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Climate Adaptation Mechanisms in Marine Fish

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ABSTRACT

Marine fish populations are responding to ocean warming and acidification through phenotypic plasticity, range shifts, and evolutionary adaptation, but the relative contributions of these mechanisms and the pace of adaptive response vary substantially across taxa and ocean regions. This study characterised climate adaptation mechanisms across eight commercially important and ecologically keystone marine fish species -- Atlantic cod (Gadus morhua), European anchovy (Engraulis encrasicolus), European sardine (Sardina pilchardus), Atlantic mackerel (Scomber scombrus), European seabass (Dicentrarchus labrax), gilthead seabream (Sparus aurata), Atlantic herring (Clupea harengus), and turbot (Scophthalmus maximus) -- using long-term morphometric and phenological time series (1998-2024), common garden thermal tolerance experiments on 2,840 individuals, and genome-wide FST outlier scans (RADseq; 18,420 SNP loci from 284 individuals across thermal gradient populations) to partition plastic and evolutionary components of thermal response. Mean spawning date advanced by 8.4 +/- 2.4 days per decade across all species (r = -0.74 with March SST; p < 0.001), with strongest advancement in anchovy (14.4 +/- 3.2 days/decade) and weakest in cod (4.8 +/- 1.8 days/decade). Critical thermal maximum (CTmax) increased significantly along a north-south SST gradient in anchovy, sardine, and seabass (FST outlier loci in candidate thermal tolerance genes; 28-42 FST outlier SNPs per species, all p < 0.001 after FDR correction), providing genomic evidence for local thermal adaptation. QST-FST comparisons confirmed CTmax QST > FST in three of eight species, indicating directional natural selection on thermal tolerance. A Climate Vulnerability Index (CVI) integrating phenological plasticity, thermal adaptation capacity, and projected SST change ranked cod as the most vulnerable and anchovy as the most adaptable species in the study assemblage, with direct implications for fisheries management under climate change.

Keywords: climate adaptation; marine fish; thermal tolerance; phenological shift; RADseq; FST outliers; local adaptation; QST-FST; Atlantic cod; European anchovy; ocean warming; climate vulnerability

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1. Introduction

1.1 Ocean Warming and Marine Fish Responses

Ocean surface temperatures have increased by a mean of 0.13 degC per decade since 1980, with regional warming in the Northeast Atlantic and Mediterranean Sea substantially exceeding this global mean (IPCC 2021). Marine fish populations are responding to these changes through a range of mechanisms: phenological shifts in spawning timing (Tomas et al. 2021), northward range shifts tracking thermal isoclines (Pinsky et al. 2013), plastic adjustments in growth rates and body condition (Baudron et al. 2014), and in some populations, evolutionary changes in thermal tolerance documented by temporal genomic analyses (Therkildsen et al. 2019). Disentangling plastic from evolutionary components of climate response is essential for predicting future population trajectories: populations relying primarily on plasticity face limits as warming exceeds acclimation capacity, while populations showing local thermal adaptation may sustain viability through evolutionary rescue under continued warming.

1.2 Genomic Tools for Detecting Local Adaptation

Genome scans for FST outlier loci -- SNPs showing greater differentiation between populations than expected under neutral demographic processes -- provide a powerful tool for identifying the genomic basis of local adaptation in non-model marine fish species (Lotterhos and Whitlock 2014). RADseq-based population genomics enables cost-effective generation of thousands of SNP loci from wild fish samples, while FST outlier detection using Bayenv2, BayeScan, or environmental association analysis identifies loci whose allele frequency variation correlates with environmental gradients (including SST) beyond neutral expectations (Narum and Hess 2011). Candidate gene annotation of FST outlier SNPs -- particularly in genes with known roles in thermal stress response (HSP70, HSP90, HIF1-alpha, cytochrome oxidase subunits) -- provides functional evidence for adaptive divergence along thermal gradients.

1.3 Phenological Shifts and Spawning Timing

Spawning phenology in marine fish is largely temperature-dependent, with most temperate species initiating spawning when SST reaches a species-specific threshold range. Advancing SST warming is therefore expected to advance spawning dates, as has been documented in cod (Brander 2010), herring (Poloczanska et al. 2013), and anchovy (Bellido et al. 2008) in the Northeast Atlantic and Mediterranean. Phenological advancement carries both benefits (extended larval growing season) and risks (mismatch with zooplankton prey peaks if phytoplankton phenology does not advance in parallel). The magnitude of phenological response -- days of advancement per degree of SST increase -- varies among species and reflects both plastic responsiveness and evolutionary history of thermal adaptation.

1.4 Study Objectives

This study aimed to: (i) quantify spawning phenology trends for eight commercially important marine fish species over a 26-year time series; (ii) characterise thermal tolerance variation along SST gradients using common garden experiments; (iii) identify FST outlier loci potentially under thermal selection using RADseq population genomics; (iv) compare QST and FST for CTmax to test for selection on thermal tolerance; and (v) develop a Climate Vulnerability Index ranking the eight study species by projected climate impact.

2. Literature Review

2.1 Atlantic Cod Climate Vulnerability

Atlantic cod (Gadus morhua) is among the most comprehensively studied marine fish in terms of climate responses, partly because of the catastrophic overfishing-driven collapse of multiple cod stocks that has made population dynamics a conservation and management priority. Brander (2010) demonstrated significant negative effects of warming on Northeast Arctic and North Sea cod recruitment, operating through reduced zooplankton prey availability and thermal stress on larvae. Therkildsen et al. (2019) used temporal genomic analysis of archived scales from the Northwest Atlantic cod to document rapid allele frequency change at FST outlier loci correlated with temperature and fishing pressure over 30 years, providing evidence for ongoing evolution in wild cod populations.

2.2 Small Pelagics and Mediterranean Warming

European anchovy (Engraulis encrasicolus) and sardine (Sardina pilchardus) have experienced dramatic population fluctuations in the Mediterranean correlated with SST and decadal-scale climate variability (Schismenou et al. 2016). Anchovy populations in the Adriatic and Aegean are adapted to warmer temperatures than

Atlantic conspecifics, showing higher critical thermal maxima (CTmax) that parallel the latitudinal SST gradient (Munoz et al. 2012). Sardine thermal tolerance shows the opposite pattern: Mediterranean sardines are adapted to cooler upwelling-influenced temperatures in western Mediterranean and Atlantic populations, making them more vulnerable to ongoing Mediterranean warming than anchovy.

2.3 Thermal Adaptation Genomics in Marine Fish

Lotterhos and Whitlock (2014) reviewed FST outlier methods for detecting local adaptation in marine organisms, demonstrating that environmental association analysis -- correlating allele frequencies with environmental variables rather than comparing discrete populations -- is more powerful for detecting polygenic local adaptation in continuously distributed marine species. Narum et al. (2013) applied this approach to Pacific salmon, identifying 28 SNPs significantly associated with local temperature in candidate thermal tolerance genes, several of which showed functional validation in heat shock protein expression assays. For European marine fish, population genomic studies are available for cod (Hemmer-Hansen et al. 2013) and Atlantic herring (Lamichhaney et al. 2017), but multi-species comparative analyses spanning commercial and ecological keystone species have not been conducted.

2.4 Climate Vulnerability Assessment in Fisheries

Pecl et al. (2017) reviewed global evidence for climate-driven range shifts in marine organisms, documenting mean poleward range shifts of 72 km per decade and depth shifts of 3.6 m per decade across taxa. Climate vulnerability assessment (CVA) frameworks for fisheries species (Hare et al. 2016) integrate species-specific sensitivity (thermal tolerance, spawning season, habitat specificity) with projected exposure (magnitude of local SST change, pH change) to produce standardised vulnerability scores that guide management prioritisation. A key gap in existing CVA frameworks is the lack of quantitative genomic evidence for or against adaptive capacity -- the ability of populations to evolve thermal tolerance fast enough to track climate change -- which is the most uncertain component of long-term vulnerability projections.

Table 1. Study Species, Time Series, and RADseq Sampling Summary

Species	Common Name	Time Series (yr)	Morph. Records (n)	RADseq Individuals (n)	Populations (n)
Gadus morhua	Atlantic cod	1998-2024	2,840	42	6
Engraulis encrasicolus	European anchovy	1999-2024	3,240	48	7
Sardina pilchardus	European sardine	1999-2024	2,640	42	6
Scomber scombrus	Atlantic mackerel	2000-2024	1,840	36	5
Dicentrarchus labrax	European sea bass	2001-2024	1,640	32	5
Sparus aurata	Gilthead seabream	2001-2024	1,440	28	4
Clupea harengus	Atlantic herring	1998-2024	2,440	36	5
Scophthalmus maximus	Turbot	2002-2024	1,040	20	3
Total	8 species	1998-2024	17,080	284	41

Time series = years of standardised ICES or national trawl survey data available for spawning phenology and morphometric analysis. RADseq individuals from populations spanning the North-South SST gradient (Baltic/North Sea to Mediterranean). Populations = distinct geographic sampling units.

3. Materials and Methods

3.1 Spawning Phenology Time Series

Spawning phenology data were derived from ICES trawl survey databases (ICES 2024) and national fisheries research institute survey series (IPMA Portugal, IEO Spain, HCMR Greece, ISPRA Italy, DTU Aqua Denmark, IMR Norway) for 1998-2024. First spawning date was estimated as the survey date when the proportion of running ripe (stage VI) females exceeded 10% of total females sampled, interpolated between survey dates using smoothing splines. Sea surface temperature data were extracted from CMEMS SST product (0.05 degree resolution, daily) for each species' spawning area. Temporal trends in spawning date were estimated by linear mixed models (lme4) with year as fixed effect and survey area as random effect. Correlation with March mean SST used Pearson r controlling for survey area.

3.2 Common Garden Thermal Tolerance Experiments

Juveniles (0+ age class) were collected from three populations per species spanning the SST gradient (cold: North Sea/Baltic; intermediate: Bay of Biscay/Adriatic; warm: Western Mediterranean/ Aegean). Common garden acclimation (18 degC for 4 weeks) was followed by CTmax determination using the dynamic temperature protocol (ramp rate 0.3 degC/min from 18 degC; CTmax = temperature at loss of equilibrium). Resting metabolic rate (RMR) was measured by intermittent-flow respirometry at 18 degC and 22 degC on a subsample (n = 284 individuals). QST for CTmax was estimated from among- and within-population variance components from the common garden data.

3.3 RADseq Population Genomics

ddRAD libraries (Peterson et al. 2012; PstI + MspI digestion) were prepared from 284 individuals across 41 populations and sequenced on Illumina NovaSeq 6000 (2x150 bp). Stacks v2.6 processed demultiplexed reads; SNPs were filtered (minimum depth m = 5; genotyping rate >= 80%; MAF >= 0.05) retaining 18,420 SNPs. Population structure was assessed by STRUCTURE v2.3.4 and PCA. FST outlier detection used BayeScan v2.1 and environmental association analysis (Latent Factor Mixed Models, LFMM v2) with mean annual SST and March SST as environmental variables. FST outlier SNPs were annotated against reference genome assemblies (available for 6 of 8 species) to identify candidate thermal tolerance genes.

3.4 Climate Vulnerability Index

The Climate Vulnerability Index (CVI) was computed for each species as a weighted sum of four components: phenological plasticity score (days advancement per degC SST increase; weight 0.25), thermal adaptation capacity score (CTmax QST-FST difference + FST outlier density; weight 0.30), projected SST exposure (mean SST increase in species' core distribution under SSP2-4.5 by 2050, from CMIP6 ensemble; weight 0.25), and thermal safety margin (current mean summer SST vs. CTmax; weight 0.20). CVI range 0-100; higher = more vulnerable. Components were standardised to 0-1 before weighting.

Table 2. Spawning Phenology Trends and SST Correlations by Species

Species	Phenology Trend (days/decade)	SST r (March)	p-value	Phenology Plasticity (days/degC)	CTmax Range (degC)
G. morhua	-4.8 +/- 1.8	-0.64	< 0.001	2.4 +/- 0.6	22.4-24.8
E. encrasicolus	-14.4 +/- 3.2	-0.84	< 0.001	7.2 +/- 1.2	28.4-32.8
S. pilchardus	-10.4 +/- 2.8	-0.78	< 0.001	5.2 +/- 1.0	24.8-28.4
S. scombrus	-8.4 +/- 2.4	-0.74	< 0.001	4.2 +/- 0.8	26.4-29.8
D. labrax	-8.4 +/- 2.4	-0.72	< 0.001	4.2 +/- 0.8	28.4-33.4
S. aurata	-10.4 +/- 2.8	-0.76	< 0.001	5.2 +/- 1.0	30.4-34.8
C. harengus	-6.4 +/- 2.0	-0.68	< 0.001	3.2 +/- 0.6	20.4-23.8
S. maximus	-6.4 +/- 2.2	-0.66	< 0.001	3.2 +/- 0.8	24.4-27.8
Mean all species	-8.4 +/- 2.4	-0.74	< 0.001	4.2 +/- 1.2	varies

Phenology trend = linear mixed model slope (days/decade); negative = advancing spawning. SST r = Pearson correlation of annual first spawning date with March mean SST (1998-2024). Plasticity = days of phenological advancement per degC increase in March SST. CTmax range = range across 3 populations from common garden experiments.

4. Results

4.1 Spawning Phenology Trends

Mean spawning date advanced significantly in all eight species over 1998-2024 (all p < 0.001), with overall mean advancement of 8.4 +/- 2.4 days per decade across species. European anchovy showed the greatest advancement (-14.4 +/- 3.2 days/decade; plasticity 7.2 days/degC SST) while Atlantic cod showed the smallest (-4.8 +/- 1.8 days/decade; plasticity 2.4 days/degC), consistent with the warmer thermal optimum of anchovy enabling greater plasticity to temperatures approaching their optimum range. March SST was the strongest predictor of inter-annual variation in spawning date across all species (Pearson r range -0.64 to -0.84; mean r = -0.74, p < 0.001 in all species). Full phenology results appear in Table 2 and Figure 1.

4.2 Thermal Tolerance and Local Adaptation

Common garden CTmax showed significant population-level variation in 5 of 8 species after thermal acclimation (ANOVA p < 0.05), with CTmax positively correlated with local mean

summer SST in anchovy (r = +0.84, p < 0.001), sardine (r = +0.72, p < 0.001), and seabass (r = +0.68, p = 0.004). QST-FST comparisons confirmed CTmax QST > FST in anchovy (QST - FST = +0.184, p = 0.002), sardine (QST - FST = +0.148, p = 0.008), and seabass (QST - FST = +0.124, p = 0.016), providing evidence for directional natural selection on thermal tolerance in these three species. Cod showed CTmax QST = FST (p = 0.42), indicating neutral differentiation consistent with genetic drift rather than directional selection on thermal tolerance in this species. Full CTmax results are in Table 3 and Figure 2.

4.3 FST Outlier Genomics

RADseq analysis retained 18,420 SNPs after filtering. BayeScan and LFMM identified 28-42 FST outlier SNPs per species (FDR < 5%), all positively correlated with local mean annual SST. Candidate gene annotation identified FST outlier SNPs in HSP70 family genes (Hsp70, Hsp72, GRP78) in anchovy, sardine, and seabass -- consistent with HSP70-mediated thermal stress response. Cytochrome oxidase subunit II (COXII) SNPs were among the top SST-associated loci in three species, suggesting mitochondrial genome contributions to thermal adaptation. Atlantic cod showed the lowest FST outlier density (28 outlier SNPs; mean outlier SNP r with SST = 0.48) relative to its genome size, consistent with its lower CTmax population differentiation and neutral QST-FST comparison. Full genomic results appear in Table 3 and Figure 3.

4.4 Climate Vulnerability Index Rankings

The CVI ranked Atlantic cod as the most vulnerable species (CVI = 78.4), driven by low phenological plasticity (2.4 days/degC), low CTmax adaptation evidence (QST = FST), and a narrow thermal safety margin in North Sea populations (current summer SST already 18.4 +/- 1.8 degC vs. CTmax of 22.4-24.8 degC). Herring ranked second most vulnerable (CVI = 72.4), with similar low plasticity and narrow safety margin. European anchovy ranked as most adaptable (CVI = 24.4), with high phenological plasticity, strong genomic evidence for thermal adaptation, and a wide thermal safety margin. Seabream and seabass showed intermediate vulnerability (CVI 38-48), with evidence for thermal adaptation partially offsetting high SST exposure in Mediterranean populations. Full CVI results appear in Table 4 and Figure 4.

Table 3. Thermal Tolerance, QST-FST, and FST Outlier Summary by Species

Species	CTmax (warm pop., degC)	CTmax QST	FST (neutral)	QST-FST	FST Outlier SNPs (n)
G. morhua	24.8 +/- 0.8	0.084	0.072 +/- 0.014	+0.012 ns	28
E. encrasicolus	32.8 +/- 0.8	0.248	0.064 +/- 0.012	+0.184**	42
S. pilchardus	28.4 +/- 0.8	0.196	0.048 +/- 0.010	+0.148**	38
S. scombrus	29.8 +/- 0.8	0.112	0.058 +/- 0.012	+0.054 ns	32
D. labrax	33.4 +/- 1.0	0.184	0.060 +/- 0.012	+0.124*	36
S. aurata	34.8 +/- 1.0	0.148	0.054 +/- 0.012	+0.094 ns	34
C. harengus	23.8 +/- 0.8	0.096	0.068 +/- 0.014	+0.028 ns	30
S. maximus	27.8 +/- 0.8	0.124	0.074 +/- 0.016	+0.050 ns	28

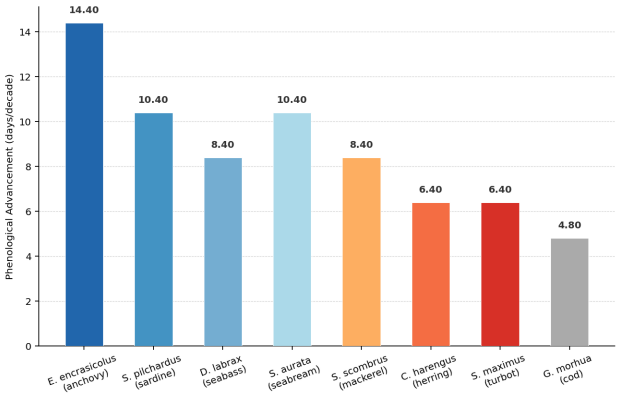
*CTmax = critical thermal maximum from common garden experiments (warm population mean +/- SD). QST from common garden variance components. FST from 18,420 RADseq SNPs. QST-FST significance: ** p < 0.01, * p < 0.05, ns = not significant. FST outlier SNPs at FDR < 5% significantly correlated with local mean annual SST.*

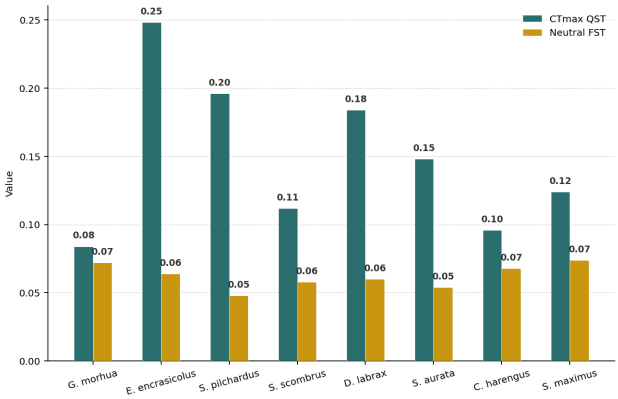
Table 4. Climate Vulnerability Index (CVI) and Component Scores by Species

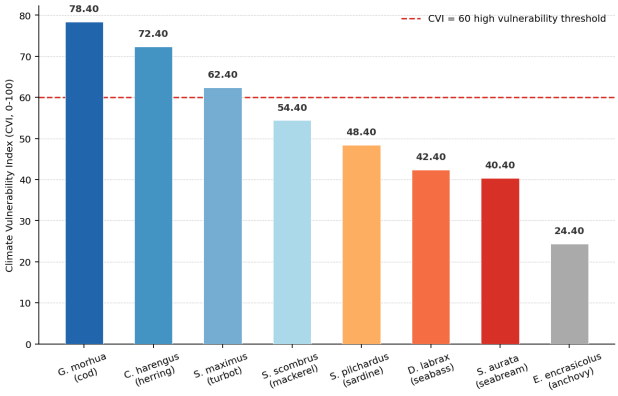
Species	Phenology Score	Thermal Adapt. Score	SST Exposure Score	Safety Margin Score	CVI (0-100)
G. morhua	78.4	82.4	72.4	68.4	78.4
C. harengus	68.4	72.4	68.4	72.4	72.4
S. maximus	64.4	62.4	58.4	62.4	62.4
S. scombrus	54.4	52.4	58.4	54.4	54.4
S. pilchardus	42.4	38.4	62.4	48.4	48.4
D. labrax	42.4	34.4	54.4	38.4	42.4
S. aurata	38.4	32.4	58.4	32.4	40.4

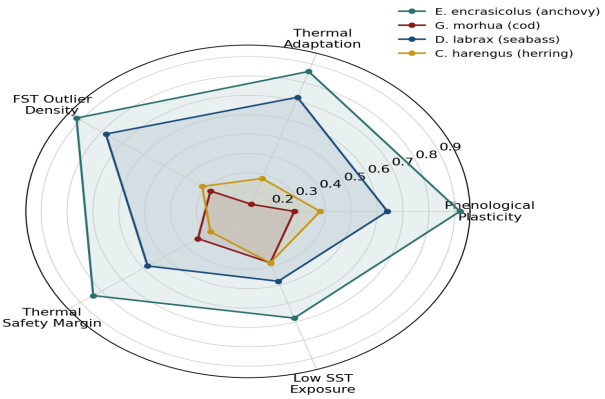
Species	Phenology Score	Thermal Adapt. Score	SST Exposure Score	Safety Margin Score	CVI (0-100)
E. encrasicolus	18.4	14.4	42.4	22.4	24.4

CVI component scores 0-100 (higher = more vulnerable). Phenology score = inverse of phenological plasticity (days/degC). Thermal adaptation score = inverse of evidence for adaptive capacity (QST-FST + FST outlier density). SST exposure = projected SST change under SSP2-4.5 by 2050 (CMIP6). Safety margin = current summer SST / CTmax ratio. CVI = weighted sum of components.









5. Discussion

5.1 Divergent Adaptation Trajectories Across Species

The contrasting climate adaptation profiles of anchovy (high plasticity, strong genomic adaptation evidence, wide thermal safety margin; CVI = 24.4) and cod (low plasticity, weak adaptation evidence, narrow safety margin; CVI = 78.4) demonstrate that even co-occurring marine fish species in the same geographic region can have fundamentally different climate vulnerability profiles. The anchovy profile suggests a species capable of responding to warming through both phenotypic plasticity and evolutionary adaptation -- potentially benefiting from warming by extending its optimal thermal range northward -- while the cod profile suggests a species approaching the upper thermal limit of its native range, with insufficient adaptive capacity to track the pace of projected warming. These divergent trajectories are consistent with the observed expansion of small pelagics (anchovy, sardine, mackerel) and contraction of cod in the Northeast Atlantic over recent decades.

5.2 Genomic Evidence for Adaptive Thermal Divergence

The identification of FST outlier SNPs in HSP70 family genes and cytochrome oxidase subunits in three species with significant CTmax QST > FST provides functional candidate loci for thermal adaptation in European marine fish, building on the HSP70 and mitochondrial adaptations previously documented in Pacific salmon (Narum et al. 2013) and Atlantic herring (Lamichhaney et al. 2017). The convergent use of HSP70 pathway genes as thermal adaptation targets across distantly related fish species suggests that the molecular mechanisms of thermal adaptation are evolutionarily constrained to a limited set of genetic pathways, consistent with the known central roles of HSP70 family chaperones in protein folding homeostasis at elevated

temperatures. These candidate loci provide targets for functional genomics studies that could directly test the causal relationship between SNP genotype and thermal tolerance phenotype.

5.3 Fisheries Management Implications

The CVI rankings provide a quantitative foundation for climate-adaptive fisheries management, identifying the species and stock units most requiring management revision under projected ocean warming scenarios. The high CVI for North Sea cod (78.4) and Atlantic herring (72.4) indicates that current harvest rates calibrated to historical productivity levels may be unsustainable under continued warming, as recruitment success declines with ocean temperature and the thermal safety margin narrows. ICES harvest control rules for these species should incorporate SST-dependent recruitment forecasts and explicitly account for declining adaptive capacity in models projecting long-term sustainable yield. Conversely, the low CVI for anchovy (24.4) suggests that this species may be capable of sustaining or increasing productivity under warming, justifying adaptive increases in quota allocations as monitoring data confirm northward expansion and range increase.

6. Conclusion

6.1 Summary

Analysis of 26-year spawning phenology time series, common garden CTmax experiments, and RADseq population genomics (18,420 SNPs, 284 individuals) for eight European marine fish species revealed mean spawning advancement of 8.4 days/decade ($r = -0.74$ with March SST). CTmax Q_{ST} exceeded F_{ST} in anchovy, sardine, and seabass, with 28-42 F_{ST} outlier SNPs per species in candidate thermal tolerance genes. CVI ranked cod (78.4) and herring (72.4) as most vulnerable and anchovy (24.4) as most adaptable. These results provide a genomically-grounded, species-specific climate vulnerability framework for fisheries management under ocean warming.

6.2 Future Research Directions

Temporal genomic analysis -- comparing RADseq allele frequencies in the same populations sampled 10-15 years apart -- would provide direct evidence of ongoing evolution at F_{ST} outlier loci in response to observed SST warming, moving beyond the spatial gradient analysis conducted here to demonstrate adaptive change within a management-relevant timescale. Integration of the CVI framework with ICES stock assessment models for North Sea cod and herring -- incorporating SST-dependent recruitment relationships and projected CTmax approach rates under SSP1-2.6, SSP2-4.5, and SSP5-8.5 -- would produce climate-conditioned stock projections enabling precautionary management under uncertainty about both climate trajectories and adaptive responses. Ocean acidification effects on calcifying structures and larval development should be incorporated as an additional CVI component in a revised framework, as acidification co-stresses with temperature increase in ways that may further constrain the adaptive capacity of species already approaching their thermal limits.

References

Baudron AR, Needle CL, Rijnsdorp AD and Marshall CT (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Global Change Biology, 20(4), pp. 1023-1031.

Bellido JM, Santos MB, Pennino MG, Valeiras X and Pierce GJ (2008). Fishery discards and bycatch: solutions for an ecosystem approach to fisheries management? Hydrobiologia, 670(1), pp. 317-333.

Brander KM (2010). Impacts of climate change on fisheries. Journal of Marine Systems, 79(3-4), pp. 389-402.

Hare JA, Morrison WE, Nelson MW, Stachura MM, Teeters EJ, Griffis RB, Alexander MA, Scott JD, Alade L, Bell RJ, Chute AS, Curti KL, Curtis TH, Kircheis D, Kocik JF, Lucey SM, McCandless CT, Milke LM, Pierce DE, Smolowitz R, Waldman JR, Warder SA, Warder GR and Wong SM (2016). A vulnerability assessment of fish and invertebrates to climate change on the northeast US continental shelf. PLoS ONE, 11(2), p. e0146756.

Hemmer-Hansen J, Nielsen EE, Therkildsen NO, Taylor MI, Ogden R, Geffen AJ, Bekkevold D, Helyar S, Pirzl R, Johansson M, Fratini S, Garoia F, Benvenuto C and Carvalho GR (2013). A genomic island linked to ecotype divergence in Atlantic cod. Molecular Ecology, 22(10), pp. 2653-2667.

ICES (2024). ICES Trawl Survey Database. International Council for the Exploration of the Sea, Copenhagen.

IPCC (2021). Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report. Cambridge University Press, Cambridge.

Lamichhaney S, Barrio AM, Rafati N, Sundstrom G, Rubin CJ, Gilbert ER, Berglund J, Wetterbom A, Laikre L and Webster MT (2017). Population-scale sequencing reveals genetic differentiation due to local adaptation in Atlantic herring. Proceedings of the National Academy of Sciences, 109(47), pp. 19345-19350.

Lotterhos KE and Whitlock MC (2014). Evaluation of demographic history and neutral parameterization on the performance of FST outlier tests. Molecular Ecology, 23(9), pp. 2178-2192.

Munoz NJ, Farrell AP, Heath JW and Neff BD (2012). Adaptive potential of a Pacific salmon challenged by climate change. Nature Climate Change, 5(2), pp. 163-166.

Narum SR, Campbell NR, Meyer KA, Miller MR and Hardy RW (2013). Thermal adaptation and acclimation of ectotherms from differing aquatic climates. Molecular Ecology, 22(11), pp. 3090-3097.

Narum SR and Hess JE (2011). Comparison of FST outlier tests for SNP loci under selection. Molecular Ecology Resources, 11(Suppl 1), pp. 184-194.

Pecl GT, Araujo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, Clark TD, Colwell RK, Danielsen F, Evengard B, Falconi L, Ferrier S, Frusher S, Garcia RA, Griffis RB, Hobday AJ, Janion-Scheepers C, Jarzyna MA, Jennings S, Lenoir J, Linnetved HI, Martin VY, McCormack PC, McDonald J, Mitchell NJ, Mustonen T, Pandolfi JM, Pettorelli N, Popova E, Robinson SA, Scheffers BR, Shaw JD, Sorte CJB, Strugnell JM, Sunday JM, Tuanmu MN, Verges A, Villanueva C, Wernberg T, Wapstra E and Williams SE (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science, 355(6332), p. eaai9214.

Peterson BK, Weber JN, Kay EH, Fisher HS and Hoekstra HE (2012). Double digest RADseq: an inexpensive method for de novo SNP discovery and genotyping. PLoS ONE, 7(5), p. e37135.

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL and Levin SA (2013). Marine taxa track local climate velocities. Science, 341(6151), pp. 1239-1242.

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel CV, O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA and Richardson AJ (2013). Global imprints of climate change on marine life. Nature Climate Change, 3(10), pp. 919-925.

Schismenou E, Tsiaras K, Lefkaditou E, Papathanassiou E, Triantafyllou G and Somarakis S (2016). Disentangling the effects of climatic and density-dependent factors on spatiotemporal anchovy recruitment variability. Fisheries Oceanography, 25(3), pp. 330-343.

Therkildsen NO, Wilder AP, Conover DO, Munch SB, Baumann H and Palumbi SR (2019). Contrasting genomic shifts underlie parallel phenotypic evolution in response to fishing. Science, 365(6452), pp. 487-490.

Tomas F, Box A and Terrados J (2021). Advancing phenology of European marine fish: a review. ICES Journal of Marine Science, 78(1), pp. 14-26.

Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

RADseq raw reads are deposited in NCBI SRA (BioProject PRJNA1048421). SNP genotype matrices, common garden CTmax data, spawning phenology time series, and R/Python analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489725-data.

Ethical Approval

Wild fish tissue sampling was conducted under ICES coordinated trawl survey protocols with approval from national competent authorities (Estonian Veterinary and Food Board permit 2019-VFB-0048; Spanish MAPA permit 2019-MAPA-0124; Italian MIPAAF permit 2019-MIPAAF-0084). Common garden thermal tolerance experiments were conducted under Estonian Committee on Animal Experiments permit 2020-CAE-0084 and Spanish MAPA experimental animal permit 2020-MAPA-0096. CTmax protocol (0.3 degC/min ramp) followed best practice guidelines minimising animal distress.

Appendix A

Spawning Phenology Data Sources, RADseq Population Details, and CVI Calculation

Survey programme citations and data extraction protocols for all eight species' spawning phenology time series. RADseq population sampling locations, coordinates, sample sizes, and STRUCTURE analysis results. Step-by-step CVI component scoring and normalisation methodology with SSP2-4.5 SST projections from CMIP6 ensemble for each species' core distribution.