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From signals to states: biologger-based classification of seabass welfare states in sea-cages

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Abstract

Background Aquaculture has grown significantly in recent years, increasing the need for advanced monitoring techniques to ensure fish welfare and optimise management practices. Understanding how fish respond to environmental and anthropogenic factors is key for improving welfare standards, and biologgers capable of measuring heart rate (HR) and external acceleration (ACC) provide valuable insights into physiological and behavioural dynamics.

Results In this study, HR and ACC were recorded from adult European seabass implanted with biologgers and monitored in sea-cages for two 14-day periods in March and July. Feeding and routine cage maintenance occurred from Monday to Friday, whereas no aquaculture-related human activity took place during weekends. A Random Forest (RF) model was developed using labelled data from controlled stress-challenge experiments to classify four welfare states: resting, regular activity, reactive response, and proactive response. Standardized ACC was identified as the main predictor for proactive responses, whereas standardized HR contributed most strongly to resting and reactive states. Application of the model to sea-cage data revealed clear diel patterns: regular activity and resting predominated at night and early morning, while proactive responses increased from midday onwards and were closely related to feeding routines. Significant differences also emerged between weekdays and weekends, with stress-related states more frequent during weekdays and resting and regular activity dominating weekends, reflecting the influence of routine operations and human activity in the farming facilities. Seasonal patterns further revealed higher HR levels and a greater prevalence of proactive responses in July, likely driven by elevated water temperatures, increased anthropogenic pressure and enhanced behavioural alertness under summer conditions.

Conclusions Overall, the integration of biologgers with machine learning classification provides a robust framework for identifying welfare states in seabass reared in sea-cages, demonstrating how physiological, behavioural, and environmental data can be combined to inform management decisions, optimise operational protocols, and ultimately enhance welfare-oriented aquaculture practices.

Keywords Heart rate, Acceleration, Machine learning, Precision fish farming, Aquaculture

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Background

The rapid expansion of aquaculture has been accompanied by an increasing demand for sustainability and ethical production practices [1]. Consequently, the welfare of farmed fish has emerged as a key concern in modern aquaculture, reflecting both societal expectations and the industry's commitment to responsible growth. Ensuring good welfare standards is not only an ethical issue but also essential for maintaining productivity, product quality, and long-term system sustainability. Fish welfare can be defined as the state of an animal as it copes with the environment [2]. In aquaculture systems, it is shaped by a wide range of factors, including those from the farmed species (i.e., ethological and physiological factors) and those derived from the farming method (i.e., environmental conditions and human-induced challenges) [3]. Thus, understanding how fish respond to environmental fluctuations and anthropogenic influences is therefore critical for improving welfare standards and optimizing management strategies. Achieving this goal requires deploying advanced monitoring technologies that provide continuous, high-resolution assessments of welfare-related parameters across seasons and environmental conditions.

Precision Fish Farming (PFF) aims to apply control-engineering principles to aquaculture production, enhancing farmers' ability to monitor, control and document biological processes through the integration of emerging technologies and automation [4]. Traditionally, welfare assessments have relied heavily on manual visual observations and subjective interpretation of fish behaviour, which can limit the accuracy and frequency of welfare evaluations. PFF reframes this process as a continuous operational cycle which includes observing, interpreting, deciding and acting, where technology progressively replaces experience-based decisions with data-driven management [4, 5]. Technological advances, such as computer vision, sonar, and artificial intelligence, are increasingly being employed to automate behavioural and physiological monitoring, allowing for more objective and scalable welfare assessments [6]. Camera systems, echo sounders, and other sensor-based tools can quantify various behavioural and environmental parameters, including fish distribution, swimming activity, and environmental variables [4]. Recent advancements in biologging sensing technologies have further facilitated the continuous recording of physiological responses, such as heart rate, internal temperature, and activity levels. This development has established a direct correlation between environmental conditions and welfare indicators, thereby providing a novel framework for understanding the relationship between ecological factors and animal welfare [7–10]. One approach that is being increasingly applied in precision livestock farming is to monitor a number of sentinel animals using sensors, allowing for continuous monitoring and early detection of health or welfare issues [5, 11, 12]. These precision approaches represent a paradigm shift from traditional, observational farming practices toward automated, knowledge-based management systems. By integrating behavioural and physiological data, PFF contributes to early detection of welfare impairments, improved decision-making, and ultimately, enhanced sustainability and fish welfare in aquaculture operations [4, 11].

Stress responses in fish are key biological indicators of welfare status [13, 14]. These responses are typically divided into three sequential phases. The primary response involves the activation of neuroendocrine pathways, leading to the rapid release of catecholamines and cortisol into the bloodstream [15, 16]. Subsequently, the secondary response is characterized by a cascade of physiological adjustments, including increased cardiac activity, elevated oxygen consumption, and alterations in glucose and lactate metabolism [17, 18]. Prolonged activation of these mechanisms can ultimately lead to tertiary responses, reflected in changes in growth, immune function, reproductive performance, and behaviour alterations [14, 19, 20]. Behavioural manifestations of stress include altered swimming patterns, reduced feeding activity, and abnormal behaviours such as erratic movements or changes in body coloration [3, 14, 21]. Monitoring both physiological and behavioural responses has therefore been recognized as an effective strategy to assess stress, health, and welfare in fish [22, 23]. Among the available monitoring tools, biologgers equipped with sensors to measure fish cardiac activity and acceleration have emerged as particularly valuable devices for assessing the physiological status of fish under varying environmental and farming conditions [24].

Most previous research employing biologgers in fish has been conducted under controlled or laboratory conditions, where environmental factors can be carefully regulated. In aquaculture research, these devices have primarily been used to assess cardiac responses and acceleration during pre-slaughter and slaughter procedures [9, 10, 25], as well as during experimentally induced stress tests [7, 26–29]. Only a limited number of studies have applied biologging in sea-cage environments, and these have largely focused on salmonid species, such as Atlantic salmon (*Salmo salar*) [30–32] and rainbow trout (*Oncorrhynchus mykiss*) [33, 34]. Fish reared under commercial sea-cage conditions are continuously exposed to fluctuating environmental variables, such as temperature, oxygen availability, and hydrodynamic forces, as well as to routine farming operations and other anthropogenic factors that can markedly influence their welfare and behaviour [11, 31, 35]. Understanding the relationships between these external drivers and the physiological and behavioural responses of fish is essential for refining operational procedures, optimizing management practices, and promoting welfare in real farming conditions.

European seabass (*Dicentrarchus labrax*) is one of the most important farmed species in Mediterranean aquaculture [36]. Despite its relevance, no studies to date have assessed seabass welfare under sea-cage conditions using biologger-derived data. Hoyo-Alvarez et al. [37] conducted laboratory-based calibrations linking oxygen consumption, swimming activity and cardiac response by exposing seabass to controlled swimming and crowding challenges. Based on these experiments, the authors described four individual welfare states derived from heart rate and acceleration data: The *resting state* is defined as the voluntary reduction of locomotor activity accompanied by decreased responsiveness to external stimuli, typically associated with a downregulation of physiological and metabolic processes. The *regular activity* state is characterized by baseline locomotor and behavioural activity, reflecting maintenance behaviours under non-stressful conditions and stable physiological parameters. The *proactive response* state is defined as an active coping state, characterized by increased locomotor activity accompanied by activation of physiological stress pathways and elevated oxygen consumption. Finally, the *reactive response* state is characterized by pronounced activation of physiological stress responses and increased cardiac output, typically accompanied by reduced locomotor activity. Importantly, these welfare states should not be viewed as discrete categories but rather as points on a continuum, where intermediate states may occur that represent varying magnitudes and durations of behavioural and physiological responses.

Overall, the objective of the present study is to assess the cardiac responses and swimming activity of European seabass reared under sea-cage conditions using biologgers, and to characterize their welfare status based on the four previously defined individual welfare states, thereby extending previous laboratory findings to an experimental sea-cage setting. Using data from surgically implantable biologgers and applying machine learning models, this study aims to classify observations into these welfare states and evaluate their distribution in fish exposed to environmental fluctuations and common operational challenges of commercial sea-cage environments.

Materials and methods

Model development and validation

Data acquisition and labelling

In order to classify observations into fish welfare states, a machine-learning model was developed prior to data collection, using data from surgically implanted biologgers in controlled experiments previously conducted by Hoyo-Alvarez et al. [37]. The laboratory-based experimental protocol included swimming tests conducted in Blažka-type swim tunnels, and crowding stress challenges (for further information about the experimental procedures see Hoyo-Alvarez et al. [37]. Biologgers (DST milli HRT-ACT, Star Oddi ®, Iceland) were surgically implanted to 12 adult seabass, and continuously recorded heart rate (HR) and average external acceleration (ACC) at 10-minute intervals. Fish were individually transferred from the housing tank to the swim tunnels, kept at rest for one hour and were then exposed to incremental flow speeds of 0.2, 0.4, 0.6, 0.8 and 1 $m.s^{-1}$ during one hour per speed continuously measuring oxygen consumption. Based on this, the resulting average optimal speed was U_{opt} = 0.74 $m.s^{-1}$ (see further details in [37]). The crowding stress challenge test was performed on all individuals together four days after completing the swimming stress challenge tests. The crowding stress test followed the protocol developed by Svendsen et al. (2021), which consisted of four steps: reducing the water level to a point at which the dorsal fin was exposed to air and then (1) refilling immediately; (2) refilling after 1 min.; (3) refilling after 5 min.; and (4) chasing the fish with a net during 5 min and then refilling. Biologgers monitored HR and ACC during the whole challenge and until four hours after the test finished, taking measurements every 10 min.

Observations were assigned to one of four welfare states based on fish physiological (HR) and behavioural (ACC) responses (for further details see [37]): (1) *Resting;* (2) *Regular activity*, (3) *Proactive response* or (4) *Reactive response.* The *resting state* is characterized by low swimming activity, heart rate and oxygen consumption, and was defined as values between 20 and 70 bpm and average ACC below 18 milli-g (mg), which mostly corresponded to nighttime observations (from 00 to 5 a.m.). The *regular activity state* involves moderate to elevated acceleration alongside low heart rate and low oxygen consumption and was defined as HR between 30 and 90 bpm and average ACC below 20 mg, corresponding to swimming speeds between 0.2 and 0.6 $m\ s^{-1}$ ($< U_{opt}$). The *reactive response state* is identified by low swimming activity and/or acceleration combined with elevated heart rate (e.g., a freezing response), and thresholds were set at HR values above 60 bpm and average ACC up to 15 mg which typically corresponded to the 270-minute post-crowding periods. Finally, the *proactive response state* corresponds to simultaneously elevated heart rate and high swimming activity, reflecting increased oxygen demand, and was defined by elevated HR (60 to 130 bpm) combined with average ACC values exceeding 15 mg and were represented at the four stress-induced peaks elicited by crowding challenge. Values falling outside the established ranges for each welfare state were excluded, as they were inconsistent with the remaining recordings for each individual.

The labelled dataset consisted of 734 observations, with a slightly imbalanced distribution: *resting and regular activity* each accounted for approximately 25%, *proactive response* 10% and *reactive response* 40%. Prior to modelling, HR and ACC were standardized within each individual using z-scores to account for interindividual physiological variability. Standardized variables are hereafter referred to as HR_{std} and ACC_{std}. Standardization followed the equation:

$$z_{ijk} = \frac{(x_{ijk} - \mu_{jk})}{\sigma_{jk}}$$

where x_{ijk} is the observed value for time *i* in individual *j* during experimental period *k*, and μ_{jk} and σ_{jk} represent the corresponding individual- and period-specific mean and standard deviation, respectively. Observations containing missing values were excluded prior to analysis, resulting in a clean dataset suitable for subsequent model training.

Model training and validation

All statistical procedures were conducted using R software (v 4.3.2) [38]. The labelled and standardized dataset was split into training (70%) and testing (30%) sets, maintaining proportional representation of each welfare state. A Random Forest (RF) classifier was implemented using HR_{std} and ACC_{std} as predictors. Hyperparameter optimization was conducted via a manual grid search of node size and class weights, while keeping *mtry* = 2 (corresponding to the total number of predictor variables), ensuring that both predictors were available for selection at every node split. Five-fold cross-validation was used to evaluate model performance. Twelve candidate models were trained, and the optimal model (v8) was selected based on the highest Kappa and accuracy values, corresponding to node size = 5 and class weights 1.5 for *proactive and reactive responses* and for *regular activity*, while the *resting state* class was weighted at 0.9 to compensate for the imbalanced class distribution.

Model training and prediction were implemented using the *randomForest* package [39], and model performance was evaluated on the independent testing dataset. Confusion matrices and associated statistics (including accuracy, sensitivity, specificity, positive predictive value, negative predictive value, and F1-scores) were computed using the *caret* package [40]. Variable importance metrics were calculated using both *randomForest* and *caret* packages. A normalized confusion matrix was generated using the *pheatmap* package [41] to facilitate comparison across welfare state classes. Receiver operating characteristic (ROC) curves and class-specific area under the curve (AUC) values were computed using the *pROC* package [42] to quantify discriminative performance across the four welfare states. Scatterplots of predicted welfare states and heatmaps of classification proportions were generated using *ggplot2* [43].

To further assess model stability under repeated resampling and to prevent overfitting, a 20-fold cross-validation procedure was performed using the *train()* function in *caret*, with random forest implemented via the "rf" method. This combination of classification metrics, visualization tools, ROC analysis, and cross-validation provided a comprehensive evaluation of model robustness and predictive reliability. The full workflow, including sequential steps of data collection, model training, validation, and application for welfare state prediction, is summarized in Fig. 1. All R code used for model

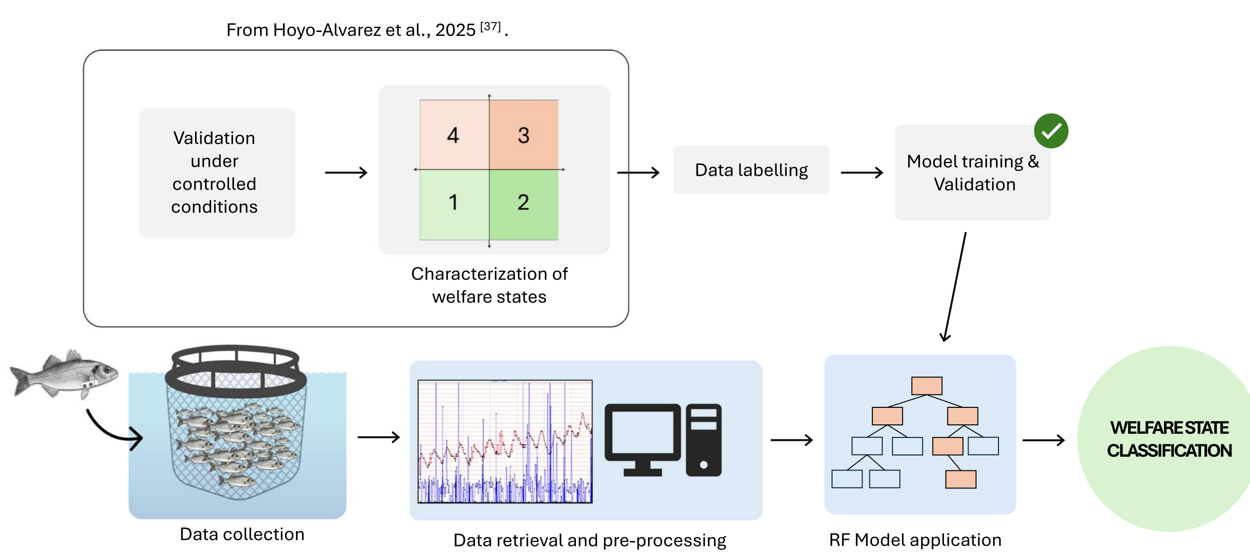

Fig. 1 Overview of the data analysis and model development pipeline, from controlled-condition data acquisition and annotation to model training and validation, followed by sea-cage data collection, processing, model application, and welfare-state classification

development, tuning, and validation is available at: https://github.com/ehoyoalvarez/RFbiologgers.

Model application: case study of seabass in sea-cages

Experimental design

The present study was conducted in open-sea cages located at the Laboratory of Marine research and Aquaculture facilities (LIMIA-IRFAP) in the coastal waters of Port d'Andratx, Balearic Islands, Spain. A total of 1000 adult European seabass (Weight = 1.00 ± 0.05 kg, Std. length = 37.4 ± 0.5 cm) were randomly distributed across four sea-cages, with 250 individuals per cage. Each net-pen replicated structures commonly used in commercial aquaculture, consisting of floating plastic rings, an anti-bird cover, and a cylindrical-conical net measuring 5.5 m in diameter and 7 m in depth. Fish were reared in the sea-cages from March to July 2023, while physiological and behavioural parameters were monitored during two experimental periods of 14 days each, conducted in March and July 2023. Fish were fed once per day from Monday to Friday, between 12:00 and 14:00 h, to apparent satiation. Routine maintenance and cleaning of the sea-cages were performed within the same time window. During weekends, the cages were left undisturbed, with no experiment-related anthropogenic activity, feeding or handling of the fish, nor experimental cages maintenance.

Biologger implantation

From each pen and for each experimental period, four individuals were surgically implanted with biologgers (DST milli HRT, Star-Oddi®, Iceland) (N_{total} = 32; Weight = 0.94 ± 0.04 kg, Std. length = 36.10 ± 0.5 cm) to continuously monitor heart rate, external acceleration, and internal temperature following surgical protocols described in Cabrera-Álvarez et al. [7] and Hoyo-Alvarez et al. [10]. The fish were initially anaesthetised by means of immersion in 0.6‰ 2-phenoxyethanol (Sigma-Aldrich®) for a period of 3–5 min, until a stage of deep anaesthesia was achieved [44]. Thereafter, the fish were positioned in a ventral-side up position on a V-shaped surgical table and maintained under anaesthesia using a 0.25‰ gill bath throughout the duration of the surgery. Prior to the start of the surgery, the ventral area of the fish was disinfected with 5% povidone-iodine (Betadine gel®, Viatris/Mylan, Lda., Portugal) to minimize the risk of bacterial infection [45]. A 2 cm incision was made in the ventral midline, posterior to the pectoral fins, and the biologger (DST milli HRT-ACT, 13 × 39.5 mm, 12 g, Star-Oddi®, Iceland) was inserted into the coelomic cavity, positioning the round end towards the pericardium and orienting the electrodes ventrally against the abdominal muscles. The sensor was secured in place with a non-absorbable suture (4.0 USP RESOLON® Blue, Resorba, Germany) attached to the rounded end of the logger, and a second stitch of silk suture (Deknatel®, Teleflex Medical, USA) attached to the flat end of the logger. Two to three interrupted stitches of absorbable glyconate monofilament suture (3.0 Monocryl antibacterial, Atramat®, Mexico) closed the abdominal incision. The surgical site was gently cleaned using sterile wipes following the application of a thin layer of Blastoestimulina® (1% ointment, Almirall, Spain) and Furacin (2 mg/g ointment, SeidLab, Spain) to minimise the risk of infection. Each fish was subsequently tagged externally with a T-bar tag (Hallprint®, Australia) near the dorsal fin and then transferred to a recovery tank with well-oxygenated seawater. An analgesic gel (Aloclair® PLUS Gel, Alliance, Spain) was applied over the sutures, tagging point, and wound area. The fish were monitored until they had recovered equilibrium and exhibited normal swimming behaviour. They were then maintained under supervision for a period of seven days, after which they were transferred to the experimental sea-cages prior to the start of the experimental trial. All individuals showed appropriate wound closure and no evidence of infection during this period. Comparable surgical procedures have previously been validated in European seabass, demonstrating rapid recovery of equilibrium and swimming behaviour following biologger implantation, as well as satisfactory wound healing, high survival, and no mid-term physiological stress effects [9, 10, 46].

Data collection

Biologgers recorded a 10-second electrocardiogram (ECG) every hour, while external acceleration and internal temperature were registered at the same hourly interval. This recording configuration was maintained throughout both experimental periods (March and July 2023). At the end of each trial, biologgers were retrieved, and data were downloaded using Star-Oddi Mercury software (v. 6.58), yielding a total of 336 data points per individual for each experimental period. An ECG quality-control procedure was then applied. All ECG recordings automatically classified by Mercury as low quality (IQ = 3) were discarded. The remaining ECG files were manually inspected, cleaned and processed using Star-Oddi HRT Analyzer tool (v. 1.3.1). Recordings exhibiting excessive background noise and/or unclear QRS complexes were removed. Following this ECG filtering process, a total of 7662 observations were retained for each variable (HR, ACC, and internal temperature) across both experimental periods. Feeding times and sea-cage maintenance operations were also registered. Hourly abiotic variables at the study site were retrieved via the Open-Meteo Historical Weather API, which draws on the ERA5 reanalysis dataset [47]. These included solar radiation and wind gusts and velocity. Additionally, hourly marine variables were obtained through the Open-Meteo Marine API, which sources data from the Copernicus Marine Environment Monitoring Service [48], and included sea surface temperature and wave height.

Data analysis

Time-series visualizations were generated to inspect temporal patterns in biologger output. To facilitate data interpretation, datasets from both experimental periods were assigned to three diel categories (morning, afternoon and night) based on period-specific sunrise and sunset times. Environmental data were integrated with biologger outputs, and prior to analysis, multicollinearity among environmental variables was assessed using Pearson correlation matrices, removing those with high determination coefficients to avoid redundancy in the set of predictors. Correlations between biologger-derived metrics (HR, ACC, internal temperature) and selected environmental variables were examined using pairwise complete observations, and correlation structures were visualized using the *ggcorrplot* package [49].

For welfare state classification, HR and ACC values were standardized using z-score transformation to account for interindividual and period variability (see "Data acquisition and labelling" section). The RF model developed in "Model development and validation" section was then applied to the data in the present study using *randomForest::predict()* [39]. Visualization of the RF classification output included a scatterplot of standardized HR vs. ACC to illustrate state separation, and barplots of state proportions across factors of interest. Differences in the distribution of predicted welfare states across categorical factors (period and day of the week) were evaluated using Chi-squared tests. Effect size was quantified using Cramer's V, and standardized Pearson residuals were used to identify over- or under-represented categories, residuals $|r| > 2$ were interpreted as deviations from expected frequencies under the null hypothesis of independence [50]. Results were considered significant at p-value < 0.05. All analyses were conducted in R version 4.3.2 [38] and all the plots were done using *ggplot2* package [43]. The full analytical workflow is summarized in Fig. 1.

Results

Cardiac and swimming activity patterns of seabass in sea-cages

Heart rate (HR) and external acceleration (ACC) exhibited clear diel structuring over the 14-day time series across both experimental periods (Fig. 2). In March, HR displayed pronounced oscillations, with daytime peaks reaching maximum values of 60.40 ± 0.79 bpm and a reduction in nighttime average values until 52.78 ± 0.74 bpm (Fig. 2A). ACC followed a similar, though less pronounced pattern, with moderate daytime values peaking at 13.68 ± 0.10 mg and reaching a minimum of 4.75 ± 0.20 mg. The minimum observed HR and ACC values coincided with weekend intervals, reflecting reduced overall activity during those periods. In July, a similar pattern in HR was found (Fig. 2B). Cardiac activity again exhibited pronounced diel fluctuations, characterized by strong daytime peaks and nighttime reductions, with overall values higher than those observed in March. Maximum HR reached 76.05 ± 1.86 bpm, while the minimum was 60.67 ± 1.13 bpm. In contrast, ACC remained relatively stable across the entire time series, with a maximum of 12.88 ± 1.37 mg and a minimum of 8.11 ± 0.51 mg, displaying limited diel variations. Weekend periods were again associated with lower HR values, whereas activity values remained nearly unchanged relative to weekdays. Internal temperature remained stable within each experimental period, averaging approximately ≈ 17 °C in March and ≈ 28 °C in July, closely matching the corresponding sea surface temperatures at each period.

Pairwise correlations between biologgers data and environmental variables were generally low to moderate. HR showed modest positive associations with internal temperature and sea surface temperature ($r \approx 0.41$ for both) which, in turn, were highly correlated ($r = 0.99$). ACC was weakly correlated with wind gusts and velocity, and solar radiation ($r \approx 0.26$–0.32). Wave height, wind, and solar radiation exhibited only minor correlations with HR and internal temperature ($|r| < 0.38$). Overall, correlations between physiological and activity metrics and environmental variables were generally weak. The full correlation matrix is available at the Additional file 1 for further information.

Model performance

The developed Random Forest model demonstrated stable performance across training, validation, and cross-validation phases. Training accuracy was 0.723 (Cohen's kappa = 0.63). Class-specific error rates ranged from 0.213 for proactive response to 0.317 for regular activity, indicating that the latter exhibited the highest overlap with neighbouring welfare states. The confusion matrix shows that misclassifications predominantly occurred between regular activity and proactive and reactive responses, whereas the resting state exhibited the clearest separation (Fig. 3A).

Validation results yielded an accuracy of 0.742 and a Kappa of 0.654. Class-level performance metrics showed sensitivity values between 0.692 (proactive response) and 0.780 (resting state), and specificity values between 0.887 (regular activity) and 0.937 (resting state). F1-scores were 0.720 (proactive response), 0.717 (reactive response), 0.696 (regular activity), and 0.814 (resting state), with balanced accuracy exceeding 0.800 for all cases.

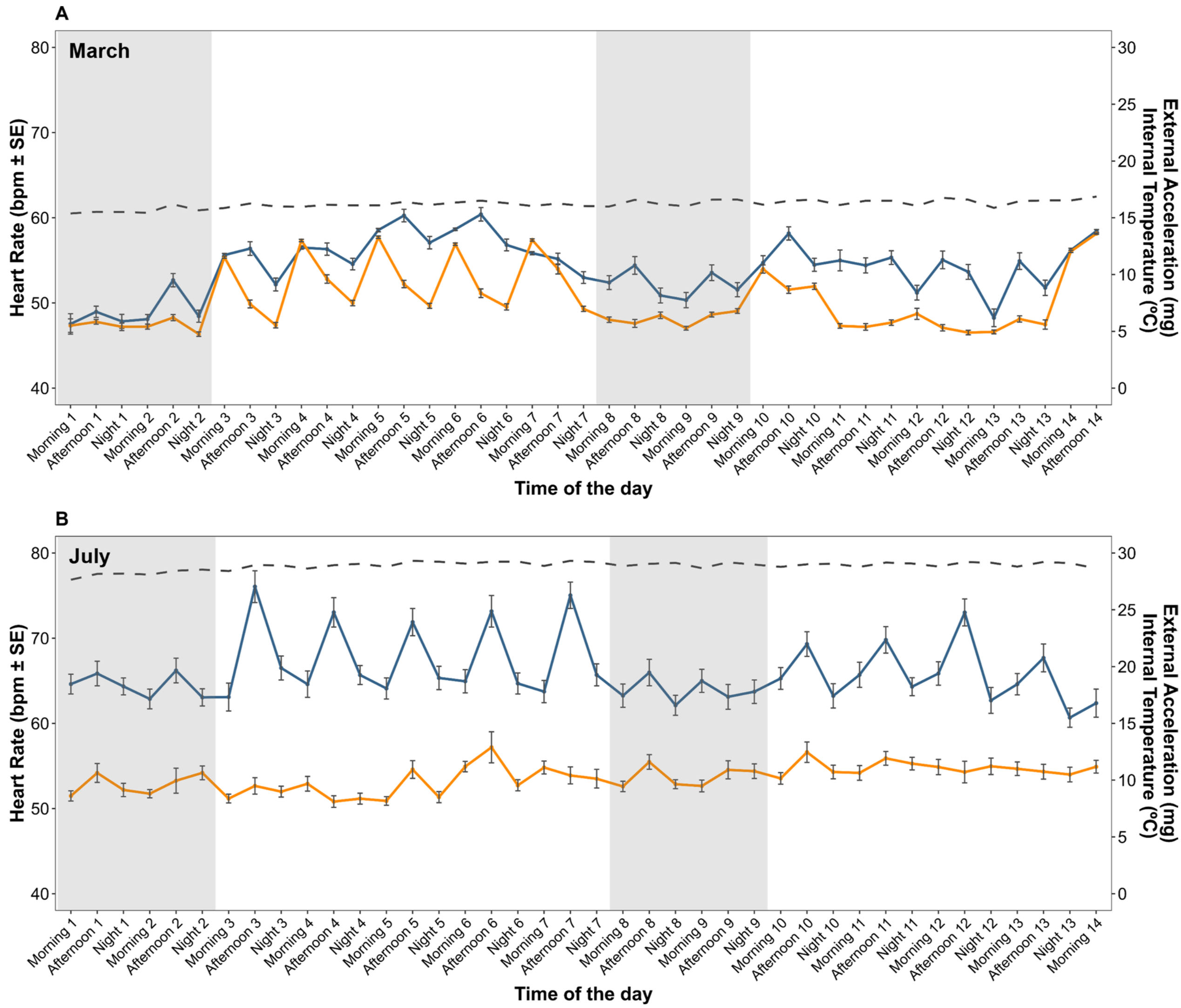

Fig. 2 Fourteen-day patterns of heart rate, external acceleration, and internal temperature across the two experimental periods. **A** March time series. **B** July time series. Mean heart rate ± SEM (HR; blue), external acceleration (ACC; orange), and internal body temperature (dashed line) recorded hourly over 14 days. Grey-shaded regions indicate weekends

Variable importance analysis demonstrated that ACC_{std} was the primary predictor for proactive response and regular activity states, while HR_{std} contributed most strongly to resting and was also a major predictor for reactive responses. Multiclass ROC analysis provided an AUC of 0.850, consistent with class-specific values obtained from pairwise comparisons. The 20-fold cross-validation produced an accuracy of 0.711 and a Kappa of 0.612, confirming the reproducibility of model performance under repeated resampling.

When the RF model was applied to sea-cage data, HR_{std} and ACC_{std} values formed distinct clusters corresponding to the four predicted states (Fig. 3B). Some degree of overlap was observed between reactive and proactive responses, as well as between reactive response and regular activity classes, which is consistent with the class-specific performance metrics and with the patterns observed during model development and validation.

Predicted welfare states

Predicted welfare states exhibited clear diel patterns over the 24-hour cycle (Fig. 4). In general terms, the proportion of proactive responses was reduced during nighttime and early morning hours, followed by a marked increase from approximately 13:00 h onwards, coinciding with feeding events and sea-cage maintenance operations. This elevated level of proactive responses persisted until the end of the day. Reactive responses remained relatively stable across all hours, accounting for roughly 25% of observations, and were generally isolated events rather than consistent, coordinated responses among individuals. Regular activity peaked during the night and early

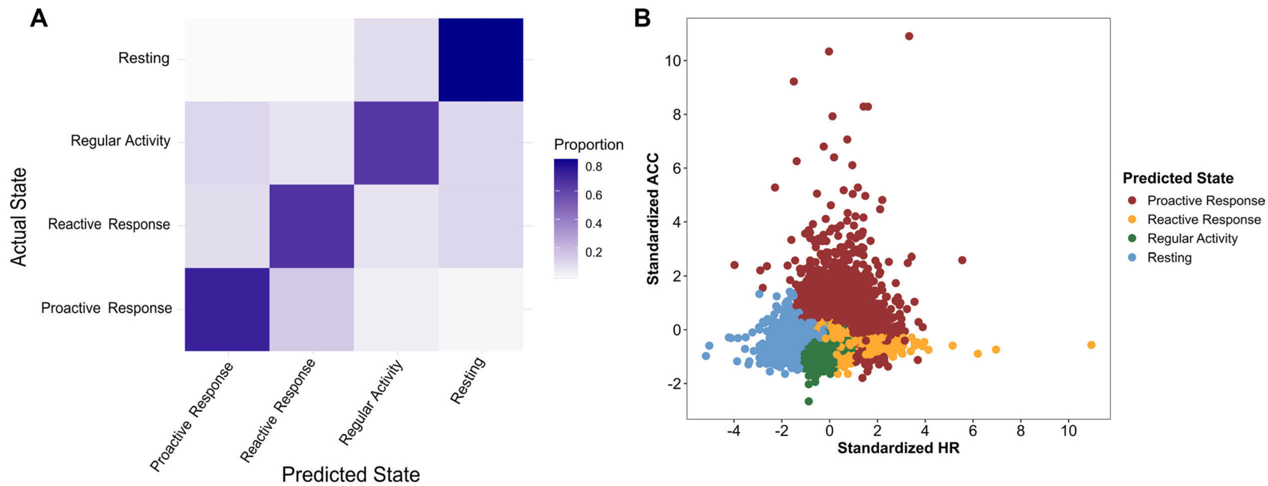

Fig. 3 Performance and classification outputs of the Random Forest (RF) model. **A** Confusion matrix of the RF classifier showing predicted versus actual welfare states. Cell shading reflects proportional accuracy within rows. **B** Scatterplot of standardized heart rate (HR) and external acceleration (ACC) from sea-cage seabass, coloured by the predicted welfare state

Fig. 4 Distribution of classified observations across the 24-h cycle for each of the four welfare states

morning, reaching a maximum at 5:00 h, coinciding with sunrise, and gradually declined throughout the afternoon to approximately 25% of observations. Resting state was slightly elevated during the late night and early morning hours, while decreasing substantially during the afternoon (Fig. 4).

When comparing experimental periods, statistically significant differences in prevalence of welfare predicted states were observed ($\chi^2 = 89.20$, $p < 0.0001$). The effect size was small-to-moderate (Cramer's V = 0.112), showing that seasonality exerted a relatively limited influence on welfare states. Standardised residual analysis revealed that in March, proactive responses and resting states were less detected than expected (r = −4.48 and r = −3.80, respectively), and an over-representation of regular activity was observed (r = 9.32), while differences in reactive responses were comparatively minor (Fig. 5A). Conversely, July was characterised by increased proactive responses and resting states (r = 4.48 and r = 3.80, respectively), and a substantially lower than expected proportion of regular activity was detected (r = −9.32).

Significant differences in prevalence of seabass welfare states were also detected between weekdays and weekends ($\chi^2 = 191.11$, $p < 0.0001$). The effect size was moderate (Cramer's V = 0.164), indicating a limited yet consistent influence of day type on welfare state classification. Weekdays showed a significantly higher occurrence of proactive and reactive responses than expected (r = 11.235 and 4.048, respectively). Additionally, a significant increase in regular activity and resting states was detected during weekends compared to weekdays (r = 8.079 and 7.178, respectively) (Fig. 5B).

Patterns in the distribution of predicted welfare states across the 24 h cycle visually differed between experimental periods and between weekdays and weekends (Fig. 6). Proactive responses showed the greatest variability among conditions. In March weekdays, proactive responses increased during the early morning and again sharply from approximately 13:00 h onwards. In July weekdays, the early-morning peak was still evident, but proactive responses increased progressively throughout the day, reaching their highest proportions between 21:00 and 23:00 h. A similar but less pronounced afternoon increase was observed during July weekends, beginning around 14:00 h. In contrast, proactive responses were nearly absent during March weekends. Reactive responses remained comparatively stable across all four period-day combinations, generally representing around 25% of observations. The only notable deviation was observed during March weekends, where reactive responses decreased to approximately 15% of observations. Regular activity showed clearer differences between periods and day types. In March weekends, regular activity accounted for a substantial proportion of observations across most hours, often alternating with resting behaviour. In July, regular activity was less prevalent during weekdays, whilst the reverse was true for weekends. Resting behaviour also varied across conditions. In March weekends, resting accounted for a high proportion of observations, especially during nighttime and early morning hours. A similar pattern was present during July weekdays, although resting declined markedly from midday onwards.

Taken together, March and July weekdays displayed a consistent structure: regular activity dominated the night and early morning, whereas proactive responses became the predominant state from midday. July weekends showed a comparable temporal organization, although proactive responses reached lower proportions and resting was slightly more frequent. March weekends differed markedly from all other conditions, with substantially higher proportions of regular activity and resting, and a clear reduction in both proactive and reactive responses.

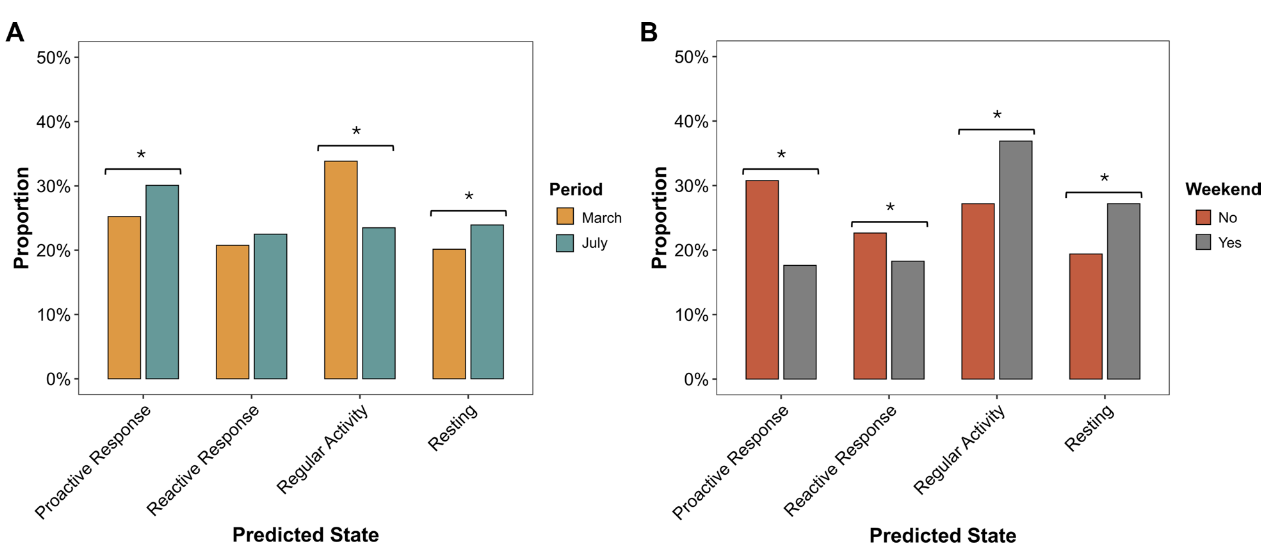

Fig. 5 Proportion of observations assigned to each welfare state by **A** day of the week, and **B** experimental period. Asterisks indicate significant deviations from the expected frequencies (standardized Pearson residuals |r| > 2)

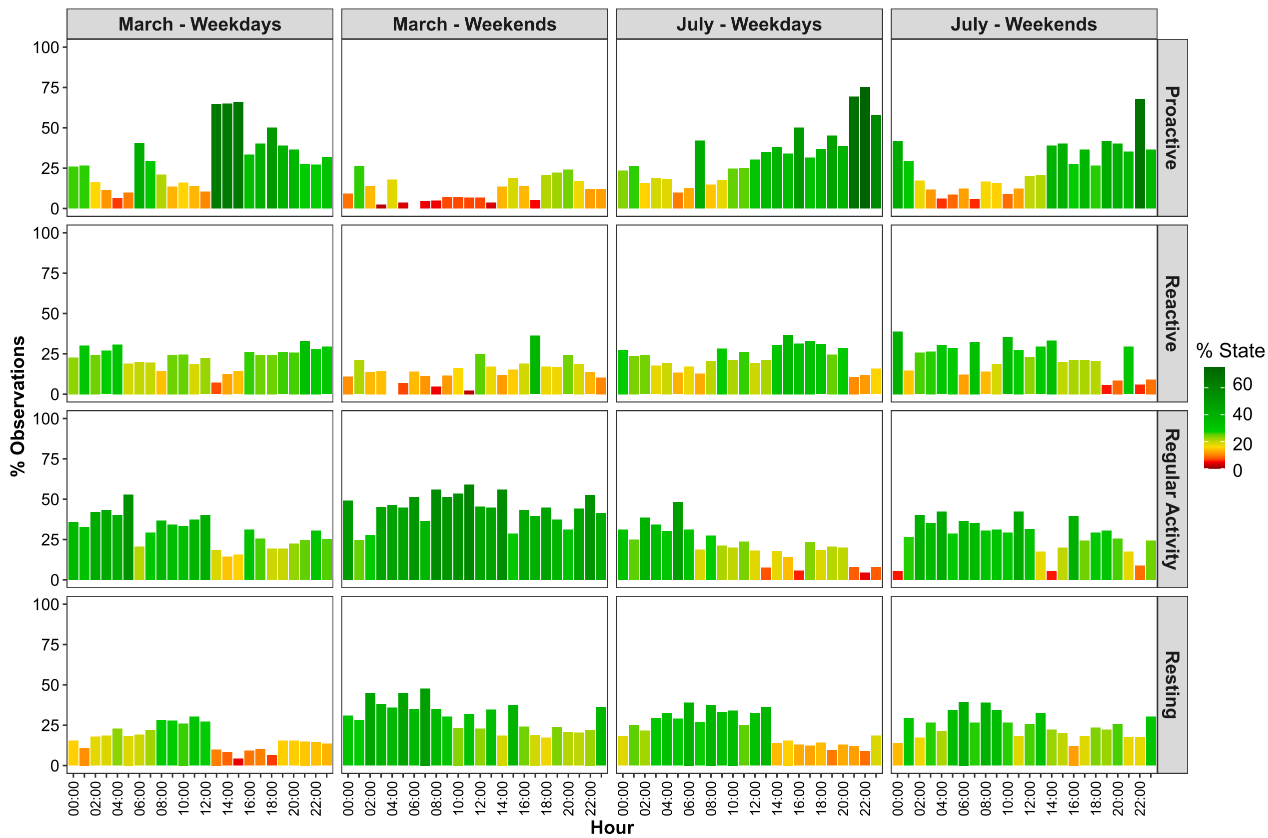

Fig. 6 Combined distribution of classified observations across welfare states by day-type and period

Discussion

The analysis of European seabass physiology and behaviour using biologger data combined with machine learning enabled robust classification of welfare states and the elucidation of complex interactions among seasonality, anthropogenic pressure, and fish welfare. This integrative approach captured meaningful physiological and behavioural patterns reflecting both environmental conditions and human-induced challenges.

Notably, HR values were consistently higher in July than in March, consistent with the temperature dependence of cardiac physiology in ectotherms, where elevated water temperatures increase metabolic and cardiac demand [51]. In contrast, maximum external ACC remained similar between periods, while minimum ACC in July was nearly twice that observed in March, resulting in reduced diel ACC variation. This pattern likely reflects elevated baseline metabolic activity associated with warmer water, increasing baseline movement levels while still allowing comparable peak accelerations relative to cooler conditions [52–54]. In this sense, although sea surface temperature correlated strongly with both HR and internal temperature of seabass, other climatological variables exhibited limited explanatory power for the observed physiological and behavioural patterns. This might be attributable to the short duration of the experimental periods and the coarse temporal resolution of environmental datasets. Higher frequency climatological measurements and extended monitoring windows would likely improve understanding of the non-linear associations between environmental conditions and biologger-derived metrics. Indeed, such relationships have been extensively documented in salmonids, where behavioural and physiological rhythms are tightly linked to environmental dynamics [32, 34, 54, 55].

However, descriptive observations alone represent only part of the picture. Resolving how such patterns translate into welfare states requires analytical approaches that integrate diverse data streams. In this context, the Random Forest (RF) model provides a structured means to classify biologgers data into seabass welfare states. The RF classifier demonstrated strong performance in discriminating welfare states from HR and ACC with a resolution exceeding descriptive analyses. Temporal trends detected by the model were consistent with the descriptive patterns, while allowing more precise categorisation of behavioural and physiological data. This capacity to infer group-level welfare conditions from a limited number of tagged individual underscores the value of sentinel fish approaches in sea-cage systems [30, 35]. However, as noted in comparable tagging studies, caution is needed when extrapolating individual-level measurements to population-level patterns, and increasing sample size would improve the statistical power of future analyses [12, 31]. In the present study, the relatively low inter-individual variability observed across physiological and behavioural metrics supports the robustness of extrapolating trends at the population level. Moreover, in commercial aquaculture settings, fish are typically exposed to similar environmental and operational conditions, which may contribute to comparable physiological and behavioural responses among individuals. While increasing the number of tagged fish would enhance statistical power and strengthen population-level inference, it would also entail greater operational constraints and ethical considerations associated with surgical implantation and handling. Importantly, despite these considerations, the RF model remained robust despite class imbalance, with high recall and precision for proactive and reactive responses, reflecting sensitivity to stress-related behaviours. In contrast, the lower recall observed for regular activity reflects the broad physiological and behavioural variability encompassed within this category, which makes its boundaries more diffuse relative to the other welfare states. Variable-importance analyses further clarified the relative contribution of each parameter: HR was especially influential in identifying reactive responses and resting states, whereas ACC was the primary driver of proactive responses. In contrast, regular activity and resting states exhibited a balanced contribution of both variables, consistent with the multifactorial interplay between locomotion, metabolic demand and arousal level. These results align with previous studies demonstrating HR and ACC as reliable proxies for energy expenditure and stress in fish [37, 56, 57], highlighting the versatility and scalability of machine learning for welfare assessment in sea-cage environments.

Despite these strengths, several limitations should be acknowledged. The model showed occasional misclassifications among states, which is not surprising given that welfare states exist along a physiological-behavioural continuum rather than as strictly discrete categories. Class imbalance also remains a challenge, expanding the training dataset by conducting more laboratory-based calibrations providing baselines for interpreting biologgers data would likely improve the delineation of minority classes and enhance overall model stability. Although cross-validation indicated satisfactory generalisation, the balance between avoiding overfitting and capturing the relevant structure of the training data is inherently delicate in ecological and ethological datasets [6].

However, despite these sampling constraints, the model's performance provides a sufficiently robust basis to extract biologically meaningful patterns regarding seabass welfare in sea-cage environments. The application of the RF classification to the dataset in the present study revealed detailed circadian patterns in seabass. Proactive responses peaked around midday, coinciding with scheduled feeding events, and persisted into the evening. This sustained post-prandial activity might reflect the allocation of energy from food not only to basal maintenance but also to active cardiovascular and locomotor functions, representing the metabolic costs of digestion and nutrient assimilation. In seabass, feeding induces a pronounced specific dynamic action (SDA), manifested as increased oxygen uptake, cardiac output, and gastrointestinal blood flow [58]. During digestion, the gut receives a high share of cardiac output, indicating active cardiovascular support for nutrient processing [59]. This elevated metabolic demand is accompanied by significant tachycardia, driven by vagal withdrawal while adrenergic drive remains low [60], consistent with the persistent high HR observed post-feeding. Gastric evacuation studies indicate that half of stomach contents are processed over ≈ 6 h at 26 ± 1 °C [61], aligning with the prolonged proactive responses and subsequent recovery of regular activity 10–13 h after feeding. Reactive responses remained around 25% throughout the day, suggesting they represent short and isolated events rather than coordinated group behavioural responses. Higher resolution HR and ACC measurements could further elucidate the drivers of these isolated reactive responses. Resting behaviour predominated in the early morning but decreased sharply after feeding, highlighting the strong influence of aquaculture routines on daily and circadian rhythms on farmed seabass [62].

The RF analysis also highlighted clear anthropogenic effects on welfare state distributions. Weekdays were generally associated with a higher occurrence of stress-related states (i.e., proactive and reactive responses), whereas weekends were dominated by regular activity and resting, coinciding with reduced human presence and minimal operational disturbance in the experimental sea-cages. Routine aquaculture operations, such as feeding and cage maintenance, are known to elevate HR while producing only minor effects in activity [31]. Within the context of the RF applied in the present study, such conditions translated into an increased proportion of reactive responses, characterized by elevated cardiac activity without a concomitant rise in swimming activity. The reactive responses observed in March likely result from feeding and cage maintenance operations, as seabass at that stage of the study might not have been fully acclimated to human presence exhibiting short duration freezing responses. These observations are consistent with previous studies in Atlantic salmon, where operational disturbances increased cardiac output but had limited influence on locomotor activity [31]. In this context, the interaction between seasonality and anthropogenic influences further modulated welfare state distributions.

July was characterized by a higher prevalence of proactive responses and resting, reflecting both elevated water temperatures and greater human presence, including boat traffic, that may enhance environmental alertness. Additionally, weekends in July showed more proactive responses compared to weekends in March, aligning with the patterns observed during weekdays in July, which may reflect adaptation to feeding schedules and feeding anticipatory responses [21], while potentially also being influenced by the higher anthropogenic pressure during summer. In contrast, March was dominated by regular activity, consistent with cooler, more stable early-spring conditions and lower anthropogenic disturbance, favouring natural behaviours and reducing the occurrence of stress-related states. Taken together, these seasonal and anthropogenic patterns underscore the combined influence of environmental context, routine aquaculture operations, and human-induced challenges on behavioural dynamics in sea-cage production systems. Although effect sizes were modest, the observed trends highlight that both natural and anthropogenic factors should be considered when interpreting biologger-derive welfare assessments in farmed fish.

The use of biologgers in this study highlighted both their potential and inherent limitations. These devices provide high-resolution, continuous measurements enabling welfare assessments beyond traditional methods, yet practical constraints remain [34]. Signal noise, partial data loss, battery depletion, and the need to recover loggers for data download limit long-term monitoring. In addition, while HR and ACC effectively served to classify welfare states, adding environmental variables to the model could enhance its predictive power. Importantly, the reference points of the developed model are based on laboratory-derived data and, despite inherent environmental differences, provide a structured baseline that facilitates welfare assessment under sea cage conditions and supports the practical applicability of the model in commercial settings. Moderate class imbalance and limited labelled observations contributed to difficulties distinguishing regular activity and resting states, which form a behavioural continuum. Thus, expanding the training dataset, increasing temporal resolution of HR and ACC measurements and enlarging sample size would capture short-duration events and reduce inter-individual variability, enabling a more accurate welfare state classification. Therefore, future research should prioritize broader datasets encompassing diverse environmental, behavioural and physiological contexts to improve model robustness and generalizability. Additionally, given the influence of feeding schedules on seabass behaviour [62], finer-scale monitoring could unravel immediate responses during feeding and routinary operations. Complementary sensors, including hydrophones and acoustic telemetry would provide richer context for machine-learning based classifications [63]. Moreover, long-term validation in commercial settings remains essential to account for interactions among environmental stressors, stocking densities, and operational routines, supporting the development of industry-ready monitoring tools [31].

Despite these limitations, combining biologgers with advanced analytical methods revealed biologically meaningful patterns linking physiology, behaviour, environmental context, and anthropogenic pressures. Consistent with previous work (e.g., Toomey et al., 2025), this study highlights the value of integrated multi-disciplinary approaches for assessing fish welfare under production conditions. Furthermore, the feasibility of classifying welfare states in sea-cage environments illustrates how physiological, behavioural, and environmental data can be combined with analytical tools to support more informed practices, optimise operational protocols, and potentially improve fish welfare in aquaculture.

Supplementary Information

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Supplementary Material 1

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Author contributions

E. H-A.: Conceptualization, Methodology, Formal analysis, Investigation, Writing—Original draft; M.J. C-A.: Methodology, Writing—Review and Editing; M. V-V.: Methodology, Resources, Writing—Review and Editing; A.P. P.: Methodology, Investigation, Resources, Writing – Review & Editing; P. A-L.: Conceptualization, Investigation, Resources, Writing—Review and Editing, Supervision, Funding acquisition.

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Data availability

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

All procedures were conducted by qualified personnel in accordance with European Directive 2010/63/EU. Experimentation procedures were approved by the Ethics Committee of the University of the Balearic Islands (CEEA 207/12/22) and authorized by the Conselleria d'Agricultura, Medi Ambient

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Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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