Title - Unbounding fish: Assessing vulnerability to overexploitation for transboundary fish populations

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Abstract

Tropical fish populations often traverse management boundaries, making it difficult to evaluate species vulnerabilities and optimise sustainable fishing goals. Most vulnerability assessments rely on life histories and gear susceptibility, but ignore transboundary differences in management, which can strongly affect vulnerability. We propose a novel vulnerability matrix, the Biology – Transboundary Management (BTM) index for individual fish populations based on 1) Species specific vulnerability 2) distribution of genetically-distinct populations with respect to jurisdictional boundaries and 3) sustainability of management practices across jurisdictions. Combining single-nucleotide polymorphism (SNP) analyses and policy assessments, we evaluate relative vulnerabilities of nine commercially relevant fish populations over a 3400km stretch of India's west coast, across multiple jurisdictions. The BTM matrix indicates that transboundary differences in management strongly influences biological vulnerability. The matrix is sensitive to population-level differences and policy changes. Our analyses emphasise the need for population-level assessments and transboundary cooperation in achieving sustainable multi species fisheries.

Introduction

The global defaunation of biodiversity once characteristic of terrestrial ecosystems, now pervades the seas and oceans as well. Historically described as an inexhaustible natural resource[1], marine fish today face a crisis of overfishing[2]. Recent global analyses indicate that of 4,713 global fish stocks (77%) show worrying declines in catch despite increasing fishing efforts[3]. Some groups like elasmobranchs are more susceptible than others. More than 390 species of elasmobranchs are threatened with extinction[4]. With the livelihoods of ~260 million people involved in marine fisheries worldwide, this is not merely an ecological problem, but a crisis of food security, livelihoods and equity[5]. This crisis is particularly acute in the global south, where dependent coastal communities target a diverse community of fish, and where

the resources available to adequately monitor and regulate the fishery are limited[6]. Finding ways to effectively manage fish resources at spatio-temporal scales that are biologically meaningful, economically viable and managerially effective is the principal challenge confronting global fisheries[7].

Bio-economic harvest models based on Maximum Sustainable Yield (MSY) calculations are the most widely used tool for fisheries management[8,9]. However, this approach has been widely criticised because it is simplistic and does not take into account differences in life history traits, ecological factors, and variations between regions[8–10]. Also, while this approach may work for managing single species typical of many temperate fisheries, its applicability to complex multi-species tropical fisheries is questionable[8,11]. Identifying biologically and ecologically relevant approaches that work for the tropics is crucial to inform fisheries policies and help managers protect tropical fish stocks.

In evaluating the sustainability of fisheries, most recent work has focused on matching fisheries effort with the productivity of each fish stock based on its natural susceptibility to resource offtake[12–17]. These approaches fall under the broad umbrella of Productivity Susceptibility Analyses or PSA. They attempt to be biologically comprehensive, incorporating population growth rates, trophic level, breeding strategies and other crucial elements of fish biology in their assessments[13]. A typical PSA approach incorporates multiple species harvested in the area of concern, making them much more appropriate than MSY approaches for multi species fisheries. They are also much more realistic about fisheries practices and the susceptibility of fish species to different gear.

To bridge the gap between being an analytical useful tool to one that is directly applicable to fisheries policy, a few limitations of the PSA approach need to be addressed. For most available PSA's, the unit of analysis is the geographic range of the species (but see Patric et al. 2010[18]) within the area of concern[12,14–17]. While this is a convenient simplification, it has been long understood that, to be effective, genetically distinct populations of the same species should be managed as separate management units[19–21]. Not incorporating this population level information in PSA analyses significantly limits their applicability to real-world fisheries management.

Along with species-centric analyses, most PSAs also assume a uniform harvest regime along the entire geographical range of analysis. However, for coastal and nearshore fisheries this assumption is seldom true. Apart from the EU, most countries manage the coastal waters under their jurisdiction with little transboundary coordination. This transboundary problem repeats within national borders as well. In most tropical countries with large coastlines like Brazil, Indonesia, Philippines, India and Mexico, coastal fisheries are often decentralised and governed by provinces which have significant autonomy in terms of fisheries management[22–25,26]. Rarely is there a uniform harvest regime across the geographical area considered within a PSA.

Between the multiple genetically distinct populations of a species and decentralised harvest regimes there is often a mismatch between the biological boundaries of fish populations and the management boundaries of fisheries. These mismatches lead to an increased risk of local depletion of populations[27]. The consequences of these mismatches have been well documented in the North Eastern Atlantic, where species like the Atlantic cod (*Gadus*

morhua)[28] and the North Atlantic mackerel (*Scomber scombrus*)[29] have experienced serious overharvest and overfishing as a result of a misalignment between management and biological boundaries.

Here we propose population-wise vulnerability matrix as a heuristic extension of the PSA by incorporating 1) the inherent resilience and susceptibility attributes of species characteristic of a typical PSA analysis, 2) the biological relevance of present management regulations[26] and 3) information on whether the population is managed through single or multiple management regimes. As a case study, we present a vulnerability assessment for nine commercially important fish species harvested along the west coast of India. Marine Fisheries in India is a paradigm case of a multi species multi-management fishery where individual states (provinces) manage fisheries in their waters semi-autonomously with little dialogue amongst them. The current fishery is managed within provincial waters (Indian states) with little regard to the underlying geographical spread of fish populations[26]. This makes Indian fisheries an ideal system in which to test the application and relevance of the combined vulnerability matrix. We used single nucleotide polymorphism (SNP) analysis of the target species to identify their population boundaries along the 3400 km stretch of the west coast of India. We combined this with a detailed analysis of management policies across all west-coast states to determine; i) how closely these policies and management regimes matched the biological susceptibility of the species and ii) whether the genetically contiguous population straddled a single or multiple management regime. This information was used to construct a population-wise vulnerability matrix. We then discuss the utility of this matrix in guiding policy and management decisions.

Methods

We first describe a heuristic framework to assess the relative vulnerability of genetically distinct, transboundary fish stocks based on an extension of a standard PSA analysis. We then demonstrate the utility of this framework based on a case study of species from an extensive coastline along the west coast of India. We use Single Nucleotide Polymorphism (SNP) analysis to identify the genetic boundaries of nine commercially targeted species and determine their population-level vulnerability after evaluating management practices across the range of each population.

1. Constructing the Biology- Transboundary management vulnerability matrix (BTM)

We propose that the vulnerability of fish populations to overharvest is a function of both, the inherent life history and catchability of each species (PSA), as well as number of management regimes and their impacts that the population is exposed to across its range. This management associated vulnerability is determined largely by (i) how prevalent management practices align with sustainability based on known species biology and (ii) different management and harvest regimes that population is subject to across its geographical distribution. Fig. 5 outlines a schematic representation of this matrix and the Rationale section details the steps we employed in its construction.

Evaluating the biological relevance of present management regimes

We first evaluate the congruence of current management practices with known species biology. For every management regime within the geographical area of the assessment we

first catalogue all available policy instruments, regulations or subsidies related to the fishery. These can also encompass catch and effort attributes of a particular fishing regime. We then evaluate each of these practices and policies based on their congruence (or disparity) with sustainability goals based on what is known of species' biology. We then assess the overall biological veracity of the management regime in question to the assessed population by calculating a percent disparity. The percent disparity is the proportion of all policy/practice attributes that do not align with the biology of the assessed population of a given species presented in percentage form. For simplicity, in the current assessment, we assume that all attributes have an equal weightage on sustainable harvest. However, it is quite possible to assign different weights to each attribute if there is a sufficient justification to do so. Weightages can also be assigned based on reliable knowledge of how effectively each policy attribute is implemented on the ground. Table 1 provides a tabular explanation of this procedure with the help of a hypothetical example.

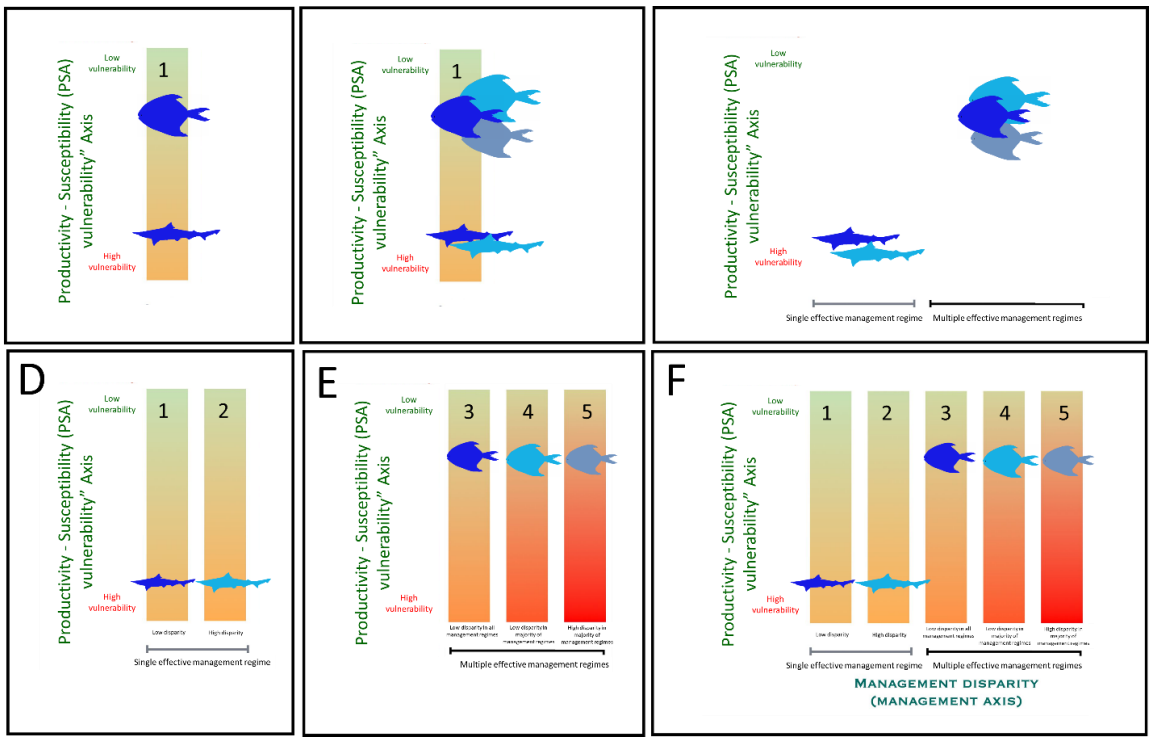
Table 1 - Evaluating the biological veracity of present management regime

Sr. No	**Attribute and its intended consequence**	**Prescribed policy**	**Species biology**	**Assessment**
1	Temporal/seasonal ban on mechanised fishing to protect breeding individuals	Ban period: June – August	Breeding period of target species: June to September	Congruence between species biology and policy attributes
2	Prescribed Minimum Legal Size (MLS) to protect juveniles from overfishing	No prescription (all size individuals are legal to catch)	Length at Maturity (L50) – 20 cm	Disparity between species biology and policy attribute
	Total disparity percentage			50% policy attributes show disparity **– High disparity combination**

Rationale for constructing the BTM vulnerability matrix

Figure 1 – Steps in the construction of the Biology - Transboundary Management (BTM) vulnerability matrix.

Legend: Silhouettes represent different fish species while different colours represent genetically distinct populations within the study area



Rationale for construction of proposed vulnerability matrix

Figure 1A: The vertical axis of the Biology - Transboundary vulnerability matrix is the score assigned by classical Productivity Susceptibility Analyses which typically assign a vulnerability score to their sampling units (usually species)[14,16,18] (figure 1A).

Figure 1B With the help of genetic tools, we identify and separately depict distinct populations in the study area. In species-based PSAs these populations would occupy the same positions on the vulnerability axis as shown in figure 1B.

Figure 1C The horizontal axis of the matrix is premised on the observation that in addition to species-based vulnerability indicated by PSA analysis, the vulnerability of a particular population is mediated by the degree to which the spatial extent of the population matches the spatial extent of the management regime. Therefore, populations can be grouped in two broad vulnerability categories i) Populations located entirely within a single management jurisdiction ii). Note that the species-specific vulnerability (based on PSA) does not change in these assessments between populations.

Figure 1D If the assessed population is entirely located within a single jurisdiction, we classify its management-based vulnerability by calculating the percent disparity: Low disparity <33%; High disparity >=33%. Management-based vulnerability increases as we move from bar 1 to bar 2.

Figure 1E If a population spans multiple management regimes, we assess its transboundary management vulnerability by calculating the percent disparity of the population within each jurisdiction separately. Based on the proportion of jurisdictions with more than 33% disparity with species biology we assign the population in three assessment categories. 1) All jurisdictions with <33 % disparity (vertical bar no. 3 in figure 1E), 2) majority of management regimes with <33% disparity (vertical bar no. 4 in figure 1E), 3) Majority of management regimes with >33% disparity (vertical bar no. 5 in figure 1E). Management-based vulnerability increases from left to right.

Figure 1F The Biology - Transboundary Management (BTM) vulnerability matrix combines management-based vulnerability assessments of i) Populations that are entirely located under jurisdiction of single management regime (Figure 1D) ii) Populations that are spread across justification of multiple management regimes (Figure 1E), keeping the common axis of species-specific vulnerability (as shown in Figure 1C). We assume that populations entirely located in a single management jurisdiction have an inherently overall lower vulnerability than populations spread across jurisdiction of multiple management regimes due to inherent differences in implementation between jurisdictions and the added complications of transboundary co-ordination, if there is any.

2. Case study: West coast of India

We apply the BTM matrix to evaluate the vulnerability of populations of nine commercially important fish species along the west coast of India. We use SNP based genomic data to identify species population boundaries for these target species and an analysis of management practices across all regimes to populate the matrix.

Study area

The study region extends from the western shores of the Kutch peninsula to Kanyakumari at the southern tip of India - a stretch of approximately 3400 km of coastline (Refer Figure.2A) The region represents a single eco-region based on its faunal community composition[30]. While fish composition and bathymetry are relatively consistent, the governance of the coast is distributed across five states (Gujarat, Maharashtra, Goa, Karnataka and Kerala). Each state manages its own fisheries with policy instruments in the form of Marine Fisheries Regulation Acts (MFRAs), as well as schemes and subsidies to manage the coastal waters under its jurisdiction. The uniformity of the habitat across the coastline together with its disjunct governance regimes makes the west coast an ideal case study to understand how differences in fisheries management can mediate the vulnerabilities of individual fish populations. As potential outliers, we also sampled individuals from a single location on India's east coast, in Balasore, Odisha, approximately 1700 km away from southernmost sampling locations on the west coast. These east coast samples are expected to act as a separate population in our analysis.

Choice of species

We identified nine fish species commonly caught in trawls on the west coast of India. The choice of species was dependent on their ubiquity, the frequency with which they occur in trawl catches across the west coast, and ease of identification in the field. They were also chosen to represent different trophic groups, habitats, taxonomic groups and commercial value.

The selected fish species were silver pomfret (*Pampus argenteus*), ribbonfish (*Trichiurus lepturus*), Japanese threadfin bream (*Nemipterus japonicus*), spiny cheek grouper (*Epinephelus diacanthus*), spade nose shark (*Scoliodon laticaudus)*, wolf herring (*Chirocentrus nudus*), Indian oil sardine (*Sardinella longiceps),* ladyfish (*Sillago sihama*), and Indian mackerel (*Rastrelliger kanagurta*),

Table 2 – Target species with their life history characters and comparative commercial values

Common name		Scientific name	Habitat	Food	Value
	Silver Pomfret	*Pampus argenteus*	Muddy bottoms	Zooplankton	Very high
	Ribbonfish	*Trichiurus lepturus*	Muddy bottoms	Fish, squid etc	High
	Japanese threadfin bream	*Nemipterus japonicus*	Mud and Sand bottoms	Small fish, Crustaceans etc	Low
	Spiny cheek grouper	*Epinephelus diacanthus*	Muddy substrate	Fish	Low
	Spade nose shark	*Scoliodon laticaudus*	Rocky substrate	Small fish, shrimp	Moderate
	wolf herring	*Chirocentrus nudus*	Inshore waters	Small fish, crustaceans etc	High
	Indian oil sardines	*Sardinella longiceps*	Coastal pelagic	Phytoplankton, crustaceans etc	Low
	ladyfish	*Sillago sihama*	Beach, sandbank, estuaries	Polychaete, shrimps,	low
	Indian Mackerel	*Rastrelliger kanagurta*	Coastal pelagic	Small Zooplankton	Moderate

Identifying the geographical extent of individual fish populations.

i. Data collection

We collected tissues samples using fin-clips taken from the fish directly at the landing site. Sample collection along the west coast of India was conducted in April 2018, February-March 2020 and November 2020. The samples from one east coast site (Balasore, Odisha) were collected in January 2023

Fin clips of ~ 10-18 individuals were collected from each species at each sampling location with the help of sterilised instruments and stored in 100% ethanol. We limited our sampling to fish landed from small boats with low engine capacity to ensure (as much as possible) that the fish sampled were sourced from local waters. We sampled only adult fish from each location.

ii. Data generation

We used genome-wide SNP (Single Nucleotide Polymorphism) markers to identify genetically distinct populations and their geographical extent for all nine chosen species. We used the Double Digest Restriction Associated DNA (ddRAD) approach to generate genomic data[31]. The sample collection protocol along with detailed protocols of DNA extraction, library preparation is given in the supplementary material, section 3.

iii. Data analysis

We used two approaches for SNP calling: with reference genomes and deNOVO SNP calling. For silver pomfret (*Pampus argenteus*) and Indian mackerel (*Rastrelliger kanagurta,*) we used available reference genomes from the NCBI database for SNP calling (*Rastrelliger kanagurta* - GCA_024605255.1, *Pampus argenteus* - GCA_000697985.1). For spiny cheek grouper (*Epinephelus diacanthus*) and spade nose shark (*Scoliodon laticaudus)* we used the reference genomes of the nearest taxonomically related species. We used the *Epinephelus coioides* (GCA_900536245.1) genome for *Epinephelus diacanthus* and *Scyliorhinus canicular* (GCA_902713615.1) genome for *Scoliodon laticaudus* from the NCBI database. There were no available reference genomes that we could use for any of the other species, so we used a de novo variant calling pipeline by STACKS. The detailed bioinformatic protocol (quality control of reads and SNP discovery) are provided in supplementary materials, section 3 and section 4.

After SNP discovery, we used three indices to identify evidence of genetic similarity and dissimilarity between samples and ultimately identify genetically distinct populations for all nine species. These indices were:

1. Visualisation based on a principal component analysis (PCA) using PLINK[32].
2. Visualisation based on admixture probabilities using the programme ADMIXURE[33]. We ran admixture for K ranging from 1 to n, where n = the number of sites in which we have information of that particular species, for 10 replicates each, the best K was determined by estimating the cross-validation error. The results were analysed and plotted using a web-based server, CLUMPAK[34].
3. A pairwise mean F_{ST} calculation conducted using STACKS[35].

Calculating "Productivity - Susceptibility (PSA) vulnerability axis

We used the Productivity Susceptibility Analysis conducted by[16] Mohammad et al. (2021) for 133 species found in Indian waters as the base vulnerability for our target species. They formulated an index of Resilience and Vulnerability (IRV) based on the Growth coefficient (K), Longevity: Asymptotic length (L_∞), Reproductive load, Number of spawning months (NSM), Fecundity and Mean trophic level (MTL) as vulnerability attributes and species geographic distribution, body length depth ratio (BLD), exploitation ratio, recruitment, susceptibility to gear and price as resilience attributes. This study is the most rigorous assessment of species susceptibility of marine fish from the region.

We used IRV index values along the species-specific vulnerability axis (the vertical axis of our matrix) for all nine species (Refer Figure 3A). Mohammad et al. did not assess the IRV index of *Silago sihama*, so we calculated its IRV index based on the formula given by Mohammad et al. (See supplementary material, section 1).

Identifying disparity between species biology and management attributes

Across the west coast of India, we surveyed fisheries regulations and policy instruments relevant to our study species. In a related study, we reviewed fisheries policies across the west coast of India and identified a total of nine different regulations as the key management attributes of the regimes prevalent in the five states of the Indian west coast[26]. They were 1) partial or complete fishing ban during monsoon months (June to August) 2) maximum allowable engine capacity of a fishing vessel 3) minimum allowable mesh size for cod end of trawl operation 4) minimum allowable mesh size for gill nets 5) minimum allowable mesh size for purse nets / ring seine nets 6) minimum allowable legal size for a species 7) ban on bull / paired trawling 8) ban on fishing using lights 9) restriction on mechanised fishing in shallow waters. These nine regulations were used to assess state-wide disparity with fish biology. Although we would ideally have included catch and effort details with respect to MSY as independent attributes, no adequate data exists for these nine species at the individual population level. See discussion for more details. The details and justifications for the percent disparity calculations are provided in detail in Supplementary material, section 2.

Populating the Biology - Transboundary Management (BTM) vulnerability matrix

We used information of the geographical extent of individual populations from genomic data, the IRV index and percent disparity (as described in above sections), to map the population-level vulnerability of the 9 target species using the Biology - Transboundary Management (BTM) vulnerability matrix.

Results

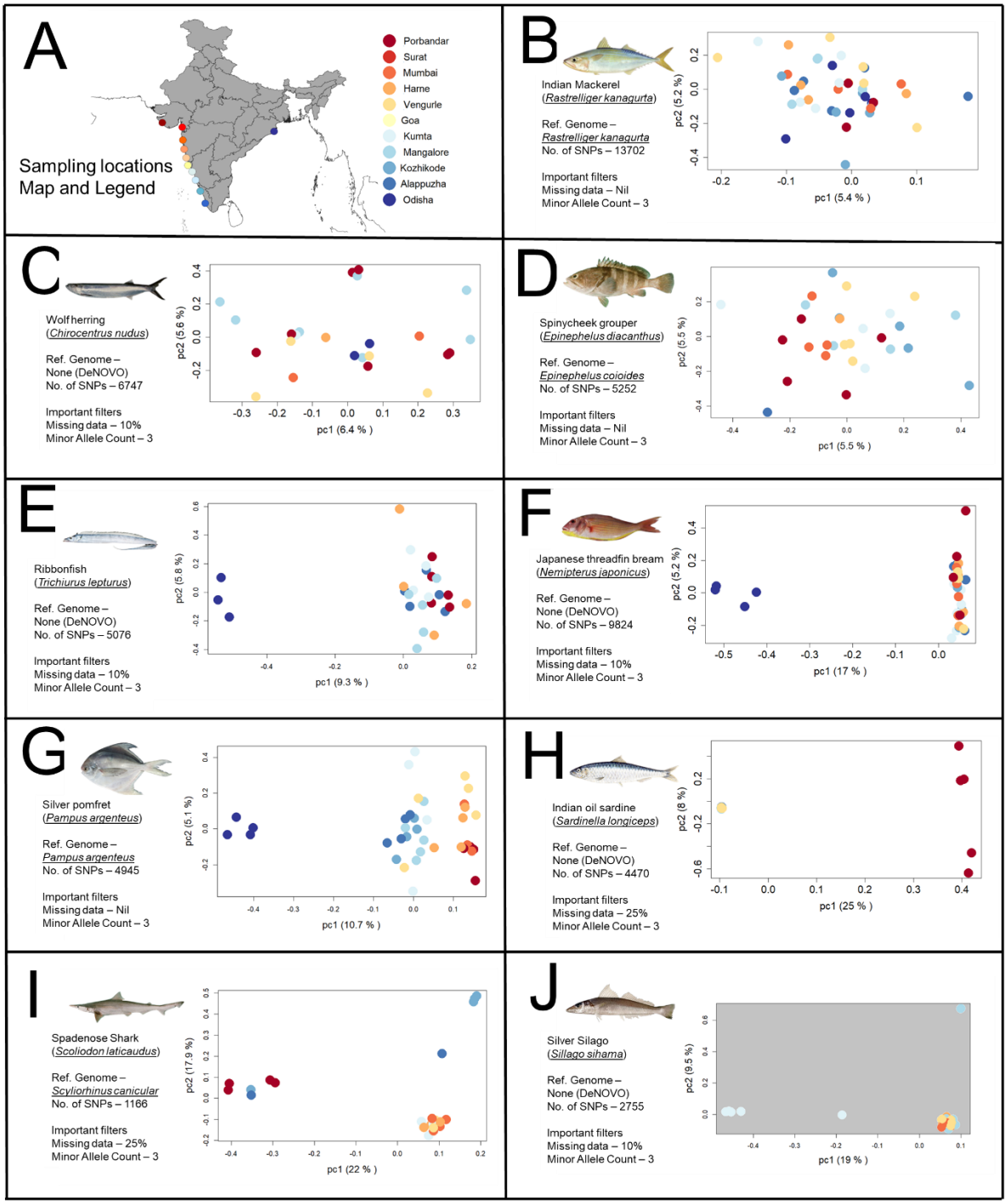
2. Establishing geographical boundaries of target fish populations

Single Nucleotide Polymorphism (SNP) analysis indicates that the degree of gene flow between individuals across the west coast of India varies considerably with species, as is evident from the Principal Component Analysis (PCA) as shown in Fig. 2. We substantiated our inference of population structure using pairwise F_{ST} and Admixture analysis[33] in addition to PCA. For more details about these analyses refer to the section 3 of the supplementary material.

Rastrelliger kanagurta and *Chirocentrus nudus* show a completely panmictic population across the west and east coast (Figure 2B & 2C). *Epinephelus diacanthus* shows evidence of a single population across the entire west coast (Figure 2D). *Trichiurus lepturus* and *Nemipterus japonicus* also show a single population across the entire west coast however they have clear divergences from conspecific populations from the east coast (Figure 2E & 2F).

The remaining four species show multiple genetically distinct population along the west coast of India. Genetic data indicate two potential *Pampus argenteus* populations along the west coast of India, one between northern Gujarat to central Maharashtra, and another from southern south Maharashtra to Kerala (Figure 2G). *Sardinella longiceps* also shows evidence of two populations, with a Gujarat population that separates clearly from the rest of the west coast population (Figure 2H). *Sillago sihama* shows evidence of an isolated population near the town of Kumta which is separate from the coastwide Maharashtra - Karnataka population (Figure 2J). Finally, genetic data from *Scoliodon laticaudus* shows evidence of three distinct west coast populations: a northern Gujarat population, a middle Maharashtra-Goa-Karnataka population, and a southern Kerala population (Figure 2I).

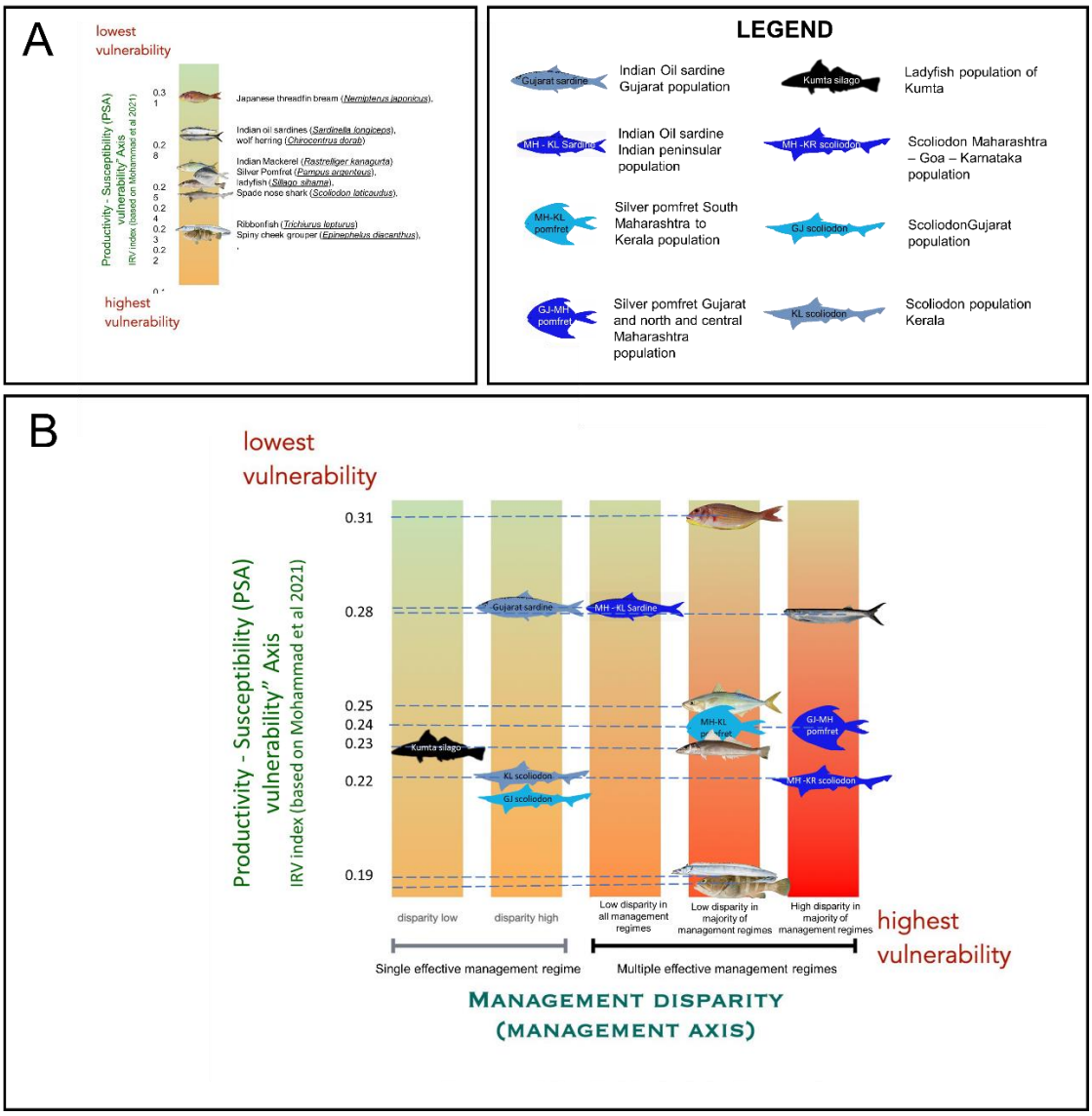
Figure 2. Principal Component plots for nine chosen species across the west coast of India



3. Formulating the vertical “Productivity - Susceptibility (PSA) vulnerability” axis

IRV values can range between 0 (most vulnerable) to 1 (least vulnerable)[16]. Among the 133 species Mohammad et al. analysed, *Solenocera crassicornis* (coastal mud prawn) had the highest IRV value of 0.512 where *Carcharhinus sorrah* (spot-tail shark) had lowest IRV value of 0.022. the nine target species we chose, *Nemipterus japonicus* had the highest IRV index value of 0.31 and thus the lowest vulnerability to overexploitation on the vertical axis whereas *Epinephelus diacanthus* had the lowest IRV index value of 0.195 making it most vulnerable on the vertical axis. We calculated an IRV index of 0.237 for *Sillago sihama* (See supplementary material, section 1). Our target species occupied a narrower portion of the range of species analysed by Mohammad et al. 2021. Figure 3A illustrates the spread of target species along the IRV axis.

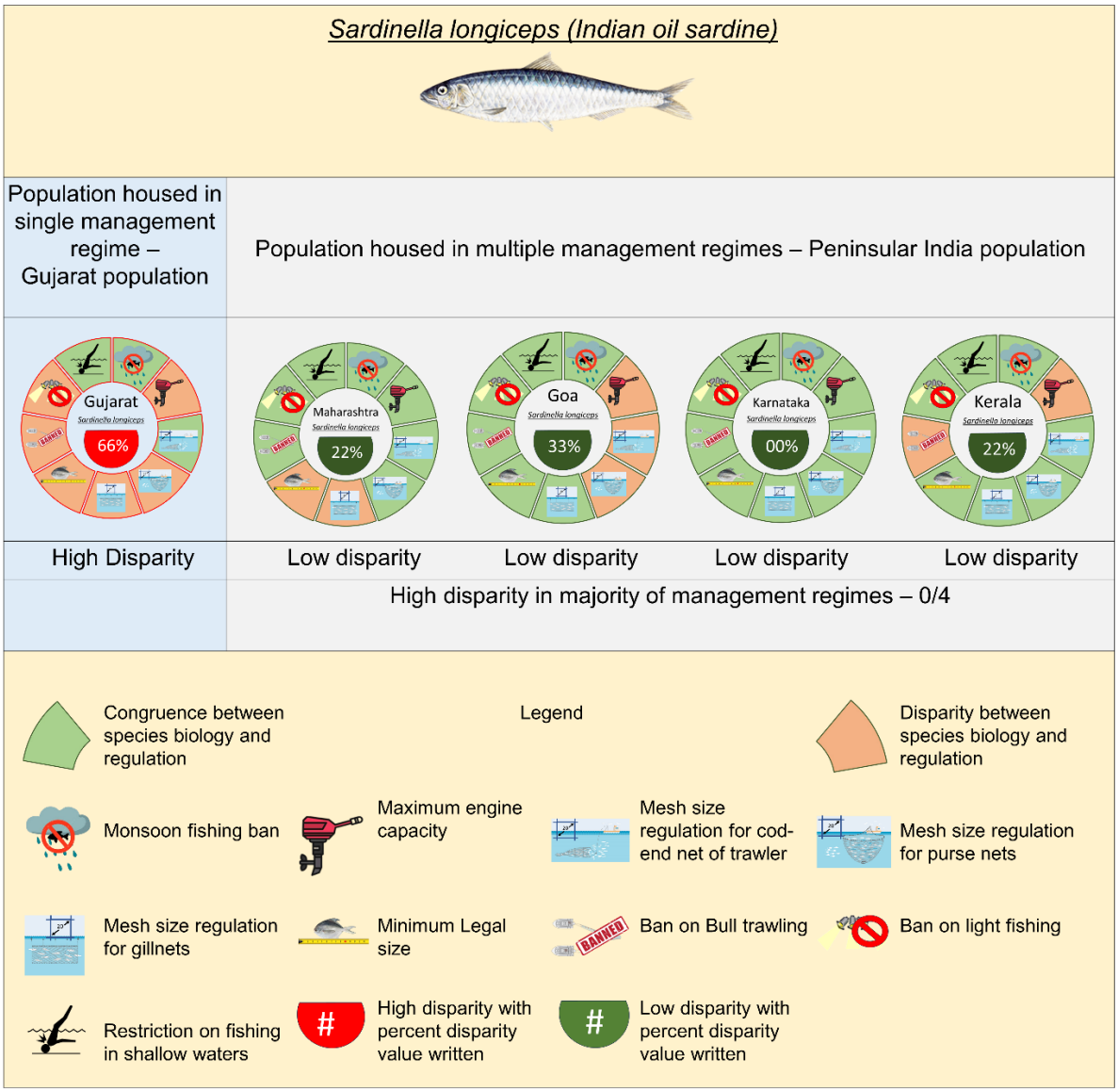
Figure 3. Biology – Transboundary Management (BTM) vulnerability matrix for nine species along the west coast of India



4. Identifying percent disparity between species biology and regulations

We identified the percent disparity between biology and regulation for each individual population - state (management regime) combination based on the rationale described in the methods section. Results of the disparity analysis for the Indian oil sardine are shown in Figure 4. The Gujarat population (which is housed in a single management regime) has a high disparity (66%), while the peninsular India population, despite being shared across four states, has a low disparity across the entire coast. Further results of all species are provided in the supplementary materials, section 2.

Figure 4. Disparity analysis for Indian oil sardine, with populations housed in single as well as multiple management regimes.



5. Mapping the vulnerability of west coast populations using the BTM matrix

We used species specific IRV values from Mohammad et al. and state wise percent disparity for each population identified by genetic analysis, to construct a Biology - Transboundary Management (BTM) vulnerability matrix for the west coast[16] (Figure 3B). There was a considerable spread on both axes of the matrix. Critically, species with multiple populations along the coast could have vastly different vulnerabilities based on the management disparity axis. This was most clear for the spade nose shark, where the transboundary southern population had a much higher vulnerability than the Kerala and Gujarat populations. For populations of pomfret and sardines the differences were not as stark, although differences in management practices between states still clearly influenced the vulnerability of each population. While panmictic species (with a single population across the coast), occupied a wide range of PSA vulnerabilities, the inherent transboundary nature of these species strongly mediated their inherent vulnerability.

Discussion

Achieving sustainability in multi species, poorly monitored and data-poor tropical coastal fisheries is often considered a wicked problem with no easy solutions[36],[6]. Although recent approaches like the Productivity Susceptibility Analysis (PSA) comprehensively incorporate complex species biology, they do not account for management complexities arising from the transboundary nature of most coastal fish populations. The BTM matrix we propose combines genomic techniques and policy analysis for a more realistic assessment of fish stock vulnerability. Our case study demonstrates that many target coastal species across the Indian coast are transboundary in nature, spanning multiple harvest regimes with differing approaches to biological sustainability. This has critical implications for tropical fisheries management. On the one hand, within a species, each population could face very different vulnerability threats. On the other, different fisheries harvesting the same population can potentially influence vulnerability of that population to overexploitation. These complexities are captured elegantly in the BTM matrix. It provides a framework for sustainable management of transboundary stocks, allowing fisheries managers to more transparently assess the vulnerability of populations, evaluate fisheries options and negotiate pragmatic transboundary arrangements based on known the boundaries of susceptible species.

A novel approach to predict vulnerability to overharvest

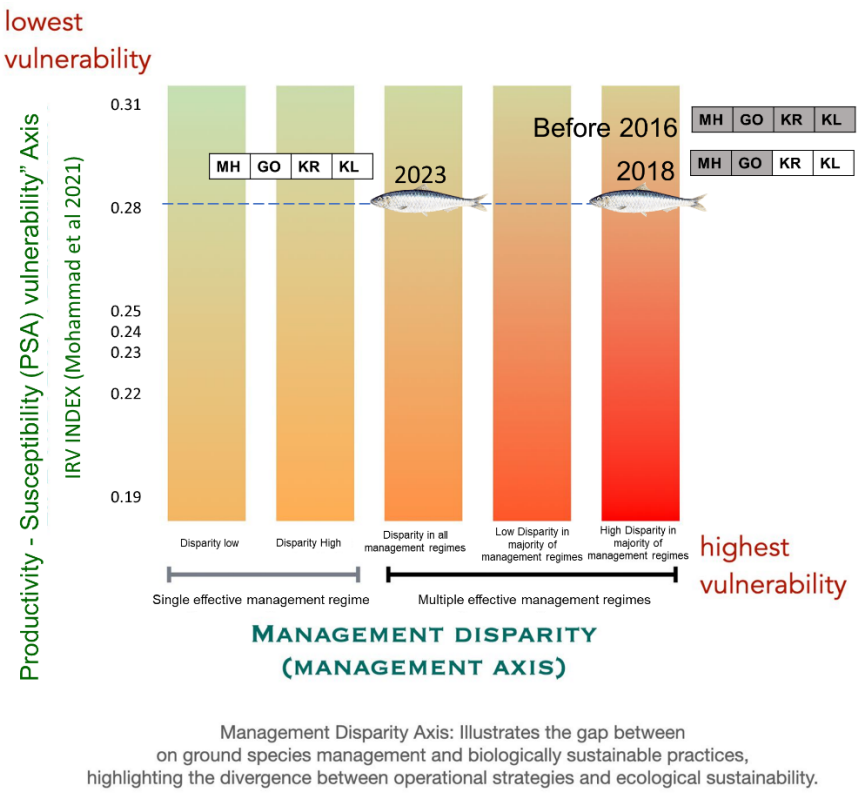
Our analysis demonstrates the vital importance of evaluating fish vulnerability for every population individually, something that most assessments do not allow. A case in point is the silver pomfret. With an vulnerability score of 0.24 (based on the IRV index, see methods), it is a species of intermediate vulnerability. However, our population genetic analysis shows that there are two populations of silver pomfret along the west coast of India, a northern population that extends from Gujarat to the central coast of Maharashtra, and a southern population that extends further south to Kerala. Although both of these populations share the same IRV index, they vary in their vulnerability along the transboundary management axis. Specifically, the southern population is governed by more stringent harvest rules for pomfret than the northern population. Karnataka and Kerala both have regulations on minimum mesh size for gill nets, and there are pomfret-specific minimum legal-size regulations in place in Goa, Karnataka and Kerala. These regulations are absent in the northern states. As a result, the southern

population experiences considerably lower disparity between pomfret biology and fisheries regulations across its range than the northern population, making it much less vulnerable to overexploitation. This example demonstrates how by shifting the assessment focus to spatially explicit populations, our vulnerability matrix considerably enhances the value of the original IRV assessment. Further, by identifying the specific management attributes responsible for differences in vulnerability, the BTM vulnerability matrix approach is highly transparent, providing actionable recommendations to policy makers on how to reduce species vulnerability with changes in policy and transboundary cooperation.

Another aspect of this vulnerability matrix is that it is dynamic and sensitive to periodic revisions in fishery policy across management regimes. The Indian oil sardine demonstrates this well. The west coast has a largely panmictic population except for Gujarat, which has a distinct population. Fewer than 10 years ago no west coast Indian states had regulations on fishing methods like bull trawling, light fishing etc. In addition, there were no mesh size regulations for purse nets or gill nets and none of the states had defined minimum legal sizes for the Indian oil sardine. Based on our assessment, until 2016, the Indian oil sardine was in the highest category of transboundary management vulnerability. The subsequent adoption of these regulations by all west coast states has significantly reduced its vulnerability to overharvest. The advantage of this analysis is that it can be used to keep track of the direction of fisheries policies across boundaries, and can update population vulnerabilities based on policy decisions (Figure 5).

Figure 5. Shift in vulnerability of the peninsular population of Indian oil sardine along the management axis as a direct result of changing management practices

Legend: Matrix legend is similar to figure 3C. The peninsula population of Indian oil sardine saw a recent improvement in its vulnerability as a direct result of actions by states within its population range. While before 2016, there was high management disparity (represented by greyed out boxes) in all states in its range before 2016, there has been a gradual improvement in management practices, with Karnataka (KR) and Kerala (KL) reducing its disparity in 2018, and Maharashtra (MH) and Goa (GO) following suit in 2023, resulting in an overall reduction in the transboundary vulnerability of this population.



We assume that IRV values remain relatively constant for a species. However, it is possible that critical life-history traits could vary between genetic stocks. For instance, Patrik et al. show that the PSA vulnerability of different populations of the same species could differ considerably[18]. In evaluating the disparity between biology and management regime information for our nine target species, we identified considerable differences in basic life history characters like length at first maturity (l50) between Pomfret [37,38] and spade nose shark[39,40] caught at different locations. These traits could potentially also influence their catchability in gear operating along the coast. Such differences could potentially lead to varying inherent population-level susceptibilities and slightly different IRV values for each species. Unfortunately, comprehensive life-history data of this granularity is unavailable for most tropical species. Before it is possible to biologically characterise each individual population more accurately, a more fundamental problem is identifying the population boundaries. Additional life-history studies could help update IRV values for a more nuanced vulnerability assessment.

While IRV values may vary slightly as we learn more about each population, they represent a largely unchanging inherent property of each taxon. However, a central feature of our matrix is that real-world vulnerability is as much a characteristic of the management jurisdiction in question as it is of the biological character of the species. This explicitly recognises the fact that fisheries regimes vary widely between locations, and that transboundary agreements (or the lack of them), can strongly mediate the inherent vulnerability of fish stocks. It is critical to keep this in mind when applying the matrix to a specific fishery. For instance, we classified the Gujarat population of the Indian oil sardine as belonging to a single jurisdiction, reducing its overall vulnerability within the matrix. Broadening the geographical scale of our analysis may well have shown that this population is contiguous with sardines from Pakistan and beyond, making it potentially subject to trans-national management differences that we did not evaluate here. This could equally apply to the spade nose shark of Gujarat and Kerala or the isolated ladyfish / silver sillago population from Kumta. A fuller analysis would require establishing genetic boundaries for the entire range of the species in question before determining its overall vulnerability. This will have important implications for the kinds of transboundary arrangements required to reduce the overall susceptibility of the population – between coastal nations or between sub-national jurisdictions. The fact that management differences can so strongly mediate inherent vulnerability indicates that assessments of this kind are most meaningful when designed for every region, making them jurisdictionally and biologically appropriate across the range of the species.

Transboundary management of fish populations in tropical waters

How could this vulnerability matrix (or exercises such as these) inform sustainable tropical fisheries? Vulnerability assessments of this sort go a long way in sharply defining the management needs for each population across its natural range and help define the scale at which fisheries management would be most biologically meaningful. It offers a clear set of directions to better align species biology with management, setting the stage for cross-boundary cooperation on specific aspects of policy and practice. How tropical regions negotiate these arrangements however continues to remain tricky.

Countries in Western Europe have had a long history of hard-won transboundary fishing arrangements[41], driven by decades of conflict over shared resources. There is also significantly better information on geographically identifiable, genetically distinct populations of fish that form the basis of these arrangements[28]. Tropical fisheries clearly have a considerable distance to travel before they arrive at this state of knowledge or policy engagement. For one, there exists no precedent of international transboundary arrangements for coastal tropical fisheries although there are non-binding international arrangements for pelagic species, like tuna[42].

More importantly, most tropical fisheries are organised and managed in very different ways from their temperate counterparts. In many countries coastal fisheries are managed in a highly decentralised manner where regions and provinces have considerable autonomy over local fisheries management[22–25]. In addition, the allied problems of equity and social justice associated with coastal fisheries are seeing an increasing movement towards even further localisation of fisheries, with approaches like TURFs (Territorial User Rights for Fishing) gaining popularity[43]. These are usually smaller than regional government fisheries management units. Most TURFs in Chile, Mexico and Japan are smaller than the dispersal

ability of fish larvae and adults[44]. While these efforts are a welcome direction to secure the livelihood of marginalised coastal communities, they are also subject to boundary paradoxes, where increasing fisheries boundaries come at the cost of increasingly complex transboundary negotiations[45]. Our analysis raises serious questions of how to ensure the success of these pockets of community managed fishing in a wider ocean of a rapidly expanding fishery sector. Without adequate coordination across biological bounds, these efforts may also result in inadvertent overharvest, and it is important to create forums of dialogue between these community managed and larger regional fisheries, keeping in mind the genetic boundaries of fish stocks.

Conclusion

For multi-specific tropical fisheries, transitioning to population-specific management of fish stocks may seem like a distant horizon. Eventually though, if coastal tropical nations are serious about stemming the collapse of coastal fish stocks, population-wise management is likely to be critical, at least for the most vulnerable of coastal species. Coastal transboundary arrangements of the kind that are already in place for open-water migratory species like tuna[42] offer a possible template that can be built on. Our results demonstrate the need for such agreements for nearshore species of fish and for individual provinces and community managed areas within a single nation state, which was largely considered less important in tropical context. For this, the BTM vulnerability matrix can be a useful prioritisation tool. Because the management axis allows for dynamic mobility based on changes in policy, it can be used to strategically evaluate which set of policy directions could reduce the susceptibility of the widest number of fish populations across a shared coastline. As our analyses shows, the inherent vulnerability of fish can be strongly mediated by what managers do at local levels, and how closely they coordinate their actions with neighbours that share the same genetic resource pool. This offers the principal challenge but also the best hope for rational management of dwindling fish stocks.

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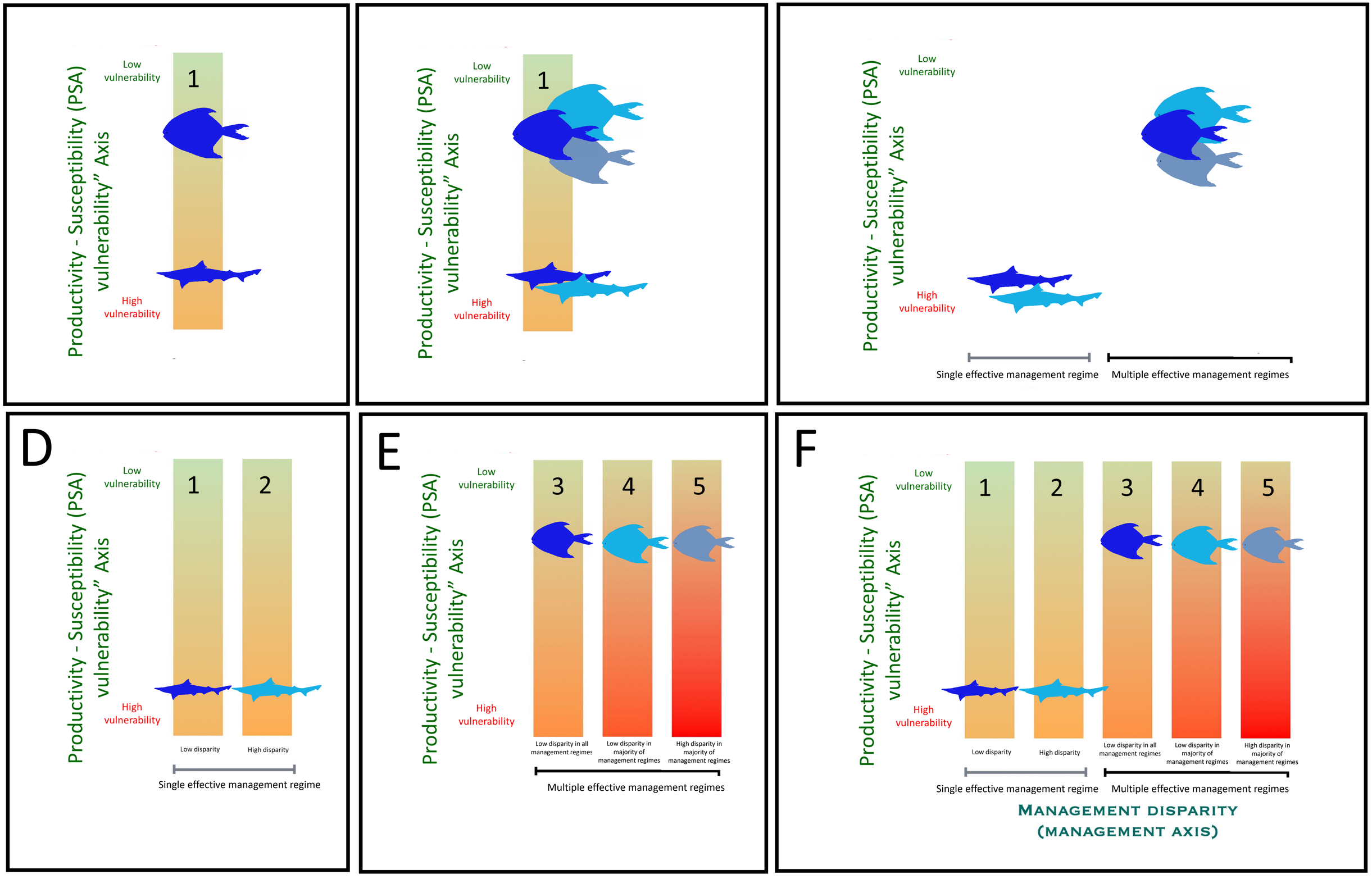
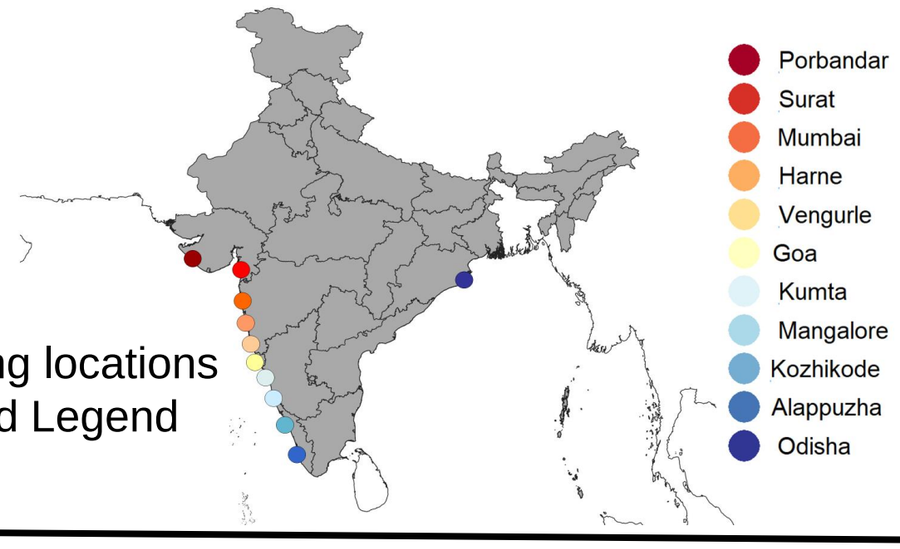

Productivity - Susceptibility (PSA) vulnerability" Axis
Low vulnerability
High vulnerability
1
Single effective management regime
Multiple effective management regimes
D
2
Low disparity
High disparity
E
3
4
5
Low disparity in all management regimes
Low disparity in majority of management regimes
High disparity in majority of management regimes
F
Management disparity (management axis)

A



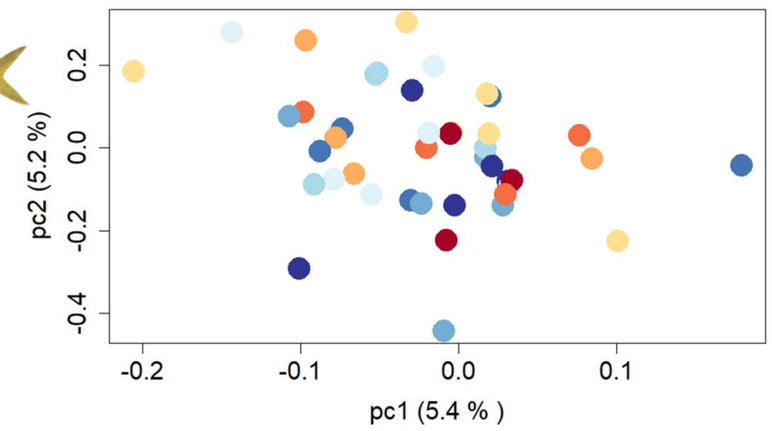
Sampling locations
Map and Legend

B

Indian Mackerel
(*Rastrelliger kanagurta*)

Ref. Genome –
Rastrelliger kanagurta
No. of SNPs – 13702

Important filters
Missing data – Nil
Minor Allele Count – 3



C

Wolf herring
(*Chirocentrus nudus*)

Ref. Genome –
None (DeNOVO)
No. of SNPs – 6747

Important filters
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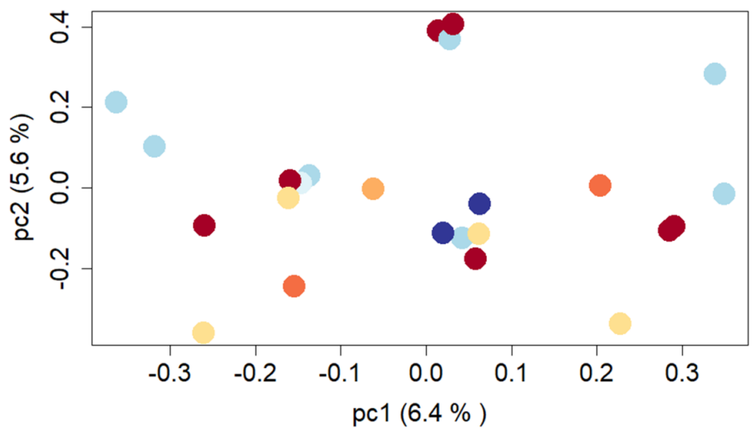
Minor Allele Count – 3



D

Spinycheek grouper
(*Epinephelus diacanthus*)

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No. of SNPs – 5252

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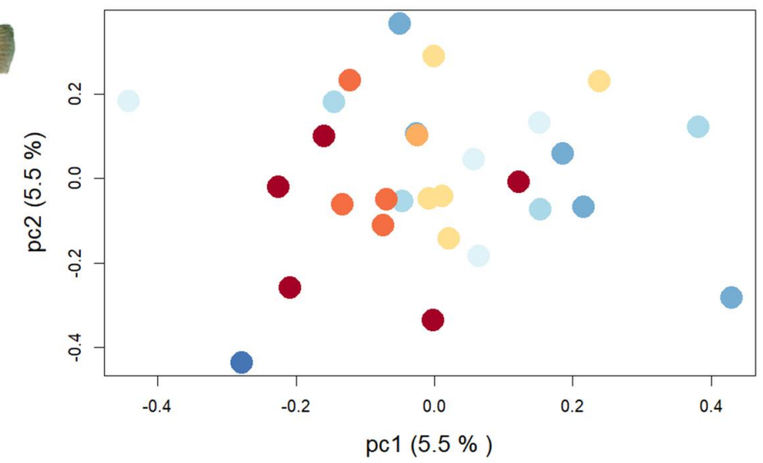
Minor Allele Count – 3



E

Ribbonfish
(*Trichiurus lepturus*)

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No. of SNPs – 5076

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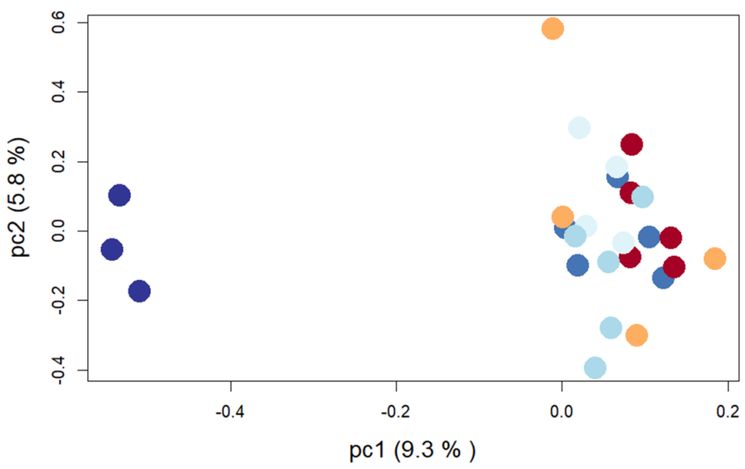

F

Japanese threadfin bream
(*Nemipterus japonicus*)

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No. of SNPs – 9824

Important filters
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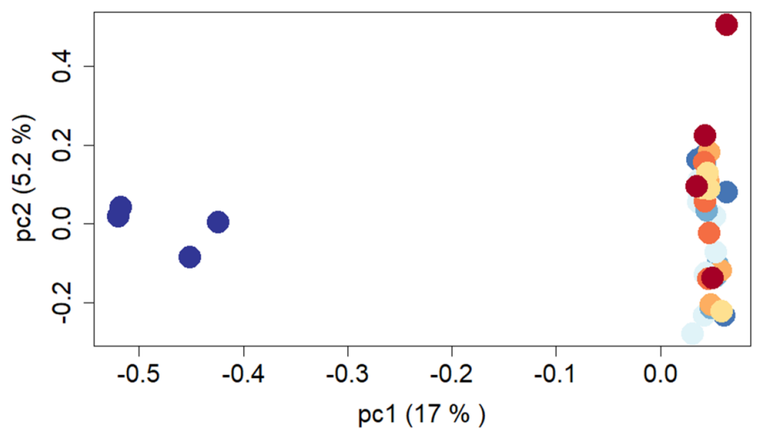
Minor Allele Count – 3



G

Silver pomfret
(*Pampus argenteus*)

Ref. Genome –
Pampus argenteus
No. of SNPs – 4945

Important filters
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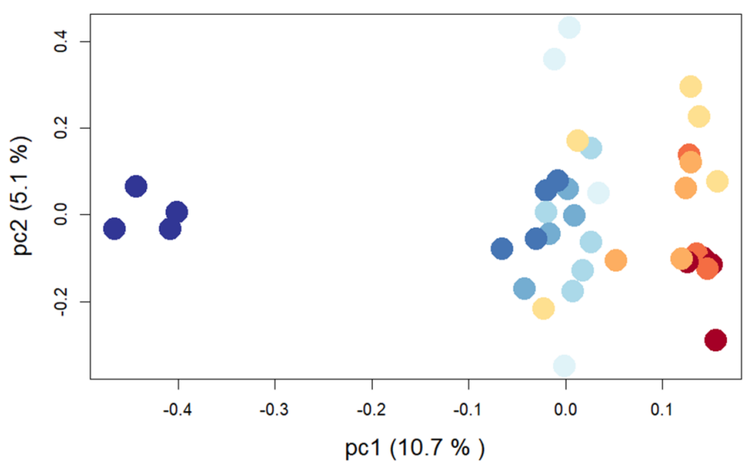
Minor Allele Count – 3

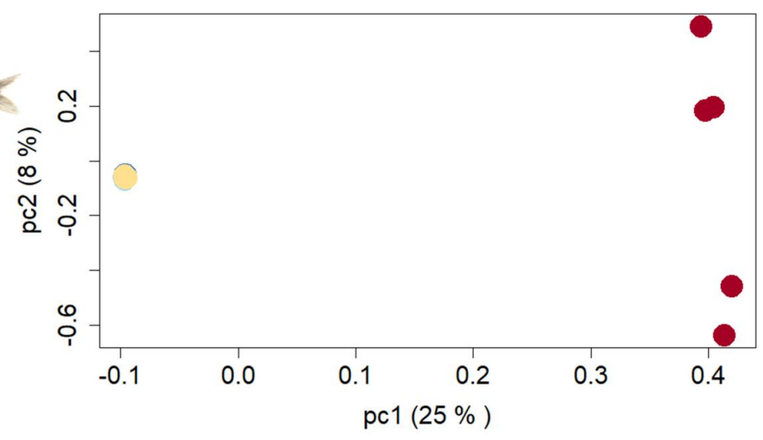


H

Indian oil sardine
(*Sardinella longiceps*)

Ref. Genome –
None (DeNOVO)
No. of SNPs – 4470

Important filters
Missing data – 25%
Minor Allele Count – 3



I

Spadenose Shark
(*Scoliodon laticaudus*)

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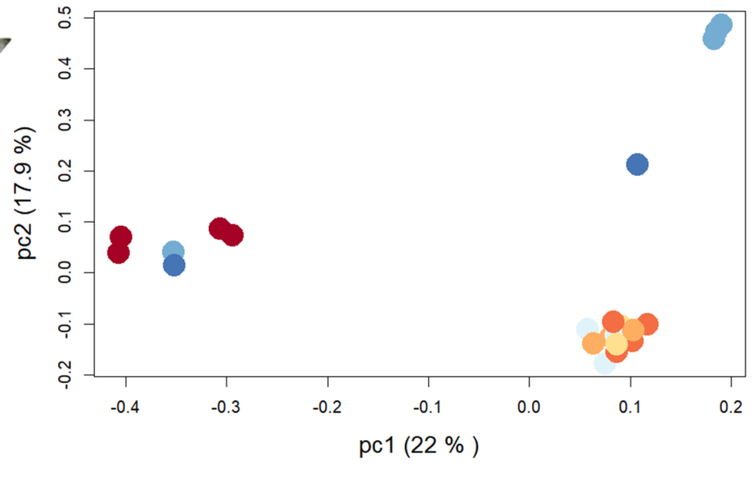
Scyliorhinus canicular
No. of SNPs – 1166

Important filters
Missing data – 25%
Minor Allele Count – 3



J

Silver Silago
(*Sillago sihama*)

Ref. Genome –
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No. of SNPs – 2755

Important filters
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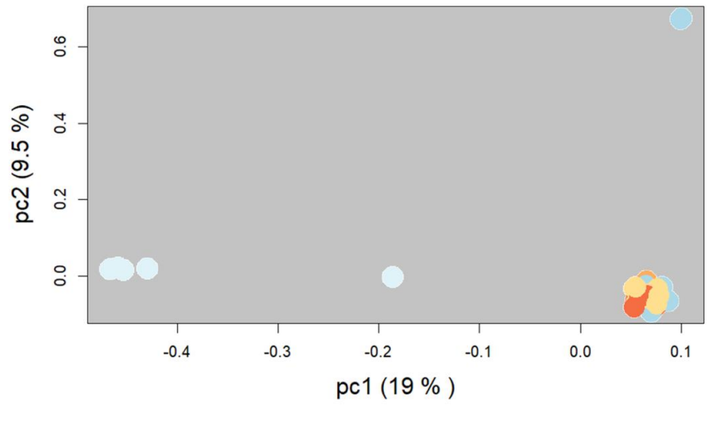
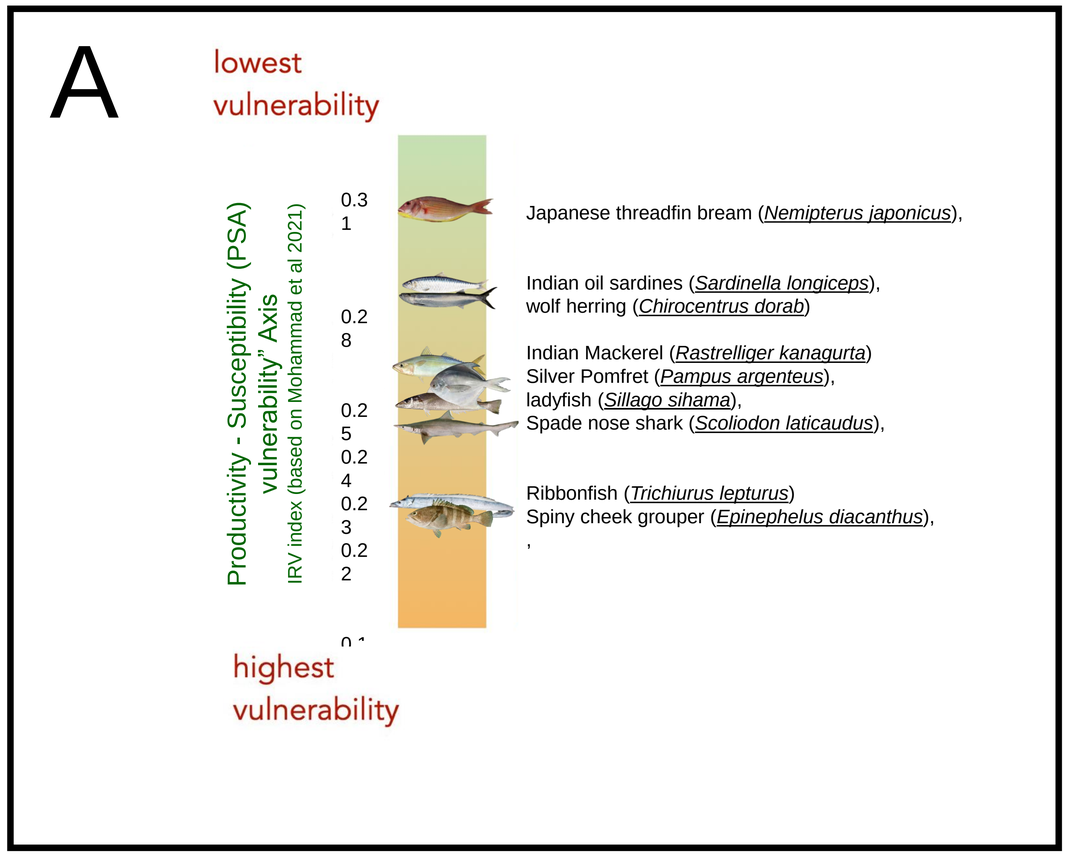
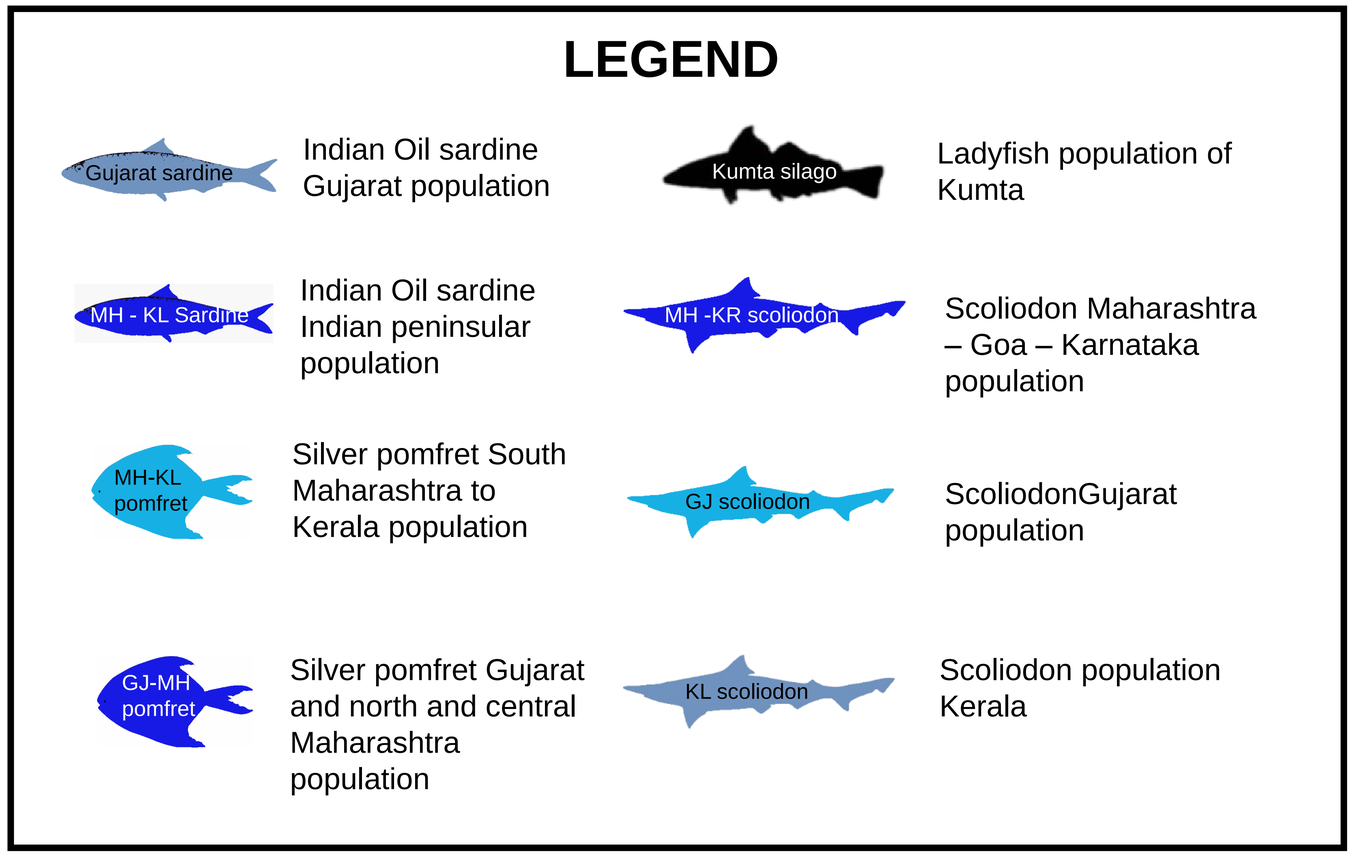
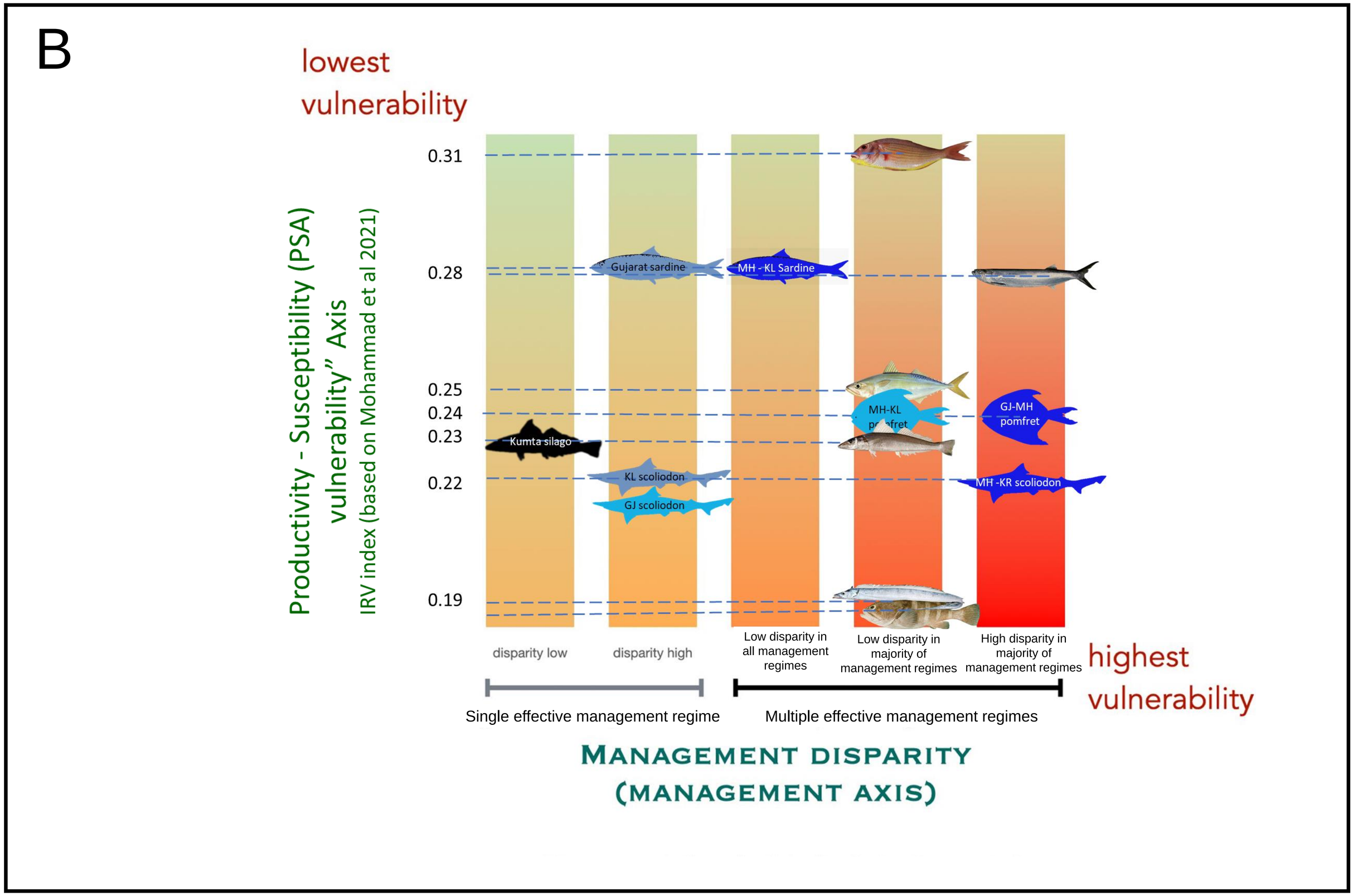
Minor Allele Count – 3

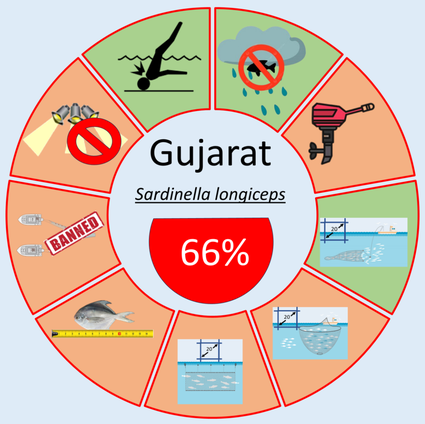
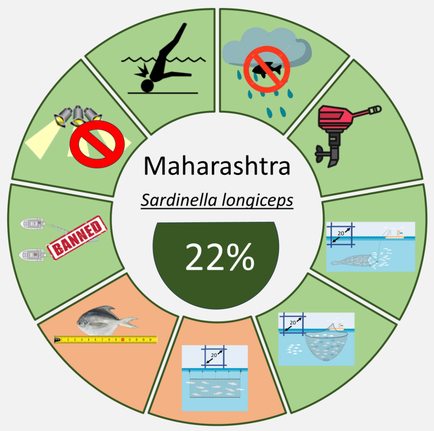
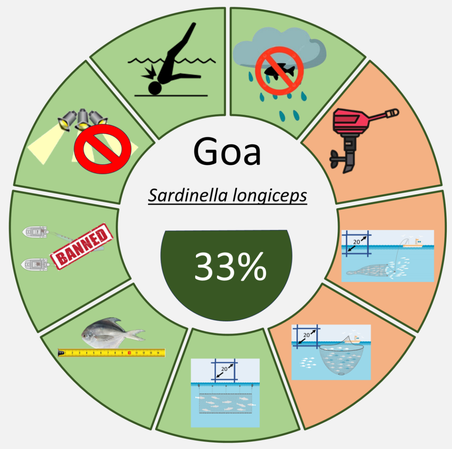
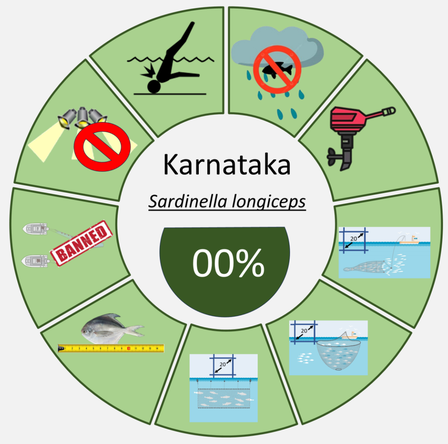
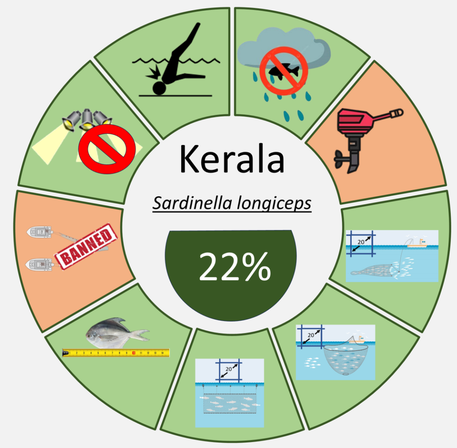



A
lowest vulnerability
Productivity - Susceptibility (PSA) vulnerability" Axis
IRV index (based on Mohammad et al 2021)
0.31
0.28
0.25
0.24
0.23
0.22
0.19
Japanese threadfin bream (Nemipterus japonicus),
Indian oil sardines (Sardinella longiceps),
wolf herring (Chirocentrus dorab)
Indian Mackerel (Rastrelliger kanagurta)
Silver Pomfret (Pampus argenteus),
ladyfish (Sillago sihama),
Spade nose shark (Scoliodon laticaudus),
Ribbonfish (Trichiurus lepturus)
Spiny cheek grouper (Epinephelus diacanthus),
highest vulnerability


LEGEND
Gujarat sardine
Indian Oil sardine Gujarat population
Kumta silago
Ladyfish population of Kumta
MH - KL Sardine
Indian Oil sardine Indian peninsular population
MH -KR scoliodon
Scoliodon Maharashtra – Goa – Karnataka population
MH-KL pomfret
Silver pomfret South Maharashtra to Kerala population
GJ scoliodon
ScoliodonGujarat population
GJ-MH pomfret
Silver pomfret Gujarat and north and central Maharashtra population
KL scoliodon
Scoliodon population Kerala

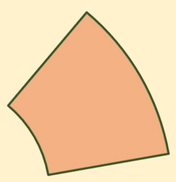

B
lowest vulnerability
Productivity - Susceptibility (PSA) vulnerability" Axis
IRV index (based on Mohammad et al 2021)
0.31
0.28
0.25
0.24
0.23
0.22
0.19
Gujarat sardine
MH - KL Sardine
Kumta silago
KL scoliodon
GJ scoliodon
MH-KL pomfret
GJ-MH pomfret
MH -KR scoliodon
disparity low
disparity high
Low disparity in all management regimes
Low disparity in majority of management regimes
High disparity in majority of management regimes
highest vulnerability
Single effective management regime
Multiple effective management regimes
MANAGEMENT DISPARITY (MANAGEMENT AXIS)

Sardinella longiceps (Indian oil sardine)

Population housed in single management regime – Gujarat population	Population housed in multiple management regimes – Peninsular India population			
				
High Disparity	Low disparity	Low disparity	Low disparity	Low disparity
	High disparity in majority of management regimes – 0/4			

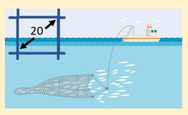
Legend

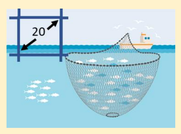
Congruence between species biology and regulation

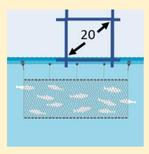

Disparity between species biology and regulation

Monsoon fishing ban

Maximum engine capacity


Mesh size regulation for cod-end net of trawler


Mesh size regulation for purse nets

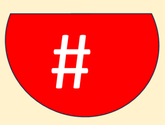

Mesh size regulation for gillnets

Minimum Legal size

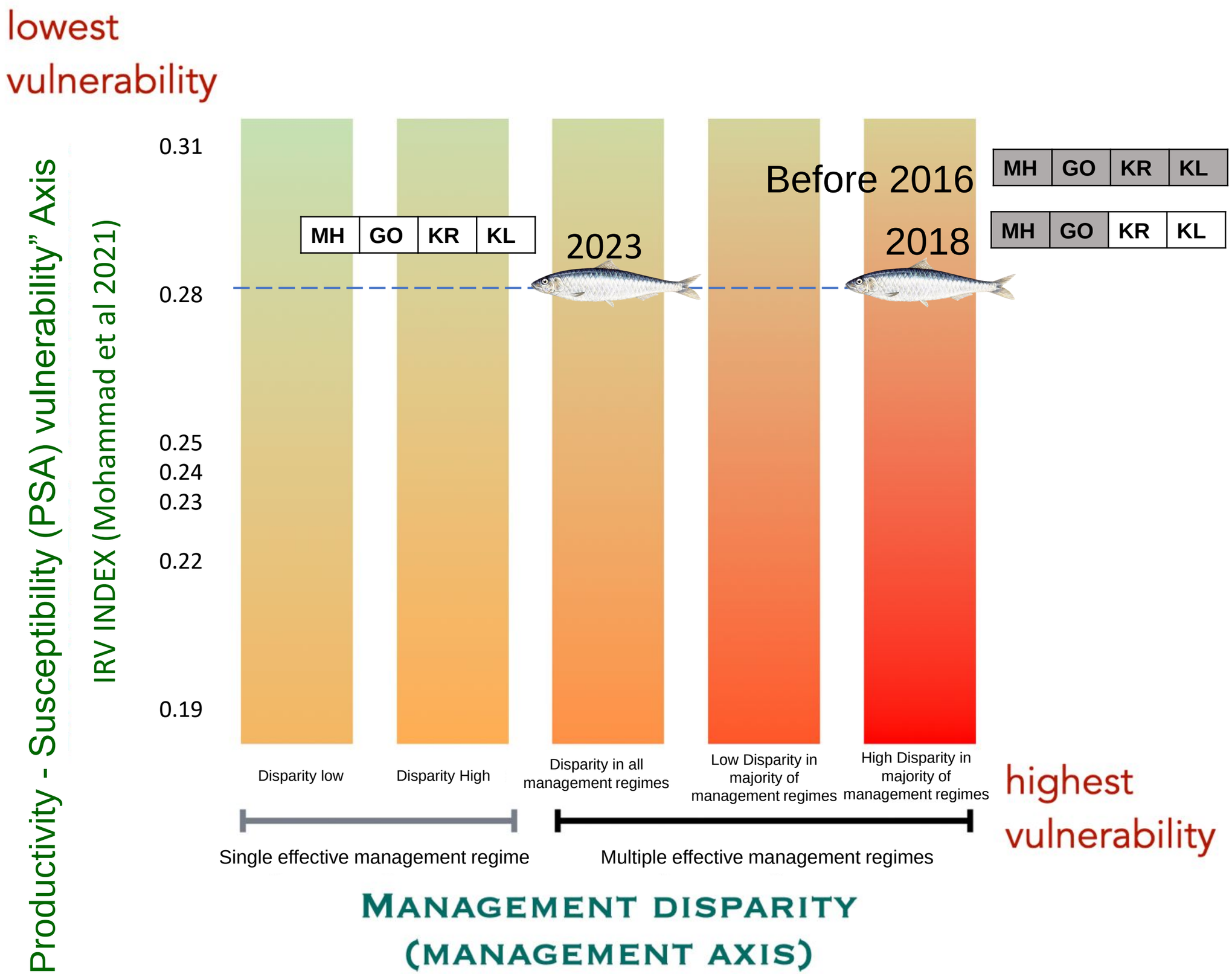
Ban on Bull trawling

Ban on light fishing

Restriction on fishing in shallow waters


High disparity with percent disparity value written

Low disparity with percent disparity value written



Management Disparity Axis: Illustrates the gap between on ground species management and biologically sustainable practices, highlighting the divergence between operational strategies and ecological sustainability.