits, Diehl et al. 2023). Also, recent advances in our understanding of adaptive

genetic diversity of other seaweeds can help to assess species' vulnerabilities and determine mitigation strategies. Genomics studies in Australia demonstrated strong population structure in native kelp and isolation-by-distance along both coasts (Vranken et al. 2021, Coleman et al. 2011), as well as adaptation to local thermal environments. This indicates that the conservation of warm adapted genotypes is critical for the persistence of this species at warm range edges and can enable management techniques such as assisted evolution (Coleman et al. 2020). Together, these findings demonstrate the need for a more holistic approach to understanding the drivers of intraspecific variation in coastal species, one that takes into account both genetic and environmental factors.

Concluding remarks and recommendations

The IUCN Red Lists have a critical blind spot as they do not account for intraspecific diversity. For species with limited population connectivity, crucial genetic diversity may therefore be lost unnoticed (cryptic extinction). The two North Atlantic coastal species presented here, cod and sugar kelp, with contrasting life histories and strong population structure have experienced range contractions in marginal areas as well as functional loss without being reflected in the national Red List status. While the assessment opens for use of criteria considering loss of subpopulations and reduction in distribution range, opportunities offered by new methods are insufficiently embedded in the set of criteria, and the focus is on interspecific diversity both at a national and global level. Better understanding of population structure and distribution of genetic diversity in coastal species is urgent and achievable and should, together with increasing the understanding of how intraspecific variation is linked to function and traits, including tolerance and resilience to future global changes, be integrated in global biodiversity conservation frameworks. In addition, we recommend actions to address key knowledge gaps and for amending the IUCN criteria:

1. Develop the species-oriented framework of the IUCN Red List to better account for intraspecific diversity, providing valuable information for conservation, and ensuring accurate reflection in the Red List status. Recent advancements in simple indicators offer the opportunity to better account for small populations, proportions of maintained subpopulations and the extent to which DNA-based methods are being used in monitoring (Hoban et al. 2020; 2022). Recognizing that the population structure remains largely obscure for many species, we suggest combining life history traits describing dispersal potential and environmental factors and describing physical barriers into alternative indicators for potential population structure to be used in assessments until confirmed by genetic data.

2. Increase and target efforts for genetic or genomic assessment of species with low dispersal potential living in semienclosed environments. This is particularly urgent for marine species, which are underrepresented on the IUCN Red List in general. As the number of sequenced species increases, practical indicators for systematical monitoring of temporal trends in genetic diversity in natural populations should be adopted.

3. We also recommend emphasising more on available long-term time-series for three reasons. First, genera-

tion time varies widely between species. Second, as time-series come of age, they represent the most valuable data on species and population trends. Third, catch reconstructions and recent genomics research suggest that humans have impacted the abundance of coastal species for centuries (see e.g. Atmore et al. 2022 and Sodeland et al. 2022).

It is important to note that our recommendations underpin implications for coastal management extending well beyond the IUCN Red Lists of endangered species. Fisheries management is a tangible real-world example of a field in which the integration of knowledge on intraspecific diversity into decision-making tools is urgent. In Skagerrak-Kattegat, serial depletion of once productive subpopulations has been lamented (Cardinale et al. 2017). Cadrin (2020) warned that "…ignoring spatial structure can lead to major failures in stock assessment and fisheries management." Multiple nested scales of management are probably necessary to avoid cryptic extinctions in metapopulations and the ensuing ecological, social, and economic consequences (Okamoto et al. 2020). Reconciliation of conservation with fisheries management must strive to involve the application of spatially explicit assessment models that account for population structure and vulnerability of disparate subpopulations (Cardinale et al. 2023).

Aquaculture is rapidly growing worldwide, targeting new species and representing a risk of spreading reproductive material into local populations. Macroalgae cultivation growth exceeds 6% annually in Europe (Duarte et al. 2022), and an annual production of 20 million tons of *S. latissima* in farms covering up to 3000 km^2 in total is envisioned in Norway's coastal waters (Broch et al. 2019). The risks related to introducing domesticated seaweed are largely unknown, and Campbell et al. (2019) highlighted significant potential effects by alteration of genetics in locally adapted populations. Cultivation of cod is recently increasing in Norway (Puvanendran et al. 2021) and possess a similar risk to local cod populations. In conclusion, we deem a better integration of intraspecific diversity into the IUCN criteria as a critical step in any effort to improve the ability of policy makers and managers to absorb and respond to new knowledge from the research front, as their informed actions are vital for successful, holistic species conservation in the Anthropocene. We deem this particularly urgent to preserve the adaptive potential of species living in semi-enclosed and densely populated coastal areas.

Author contributions

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Conflict of interest: The authors have no conflict of interest to declare.

Data availability

No new data were generated or analysed in support of this research.

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Handling Editor: W. Stewart Grant