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Abiotic factors and heavy metals defining eco-physiological niche in fish

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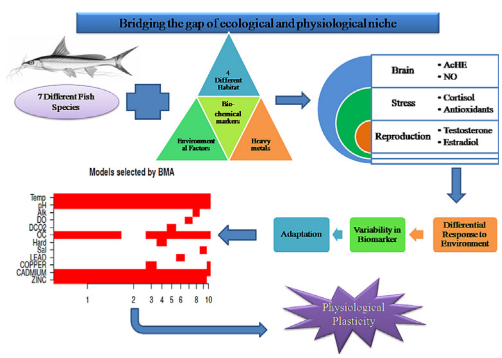
HIGHLIGHTS

- Stress tolerance can contribute to the relative vulnerability to reproductive success.
- Phenotypic plasticity can explain stress tolerance variability at intra specific level.
- Degree of adaptation depends on correlation of three axes-stress-brain- reproduction.
- Interactions of biotic and abiotic factors shape the ecophysiological niche of species.

GRAPHICAL ABSTRACT



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ABSTRACT

Ecosystem dynamics undergoing alterations in structure and function highlights the need to look into the relations between ecological parameters and organismal fitness and tolerance. Ecophysiological studies are used to understand how organisms adapt to and cope up with environmental stress. Current study uses a process-based approach to model physiochemical parameters regarding seven different fish species. Species respond to climatic variations via acclimation or adaptation through physiological plasticity. Four sites are differentiated into two types based on the water quality parameters and metal contamination. Seven fish species are clustered into two groups, each group depicting separate pattern of response in similar habitat. In this manner, biomarkers from three different physiological axes-stress, reproduction, and neurology were taken to determine the organism's ecological niche. Cortisol, Testosterone, Estradiol, and AChE are the signature molecules estimated for the said physiological axes. The ordination technique, nonmetric multidimensional scaling, has been utilized to visualize the differentiated physiological response to changing environmental conditions. Then, Bayesian Model Averaging (BMA) was used to identify the factors that play a key role in refining the stress physiology and determining the niche. Current study confirms different species belonging to similar habitats respond to various environmental and physiological factors in a different manner as various biomarkers respond in a species-specific pattern that induces the choice of habitat preference controlling its ecophysiological niche. In the present study, it is quite apparent that adaptive mechanism of fish to environmental stress is achieved through modification of physiological mechanisms through a panel of biochemical markers. These markers organize a cascade of physiological event at various levels including reproduction.

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1. Introduction

Biological populations are spread over various ecological niches across the world with different geographical distribution which are delineated by strong environmental gradients of temperature, salinity, pollution stress and, thus, serve as suitable models to observe acclimation and adaptation (Whitehead et al., 2011). Changes in physiological resilience and locally adapted phenotypes represent two separate ways to resolve evolutionary issues that could have an effect on sustenance in dynamic environments. The adaptation of physiological resilience is solely dependent on the organism's experience with its local environmental extremes during its lifetime (Whitehead et al., 2011). Generally, species thrive in a limited range of environmental conditions, which tends to adjust according to the geographical range and species range follows this shift. Species distribution and abundance is under continuing stress due to climate change. This observation forces one to look again at the niche concept which portrays the function of species within a range of biotic and environmental interactions. The perspectives of niche concept vary substantially from the view-point of ecology and environmental physiology, though the niche concept is central to both. Environmental and physiological niche characteristics help explain a species response to altering environmental conditions. In ecology, the emphasis is given to biotic aspects of the niche, such as different types of species interactions (Pörtner et al., 2010).

For improvement of stock assessments, description of critical fish habitat, prediction of rates of post-release mortality, development of useful bycatch decrease strategies, and projection of the population effects of global temperature-rise and ocean acidification, there is a dire need for a mechanistic understanding of physiological capabilities and tolerances at population and species level. (Horodysky et al., 2015). A fish's obvious reactions to environmental change are channelled by its ability to build an eloquent stress response by initiating physiological systems via energy utilization towards defensive mechanisms and behavioral changes in order to cope with threat from its immediate environment. Mechanisms responsible for these responses involve two neuroendocrine pathways: 1) the hypothalamic-pituitary-interrenal (HPI) axis, and 2) the brain–sympathetic–chromaffin cell (BSC) axis. The latter axis plays a role in the synthesis and secretion of cortisol and catecholamines, respectively (Wendelaar Bonga, 1997). The ability of fishes to deal with environmental deviations is the crucial parameter of their fitness and depends on their stress physiology. The slow but constant rise and climate change scenarios has been impending penalties on stress physiology. The ability of fish to deal with environmental deviation is the crucial parameter of their fitness and is dependent on their stress physiology. Stress physiology has been threatened by the steady but constant rise in temperature and climate change scenarios. Fish, being ectotherms, are supposed to be vulnerable to global warming. Keeping in view the effects of climate change, where cyclic water temperatures and thermal deviations and extremes become more frequent, a deep understanding of the stress physiology controlled by temperature is crucial to forecasting the impacts of global warming on fish populations (Vasseur et al., 2014). However, scant information is available about the effects of global warming on the two main stress axes, the HPI and BSC, in the wild populations. Fish are an important model for studying translational science in order to understand how organisms function in the face of natural stressors and also provide knowledge on basic life-control mechanisms via biochemical, physiological, and developmental processes (Riesch et al., 2015).

The physicochemical stressors bestow physical, chemical, or physiological effects that affect biological processes at each level of the organization. These interactions act as effective sources of selection determining evolutionary aspects of populations and modulators of ecological processes (Nevo, 2011; Steinberg, 2012). Eventually, they pose exceptional avenues to unravel organismal biological questions about: the mechanisms connecting fitness to genomic variations (Barrett and Hoekstra, 2011); diversity as a network of ecological and evolutionary processes (Nosil, 2012); reasons concerned with the reoccurrence and prediction of evolutionary changes (Riesch et al., 2016); ecological dynamics influenced by evolutionary change (Schoener, 2011); and in conclusion, factors restraining shape, size and pattern of an organism's fundamental distribution (Sexton et al., 2009). A mechanistic niche model must envision the aspects of the physical environmental interactions with the functional traits of the organism influencing fitness (Kearney et al., 2010). Species coexisting in the same ecosystem occupying different niches invoke differential responses, which, in turn, outline the species interactions and affect the dimensions of each species' niche (Pörtner et al., 2010).

The description of ‘environment’ includes a reference to a particular organism. The experience of an organism in its ‘environment’ is an outcome of the interactions between the distinctiveness of the organism and the habitat in which it thrives. This invokes the idea that two different organisms residing in the same habitat may experience two different ‘environments’. Organisms can alter or transform their environments through physiological, behavioral, and morphological processes. The understanding of the ways an organism chooses to interact, and the types of environment it experiences within a habitat, which, in turn, affects fitness in terms of growth, survival, and reproduction, is necessary to predict a niche mechanistically (Kearney, 2006).

Physiological and adaptive responses are displayed by fish to deal with the changeable environments they dwell in. We put forward physiological acclimation to environmental stress and further predictive analysis using biomarkers in response to environmental stress. The objective of this study is to find the correlates between organisms and habitat components, to find out whether they can potentially be predicted through modelling an organism's physiological niche. This mechanistic understanding of physiological niche would be critical under new conditions such as species invasion or climate change. Our first goal is to provide a snapshot of significant findings and generalizations concerning the function of abiotic factors in modifying fish stress physiology with the alteration of habitat. The questions we have considered for this study are- 1. Whether effect of heavy metals and other water quality parameters, as part of their immediate environment, have similar effects on different fish species (acclimation or adaptation). 2. Whether heavy metal stress affects brain functioning and it ultimately results in steroid production or not. 3. Whether we can predict the major factors causing severe stress resulting maximum damage to reproductive physiology.

2. Materials and methods

2.1. Study site, sampling and hydrological data

Four sites were chosen for this study namely, Taki (Site 1; 22.62 N, 88.95E), Haroa (Site 2; 22.6N, 88.67E), Malancha (Site 3; 22.51N, 88.77E) and Dhamakhali (Site 4; 22.36N, 88.86E) (Fig. 1a). Site 1 and Site 2 mainly receive effluents from rural domestic sewage. No notable industry is located in and around the study sites. Site 3 and site 4 are surrounded by numerous industries, which were located on both sides of Vidyadhari River. Industrial wastes, agricultural manures, and domestic sewage are directly dumped in the river channels, either with fractional treatment or without any pretreatment at all. Consequently, xenobiotic pollutants, including a high concentration of metals, were detected at increasing levels in this riverine water. The region experiences hot summer (March–June), monsoon (July–October), and winter seasons (November–February). This river deposits sand-dominated sediments in its active channel and flood plain areas during the declining phase of the post-monsoon, which frequently affects agricultural practices, local vegetation, and residential life strategies. The sampling covered a total stretch of about 90 km. At each sampling site, prior to netting, hydrological parameters (water temperature, pH, total dissolved CO_2 and DO, hardness, salinity, organic carbon, unionised ammonia) were recorded following standard procedure by APHA (2005). The sampling was performed with a gill net of 20 m length, with 1 cm spacing between adjacent knots. Hand nets were also used occasionally for sampling. Nettings were performed twice per month at each site, i.e. twenty four nettings per year at each site for three consecutive years (2016–2018). All the three sites were surveyed simultaneously and for the same duration to minimize possible sampling errors.

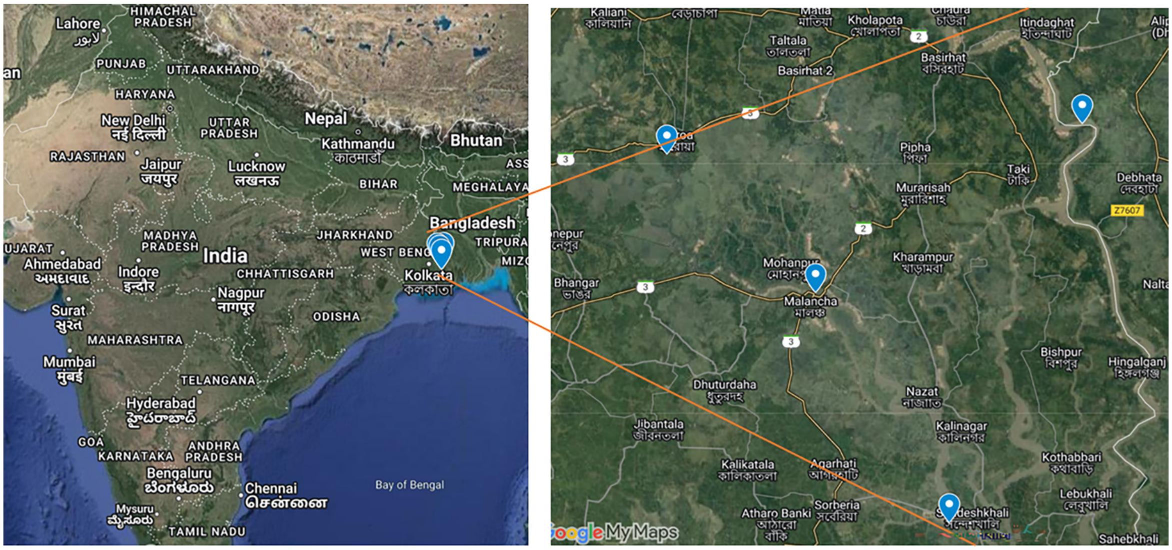

Fig. 1a. Study sites.

2.2. Design of work

Organism faces the critical challenge of to decide optimal mating time, in order to maximize reproductive success. The factors that regulate the timing of mating can broadly be categorized into two groups, "chronological" and "continuous". Chronological factors encourage reproduction in a specific and constrained time frame, while continuous factors may affect reproduction at any time of the season. Chronological factors are sex hormone production, sexual maturation and environmental influences like seasonal cues. Among the continuous factors that organisms face, are searching for food and escaping predators. Negative outcomes of either of these two factors may harm the reproductive process (Fig. 1b).

Various environmental cues and anthropogenic activities influence the aquatic ecosystem. Abnormalities in anthropogenic and/or climatic factors alter the biochemical quality of the aquatic system. Such abnormalities may cause brain dysfunction that ultimately affects the neuroendocrine system. Brain dysfunction also impacts the augmentation of stress factors. Pro-oxidant and antioxidant balance is disrupted, which may compromise the neuro-endocrine control of reproduction. In light of these information, the current study was undertaken in four different study sites (two non-polluted and two polluted) to enumerate the consequences of heavy metal pollution and abiotic factor fluctuation on brain activity. This study also aims to illuminate how brain dysfunction affects antioxidant balance and sex steroid production. We also considered whether sex steroid and stress steroid imbalance could influence habitat preference and niche separation in fish.

2.3. Selection of fish model

There were few cyclones which include Aila in 2009, Bulbul in 2019, Fani in 2019, Aamphan in 2020, Yaas in 2021 had taken toll on the Sundarbans mangroves in last decade. This kind of natural calamities causing mixing of fresh water with brackish water and brackish water with marine water are the main grounds behind the declining trend of some indigenous fish species of Sundarbans mangrove area. These natural disasters induce instability in aquatic environment resulting in fluctuations in salinity and some other physical factors of the water bodies (organic carbon, dissolved oxygen, alkalinity). Such conditions in habitat impart critical effect on the growth, reproduction and survival of aquatic organisms specially fish (Mukherjee et al., 2017). Among those fish we had selected seven stenohaline species that have been countenancing with such problems in different ways but still remaining under threat of reduction. *Parambassis ranga*, inhabits in shallow or middle layer of water column with low water flow and consumes mucus from large fish's scale, insect

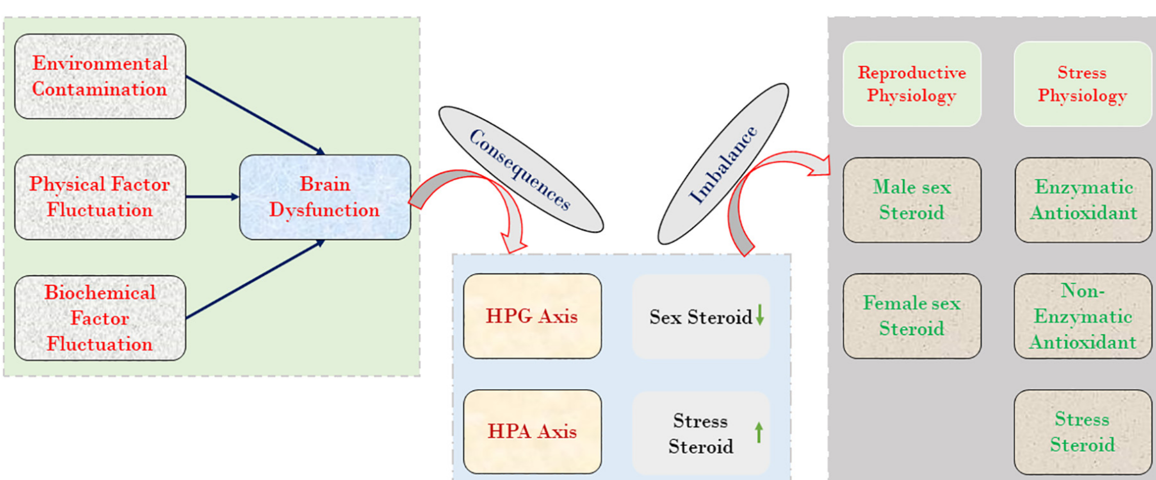

Fig. 1b. Design of work defining the basic pathways and parameters controlling the brain-reproduction pathway with stress physiology; HPG = hypothalamo-pituitary-gonadal axis, HPA = Hypothalamo-pituitary-adrenal axis.

larvae, tubifex and zooplanktons. *Badis badis* favours turbid waters with low water flow and growths of submersed vegetation. *Badis*, micropredators, feeds on small aquatic crustaceans, worms, insect larvae and other zooplankton. *Aplocheilus lineatus* is a benthopelagic, non-migratory, freshwater and brackish water fish. It can tolerate medium range of salinity stress. *Ompok bimaculatus*, dwells in ground level of water, paddy field and highly carnivorous. It preys upon small fish, crab larva, small mollusc, and shrimp. *Mystus gulio* lives in mid water with low water flow and is a benthic and detritus feeder. The population is known to be decreasing in recent years due to catching, pet trading and habitat destruction. *Notopterus chitala*, a near threatened species, lives in mid or deep water. It is carnivorous and primarily feeds on small fish, fish larvae and crustacean. *Esomus danrica*, is freshwater fish. *Esomus* is surface plankton feeder and omnivorous.

2.4. Collection of tissue samples

Adult fish of all the selected species were collected from all the four sites. All the fish were anesthetized using phenoxy-ethanol (1: 20000, v/v) immediately after the collection. Fish were sacrificed 30 min after their capture. Brain tissues of each fish was collected and stored in ice cold phosphate buffer. Tissues was homogenized and sonicated at 4 °C in a homogenizing buffer (50 mM Tris-HCl buffer, pH 7.4), for preparation of 15 % tissue homogenate. Blood was collected from caudal vein. Centrifugation was done at 5000*g* for 10 min and the serum was collected. All the samples were stored at −80 °C for biochemical analysis (Mukherjee et al., 2017).

2.5. Measurement of enzymatic as well as non-enzymatic antioxidants in the hepatic tissue

Tissue homogenates were centrifuged at 10000*g* for 15 min at 4 °C. Supernatant was collected and used to calculate the levels of different enzymatic [superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GRd), glutathione peroxidise (GPx), glutathione S-transferase (GST)] and non-enzymatic antioxidants [malondialdehyde (MDA) glutathione (GSH)], following standard protocol (Moniruzzaman et al., 2016). Protein concentrations in all the samples were determined following standard Bradford's procedure.

2.6. Analysis of heavy metals

The quantity of heavy metals [copper (Cu), lead (Pb), cadmium (Cd) and zinc (Zn)] in the water samples of each site were measured following standard protocol (APHA 1998). Water samples were collected and stored in the glass bottles. Stored samples were further acidized using 5 ml/l concentrated HNO_3. 100 ml of these acidized samples were taken and mixed with 5 ml of Concentrated HCl. The mixture was then heated for about 15 min in fume bath. After that the mixture was cooled in room temperature and filtered. Filtrates were digested by a mixture of concentrated HNO_3-$HClO_4$ and filtered again. Metal concentration was evaluated by using atomic absorption spectrophotometry (AAS) (Das et al., 2018).

All standards used were NIST Traceable Certified Reference Material. R^2 value for Calibration curve is >0.995. Cadmium standard solution (Product No. 1.19777: traceable to SRM from NIST $Cd(NO_3)_2$ in HNO_3 0.5 mol/l 1000 mg/l Cd), Copper standard solution (Product No. 1.19786: traceable to SRM from NIST $Cu(NO_3)_2$ in HNO_3 0.5 mol/l 1000 mg/l Cu), Lead standard solution (Product No. 1.19776: traceable to SRM from NIST $Pb(NO_3)_2$ in HNO_3 0.5 mol/l 1000 mg/l Pb), Zinc standard solution (Product No. 1.19806: traceable to SRM from NIST $Zn(NO_3)_2$ in HNO_3 0.5 mol/l 1000 mg/l Zn) were used as standards.

2.7. Statistical analysis

To determine whether the response of a fish species varied across sites, nonmetric multidimensional scaling (NMDS) of the physiological parameters and environmental parameters, taken from all four sites, was performed. Bartlett's test and Levene's test were applied to determine the equality of variance among the sites. Both robust Brown-Forsythe Levene-type procedures using group medians and robust Levene-type procedures using group means were used. Tukey's honest significant difference method was utilized to test the pairwise difference between the means of sites along the NMDS axes. The functions bartlett.test, levene.test and TukeyHSD were used which are available in R Software for Statistical Computation (R Core Team, 2020).

2.8. Selection of significant predictors: Bayesian Model Averaging

To check whether we can predict the major factors causing severe stress resulting in maximum damage to reproductive physiology, a multiple linear regression setup was considered. This setup identified key parameters that may act as indicators of stress. Water quality parameters and heavy metal concentration parameters were used as explanatory variables.

To optimize the uncertainty related to the selection of the most suitable model, Bayesian Model Averaging (BMA) was used. BMA incorporates a probability distribution on the set of models (called model space) and provides inference about the unknown quantity of interest by giving prediction as a weighted average of the estimates from each equation from the model space. A model's weight is equal to the posterior probability that it is correct, given that one of the models considered is correct (Raftery et al., 2005).

Given a model space M constituting all possible models S_i and the data D, probability of predicting the future outcome, Δ is done via the following equation (Raftery, 1996):

$$P(\Delta|D) = \Sigma_{i=1}^{I} P(\Delta|S_i, D) P(S_i|D), \quad (1)$$

where $P(\Delta|S_i, D)$ is the prediction of Δ according to model S_i and data D used to parametrize the model and $P(S_i|D)$ is the posterior probability of the model S_i in M. I is the dimension of the model space. The posterior model probability of S_i is given by:

$$P(S_i|D) = \frac{P(D|S_i) \times P(S_i)}{\sum_{j=1}^{I} P(D|S_j) \times P(S_j)}$$

where $P(D|S_i)$ is the integrated likelihood of the model S_i obtained by integrating over the unknown parameters as follows: $P(D|S_i) = \int_\theta P(D|\theta_i, S_i) \times P(\theta_i|S_i) d\theta_i$ where θ_i is the parameter of the model S_i and $P(D|\theta_i, S_i)$ is the likelihood for θ_i (possibly vector valued) under model S_i. Prior model probabilities $P(S_i)$ are taken to be equal. The integrated likelihood $P(D|S_i)$ is a high dimensional integral calculated using BIC approximation: $2 \log P(D|S_i) \approx 2 \log P(D|\widehat{\theta}_i) - d_i \log n = -\text{BIC}_i$, where $d_i = \dim(\theta_i)$ is the number of independent parameters in S_i and $\widehat{\theta}_i$ is the maximum likelihood estimate (equal to the ordinary least squares estimator for linear regression coefficients). The BIC approximation for determining posterior model probabilities is accurate when sample sizes are large enough (Kass and Raftery, 1995) and its use has been justified by several authors (Volinsky and Raftery, 2000).

In our problem, for each regression parameter say β_1 of a predictor variable (an attribute of the water condition, for example, salinity or hardness or even the intercept), we can replace $\Delta = \beta_1$ in Eq. (1). The BMA posterior mean of β_1 is the weighted average of the posterior means of β_1 under each of the models, that is, $E(\beta_1|D) = \sum_i \widehat{\beta}_1^{(i)} P(S_i|D)$. The estimate is essentially a model-averaged Bayesian point estimate, averaged over $\widehat{\beta}_1^{(i)}$'s, posterior mean of β_1 under model S_i. The function *bicreg* from the *BMA* package in R was used for variable selection and the integrated likelihood was approximated by the BIC. The sum over all the models was approximated by finding the best models using the fast leaps and bounds algorithm (Furnival and Wilson, 1974). Finally, variables with coefficients having posterior probability that the variable is in the model >0.55 were the ones affecting the response variable and for the final prediction 5 best models with highest

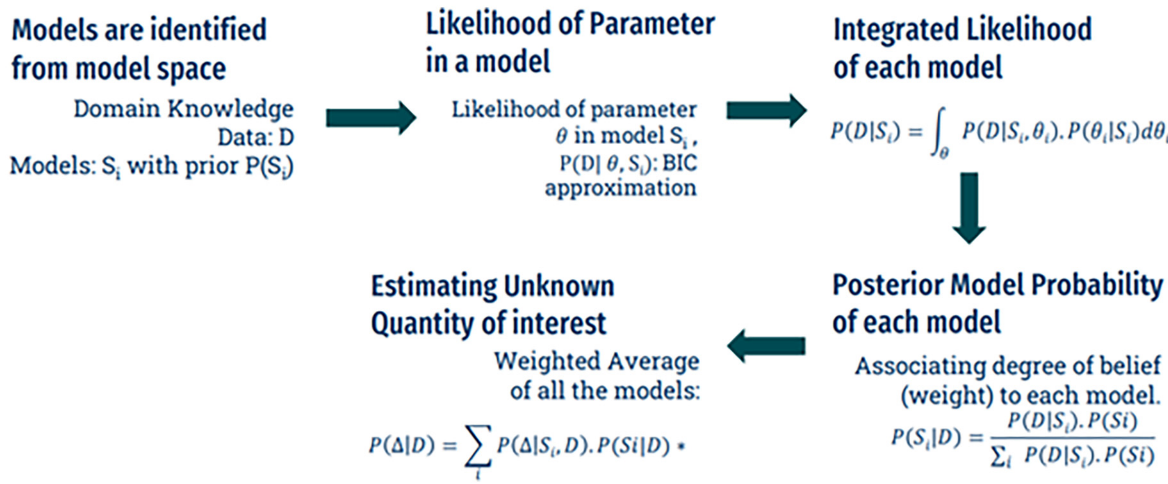

Fig. 1c. Working principle of Bayesian model averaging.

posterior model probabilities were selected. A pictorial summary of the working principles of BMA is given in Fig. 1c.

3. Results

From the exploratory analysis of water quality parameters from all the four sites, it is observed that sites 1 and 2 have a similar profile with respect to heavy metals e.g. cadmium, copper, lead, zinc. Sites 3 and 4 have a similar characteristic with more contamination of heavy metals. The scatterplot shows two distinct clusters. One corresponds to sites 1 and 2 and the other corresponds to sites 3 and 4. Similar cases arise with OC, pH, salinity, dissolved oxygen, and dissolved CO_2. The distribution of alkalinity, hardness and temperature of all the four sites is similar (Figs. 2a and 2b, Online supporting information – I & III).

For the species *Parambasis*, no significant difference was observed in the variance of the physiological parameters and environmental variables among sites along each of the first NMDS axes. However, Tukey's multiple comparison of means was statistically significant at the 0.05 level of significance along axis 1. In the ordination plot two distinct clusters of sites were observed; one cluster is composed of sites 1 and 2 and the second one is composed of the projections from sites 3 and 4 (Fig. 2a). This indicates that the species' response to environmental changes is different for two categories of water bodies.

Tukey's test confirmed that there is no significant difference between sites 1 and 2 along the first and second NMDS axis (p-value $\gg$ 0.05). A similar result is observed for sites 3 and 4 (Figs. 2a, 2b). This implies that in the defined space as ‘niche’ the environmental parameters are creating similar conditions for site 1 and site 2. In a same manner, site 3 and 4 are imposing similar conditions for the organisms living therein. A significant difference between the means of the two clusters was observed (*p*-value <0.00001). A similar physiological response as shown by *Parambasis* was noted for *Notopterus*, *Badis*, *Ompok* and *Aplocheilus (Online supporting material III)*. Hence, this group of five species has similar physiological niche and expected to respond similarly to the environmental changes which occurred either due to the heavy metal concentration or due to the variations of water quality parameters. *Mystus* and *Esomus* were found to respond in a similar way for MDA, testosterone, estradiol, cortisol and 11 KT, but different from the other five fishes. For *Mystus*, there was a significant difference in the variance of the physiological parameters among sites along the first NMDS axis at 0.05 level of significance (*Online supporting material III* Fig. 2b).

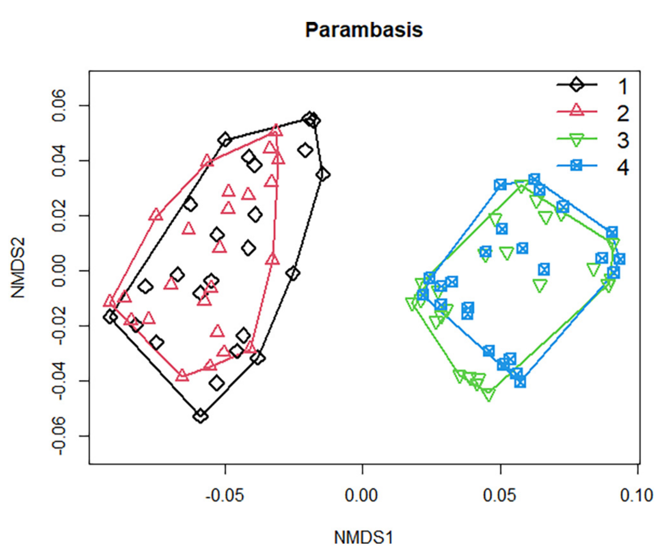

Fig. 2a. For the first NMDS axis, Bartlett's test for homogeneity of variance gives, K-squared = 1.3142, df = 3, *p*-value = 0.726 and for the second axis: K-squared = 4.8256, df = 3, *p*-value = 0.185. Similarly, Levene's test yields no significant difference along both first and second NMDS axes having *p*-values 0.689 and 0.05554, respectively.

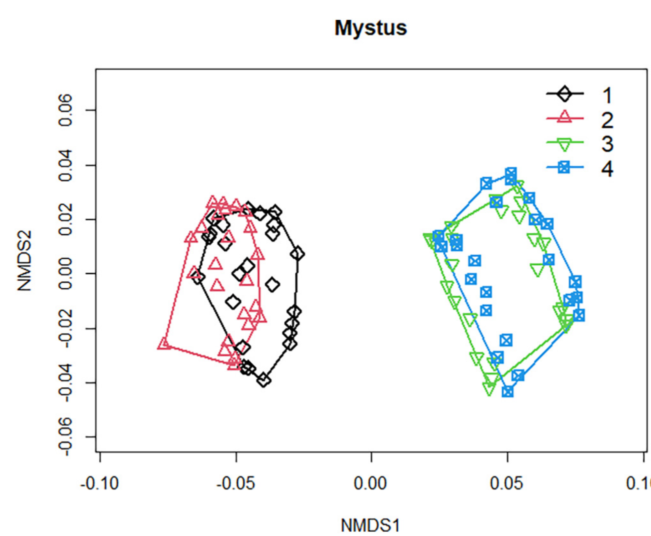

Fig. 2b. For the first NMDS axis, Bartlett's K-squared = 11.221, df = 3, *p*-value = 0.01059; Levene's test, p-value = 0.006502. Similarly, for the fish species Esomus, Bartlett's K-squared = 11.381, df = 3, p-value = 0.009836 and Levene's test, p-value = 0.009016 along the first NMDS axis.

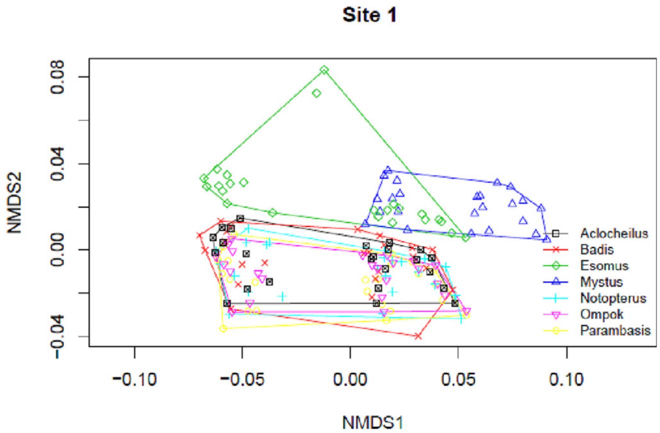

Fig. 3. For the first NMDS axis, Bartlett's K-squared = 4.5239, df = 6, p-value = 0.6062; Levene's test, p-value = 0.5744. For the second axis, Bartlett's K-squared = 11.532, df = 6, p-value = 0.0165; Levene's test, p-value = 0.6882.

To test whether the physiological response of different fish species occupying similar niche for different sites, nonmetric multidimensional scaling unconstrained ordination of physiological factors was carried out for each site and same statistical tests (as above) were utilized to group the species into clusters which had a similar physiological response. The ordination plot of the fishes in site 1 and site 2 clearly indicates that there is a large interesting region of the convex hulls in the NMDS space of the species *Aplocheilus*, *Badis*, *Notopterus*, *Ompok* and *Parambasis* (only site 1 is depicted in Fig. 3). Hence, in a stable environmental condition, these species have similar niche (Tukey's pairwise comparison test results p-value < 0.05).

Mystus and *Esomus* responded differently than the other five species which was confirmed by Tukey's pair wise comparison (p-*value* < *0.05*). It is interesting to note that the large intersecting region of the five species gets distorted in the ordination plot of physiological factors in site 3. *Aplocheilus, Parambassis* and *Ompok* form a cluster, whereas *Badis* and *Notoperus* forms a different cluster and the clusters' means are significantly different along the NMDS axis 2 (Tukey's pairwise comparison test, p-value < *0.05*). Hence, although they have a similar physiological niche, but under different environmental conditions they respond differently (Fig. 4). The same dynamics are also observed for the site 4. The convergence of the method is measured by the stress plot which indicates the performance of the ordination method as the function of the subspace dimension. For all the nonmetric MDS exercises which have been carried out in the manuscript, the stress values are found to be <0.2 when the number of NMDS axes is 2. Therefore, a two-dimensional representation is sufficient to determine the species differentiated physiological responses to different climatic conditions (Figs. 2a–4).

3.1. Results of BMA analysis

The BMA posterior density function of each regression coefficient was investigated. The density functions (shown in Fig. 5) are approximated by a finite mixture of normal densities and scaled so that the height of the density curve is equal to the posterior probability that the variable is in the model. Hence, variables whose curves are almost centered about 0 have lower probability to be included in the model as compared to the variables whose curves are centered far away from 0 to be included in the model. The spike in the curve at 0 shows the probability that the variable is not in the model.

As we further look into the responses of all the seven species with all the physiological or biochemical variables along with the environmental factors and heavy metals to find out the role of each independent variable to determine their impact on the biomarkers, we found some interesting insights. For *Parambasis*, the impact of the water quality parameters on AchE, was performed using BMA (Fig. 5). In the best 5 linear regression models (with the highest posterior probabilities), Temperature, pH, OC (Oxygenated Carbon), Cadmium and Zinc gave non-zero coefficients in almost all the models. This indicated their presence in the final model and significant effect on the AchE level of *Parambasis* (Fig. 6). A visual summary of the BMA output was obtained by the *imageplot.bma* function (Fig. 6). Carrying an analysis in the similar manner with the same set of predictor variables the following variables are identified to be the ones having higher probabilities of affecting the levels of AchE, Cortisol, Testosterone and Estradiol in *Parambasis*: (Cortisol - pH, DO, Copper; Testosterone – Temperature; Estradiol- Temp, pH, DO, Hardness, Salinity). The list of important predictors for other species are given in Table 1.

BMA has been performed for all the fish species; imageplots are given in the supplementary material (Supplementary Online information II). A similar BMA analysis has been done for understanding which predictor variables from the set of the same ones considered before affect the levels of AchE, Cortisol and Testosterone, Estradiol in the other species. AchE, Cortisol, Testosterone and Estradiol are the signature response variables to take

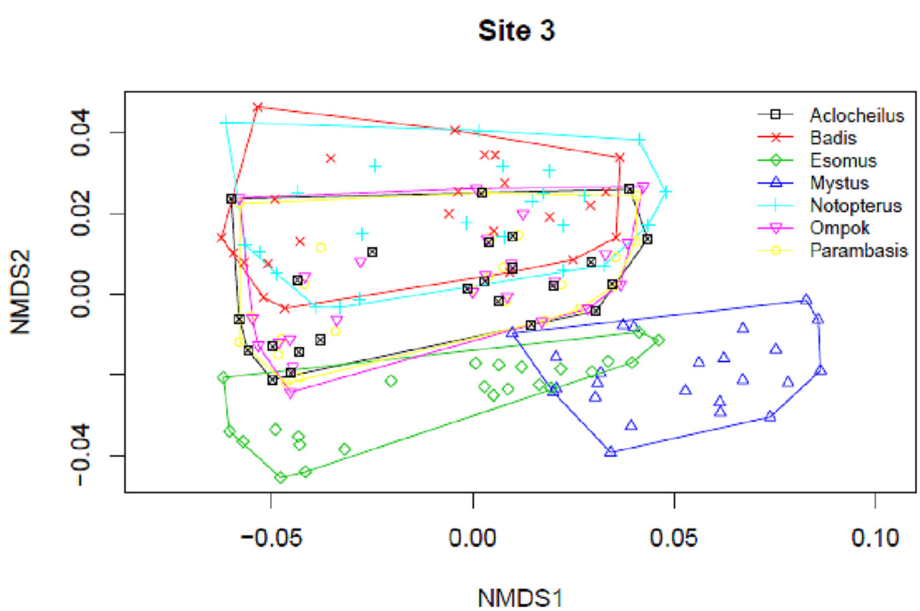

Fig. 4. For the first NMDS axis, Bartlett's K-squared = 5.2506, df = 6, p-value = 0.5121; Levene's test, p-value = 0.533. For the second axis, Bartlett's K-squared = 6.2749, df = 6, p-value = 0.3931; Levene's test, p-value = 0.409.

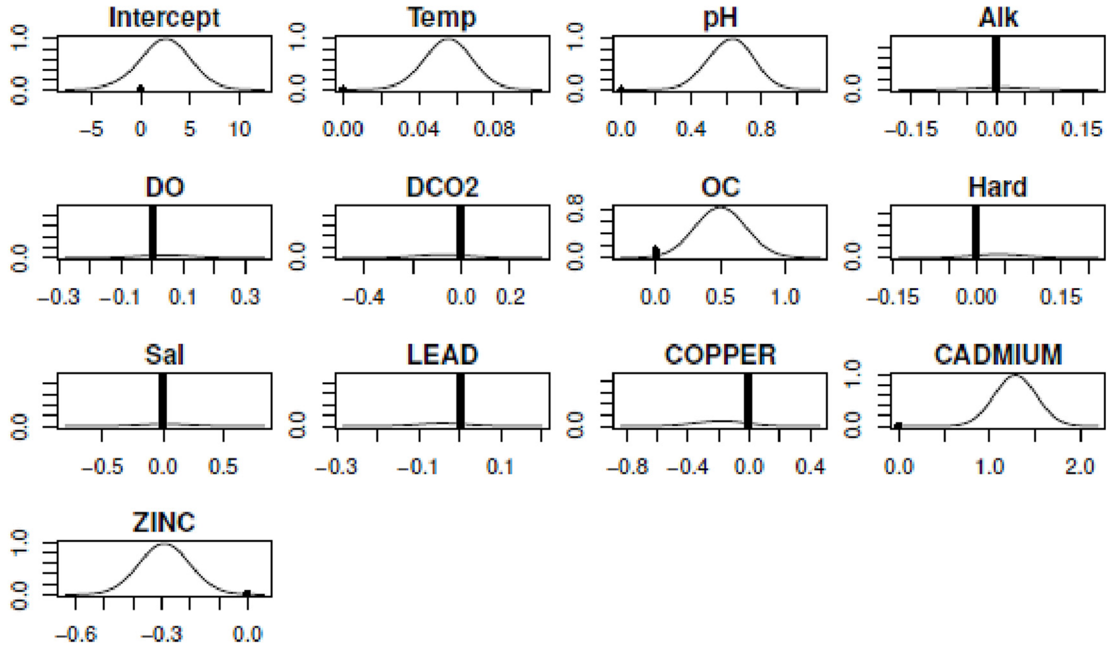

Fig. 5. BMA posterior distribution of all the coefficients for the attributes of water for predicting the AchE level in Parambasis. Let us consider the BMA posterior distribution of the coefficient of the predictor variable “Copper”. From the complete summary of the best five linear regression models, we observed that the posterior probability that the variable is in the model is 0.094. Hence the height of the spike at 0 (the probability that the variable is not in the model) is 0.906 (1–0.094) which is high. So, the variable “Copper” has high chance of getting not included in the model. It is also supported by the fact that the posterior density of the variable “Copper” is centred about zero. Similar inference can be carried out for each of the coefficients of the predictor variables.

note on the neurological, stress and reproductive axes of fish. The findings are provided in the table below:

4. Discussion

4.1. Effect of heavy metals and other water quality parameters on physiology

The current study makes it obvious that temperature, pH and dissolved oxygen are the key factors among all the physical variables to regulate stress response (Table 1). A combination of stress factors and sex steroids could influence the reproductive output and distribution pattern of fish species in a particular habitat. Spatial heterogeneity within a habitat due to the influence of environmental factors and nutrient can control the assemblage structure which induces the selection of life history pattern of fish (Moniruzzaman et al., 2021). Fish would prefer habitat where they are able to maintain a stable environment and suitable conditions. Outcome of the current study bases the Shelford's Law of Tolerance (1912) that describes that the growth and distribution of an individual, is limited by abundance and scarcity of environmental factors (as evident from Fig. 4).

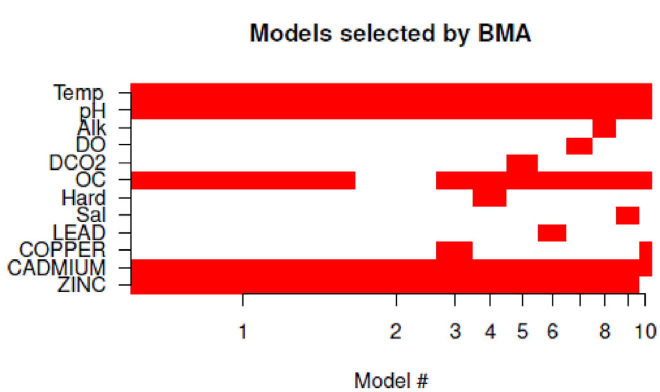

Fig. 6. Image plot indicating the presence or absence of a predictor variable in a model for determining the AchE level in Parambasis. Each row corresponds to a predictor variable and each column corresponds to a model. The corresponding rectangle is red if the variable is in the model and white otherwise. The width of the column is proportional to the model's posterior probability. It can be easily observed that variables: Temp, pH, Cadmium and Zinc are present in all 10 models while Alk (Alkalinity), Hard (Hardness), etc. are not. The OC (oxygenated-carbon) variable appears in all the models except the second model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
List of significant predictors obtained using the BMA.

Fish species	Response	Important variables affecting response
Parambasis sp	AchE	Temp, pH, OC, Cadmium, Zinc
	Cortisol	pH, DO, Copper
	Testosterone	Temp
	Estradiol	Temp, pH, DO, Hardness, Salinity
Mystus sp	AchE	Temp, pH, OC, Cadmium, Zinc
	Cortisol	Lead
	Testosterone	Temp, pH, DCO_2, Hard
	Estradiol	Temp, Alkalinity, DCO_2, Hardness, Salinity
Notopterus sp	AchE	Temp, pH, DCO_2, Sal, Cadmium, Zinc
	Cortisol	pH, DCO_2, Lead, Cadmium
	Testosterone	Temp, pH, DO, Sal
	Estradiol	Temp, DO, Hardness
Badis sp	AchE	Temp, pH, OC, Cadmium, Zinc
	Cortisol	pH, DO, Lead, Cadmium
	Testosterone	Temp
	Estradiol	Temp, DCO_2, Copper
Esomus sp	AchE	Temp, pH, OC, Cadmium, Zinc
	Cortisol	Temp
	Testosterone	Temp, pH, DCO2, OC, Hard
	Estradiol	Temp, Alkalinity, DCO2, OC, Hardness, Salinity
Ompok sp	AchE	Temp, pH, OC, Cadmium, Zinc
	Cortisol	pH, DO, Copper
	Testosterone	Temp, OC
	Estradiol	Temp, pH, DO, Hardness, Salinity
Aclocheilus sp	AchE	Temp, pH, OC, Cadmium, Zinc
	Cortisol	pH, DCO2, Copper
	Testosterone	Temp, OC
	Estradiol	Temp, pH, DO, Hardness, Salinity

Interaction between biochemical factors within the organism and its environmental landscape kindles and spurs its adaptive response and ultimate expansion. The fitness of an organism is determined by how effectively its central organ, the brain, responds to environmental influences.

Present study aims to visualize the adaptive response of different fish population under fluctuating environmental conditions using previously established biomarkers (Mukherjee et al., 2017; Mukherjee et al., 2020; Moniruzzaman et al., 2016). Stress affects tissue metabolism and initiates the production of free radicals. The SOD-CAT system constitutes the preliminary defense machinery against free radical induced damage. Our results indicated that temperature, pH, and salinity are the key environmental factors that affect the levels of both SOD and CAT. Metals that affect this system are zinc for SOD and copper for CAT (Table 1). Fluctuations in temperature may produce high physiological demands that could reduce the oxygen saturation levels of the system. Thus, the combination of increased metabolic demand and decreased oxygen availability can be a limiting factor for species survival (Morgan et al., 2006). Temperature affects the community composition of aquatic fauna and limits the niche range of particular species (Grossman and Ratajczak, 1998; Matthews and Berg, 1997). Temperature is also an important factor that has the potential to govern ecophysiological changes in fish as evident from our study (Table 1). A pH values above 9 and below 5 can cause severe osmotic damage to fish (Mukherjee et al., 2020). A simultaneous alteration of temperature and pH disrupts fish osmotic balance and creates oxidative stress that eventually affects the SOD-CAT system. Glutathione (GSH) together with its enzyme complexes (GPx, GST and GRd) constitutes an imperative line of defense against oxidative stress. This study confirms that temperature, pH, salinity, copper and zinc could manipulate the different variables of the glutathione system. GSH imbalance indicates accumulation of free radicals in the tissue. Increase in lipid peroxidation and MDA production indicate oxidative stress (Zheng et al., 2016; Moniruzzaman et al., 2016). DCO_2, OC and salinity are the major environmental factors that could regulate lipid peroxidation, as found in the present study. AChE and MAO regulate specific neurotransmitter and control neuronal activity of the central nervous system (Basha et al., 2012). NO acts as a neurotransmitter and is a major constituent of the signal transduction pathway in the brain (Garry et al., 2015). In the present study, AChE, MAO, and NO are noted to be altered with 'environment'. Temperature and dissolved CO_2 was earlier documented to have a high impact on brain function through its interference with neurotransmitter activity (Montgomery and Macdonald, 1990). Our study shows that AchE in all the selected fish species is influenced by temperature (see Table 1). Our result also confirms that Zn and Cd are the key elements responsible for disruption of neurological functions by affecting AChE level. Although cadmium is not accumulated in significant quantities in the brain cells, it could hamper the metabolism of copper. Cadmium decreases calcium incursion and hampers the release of specific neurotransmitter (Wang and Du, 2013). Cadmium also has a direct effect on the central nervous system which leads to alteration of brain enzymes. Sites 3 and 4 are more contaminated compared to the other sites (Online supplementary Information I). An excess of metals in a freshwater ecosystem induces decrease in pH, making the metals more soluble and mobile. Metal accumulation in fish bodies destroys the homeostatic balance by producing an excess amount of superoxide radicals, which, in turn, leads to increase in oxidative stress.

4.2. Major factors causing severe stress resulting maximum damage to reproductive physiology

Different fish species have different tolerance levels to toxic or environmental stress, as evident from our study (Fig. 6, Online Supporting Information - II). This implies that for a combination of stressors, severity of damage varies depending on the species. Fluctuation in physical factors, therefore, affects the timing and amplitude of different components of the reproductive endocrine axis. As we can observe through our analyses that the testosterone and estradiols levels of different species inhabiting in the separate habitats are not same. More specifically, modulation of male (testosterone) and female (17β-estradiol) sex steroids may delay or shift the maturation process and reproduction (Juntti and Fernald, 2016). However, some species even respond by exhibiting complete inhibition of reproduction (Schreck et al., 2001). Different strategies for coping with stress often significantly affect reproductive fitness either in terms of gamete quality and/or fertilization rate. Neuroendocrine physiology associated with reproductive maturation and spawning appears firmly associated with stress. Environmental variables are ultimately imperative in optimizing the maturation process and reproductive timing. The physiological response to stressors is also quite flexible and plastic, both within and between species (Balasch and Tort, 2019). However, the crosstalk between sex steroids and stress steroids is the key factor in guiding the reproductive output of the aquatic organisms. Current research is, therefore, very practical and indicative of the crosstalk between endocrine physiology and reproductive fitness under a longer period of stress in the aquatic systems that directs different species for acclimation and further adaptation in different habitats. Thus, it can be hypothesized that the acclimation process and reproductive fitness responses to chronic stress are species-specific and habitat dependent (Figures in Online Supplementary Information III).

The optimal adaptive strategy of organisms is determined by environmental fluctuation and ecosystem health. A polluted and detrimental environment (Site 3 and Site 4) fluctuates between discrete states. The brain, the neuroendocrine center, systematizes an organism to phenotypic plasticity if its environment is out of balance during any of the stages of development. In a stable environment (here, Sites 1 and 2), an individual encounters homogeneous abiotic factors, resulting in a lower total energy requirement during the acclimation process and, as a result, improved reproductive performance and fitness. The importance of plasticity and adaptation will be determined first by the relationship between life strategy and the rate of environmental change, and then by the rate of physiological, reproductive and behavioral changes in comparison to the rate of environmental fluctuations. Species with rapid reproductive maturity and shorter life spans may experience minimal environmental vacillation. *Mystus* sp. and *Esomus* sp. are currently observed to have an improved adaptive strategy under toxic and environmental stress, which will aid the organisms in expanding phenotypic plasticity to acclimate to the extreme environment.

4.3. Bridging the gap between ecological and physiological niche

The study of ecophysiology deals with the environmental signals that affect an organism's functional traits, which show a fundamental role in the adaptation to the constantly shifting 'environment' and control the distribution and responses of the organisms in their natural habitat (Sánchez-Moreiras and Reigosa, 2018). Phenotypic plasticity can be described as the capability of an organism with a particular genotype to alter its phenotype as a function of its environment. Based on different situations, an individual, population or species is free to choose among the various behaviours that can have substantial ecological and evolutionary implications (Bhat et al., 2015). Among the three types of phenotypic plasticity, namely, reversible, developmental, and transgenerational (Angilletta, 2009; Donelson et al., 2018); reversible plasticity, which is also labeled as "acclimatization" or "acclimation", indicates supple variations in physiological phenotypes as an outcome of environmental interactions in a varying time range of days to months, e.g., seasonal acclimatization in temperate fish (Schulte et al., 2011). In several species, behavioral dissimilarity is a significant strategy for coping with environmental variability (Bhat et al., 2015). Plasticity can act as the basis of local adaptation to various forms of stresses, e.g., decreasing sensitivity to thermal stress (Pörtner, 2002). This type of phenomenon of tolerance to environmental stress may have ecological and evolutionary consequences, regardless of whether it reveals plasticity or adaptation. Eventually, a clear, detailed knowledge using observed data on the intricate network of environmental and physiological interactions, as analyzed in this study brings forward information about the regulatory and ecophysiological events in the light of adaptation and/or plasticity.

The strength and magnitude of environmental and biotic interactions could influence the distribution of populations among different habitats

(Gilliam and Fraser, 1987; Rosenzweig, 1987; Morris, 1988). A reason for the habitat selection of aquatic organism is to get them into an optimum and profitable physical condition to ensure greater fitness per individual (Lefevre et al., 2017) by maximizing energy gain and minimizing extinction risk (Gilliam and Fraser, 1987). Furthermore, organisms undergoing physiological niche shifts as a result of changes in their interaction or habitat choice at various stages of their life cycle may alter the population itself as well as other populations (Ebenman and Persson, 1988). Eventually, interactions within and among populations with physiological niche shifts will influence the whole fish community. An abiotic and biotic interaction influences fish community structure directly (Kerfoot and Sih, 1987; Strauss, 1991). In present study, different environmental factors exert influence at different level of physiological interactions (Table 1).

Temperature and dissolved oxygen levels, temporal heterogeneity of the environment at different levels are important factors for fish reproductive physiology (Menge & Sutherland, 1996). Chemical toxins, such as heavy metals, contribute to the adaptive and reproductive fitness of fish. Being ectothermic organisms, fish are dependent on the surrounding temperature and oxygen level for physiological activity, which allows for mobility, growth, and reproduction. However, the total energy cost of survival increases with these two factors, which may ultimately lead to niche separation. According to the findings of the current study, greater variation in habitat preferences determines better profitability during niche separation.

The concept of the realized niche demonstrates the connection between environmental parameters and the existence and success of a species at the ecosystem level. The fluctuation of environmental factors within a species' habitat occurs between the species' tolerance windows. However, the ways in which the physiological characteristics of a species may relate to its realized niche have not been fully elaborated in this study. From a physiological point of view, the response of a measured trait across a combined set of biotic and abiotic variables would represent an approximation of the niche. (Pörtner et al., 2010). The threat of global climate change to biodiversity loss can be viewed from a niche conservation perspective. If the climatic tolerance of a species is not wide enough to encompass the new conditions or acclimatize to them (physiologically or behaviorally), species with strong climatic niche conservation must either migrate or go extinct, whereas more evolutionarily tolerant species can potentially adapt (Holt, 1990).

Although the univocal concept is that having greater variations in tolerance of stress should lower the chances of extinction risk due to impacts of global changes. There are no sufficient data on fishes to offer insights into specific mechanisms by which this may take place. Our study can be used as a generalized model to take steps for management aspects of species which are under environmental stress. The model can be modified according to species-specific and site-specific manner. Our model can indicate a panel of biomarkers which could be the player of organismal conservation needs. This study can contribute to the emerging field of conservation physiology by linking environmental changes with ecosystem approach via the application of physiological aspects to conserve species.

Overall, the authors of this study are far-off from understanding how the variation at the genetic level for stress tolerance among species can contribute to their relative vulnerability to reproductive success, and whether this occurs by any of the mechanisms proposed earlier. Improvements in technologies for rapid molecular markers of fishes, coupled with advances in sequencing, may provide access to testing the theories.

5. Conclusion

In the present study, it is evident that the adaptive mechanism of fish to environmental stress is achieved through modification of physiological mechanisms through a panel of biochemical markers. These markers organize a cascade of physiological event at various levels including reproduction. Simultaneously, different environmental factors exert variety of effects on these stress markers in a species-specific manner. If phenotypic plasticity can explain the stress tolerance variability at the intra-specific level, then the degree of adaptation modifies all the three components of the stress-brain-reproduction-axis among the closely related species in varying environments.

This study will introduce comparative systems informative to the variations taking place from ecological alterations, leading to adaptation, speciation, and evolution, as such. The current systems ecology study is unfolding the gateways to understanding the function of abiotic factors in inducing mechanistic physiological changes, which in turn drive species to substantiate their ecological niche, providing insight from species to ecosystem. The observables of this study are dimensions of the selected species' performances, ranging from niche selection to minute metabolic sketching. This endeavor simplifies the biochemical pairing with the species adapted to spatial and/or temporal states which is the central premise in natural environments, and this was revealed in detail using different statistical tools.

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CRediT authorship contribution statement

Mahammed Moniruzzaman: Conceptualization, Investigation, Formal analysis, Methodology, Writing - original draft, Funding acquisition. Urbi Dutta: Data curation and Methodology. Nimai Chandra Saha: Funding acquisition, Writing - review & editing. Amiya Ranjan Bhowmick: Conceptualization, Software, Formal analysis, Supervision, Writing - review & editing. Joyita Mukherjee: Conceptualization, Visualization, Project Writing - review & editing administration, Resources, Supervision, Writing - original draft.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors 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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