



Northern shrimp exhibit origin-specific proteomic remodelling under ocean acidification, with limited response to ocean warming

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ABSTRACT

The Northern shrimp (*Pandalus borealis*) is an ecologically important species and the target of one of the world's largest shellfish fisheries. Yet, its habitats are rapidly changing due to human-driven climate change, with temperatures projected to increase by ~4 °C and seawater pH to decline by 0.3 pH units the end of the century. These stressors may cause interactive effects, with responses differing among origins due to local adaptation or long-term acclimatisation. We investigated the impacts of ocean warming and acidification (individually and combined) on the proteome of female *P. borealis* from four geographic origins. Shrimp proteomes responded to ocean acidification, but not to warming, with marked origin-specific differences. Comparing the most favourable condition (2 °C, pH 7.75) to low pH (7.35) across tested temperatures, we detected 109 differentially abundant proteins (DAPs) in shrimp from the Saint Lawrence Estuary (SLE), six in those from the Northeast Newfoundland Coast (NNC) and Eastern Scotian Shelf (ESS), and three in the Esquimaux Channel (EC). SLE shrimp showed widespread downregulation across metabolic, genetic information processing, and signalling pathways, suggesting higher sensitivity to acidification relative to other origins, where responses were muted. These findings highlight intraspecific variation in proteomic responses to ocean acidification in this commercially valuable crustacean. They confirm ocean acidification as a major concern in the context of rapid environmental change and suggest that uniform conservation strategies may be ineffective. Instead, management efforts should account for origin-specific sensitivities, reflecting the complex adaptive landscape shaping the resilience of *P. borealis* and other exploited marine species.

1. Introduction

Numerous studies have been conducted on a multitude of organisms using traditional phenotypic measurements to examine their physiology. Additionally, recent advances in omics technologies (Manzoni et al., 2018; Page and Lawley, 2022; Stillman and Armstrong, 2015; Viant, 2007) have allowed researchers to acquire a deeper understanding of the

molecular mechanisms that underlie whole-organism physiology (Calosi et al., 2017; Noisette et al., 2021; Turner et al., 2025). This in turn has generated significant breakthroughs in our critical appreciation of the functioning and evolution of physiological systems. Among the different omics approaches, proteomics enables the comprehensive analysis of the proteins expressed by an organism, providing insights into the alterations in protein abundance, post-translational modifications, and

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protein-protein interactions in response to environmental changes (Aebersold and Mann, 2003; Carroll and Coyne, 2021; Madeira et al., 2020). Further, proteomics has emerged as a valuable tool for providing insights on various aspects of an organism's fundamental biological processes, such as functional characterization of proteins, gene expression and regulation, and identification of biomarkers (Heck and Neely, 2020; López, 2007). In this sense proteomics specifically, can be used to identify both key proteins and pathways involved in the physiological responses of marine organisms under the effect of environmental changes or stressors, potentially unravelling the molecular basis of their adaptation and acclimatisation processes (Araújo et al., 2018; Madeira et al., 2020; Nesatyy and Suter, 2007; Tomanek, 2014). This in turn can support the development of effective conservation strategies in the face of global climate change (Domínguez-Pérez et al., 2019), improve management of global change impacts and risks on populations of marine species, as well as guide stock assessment and management of important fisheries (Chellapandian and Sivakamavalli, 2022; Karr, 2008; Kershaw et al., 2024).

Since the industrial revolution (ca. 1850), ocean temperature has increased by ca. 1 °C and surface water pH has declined by ca. 0.1 pH units (IPCC, 2022). These environmental changes are occurring more rapidly in some locations (e.g., Lavoie et al., 2019), therefore impacting marine organisms differentially depending on, but not limited to, location, previous acclimatisation history to prevalent environmental regimes, and species (DuBois et al., 2022; Somero, 2012; Vargas et al., 2017). Commercial species may be particularly at risk, as the combination of global change forcing with fishing pressure may result in abundance declines and distributional shifts due to the progressive reduction in habitat suitability (Townhill et al., 2023).

Pandalus borealis Krøyer 1838 is widely distributed in the North Atlantic and supports an important commercial fishery, being the third most lucrative fishery in Canadian waters (DFO, 2021a), and target of one of the world's largest shellfish fisheries (Government of Canada, 2016). This species is of great economic and cultural importance in the Northeast Atlantic region (Dupont et al., 2014; Søvik and Thangstad, 2016). Further, *P. borealis* is an ecologically important species, representing a major prey species for many fish and marine mammals (Brown-Vuillemin et al., 2022; Dawe et al., 2012; Jónsdóttir et al., 2012; Zabihi-Seissan et al., 2024). Changes in ocean temperature and other environmental drivers, including anthropogenic stressors, have likely caused the abundance of *P. borealis* to decline in some regions (DFO, 2023; Richards and Hunter, 2021). This adds to the evidence that cold-water species abundance is decreasing in warming oceans (Logerwell et al., 2022). Recent studies have highlighted that the survival and (broadly speaking) the metabolic performance of *P. borealis* from different geographical locations is negatively affected, in a comparative manner, by seawater temperatures above 6 °C and low pH (Guscelli et al., 2023b). Different from whole-organisms traits, shrimp metabolomic and lipidomic responses showed marked intraspecific differences among geographical locations (Feugere et al., 2025; Guscelli et al., 2023a), with shrimp from some origins being more sensitive to ocean warming (OW) and ocean acidification (OA), in isolation and combined, than those from others. Differently, at the transcriptome level, only the response to temperature was characterised, and Leung et al. (2023) highlighted that the thermal transcriptomic response of northern shrimp from different origins was comparable. These apparent idiosyncrasies may be reconciled by investigating the remodelling that may occur in other cell layers in response to OW and OA. Specifically, the proteome connects functionally the transcriptome to the lipidome and metabolome, and helps defining whole-organism phenotypes. In the current study, a proteomic screening of abdominal muscle samples from females of the Northern shrimp *P. borealis* was performed, with specimens being collected from four different locations in Atlantic Canada and exposed for a month to different combinations of three temperatures and two pH levels (Guscelli et al., 2023b). Our results on shrimp proteome response were used to explore the sensitivity and plasticity of *P. borealis* from different

geographic origins to predicted changes in seawater temperature and pH. Based on previous evidence of the impact of different global change drivers on *P. borealis* (Arnberg et al., 2013; Chabot and Ouellet, 2005; Chemel et al., 2020; Feugere et al., 2025; Guscelli et al., 2023a, 2023b) we hypothesise that: (i) OW exerts a greater effect on the proteome when compared to OA, (ii) that OW and OA combined exert non-additive effects, and (iii) shrimp from different locations respond differently to global change drivers in isolation and combined.

2. Materials and methods

2.1. Animal collection and maintenance

Non-ovigerous females of the Northern shrimp *P. borealis* were collected for experiments performed by Chemel et al. (2020) and Guscelli et al. (2023a, 2023b). Briefly, individuals were collected from one of four geographic locations within the northwest Atlantic: St. Lawrence Estuary (SLE, 48° 35' N, 68° 35' W; May 2018), Esquiman Channel (EC, 50° 44' N, 57° 29' W; July 2019), Eastern Scotian Shelf (ESS, 45° 23' N, 61° 04' W; February 2019), and Northeast Newfoundland Coast (NNC, 50° 18' N, 54° 16' W; November 2019) (Fig. 1) with shrimp traps or trawls and then transported to the Maurice-Lamontagne Institute (MLI), Fisheries and Oceans Canada (Mont-Joli, QC, Canada) in well-oxygenated, 750-L water tanks at 2 °C. Shrimp were maintained in 1700-L flow-through tanks that were continuously supplied from the nearby Saint Lawrence Estuary at MLI for approximately eight weeks following collection to adjust to laboratory conditions. The sea water supplied from the estuary was filtered through a large sand bed, and salinity was automatically adjusted by addition of aquaculture quality salt and kept at 32. Average conditions of the supplied sea water were 4.5 °C and pH_T 7.9 (pH total scale, pH_T). Water was supplied at a flow rate of 3.5 L min⁻¹. Shrimp were fed *ad libitum* three times a week, with a diet consisting of equal parts of frozen capelin (*Mallotus villosus*) and shrimp (*Pandalus* spp.) (Guscelli et al., 2023b). Water parameters were monitored using temperature probes (HRSTD-3-100-A-240-E, Omega Engineering Inc., Norwalk, CT, USA) and pH probes (1001 modules, IKS Aquastar, Karlsbad, Germany), and mean environmental conditions are summarised in Chemel et al. (2020) & Guscelli et al. (2023b).

2.2. Experimental design, system, and protocol

After the pre-exposure period, 60 females from each geographic origin were randomly assigned to one of 12 experimental tanks (240 L), being stocked at five shrimp per tank. Shrimp were exposed for 30 d to one of six experimental treatments, with two experimental tanks per treatment. The detailed experimental design can be found in (Chemel et al., 2020; Guscelli et al., 2023a, 2023b) and is summarised in Table 1. Briefly, the treatments and corresponding target values used were as follows: low temperature and current pH (2C: 2 °C and pH_T 7.75), low temperature and low pH (2A: 2 °C and pH_T 7.40); intermediate temperature and current pH (6C: 6 °C and pH_T 7.75); intermediate temperature and low pH (6A: 6 °C and pH_T 7.40); elevated temperature and current pH (10C: 10 °C and pH_T 7.75); and elevated temperature and low pH (10A: 10 °C and pH_T 7.40). Temperature treatments were chosen based on the suggested, most favourable temperature for this species (2 °C, Shumway et al., 1985). The current average temperature experienced by shrimp in EC (6 °C, Bourdages, 2022), also corresponds to the predicted temperature for 2100 (+4 °C) under the representative concentration pathway 8.5 by the Intergovernmental Panel on Climate Change (IPCC, 2013) for other origins (Fig. 1). The elevated temperature (10 °C) represents the IPCC scenario for shrimp from EC. Levels of pH were selected as the current pH_T (7.75) experienced by SLE and EC shrimp and future predicted level for shrimp from ESS and NNC. The pH_T of 7.40 was selected as equivalent to a −0.3/−0.4 unit decrease in pH by the end of the century (IPCC, 2013) for shrimp from the SLE and EC (Fig. 1).

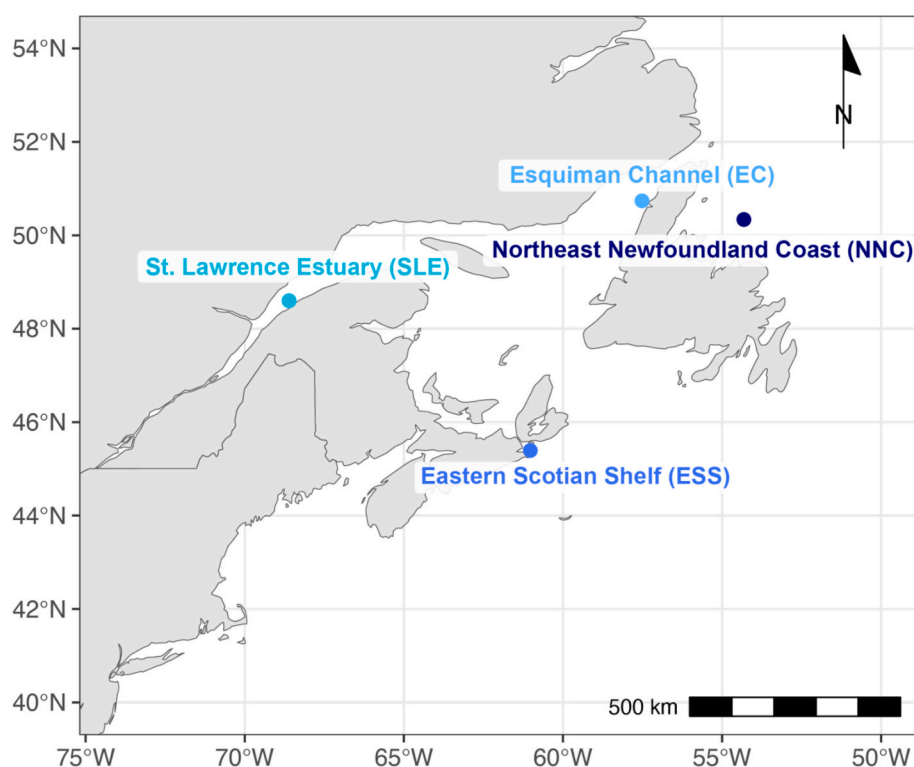


Fig. 1. Map showing collection sites of the Northern shrimp *Pandalus borealis* used in the present study. Female shrimp were collected from: St. Lawrence Estuary, Esquiman Channel, Eastern Scotian Shelf, and Northeast Newfoundland Coast.

Table 1

Summary of experimental culture conditions corresponding to each experimental group. Shrimp from all origins were assigned in equal numbers across the six experimental treatments.

Treatment	Temperature (°C)	pH	Replicate tanks	Number of individuals per tank
2C	2.0	7.75	2	5
2A	2.0	7.40	2	5
6C	6.0	7.75	2	5
6A	6.0	7.40	2	5
10C	10.0	7.75	2	5
10A	10.0	7.40	2	5

Details of daily husbandry of shrimp from all geographic locations and monitoring of the experimental system and seawater chemistry measurements can be found in [Chemel et al. \(2020\)](#) and [Guscelli et al. \(2023a, 2023b\)](#). To avoid energy demands related to food ingestion, shrimp were fasted from day 23.

After 30 d exposure to treatment conditions, 10 individuals *per* treatment *per* geographic origin (five individuals *per* treatment tank) were removed from their respective treatments and used to determine metabolic rates *via* the measurement of individual oxygen uptake (methods and results are presented in [Guscelli et al. \(2023a, 2023b\)](#), and [Guscelli et al. \(2024\)](#)). Shrimp were then quickly and rapidly patted dry, and muscle tissue (from the abdomen) was dissected and flash-frozen in liquid nitrogen. Muscle tissue was chosen to continue with similar sampling protocols used in previous studies by the research team and allow a reliable comparison with other omics compartments ([Feugere et al., 2025](#); [Guscelli et al., 2023a, 2023b](#)). Moreover, it provides the most tissue for analyses, representing the largest proportion of body mass of northern shrimp, which is also an important source of protein for predators in the wild, as well as for human consumption. Samples were then stored at -80°C until they were shipped in a dry shipper to ECOMARE - Laboratory for Innovation and Sustainability of Marine

Biological Resources at the University of Aveiro (Aveiro, Portugal). Here samples were kept at -80°C , until analyses were carried out.

2.3. Quantitative proteomics

2.3.1. Protein extraction

Protein extractions were performed at ECOMARE on flash-frozen muscle tissue of *P. borealis*. Shrimp muscle tissue samples (≈ 100 mg) were homogenised in 2 mL of modified Laemmli buffer (60 mM Tris-HCl, pH 6.8, 2 % SDS - sodium dodecyl sulfate) using a tissue homogenizer (Omni TH, Bebenssee, Germany). Subsequently, samples were sonicated (Sonifier 250, Branson) (output control 1.5, time 5 s + 10 s on ice, $3\times$) and centrifuged for 15 min at $10,000\times g$ at 4°C , and homogenates were spun down and supernatant containing extracted protein was collected. Samples were stored at -80°C until being transported *via* dry shipper with liquid nitrogen for proteomic analyses to the Center for Neuroscience and Cell Biology – University of Coimbra (Cantanhede, Portugal).

2.3.2. Sample preparation for proteomics, LC-MS analyses and pre-processing of proteomics data

Protein identification and relative quantification were performed on previously frozen protein extracts following a similar method described in [Trindade et al. \(2022\)](#) with slight modifications. Briefly, protein extracts (1 mL) of muscle tissue were diluted with 1 mL $1\times$ Laemmli sample buffer ([Laemmli, 1970](#)) and sonicated using a cup-horn (Ultrasonic processor, 750 W). Total protein concentration was measured for each sample using an assay kit (Pierce 660 nm Protein Assay kit, Thermo Scientific™ Waltham, MA). For data-dependent acquisition (DDA) experiments, replicates from two independent variables (geographic origin – four levels – and temperature – three levels) were pooled into twelve different sample pools (SLE-2, SLE-6, SLE-10, EC-2, EC-6, EC-10, ESS-2, ESS-6, ESS-10, and NNC-2, NNC-6, NNC-10) before protein separation by gel electrophoresis. These pools included all pH groups within the temperature $\times$ population pools, to ensure proteins occurring across all

treatments (temperature, population/origin, and pH) were captured and well represented (3). For data-independent acquisition (DIA) each sample was processed individually. The data from the DDA experiment runs were used to build the spectral library, which was used to mine the DIA data from each sample for quantification. The protein content from each sample/pool ($\approx 50 \mu\text{g}$) was alkylated with acrylamide, separated by the Short-GeLC Approach (Anjo et al., 2015), and digested with trypsin for 16 h. Extracted peptides were then resuspended to 25 μL (for DDA experiments) and 30 μL (for DIA experiments) with 2 % acetonitrile and 0.1 % formic acid. For each sample 10 μL of extract were analysed using a NanoLC™ 425 System (Eksigent) coupled to a Triple TOF™ 6600 mass spectrometer (Sciex) and the ionization source (ESI DuoSpray™ Source) and the parameters used for the DDA and SWATH/DIA acquisitions are described in (Trindade et al., 2022).

Ion-library construction followed methods detailed in (Trindade et al., 2022), with one deviation from using the Decapoda database (NCBI; 342,483 protein sequences) for searching. Relative quantification of proteins (SWATH-MS) was also conducted following methods detailed in Trindade et al. (2022) and was normalised for total sum of peak areas for each respective sample. The MS proteomics data have been deposited to the ProteomeXchange Consortium via the PRIDE (Perez-Riverol et al., 2025) partner repository with the dataset identifier PXD068332.

2.3.3. Statistical & bioinformatic analyses

All analyses were performed in R (v 4.2.2). Initially, principal component analysis (PCA) was performed on raw data to check for batch effects (Fig. S1). Batch effects were identified (Fig. S1). Following this, proteomic data were pre-processed by filtering out rows (variables) with <50 % valid values, then the function *ComBat* in the package *sva* (Leek et al., 2012) was used to remove batch effects in the data by using an empirical Bayes framework to adjust for batch effects (Fig. S2). The batch effect corrected data was then normalised by Z-scoring the matrix. Missing data imputation was done by replacing missing values, which were considered to be zeroes in this dataset, from a normal distribution (width 0.3, down shift 1.8, separately for each sample) (Madeira et al., 2021). A p value ≤ 0.05 was considered significant and a p value between 0.05 and 0.10 was considered to be “marginally significant” (along the lines of the framework outlined by Muff et al., 2022). Missing data imputation did not distort the distribution of the data (Fig. S3).

Subsequently, a permutation analysis of variance (PERMANOVA) was applied to filtered proteomics data from the four geographic origins surveyed ($N = 215$) used in this study to test the effects of temperature, pH, and origin on the response of 592 proteins. The function *adonis2* in the package *vegan* (Oksanen et al., 2022) was used with the following parameters: permutations = 9999, distance method = euclidean. Temperature, pH, and origin were set as the independent variables.

Differentially abundant proteins (DAPs) were identified, per origin, by applying empirical Bayes statistics on protein-wise linear models using *limma* (Ritchie et al., 2015) in the *DEP* package (v 3.17) (Zhang et al., 2018). Missing values were removed from origin-based datasets by filtering for proteins that were quantified in eight out of the ten replicate individuals of at least one treatment condition within an origin. Data was then normalised by variance stabilising transformation. Missing values were imputed using random draws from a Gaussian distribution centred around a minimal value for missing not at random (MNAR) with option “MinProb”, $q = 0.01$. Comparisons of conditions (temperature, pH, and origin) were conducted to identify significant DAPs between groups. Correction from testing was done in *DEP* with the package *fdrtool* (Strimmer, 2008). Proteins were considered differentially abundant between groups with an FDR-corrected p -value < 0.05 and a $\log_2$ -fold change (lfc) beyond ± 1 .

Protein sequences were obtained through the *efetch* command in NCBI's freely available E-utilities (<https://www.ncbi.nlm.nih.gov/books/NBK25497/>). eggNOG-mapper v2 was used to obtain protein descriptions, Kyoto Encyclopedia of Genes and Genomes (KEGG) terms,

and gene ontology (GO) annotation for DAPs using default parameters (Cantalapiedra et al., 2021; Huerta-Cepas et al., 2019). Functional overrepresentation analysis of DAPs was performed in the Cytoscape (Shannon et al., 2003) plugin BiNGO (Heymans et al., 2005), where hypergeometric tests of GO categories were used, specifically “biological process”, with the annotated genome of *P. borealis* as a “background”. A p -value (Benjamini-Hochberg FDR correction) cut-off of 0.05 was used. To predict and identify protein-protein interaction networks associated with DAPs from different origins of *P. borealis*, STRING analysis (Search Tool for the Retrieval of Interacting Genes/Proteins; <https://string-db.org/>) (Szklarczyk et al., 2023) was performed using default parameters with high confidence (≥ 0.7) and the whiteleg shrimp, *Penaeus vannamei*, as the representative database, and only decapod species available (Szklarczyk et al., 2025). Protein networks were generated and visualised in Cytoscape (Shannon et al., 2003) using the StringApp plugin (Doncheva et al., 2019). KEGG mapper (Kanehisa and Sato, 2020) was used to assign KEGG BRITE descriptors to DAPs.

3. Results

3.1. Overall proteome response in female *P. borealis*

The proteome of the abdominal muscle of females of the northern shrimp *P. borealis* from different origins responded differently to OA conditions, as indicated by the presence of a significant interaction between seawater pH and shrimp's origin (Pseudo- $F_{(3,192)} = 2.391$, $p = 0.031$, Table 2).

Based on the PERMANOVA results, analyses focused on the effect of pH and origin on proteomic response of *P. borealis*, and in particular on the comparison of the favourable condition (i.e., 2 °C at 7.75 pH - 2C) vs. the low pH treatments (i.e., those at 7.35 pH - A) at 2, 6, and 10 °C (2A, 6A, and 10A - Fig. 2).

3.2. Differentially abundant proteins

Differentially abundant proteins (DAPs) were identified across the four geographic origins when comparing 2C to 2A, 6A, and 10A (Fig. 3). SLE showed the most DAPs (109), when comparing 2C to 2A, 6A and 10A (Fig. 3). We found six DAPs in the NNC and ESS origins, and three in the EC origin (Fig. 3).

3.3. Enrichment analyses

KEGG pathway analyses were performed to categorise DAPs (Table 3) and showed differential regulation of a number of cellular processes. The most represented terms were found in protein families relating to genetic information processing and protein families relating to cell signalling (Tables 3, S2).

Table 2

Summary of results from the PERMANOVA test used to investigate the effects of temperature, pH, and origin, in isolation and combined, on the muscle proteome of females of the northern shrimp *Pandalus borealis*. Text in bold indicates statistically significant terms ($p \leq 0.05$). The * indicates marginally significant results (P).

Source	df	SS	R2	Pseudo-F	P (perm)
Temperature (T)	2	33.337	0.010	1.081	0.329
pH	1	18.132	0.005	1.176	0.274
Origin (O)	3	91.337	0.027	1.974	0.073*
T*pH	2	4.318	0.001	0.140	1.000
T*O	6	88.459	0.026	0.956	0.475
pH*O	3	110.649	0.033	2.391	0.031
T*pH*O	6	71.765	0.021	0.776	0.666
Residuals	192	2961.252	0.876		
Total	215	3379.249	1.000		

Analysis used 9999 permutations and a Euclidean distance method.

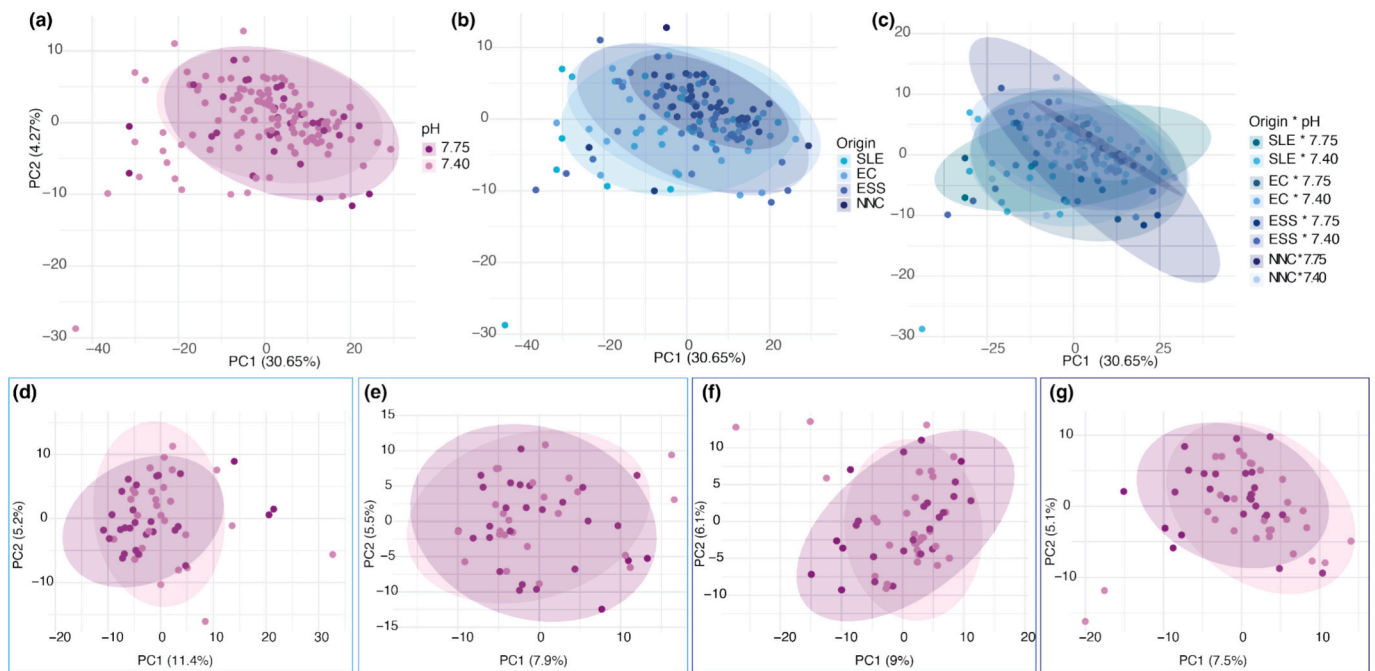


Fig. 2. Principal component analysis (PCA) plots displaying PC1 and PC2 shrimp *P. borealis* from 2C (2 °C at 7.75 pH), 2A (2 °C at 7.35 pH), 6A (6 °C at 7.35 pH), and 10A (10 °C at 7.35 pH) treatments comparing seawater pH conditions (a), origin (b), and the interaction between origin and seawater pH (c), where points represent individual shrimp samples from all geographic origins sampled. Plots d, e, f, and g represent PCAs comparing seawater pH levels of 7.75 and 7.40 separately for each origin: SLE (d), EC (e), ESS (f), and NNC (g).

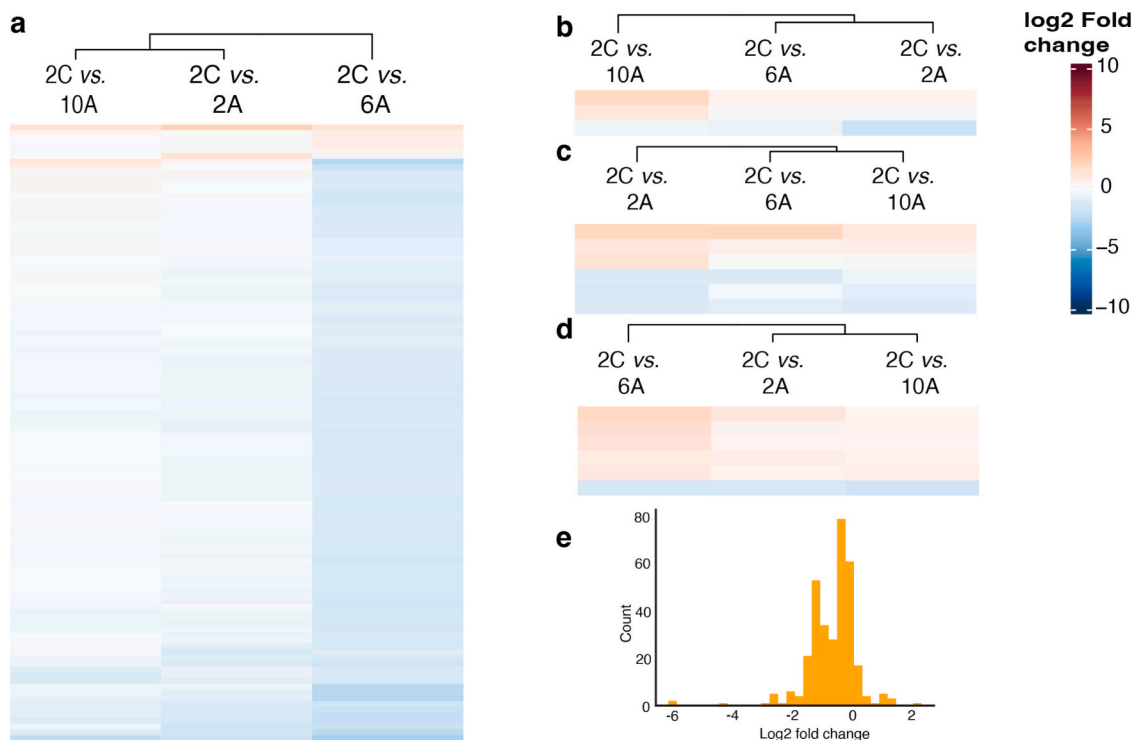


Fig. 3. Heatmaps of $\log_2$ -fold-change FDR values < 0.05 with up- (red) and down-regulated (blue) proteins from (a) SLE, (b) EC, (c) ESS, and (d) NNC. The histogram (e) illustrates the overall distribution of $\log_2$ fold-changes across all significant proteins in the SLE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Protein-protein interaction networks were created for each geographic origin from inputting DAPs found resulting from treatment comparisons of 2C to 2A, 6A and 10A (Fig. 4). The resulting network for SLE contained 99 proteins (nodes) and 91 predicted or known protein

interactions (edges) (Fig. 4a). The EC and NNC networks contained proteins, three and six respectively, with no predicted or known interactions (Fig. 4b, d). The ESS network resulted in five proteins and one interaction (Fig. 4c).

Table 3

Differentially abundant proteins ($FDR < 0.05$) across treatment comparisons of 2C to 2A, 6A, and 10A and origins were assigned KEGG BRITE (Kanehisa and Sato, 2020) identifiers using eggNOG mapper. The number of proteins associated with each KEGG BRITE identifier was obtained from DEP analyses of the proteome of shrimp from each origin. Saint Lawrence Estuary (SLE), Esquiman Channel (EC), Eastern Scotian Shelf (ESS), and Northeast Newfoundland Coast (NNC). A total of 105 proteins returned KEGG identifications.

Origin	SLE		EC		ESS		NNC	
	Increase	Decrease	Increase	Decrease	Increase	Decrease	Increase	Decrease
KEGG BRITE identifier								
<i>Protein families: metabolism</i>								
Enzymes	2	34	-	-	2	1	2	-
Protein kinases	-	4	-	-	-	-	-	-
Protein phosphatases and associated proteins	-	2	-	-	-	-	-	-
Peptidases and inhibitors	-	3	-	-	-	1	-	-
<i>Protein families: genetic information processing</i>								
Transcription factors	-	3	-	-	-	-	-	-
Transcription machinery	1	5	-	-	-	-	-	-
Messenger RNA biogenesis	2	12	-	1	-	-	-	-
Spliceosome	-	7	-	-	-	-	-	-
Ribosome	-	3	-	-	1	-	-	-
Ribosome biogenesis	-	1	-	-	-	-	-	-
Transfer RNA biogenesis	-	2	-	-	-	-	-	-
Translation factors	-	3	-	1	-	-	-	-
Chaperones and folding catalysts	-	6	-	-	-	-	-	-
Membrane trafficking	-	18	-	-	-	-	-	-
Ubiquitin system	-	2	-	-	-	-	-	-
Proteasome	-	2	-	-	-	1	-	1
Chromosome and associated proteins	-	11	1	-	-	-	-	1
DNA repair and recombination proteins	1	1	-	-	-	-	-	-
Mitochondrial biogenesis	1	5	-	-	-	-	-	-
<i>Protein families: signalling and cellular processes</i>								
Transporters	-	2	-	-	-	-	1	-
Secretion system	-	2	-	-	-	-	-	-
Cilium and associated proteins	-	1	-	-	-	-	-	-
Cytoskeleton proteins	2	20	1	-	-	-	1	-
Exosome	3	46	-	1	-	-	-	-
Ion channels	-	1	-	-	-	-	-	-
GTP-binding proteins	-	5	-	-	-	-	-	-
CD molecules	-	1	-	-	-	-	-	-
Proteoglycans	-	2	-	-	-	-	-	-
Glycosaminoglycan binding proteins	-	-	-	-	-	-	1	-
Unclassified	-	3	-	-	-	-	-	-

A total of 131 significantly enriched biological processes were generated from STRING analyses for DAPs, from the comparison of 2C to 2A, 6A, and 10A (independently) in the SLE and one biological process was enriched in the ESS, specifically the process of negative regulation of innate immune response. Enrichment analyses found no significantly enriched biological processes in the EC or NNC. In the SLE, the enriched biological processes containing the highest number of proteins were cellular processes and metabolic processes (Fig. 5).

3.4. Origin comparison

When comparing DAPs from pairwise comparisons of 2C to 2A, 6A, and 10A across shrimp origins, shrimp from SLE had 107 unique proteins that were differentially abundant, ESS had five, and NNC and EC had three each (Fig. 6). Two proteins were shared between SLE and NNC, a likely histone H4 protein (KAG0692637.1) and calcium-transporting ATPase type protein (KAG0715187.1) (Fig. 6), and a peroxiredoxin (AET34923.1) was shared between ESS and NNC (Fig. 6).



Fig. 4. Protein-protein interaction networks of differentially abundant proteins (FDR ≤ 0.05) when comparing 2C to 2A, 6A, and 10A across all origins and their database description. (a) Network for the SLE. Purple nodes represent terminal nodes, and pink nodes are highly connected (>5 connections). Colours surrounding nodes in the SLE network show nodes involved in glycolysis, metabolic processes, cellular response to stress, cellular Na⁺ homeostasis, cellular K⁺ homeostasis, metabolism of amino acids, and pyruvate metabolism. For visualisation, singletons were not shown in the SLE network. (b, c, d) Networks for EC, ESS, and NNC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Origin-specific proteomic responses to ocean acidification

Here, we show the presence of origin-specific responses in the proteome of Northern shrimp from four distinct geographical origins to low seawater pH conditions predicted to occur by the year 2100. Similarly to our previous studies on other omics layers of the Northern shrimp (Feugere et al., 2025; Guscelli et al., 2023a), individuals from SLE are the most sensitive to ocean acidification (OA), having by far the most differentially abundant proteins (DAPs). Based on our findings, and genetic evidence from Bourret et al. (2024), we suggest the presence of a certain degree of long-term acclimatisation to regional conditions, which helps define how shrimp will respond to the physiological challenge imposed by OA. Our results, together with those from previous studies (Arnberg et al., 2013; Chabot and Ouellet, 2005; Chemel et al., 2020; Feugere et al., 2025; Guscelli et al., 2023a, 2023b; Leung et al., 2023) show that the Northern shrimp has a relatively wide thermal breadth for a cold-adapted species. While OW appeared to be the main driver shaping *P. borealis* whole-organism responses (Guscelli et al., 2023b), metabolomics (Guscelli et al., 2023a), and lipidomics profiles (Feugere et al., 2025), OA is the dominant driver shaping the proteome of shrimp.

4.2. Comparative influence of ocean acidification and warming across origins

At the proteome level, *P. borealis* appears to be sensitive to OA but not to OW, this pattern being consistent across origins. However, the presence of a significant interaction between origin and seawater pH emphasises origin-specific responses to OA, suggesting a higher sensitivity and/or the presence of plastic compensatory or adaptive responses to this global change driver in shrimp from some origins versus others.

This result differs from that by Guscelli et al. (2023b), who showed females of *P. borealis* from different origins to display comparable whole-organism level responses to OA and OW among all origins. It appears that *P. borealis* remodels preferentially (and in some cases profoundly) its molecular dynamics, with all omics layers displaying origin-specific responses to global change drivers, in order to maintain a stable performance at the whole-organism level (as also observed for American lobster (*Homarus americanus*) larvae by Noisette et al., 2021). However, while non-additive responses (*sensu* Piggott et al., 2015) between OW and OA were dominant for both metabolomic (Guscelli et al., 2023a) and lipidomic layers (Feugere et al., 2025), for the proteome we do not report non-additive responses to OW and OA. Furthermore, the proteome is unresponsive to temperature, a pattern that may be rather common in warm-adapted species or species with broad thermal breadths (Araújo et al., 2018; Dineshram et al., 2016). This finding was surprising, however, for a cold-adapted species such as *P. borealis*, where an increase in temperature was expected to enhance processes such as chaperoning, cytoskeleton dynamics, redox regulation, and energy metabolism (see for example Lipaeva et al., 2023; Fields et al., 2012; and Truebano et al., 2013). Nonetheless, it is important to note that *P. borealis* is not a stenothermic species, as it occupies habitats with temperatures ranging from −1.6 to 16.3 °C (Zabihi-Seissan et al., 2024). Several authors have proposed, using different model organisms, that proteome composition may remain stable over a range of temperatures, whereas proteins' activity may increase due to temperature effects on enzyme kinetics and reaction rates (Madeira et al., 2020; Mair et al., 2021). Enzyme/protein abundance levels can be regulated not only through gene expression changes, but also *via* post-translational modifications, which are known to affect proteins' stability and degradation (Lee et al., 2023). Shifting an enzyme activity instead of its abundance may be the most energetically advantageous mechanism within a certain thermal range, while protein content adjustments may only be necessary at extreme temperatures (Madeira et al., 2020; Mair et al., 2021). Still,

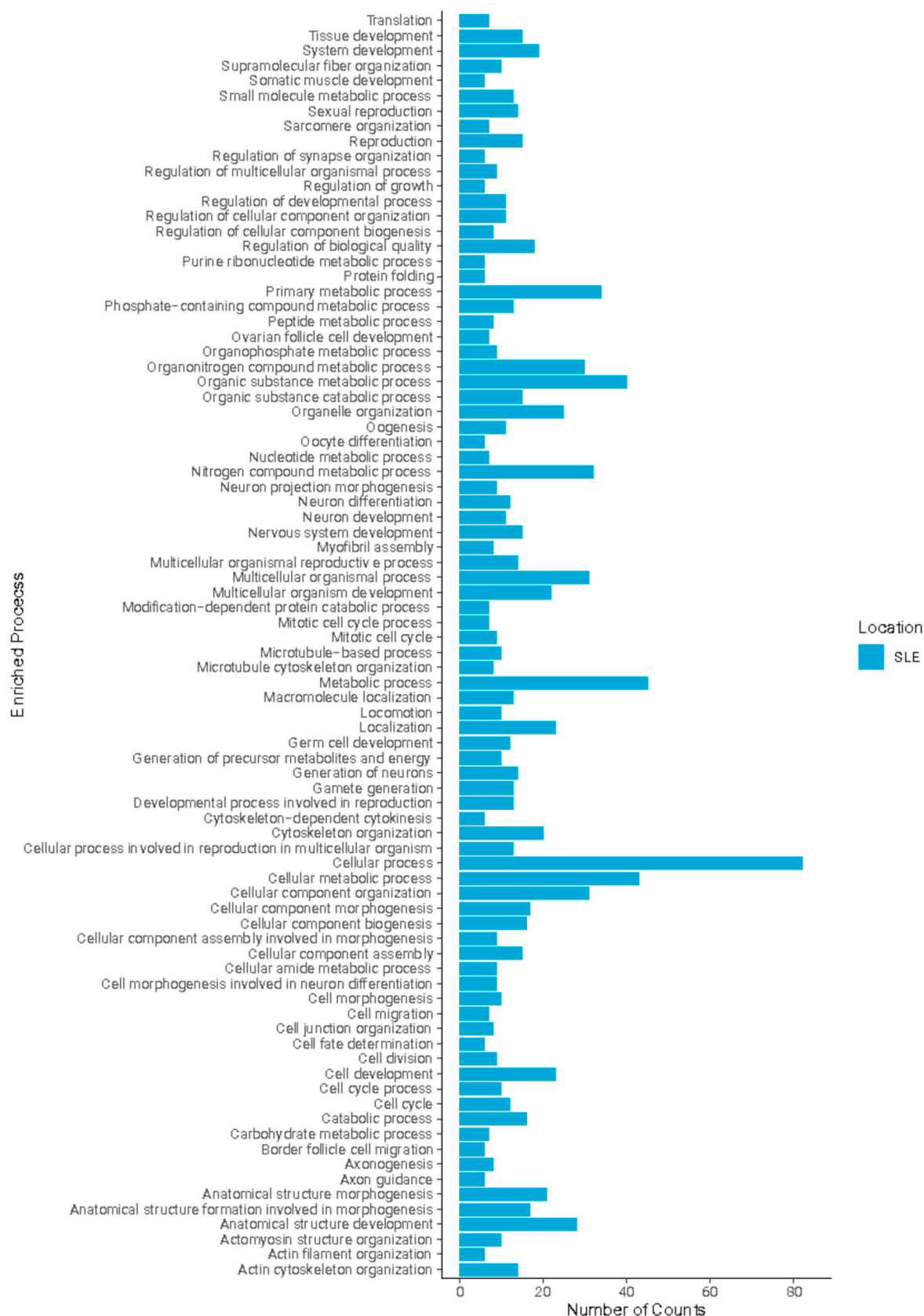


Fig. 5. Gene ontology (GO) enrichment analyses of proteins with a false discovery rate of ≤ 0.05 . Only processes containing ≥ 5 counts are shown in the figure, only the SLE origin is therefore shown. GO terms of enriched processes are given and the corresponding number of proteins found within these processes is given as counts.

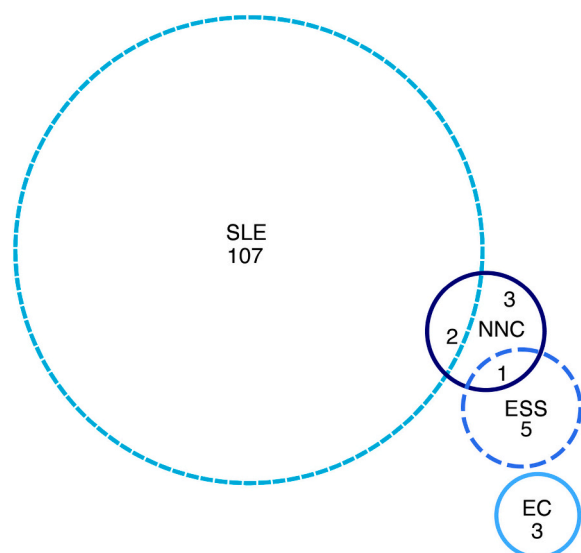


Fig. 6. Area-proportional Venn diagram illustrating unique and common differentially abundant proteins across the four origins: SLE, EC, ESS, and NNC, from comparison of 2C to 2A, 6A, and 10A. Generated using DeepVenn (<https://www.deepvenn.com>).

our previous work has shown that *P. borealis* displays origin-specific metabolic enzymes (i.e., citrate synthase, cytochrome C oxidase or lactate dehydrogenase) activity levels, with no effects of temperature or pH being detected (Guscelli et al., 2023b). Different baseline enzymatic activity levels may thus reflect the long-term acclimatisation to regional conditions, with SLE displaying the lowest activity levels for these enzymes. Here, we found a marginally significant effect of origin on proteins' abundance as well, suggesting that both abundance and activity may be determined by long-term acclimatisation processes.

4.3. Strong OA-induced proteomic disruption in SLE shrimp

Contrary to elevated temperature, low pH elicits a proteomic response on *P. borealis* muscle, with shrimp from SLE displaying widespread decreased abundance in proteins across metabolic, genetic information processing, and signalling and cellular process pathways (109 DAPs), suggesting OA is triggering a strong response in shrimp from this location. This suggests a heightened sensitivity to OA compared to shrimp from other localities, where we see more muted responses to OA (< 6 DAPs), likely indicating the presence of less responsive phenotypes. Shrimp from SLE showed a staggering 18–36 times more DAPs when compared to shrimp from other origins. The number of proteins associated with enzymes across the origins varied, with the abundance of these proteins mostly decreasing in SLE, but increasing in shrimp from NNC, however minimally, and with minimal overall change in shrimp from ESS and EC shrimp origins. More in general, differences in enzyme abundance may reflect origin-specific strategies for coping with environmental challenges, ranging from an intense reduction in cell functions (SLE) to minimal remodelling (other origins) aimed at sustaining cellular performance. SLE shrimp exhibited the most extensive and highly interconnected network of DAPs (Fig. 4), with enriched connections in pathways associated with glycolysis, pyruvate metabolism, amino acid metabolism, cellular stress responses, and ionic homeostasis. This complex network structure suggests broad molecular remodelling, where most proteins decreased their abundance under OA. This possibly reflects an energy-saving strategy, where energetically expensive processes are reduced to stabilize ATP:ADP levels (as observed by Guscelli et al., 2023b), but the cell still attempts to maintain its integrity and basic function. This is supported by the evidence of mixed regulation of specific functions, where most proteins decreased but some also

increased, involving transcription, DNA repair, mitochondrial biogenesis, cytoskeleton dynamics, and exosomes. Such processes may be essential for the cell to produce exclusively key proteins, regulate DNA repair, control mitochondrial metabolism, maintain structure and adjust cell-to-cell communication, with exosomes potentially playing an important role in mediating innate immune responses under stress (Beninson and Fleshner, 2014). In our previous metabolomics study (Guscelli et al., 2023a), we found evidence of increased tyrosine concentration in SLE shrimp exposed to OA, also suggesting a modulation of the immune response (see Huang et al., 2020; Parthasarathy et al., 2018; Shang et al., 2023). Interestingly, ESS-origin showed an enrichment of the pathway for negative regulation of innate immune response. Thus, OA seems to affect innate immunity in shrimp from both of these origins, albeit it is unclear if they show opposing or concordant responses. Several studies have shown that medium and long-term exposure to OA could lead to immune suppression and increased susceptibility to disease in crustaceans (Hernroth et al., 2012; Weerathunga et al., 2021) and other taxa (Bibby et al., 2008; Leite Figueiredo et al., 2016). However, negative regulation of innate immune response may also be important to keep immune balance and control tissue inflammation levels (see Mulay and Lech, 2022). Therefore, we should not exclude the possibility that differential fine-tuning of immune responses across origins may be needed, depending on origin-specific sensitivities to OA. Additionally, proteins involved in Na^+ and K^+ homeostasis are found among DAPs in the SLE shrimp, with lower abundance under OA, further underscoring the likely disruption of acid-base balance and ion transport processes, which are commonly affected under OA conditions (Melnzer et al., 2020; Turner et al., 2015; Zhu et al., 2022). Shrimp from the remaining origins (EC and NNC) exhibited fewer DAPs, no enriched processes, and simpler protein-protein interaction networks, with minimal inter-connectivity. Again, these limited responses may indicate reduced sensitivity or reduced ability to mount a plastic response to OA, as observed for *P. borealis* metabolome (Guscelli et al., 2023a) and lipidome (Feugere et al., 2025). The lack of stress-related enriched proteins and an absence of large, interconnected networks in shrimp from EC, ESS, and NNC suggests a lack of systemic proteome remodelling compared to SLE. Shrimp from SLE have more protein families that are impacted by OA, this further supporting the idea that SLE shrimp experience a more pronounced physiological disruption in response to OA. This potentially reflects the negative effects of shrimp prolonged exposure to stressful conditions *in situ* (see also Guscelli et al., 2023a). This pronounced proteome response in shrimp from SLE is comparable to the response reported in the phospholipidome, where shrimp from this same location showed the largest remodelling among all origins (Feugere et al., 2025). Whilst shrimp from SLE show the greatest level of response to OA, the limited response (at the proteome and metabolome levels) in EC shrimp may however suggest that Northern shrimp at this location are more vulnerable. This is also supported by findings at lipidome level (Feugere et al., 2025), which pointed to EC shrimp as being the most vulnerable at the cellular membrane level. Further, this should also be considered in light of the local oceanographic-geomorphological conditions. Shrimp from the EC location have not moved to shallower depths in recent years despite the progression of global changes, likely due to a lack of suitable habitats for these specimens in shallower waters or because conditions in deeper water were not (yet) extreme enough to influence their bathymetric migration to more favourable conditions (Guscelli et al., 2023b). Differently, shrimp from SLE have migrated bathymetrically in recent years to shallower, cooler, less acidic, and better oxygenated waters (DFO, 2022, 2021b). By interpreting all omics layers investigated, we conclude that *P. borealis* responds to global change drivers in a highly origin-specific manner. The convergence of metabolomic, lipidomic, and proteomic evidence reinforces the notion that the SLE origin is regionally more responsive at various levels of the biological organisation to OA, featuring metabolic, lipidomic, and proteomic remodelling not observed in other origins. However, SLE origin is not necessarily the most vulnerable, considering that survival (under

laboratory conditions) to exposure to OW and OA was comparable among origins (Guscelli et al., 2023b), and suitable habitats are still present at this locality.

4.4. Value of multi-layer biological integration for understanding vulnerability

Our work further highlights the importance of understanding the differences in inter-origin phenotypic responses to global change drivers, here specifically OA, to inform management and conservation strategies under future global change scenarios (Calosi et al., 2017; Vargas et al., 2017). Furthermore, by integrating information from multiple layers of an organism, we show the importance of accounting for the inherent complexity of biological systems (Bartholomew, 1986; Madeira et al., 2024). This enables us to reconcile what may appear to be contrasting responses, and avoid under- or over-estimating the assessment of a population or species vulnerability to the ongoing environmental change (Calosi et al., 2016). Moreover, it also allows to provide a mechanistic underpinning for decreasing trends in density with the progression of global changes (for OW in *P. borealis* see Zabihi-Seissan et al., 2024). Our proteomic analysis provides an essential layer that helps to reconcile differing responses observed at other 'omic and whole-organism levels (Feugere et al., 2025; Guscelli et al., 2023a, 2023b). In fact, while metabolomics reveals rapid shifts in the metabolism of organisms, and lipidomics captures membrane-specific mitolting, among other functions, proteomics reveals the molecular machinery regulating these responses (Aebersold and Mann, 2003; Carroll and Coyne, 2021; Griffiths and Wang, 2009; Madeira et al., 2020). When integrated, these omics levels provide a more complete picture of vulnerability, and acclimatory and adaptation capacity under global change scenarios in marine ectotherms, thus more appropriately informing effective global change smart-management and conservation strategies and practices (Madeira et al., 2024).

5. Conclusions

Our study demonstrates that ocean acidification is the primary driver of proteomic remodelling in the Northern shrimp *P. borealis*, while warming elicits no detectable proteomic response across origins. Despite shrimp's general lack of responsiveness to temperature at proteome level, responses to low pH/elevated pCO_2 are strongly origin-specific. In more detail, shrimp from the SLE exhibited extensive proteomic remodelling under ocean acidification conditions, whereas shrimp from the other origins displayed minimal changes, reflecting divergent regional sensitivities linked to shrimp's long-term acclimatisation histories. These findings align with previously observed metabolomic and lipidomic patterns (Feugere et al., 2025; Guscelli et al., 2023a), highlighting how molecular responses to global change drivers are mostly shaped by local environmental conditions (e.g., Vargas et al., 2017; Garlaschè et al., 2025). Importantly, pronounced proteomic remodelling does not necessarily indicate greater vulnerability, as whole-organism survival remains comparable among origins, underscoring the difficulty of linking molecular disruption to organismal resilience. By integrating multiple 'omics layers, it is possible to provide a mechanistic understanding of origin-specific responses to environmental change. Overall, multi-omics approaches can more accurately assess the vulnerability of populations to climate change, therefore allowing more informed conservation and management strategies for cold-adapted marine ectotherms.

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CRediT authorship contribution statement

Tessa M. Page: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data

curation, Conceptualization. **Miguel Rosado:** Writing – review & editing, Formal analysis, Data curation. **Vera M. Mendes:** Writing – review & editing, Formal analysis, Data curation. **Ella Guscelli:** Writing – review & editing, Methodology, Investigation. **Joana Filipa Fernandes:** Writing – review & editing, Investigation. **Denis Chabot:** Writing – review & editing, Resources, Investigation. **Ricardo Calado:** Writing – review & editing, Funding acquisition. **Bruno Manadas:** Writing – review & editing, Funding acquisition. **Piero Calosi:** Writing – review & editing, Writing – original draft, Supervision, Resources, Funding acquisition, Conceptualization. **Diana Madeira:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Denis Chabot has patent issued to Crown. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Proteomic quantification data used to construct the principal figures of this manuscript have been uploaded on figshare (doi: <https://doi.org/10.60270/figshare.2025.119152>).

org/10.6084/m9.figshare.30009802). The mass spectrometry proteomic data have been deposited to the ProteomeXchange Consortium under dataset identifier PXD068332.

References

- Aebersold, R., Mann, M., 2003. Mass spectrometry-based proteomics. *Nature* 422 (6928), 198–207. <https://doi.org/10.1038/nature01511>.
- Anjo, S.I., Santa, C., Manadas, B., 2015. Short GeLC-SWATH: a fast and reliable quantitative approach for proteomic screenings. *Proteomics* 15 (4), 757–762. <https://doi.org/10.1002/pmic.201400221>.
- Araújo, J.E., Madeira, D., Vitorino, R., Repolho, T., Rosa, R., Diniz, M., 2018. Negative synergistic impacts of ocean warming and acidification on the survival and proteome of the commercial sea bream, *Sparus aurata*. *J. Sea Res.* 139, 50–61. <https://doi.org/10.1016/j.seares.2018.06.011>.
- Arnberg, M., Calosi, P., Spicer, J.I., Tandberg, A.H.S., Nilsen, M., Westerlund, S., Bechmann, R.K., 2013. Elevated temperature elicits greater effects than decreased pH on the development, feeding and metabolism of northern shrimp (*Pandalus borealis*) larvae. *Mar. Biol.* 160 (8), 2037–2048. <https://doi.org/10.1007/s00227-012-2072-9>.
- Bartholomew, G.A., 1986. The role of natural history in contemporary biology: natural history can help pose questions for and supply integrative lines between different biological disciplines. *BioScience* 36 (5), 324–329. <https://doi.org/10.2307/1310237>.
- Beninson, L.A., Fleschner, M., 2014. Exosomes: an emerging factor in stress-induced immunomodulation. *Semin. Immunol.* 26 (5), 394–401. <https://doi.org/10.1016/j.smim.2013.12.001>.
- Bibby, R., Widdicombe, S., Parry, H., Spicer, J., Pipe, R., 2008. Effects of ocean acidification on the immune response of the blue mussel *Mytilus edulis*. *Aquat. Biol.* 2, 67–74. <https://doi.org/10.3354/ab00037>.
- Bourdages, H., 2022. Assessment of Northern Shrimp Stocks in the Estuary and Gulf of St. Lawrence in 2021: Commercial Fishery and Research Survey Data. Canadian Science Advisory Secretariat.
- Bourret, A., Leung, C., Puncher, G.N., Le Corre, N., Deslauriers, D., Skanes, K., Bourdages, H., Cassista-Da Ros, M., Walkusz, W., Jeffery, N.W., Stanley, R.R.E., Parent, G.J., 2024. Diving into broad-scale and high-resolution population genomics to decipher drivers of structure and climatic vulnerability in a marine invertebrate. *Mol. Ecol.* 33 (15), e17448. <https://doi.org/10.1111/mec.17448>.
- Brown-Vuillemin, S., Chabot, D., Nozères, C., Tremblay, R., Sirois, P., Robert, D., 2022. Diet composition of redfish (*Sebastes* sp.) during periods of population collapse and massive resurgence in the Gulf of St. Lawrence. *Front. Mar. Sci.* 9. <https://doi.org/10.3389/fmars.2022.963039>.
- Calosi, P., Wit, P.D., Thor, P., Dupont, S., 2016. Will life find a way? Evolution of marine species under global change. *Evol. Appl.* 9 (9), 1035–1042. <https://doi.org/10.1111/eva.12418>.
- Calosi, P., Melatun, S., Turner, L.M., Artioli, Y., Davidson, R.L., Byrne, J.J., Viant, M. R., Widdicombe, S., Rundle, S.D., 2017. Regional adaptation defines sensitivity to future ocean acidification. *Nat. Commun.* 8 (1), 13994. <https://doi.org/10.1038/ncomms13994>.
- Cantalapiedra, C.P., Hernández-Plaza, A., Letunic, I., Bork, P., Huerta-Cepas, J., 2021. eggNOG-mapper v2: functional annotation, orthology assignments, and domain prediction at the metagenomic scale. *bioRxiv*. <https://doi.org/10.1101/2021.06.03.446934> (p. 2021.06.03.446934).
- Carroll, S.L., Coyne, V.E., 2021. A proteomic analysis of the effect of ocean acidification on the haemocyte proteome of the South African abalone *Haliotis midae*. *Fish Shellfish Immunol.* 117, 274–290. <https://doi.org/10.1016/j.fsi.2021.08.008>.
- Chabot, D., Ouellet, P., 2005. Rearing *Pandalus borealis* larvae in the laboratory. *Mar. Biol.* 147 (4), 881–894. <https://doi.org/10.1007/s00227-005-1626-5>.
- Chellapandian, H., Sivakamavalli, J., 2022. Chapter 5—proteomics and genomics as an efficient tool for biomonitoring. In: Tiwari, S., Agrawal, S. (Eds.), *New Paradigms in Environmental Biomonitoring Using Plants*. Elsevier, pp. 95–108. <https://doi.org/10.1016/B978-0-12-824351-0.00005-5>.
- Chemel, M., Noiset, F., Chabot, D., Guscelli, E., Leclerc, L., Calosi, P., 2020. Good news — bad news: combined ocean change drivers decrease survival but have no negative impact on nutritional value and organoleptic quality of the northern shrimp. *Front. Mar. Sci.* 7. <https://doi.org/10.3389/fmars.2020.00611>.
- Dawe, E., Koen-Alonso, M., Chabot, D., Stansbury, D., Mullenwey, D., 2012. Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change. *Mar. Ecol. Prog. Ser.* 469, 233–248. <https://doi.org/10.3354/meps10136>.
- DFO, 2021a. 2020 value of Atlantic & Pacific coast commercial landings, by province. <https://www.dfo-mpo.gc.ca/stats/commercial/land-debarq/sea-maritimes/s2020p-v-eng.htm>.
- DFO, 2021b. Oceanographic conditions in the Atlantic Zone in 2020. In: *Can. Sci. Adv. Sec. Sci. Adv. Rep.*, 2021/026.
- DFO, 2022. Assessment of northern shrimp stocks in the Estuary and Gulf of St. Lawrence in 2021. In: *Can. Sci. Adv. Sec. Sci. Adv. Rep.*, 2022/006.
- DFO, 2023. Assessment of northern shrimp (*Pandalus borealis*) and striped shrimp (*Pandalus montagu*) in the eastern and western assessment zones. In: *Can. Sci. Adv. Sec. Sci. Adv. Rep.*.
- Dineshram, R., Chandramouli, K., Ko, G.W.K., Zhang, H., Qian, P.-Y., Ravasi, T., Thiagarajan, V., 2016. Quantitative analysis of oyster larval proteome provides new insights into the effects of multiple climate change stressors. *Glob. Chang. Biol.* 22 (6), 2054–2068. <https://doi.org/10.1111/gcb.13249>.
- Domínguez-Pérez, D., Lippolis, J., Dennis, M., Miller, B., Tiley, K., Vasconcelos, V., de Almeida, A.M., Campos, A., 2019. The queen conch (*Lobatus gigas*) proteome: a valuable tool for biological studies in marine gastropods. *Protein J.* 38 (6), 628–639. <https://doi.org/10.1007/s10930-019-09857-0>.
- Doncheva, N.T., Morris, J.H., Gorodkin, J., Jensen, L.J., 2019. Cytoscape StringApp: network analysis and visualization of proteomics data. *J. Proteome Res.* 18 (2), 623–632. <https://doi.org/10.1021/acs.jproteome.8b00702>.
- DuBois, K., Pollard, K.N., Kauffman, B.J., Williams, S.L., Stachowicz, J.J., 2022. Local adaptation in a marine foundation species: implications for resilience to future global change. *Glob. Chang. Biol.* 28 (8), 2596–2610. <https://doi.org/10.1111/gcb.16080>.
- Dupont, S., Hall, E., Calosi, P., Lundve, B., 2014. First evidence of altered sensory quality in a shellfish exposed to decreased pH relevant to ocean acidification. *G. J. Shellfish Res.* 33 (3), 857–861. <https://doi.org/10.2983/035.033.0320>.
- Feugere, L., Fernandes, J.F., Guscelli, E., Melo, T., Aveiro, S., Chabot, D., Calado, R., Domingues, R., Madeira, D., Calosi, P., 2025. Non-additive phospholipidomic responses to ocean warming and acidification drive intraspecific variation in cell membrane vulnerability in a marine ectotherm. *Environ. Res.*, 122135. <https://doi.org/10.1016/j.envres.2025.122135>.
- Fields, P.A., Zuzow, M.J., Tomanek, L., 2012. Proteomic responses of blue mussel (*Mytilus*) congeners to temperature acclimation. *J. Exp. Biol.* 215 (7), 1106–1116. <https://doi.org/10.1242/jeb.062273>.
- Garlaschi, G., Drolet, D., Riley, C., Small, D., Howland, K.L., McKindsey, C.W., Calosi, P., 2025. Intraspecific variation in thermal performance suggests the presence of range-edge divergence and phenotypic compensation of Northern individuals in an introduced species. *Glob. Ecol. Biogeogr.*, e70163. <https://doi.org/10.1111/geb.70163>.
- Government of Canada, F. and O. C., 2016. Northern shrimp. https://www.dfo-mpo.gc.ca/species-especies/profiles-profil/northern-shrimp-crevette-nordique-eng.html?utm_source=chatgpt.com (March 6).
- Griffiths, J., Wang, Y., 2009. Mass spectrometry: from proteomics to metabolomics and lipidomics. *Chem. Soc. Rev.* 38 (7), 1882–1896. <https://doi.org/10.1039/B618553N>.
- Guscelli, E., Chabot, D., Vermande, F., Madeira, D., Calosi, P., 2023a. All roads lead to Rome: inter-origin variation in metabolomics reprogramming of the northern shrimp exposed to global changes leads to a comparable physiological status. *Front. Mar. Sci.* 10. <https://doi.org/10.3389/fmars.2023.1170451>.
- Guscelli, E., Noiset, F., Chabot, D., Blier, P.U., Hansen, T., Cassista-Da Ros, M., Pepin, P., Skanes, K.R., Calosi, P., 2023b. Northern shrimp from multiple origins show similar sensitivity to global change drivers, but different cellular energetic capacity. *J. Exp. Biol.* 226 (16), jeb245400. <https://doi.org/10.1242/jeb.245400>.
- Guscelli, E., Noiset, F., Chabot, D., Blier, P.U., Hansen, T., Cassista-Da Ros, M., Pepin, P., Skanes, K.R., Calosi, P., 2024. Seawater parameters during the experiments with multiple populations of the northern shrimp (*Pandalus borealis*) exposed to global change drivers. In: Guscelli, E., et al. (Eds.), *Survival, Metabolic Traits and Enzyme Activities of Multiple Populations of the Northern Shrimp (*Pandalus borealis*) Exposed to Global Change Drivers*, PANGAEA. <https://doi.org/10.1594/PANGAEA.966793>. dataset bundled publication.
- Heck, M., Neely, B.A., 2020. Proteomics in non-model organisms: a new analytical frontier. *J. Proteome Res.* 19 (9), 3595–3606. <https://doi.org/10.1021/acs.jproteome.0c00448>.
- Hernroth, B., Sköld, H.N., Wiklander, K., Jutfelt, F., Baden, S., 2012. Simulated climate change causes immune suppression and protein damage in the crustacean *Nephrops norvegicus*. *Fish Shellfish Immunol.* 33 (5), 1095–1101. <https://doi.org/10.1016/j.fsi.2012.08.011>.
- Heymans, K., Kuiper, M., Maere, S., 2005. BiNGO: A Cytoscape plugin to assess overrepresentation of Gene Ontology categories in Biological Networks. *Bioinformatics* 21 (16), 3448–3449. <https://doi.org/10.1093/bioinformatics/bti551>.
- Huang, Z., Aweya, J.J., Zhu, C., Tran, N.T., Hong, Y., Li, S., Yao, D., Zhang, Y., 2020. Modulation of crustacean innate immune response by amino acids and their metabolites: inferences from other species. *Front. Immunol.* 11, 574721. <https://doi.org/10.3389/fimmu.2020.574721>.
- Huerta-Cepas, J., Szklarczyk, D., Heller, D., Hernández-Plaza, A., Forslund, S.K., Cook, H., Mende, D.R., Letunic, I., Rattei, T., Jensen, L.J., von Mering, C., Bork, P., 2019. eggNOG 5.0: a hierarchical, functionally and phylogenetically annotated orthology resource based on 5090 organisms and 2502 viruses. *Nucleic Acids Res.* 47 (D1), D309–D314. <https://doi.org/10.1093/nar/gky1085>.
- IPCC, 2013. In: Stocker, T.F. (Ed.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. <https://doi.org/10.1017/CBO9781107415324>.
- IPCC, 2022. *The Ocean and Cryosphere in a Changing Climate: Special Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. <https://doi.org/10.1017/9781009157964>.
- Jónsdóttir, I.G., Björnsson, H., Skúladóttir, U., 2012. Predation by Atlantic cod *Gadus morhua* on northern shrimp *Pandalus borealis* in inshore and offshore areas of Iceland. *Mar. Ecol. Prog. Ser.* 469, 223–232. <https://doi.org/10.3354/meps09977>.
- Kanehisa, M., Sato, Y., 2020. KEGG Mapper for inferring cellular functions from protein sequences. *Protein Sci.* 29 (1), 28–35. <https://doi.org/10.1002/pro.3711>.
- Karr, T.L., 2008. Application of proteomics to ecology and population biology. *Heredity* 100 (2), 200–206. <https://doi.org/10.1038/sj.hdy.6801008>.
- Kershaw, J., Ramp, C., Sears, R., Hall, A., Deros, D., 2024. Proteome profiling reveals opportunities to investigate biomarkers of oxidative stress and immune responses in blubber biopsies from free-ranging baleen whales. *Conserv. Physiol.* 12 (1), coae059. <https://doi.org/10.1093/conphys/coae059>.

- Laemmli, U.K., 1970. Cleavage of structural proteins during the assembly of the head of bacteriophage T4. *Nature* 227 (5259), 680–685. <https://doi.org/10.1038/227680a0>.
- Lavoie, D., Lambert, N., Gilbert, D., 2019. Projections of future trends in biogeochemical conditions in the Northwest Atlantic using CMIP5 earth system models. *Atmosphere-Ocean* 57 (1), 18–40. <https://doi.org/10.1080/07055900.2017.1401973>.
- Lee, G.H., Min, C.W., Jang, J.W., Wang, Y., Jeon, J.-S., Gupta, R., Kim, S.T., 2023. Analysis of post-translational modification dynamics unveiled novel insights into rice responses to MSP1. *J. Proteome* 287, 104970. <https://doi.org/10.1016/j.jprot.2023.104970>.
- Leek, J.T., Johnson, W.E., Parker, H.S., Jaffe, A.E., Storey, J.D., 2012. The sva package for removing batch effects and other unwanted variation in high-throughput experiments. *Bioinformatics* 28 (6), 882–883. <https://doi.org/10.1093/bioinformatics/bts034>.
- Leite Figueiredo, D.A., Branco, P.C., dos Santos, D.A., Emerenciano, A.K., Iunes, R.S., Shimada Borges, J.C., Cunha, Machado, da Silva, J.R., 2016. Ocean acidification affects parameters of immune response and extracellular pH in tropical sea urchins *Lytechinus variegatus* and *Echinometra luccunter*. *Aquat. Toxicol.* 180, 84–94. <https://doi.org/10.1016/j.aquatox.2016.09.010>.
- Leung, C., Guscelli, E., Chabot, D., Bourret, A., Calosi, P., Parent, G.J., 2023. The lack of genetic variation underlying thermal transcriptomic plasticity suggests limited adaptability of the Northern shrimp, *Pandalus borealis*. *Front. Ecol. Evol.* 11. <https://doi.org/10.3389/fevo.2023.1125134>.
- Lipaeva, P., Karkossa, I., Bedulina, D., Schubert, K., Luckenbach, T., 2023. Cold-adapted amphipod species upon heat stress: proteomic responses and their correlation with transcriptomic responses. *Comp. Biochem. Physiol. Part D Genomics Proteomics* 45, 101048. <https://doi.org/10.1016/j.cbcd.2022.101048>.
- Logerwell, E.A., Wang, M., Jørgensen, L.L., Rand, K., 2022. Winners and losers in a warming Arctic: potential habitat gain and loss for epibenthic invertebrates of the Chukchi and Bering Seas, 2008–2100. *Deep-Sea Res. II Top. Stud. Oceanogr.* 206, 105210. <https://doi.org/10.1016/j.dsr2.2022.105210>.
- López, J., 2007. Applications of proteomics in marine ecology. *Mar. Ecol. Prog. Ser.* 332, 275–279. <https://doi.org/10.3354/meps332275>.
- Madeira, D., Araújo, J.E., Madeira, C., Mendonça, V., Vitorino, R., Vinagre, C., Diniz, M. S., 2020. Seasonal proteome variation in intertidal shrimps under a natural setting: connecting molecular networks with environmental fluctuations. *Sci. Total Environ.* 703, 134957. <https://doi.org/10.1016/j.scitotenv.2019.134957>.
- Madeira, D., Fernandes, J.F., Jerónimo, D., Ricardo, F., Santos, A., Domingues, M.R., Calado, R., 2021. Calcium homeostasis and stable fatty acid composition underpin heatwave tolerance of the keystone polychaete *Hediste diversicolor*. *Environ. Res.* 195, 110885. <https://doi.org/10.1016/j.envres.2021.110885>.
- Madeira, D., Madeira, C., Calosi, P., Vermandele, F., Carrier-Belleau, C., Barria-Araya, A., Daigle, R., Findlay, H.S., Poisot, T., 2024. Multilayer biological networks to upscale marine research to global change-smart management and sustainable resource use. *Sci. Total Environ.* 944, 173837. <https://doi.org/10.1016/j.scitotenv.2024.173837>.
- Mairot, F., Gouze, J.-L., de Jong, H., 2021. Optimal proteome allocation and the temperature dependence of microbial growth laws. *Npj Syst. Biol. Appl.* 7 (1), 14. <https://doi.org/10.1038/s41540-021-00172-y>.
- Manzoni, C., Kia, D.A., Vandrovova, J., Hardy, J., Wood, N.W., Lewis, P.A., Ferrari, R., 2018. Genome, transcriptome and proteome: the rise of omics data and their integration in biomedical sciences. *Brief. Bioinform.* 19 (2), 286–302. <https://doi.org/10.1093/bib/bbw114>.
- Melzner, F., Mark, F.C., Seibel, B.A., Tomanek, L., 2020. Ocean acidification and coastal marine invertebrates: tracking CO₂ effects from seawater to the cell. *Annu. Rev. Mar. Sci.* 12 (2020), 499–523. <https://doi.org/10.1146/annurev-marine-010419-010658>.
- Muff, S., Nilsen, E.B., O'Hara, R.B., Nater, C.R., 2022. Rewriting results sections in the language of evidence. *Trends Ecol. Evol.* 37 (3), 203–210. <https://doi.org/10.1016/j.tree.2021.10.009>.
- Mulay, S.R., Lech, M., 2022. Editorial: negative regulators of innate immunity and their role in host responses to injury and infection. *Front. Immunol.* 13. <https://doi.org/10.3389/fimmu.2022.891919>.
- Nesatyy, V.J., Suter, M.J.-F., 2007. Proteomics for the analysis of environmental stress responses in organisms. *Environ. Sci. Technol.* 41 (20), 6891–6900. <https://doi.org/10.1021/es070561r>.
- Noiset, F., Calosi, P., Madeira, D., Chemel, M., Menu-Courey, K., Piedalue, S., Gurney-Smith, H., Daoud, D., Azetsu-Scott, K., 2021. Tolerant larvae and sensitive juveniles: integrating metabolomics and whole-organism responses to define life-stage specific sensitivity to ocean acidification in the American lobster. *Metabolites* 11 (9), 9. <https://doi.org/10.3390/metabol11090584>.
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szocs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Evangelista, H.B., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Oulette, M.-H., Cunha, E.R., Smith, T., Stier, A., Braak, C.J.F.T., Weedon, J., 2022. *vegan*: community ecology package (version 2.6-4) (computer software). <https://cran.r-project.org/web/packages/vegan/index.html>.
- Page, T.M., Lawley, J.W., 2022. The next generation is here: a review of transcriptomic approaches in marine ecology. *Front. Mar. Sci.* 9. <https://doi.org/10.3389/fmars.2022.757921>.
- Parthasarathy, A., Cross, P.J., Dobson, R.C.J., Adams, L.E., Savka, M.A., Hudson, A.O., 2018. A three-ring Circus: metabolism of the three proteogenic aromatic amino acids and their role in the health of plants and animals. *Front. Mol. Biosci.* 5, 29. <https://doi.org/10.3389/fmolb.2018.00029>.
- Perez-Riverol, Y., Bandla, C., Kundu, D.J., Kamatchinathan, S., Bai, J., Hewapathirana, S., John, N.S., Prakash, A., Walzer, M., Wang, S., Vizcaino, J.A., 2025. The PRIDE database at 20 years: 2025 update. *Nucleic Acids Res.* 53 (D1), D543–D553. <https://doi.org/10.1093/nar/gkae1011>.
- Piggott, J.J., Townsend, C.R., Matthaei, C.D., 2015. Reconceptualizing synergism and antagonism among multiple stressors. *Ecol. Evol.* 5 (7), 1538–1547. <https://doi.org/10.1002/eece3.1465>.
- Richards, R.A., Hunter, M., 2021. Northern shrimp *Pandalus borealis* population collapse linked to climate-driven shifts in predator distribution. *PLoS One* 16 (7), e0253914. <https://doi.org/10.1371/journal.pone.0253914>.
- Ritchie, M.E., Phipson, B., Wu, D., Hu, Y., Law, C.W., Shi, W., Smyth, G.K., 2015. Limma powers differential expression analyses for RNA-sequencing and microarray studies. *Nucleic Acids Res.* 43 (7), e47. <https://doi.org/10.1093/nar/gkv007>.
- Shang, Y., Wang, X., Shi, Y., Huang, W., Sokolova, I., Chang, X., Chen, D., Wei, S., Khan, F.U., Hu, M., Wang, Y., 2023. Ocean acidification affects the bioenergetics of marine mussels as revealed by high-coverage quantitative metabolomics. *Sci. Total Environ.* 858, 160090. <https://doi.org/10.1016/j.scitotenv.2022.160090>.
- Shannon, P., Markiel, A., Ozier, O., Baliga, N.S., Wang, J.T., Ramage, D., Amin, N., Schwikowski, B., Ideker, T., 2003. Cytoscape: a software environment for integrated models of biomolecular interaction networks. *Genome Res.* 13 (11), 2498–2504. <https://doi.org/10.1101/gr.123930>.
- Shumway, S.E., Perkins, H.C., Schick, D.F., Stickney, A.P., 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Kroyer, 1838. <http://aquaticcommons.org/id/eprint/2793>. <https://aquadocs.org/handle/1834/20581>.
- Somero, G.N., 2012. The physiology of global change: linking patterns to mechanisms. *Annu. Rev. Mar. Sci.* 4 (1), 39–61. <https://doi.org/10.1146/annurev-marine-120710-100935>.
- Søvik, G., Thangstad, T.H., 2016. Results of the Norwegian bottom trawl survey for northern shrimp (*Pandalus borealis*) in Skagerrak and the Norwegian Deep (ICES Divisions IIIa and IVa east) in 2015. Scientific Council Reports of the Northwest Atlantic Fisheries Organization. <https://www.waterbouwkundiglaboratorium.be/nl/catalogus>.
- Stillman, J.H., Armstrong, E., 2015. Genomics are transforming our understanding of responses to climate change. *BioScience* 65 (3), 237–246. <https://doi.org/10.1093/biosci/biu219>.
- Strimmer, K., 2008. fdrtool: a versatile R package for estimating local and tail area-based false discovery rates. *Bioinformatics* 24 (12), 1461–1462. <https://doi.org/10.1093/bioinformatics/btn209>.
- Szklarczyk, D., Kirsch, R., Koutrouli, M., Nastou, K., Mehryary, F., Hachilif, R., Gable, A. L., Fang, T., Doncheva, N.T., Pyysalo, S., Bork, P., Jensen, L.J., von Mering, C., 2023. The STRING database in 2023: protein-protein association networks and functional enrichment analyses for any sequenced genome of interest. *Nucleic Acids Res.* 51 (D1), D638–D646. <https://doi.org/10.1093/nar/gkac1000>.
- Szklarczyk, D., Nastou, K., Koutrouli, M., Kirsch, R., Mehryary, F., Hachilif, R., Hu, D., Peluso, M.E., Huang, Q., Fang, T., Doncheva, N.T., Pyysalo, S., Bork, P., Jensen, L.J., von Mering, C., 2025. The STRING database in 2025: protein networks with directionality of regulation. *Nucleic Acids Res.* 53 (D1), D730–D737. <https://doi.org/10.1093/nar/gkac1113>.
- Tomanek, L., 2014. Proteomics to study adaptations in marine organisms to environmental stress. *J. Proteome* 105, 92–106. <https://doi.org/10.1016/j.jprot.2014.04.009>.
- Townhill, B.L., Couce, E., Tinker, J., Kay, S., Pinnegar, J.K., 2023. Climate change projections of commercial fish distribution and suitable habitat around north western Europe. *Fish. Fish.* 24 (5), 848–862. <https://doi.org/10.1111/faf.12773>.
- Trindade, F., Ferreira, A.F., Saraiva, F., Martins, D., Mendes, V.M., Sousa, C., Gavina, C., Leite-Moreira, A., Manadas, B., Falcão-Pires, I., Vitorino, R., 2022. Optimization of a protocol for protein extraction from calcified aortic valves for proteomics applications: development of a standard operating procedure. *Proteomes* 10 (3), 30. <https://doi.org/10.3390/proteomes1003030>.
- Truebano, M., Diz, A.P., Thorne, M.A.S., Clark, M.S., Skibinski, D.O.F., 2013. Proteome response to heat stress in the Antarctic clam *Laternula elliptica*. *J. Integr. OMICS* 3 (1), 34–43. <https://doi.org/10.5584/jiomics.v3i1.125>.
- Turner, L.M., Ricevuto, E., Massa-Gallucci, A., Gambi, M.-C., Calosi, P., 2015. Energy metabolism and cellular homeostasis trade-offs provide the basis for a new type of sensitivity to ocean acidification in a marine polychaete at a high-CO₂ vent: adenylate and phosphagen energy pools versus carbonic anhydrase. *J. Exp. Biol.* 218 (14), 2148–2151. <https://doi.org/10.1242/jeb.117705>.
- Turner, L.M., Madeira, D., Ricevuto, E., et al., 2025. Sibling species differently distributed around a CO₂ vent show transplantation proteomic remodelling, while displaying metabolomic signatures associated with their origin. *Sci. Rep.* 15, 33604. <https://doi.org/10.1038/s41598-025-18913-y>.
- Vargas, C.A., Lagos, N.A., Lardies, M.A., Duarte, C., Manríquez, P.H., Aguilera, V.M., Broitman, B., Widdicombe, S., Dupont, S., 2017. Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity. *Nat. Ecol. Evol.* 1 (4), 4. <https://doi.org/10.1038/s41559-017-0084>.
- Viant, M.R., 2007. Metabolomics of aquatic organisms: the new 'omics' on the block. *Mar. Ecol. Prog. Ser.* 332, 301–306. <https://doi.org/10.3354/meps332301>.
- Weerathunga, V., Huang, W.-J., Dupont, S., Hsieh, H.-H., Piyawardhana, N., Yuan, F.-L., Liao, J.-S., Lai, C.-Y., Chen, W.-M., Hung, C.-C., 2021. Impacts of pH on the fitness and immune system of Pacific white shrimp. *Front. Mar. Sci.* 8. <https://doi.org/10.3389/fmars.2021.748837>.
- Zabihi-Seissan, S., Baker, K.D., Stanley, R.R.E., Tunney, T.D., Beauchamp, B., Benoit, H. P., Brickman, D., Chabot, D., Cook, A., Deslauriers, D., Koen-Alonso, M., Lawlor, J., Le Bris, A., Mullowney, D.R.J., Roux, M.-J., Skanes, K.R., Wang, Z., Pedersen, E.J., 2024. Interactive effects of predation and climate on the distributions of marine

- shellfish in the Northwest Atlantic. *Oikos* 2024 (9), e10524. <https://doi.org/10.1111/oik.10524>.
- Zhang, X., Smits, A.H., van Tilburg, G.B., Ovaa, H., Huber, W., Vermeulen, M., 2018. Proteome-wide identification of ubiquitin interactions using UblA-MS. *Nat. Protoc.* 13 (3), 3. <https://doi.org/10.1038/nprot.2017.147>.
- Zhu, S., Yan, X., Shen, C., Wu, L., Tang, D., Wang, Y., Wang, Z., 2022. Transcriptome analysis of the gills of *Eriocheir sinensis* provide novel insights into the molecular mechanisms of the pH stress response. *Gene* 833, 146588. <https://doi.org/10.1016/j.gene.2022.146588>.