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Predish: a decision support tool for estimating risk of fish predation in aquaculture systems

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ABSTRACT

The practice of rearing multiple species within the same environment, known as polyculture, is an age-old approach that offers numerous benefits for enhancing the sustainability of aquaculture, provided the species can coexist without detrimental interactions. Predation is one of the most detrimental interactions in polyculture systems and must be avoided to ensure compatibility among species. Since many piscivorous species are commonly reared in aquaculture, it is crucial to avoid species combinations where predation might occur. To address this, we developed a model that estimates predation risk between fish based on their total length in order to avoid empirical trials and thereby uphold ethical standards. This model was calibrated based on niche allometric framework with an extensive dataset on fish predation (4,207 instances) and validated using the specificity, the sensitivity, the True Skill Statistic (TSS) and the area under the curve (AUC) method with a comprehensive dataset of fish predation and non-predation events (13,707 events). The model demonstrated high accuracy with a sensitivity (predation prediction accuracy) of 0.88, specificity (non-predation prediction accuracy) of 0.96, a TSS of 0.84, and an AUC of 0.92. As a practical application, we developed a decision-support tool, Predish, in R software to allow users to estimate predation risk between fish. Predish also includes a database to fill any missing data, making it a valuable resource for designing new polyculture systems that incorporate piscivorous species with minimal predation risk, ultimately supporting aquaculture sustainability.

1. Introduction

Aquaculture can be practiced as either monoculture or polyculture, referring to the production of a single species or multiple species simultaneously within the same farming system, respectively (Thomas et al., 2021). In fish production, polyculture is an ancient practice that remains widely used in pond aquaculture, particularly in Eurasia (review in Milstein, 1992; Thomas et al., 2021). Recently, this practice has been gaining renewed interest from producers, research and development organizations, and scientists, who aim to implement it for newly farmed species or in production systems where polyculture has rarely or never been applied (e.g., recirculating aquaculture system; RAS) (Amoussou et al., 2022; Kozłowski et al., 2014; Lecocq et al., 2024; Thomas et al., 2020). This renewed interest stems from the potential of polyculture to serve as a sustainable development option for aquaculture (Lecocq et al., 2024; Thomas et al., 2021).

Polyculture offers numerous potential advantages over monoculture: it improves the utilization of resources naturally present or supplied to the aquaculture environment (Nhan et al., 2007), recycles co-products into the farmed biomass (Biswas et al., 2020; Milstein, 1992; Thomas et al., 2021), strengthens the resilience of the system (Dumont et al., 2020), and reduces operational costs and financial risks (Thomas et al., 2021). Additionally, it can make the production of certain species economically viable when they would not be profitable in monoculture (Stickney, 2013). Polyculture can also improve the welfare of farmed fish, either directly through the beneficial interactions between combined species (Biswas et al., 2020; Papoutsoglou et al., 2001) or indirectly through reduced maintenance operations, which are partly

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carried out by other farmed species (Kozłowski et al., 2014). However, these potential benefits can only be achieved if there is interspecific compatibility or, even better, interspecific complementarity. Interspecific compatibility is the capacity of species to coexist within the same production system without detrimental interactions and competition for resources like food or space. Interspecific complementarity is the ability of species to utilize by-products from other co-farmed species, or to establish commensal or mutualistic interactions (Lecocq et al., 2024; Thomas et al., 2021). Without at least compatibility, polyculture can result in interspecific competition, stress, and even predation, with a negative impact on fish welfare and production like reduced growth and survival rate (Barcellos et al., 2007; Rahman and Verdegem, 2010; Slos and Stoks, 2008; Werner et al., 1983). Therefore, it is essential to design compatible species combinations to develop effective and beneficial polycultures for aquaculture.

Predation is defined as the swallowing of the whole living prey by a predator (definition adapted from Mihalitsis and Bellwood, 2017). Although predation can be sought in specific cases (Jiwyam, 2008; Shrestha et al., 2011), it is a major interaction to avoid when developing combinations of compatible species for aquaculture (Thomas et al., 2021). Predation is the most significant detrimental interactions that can occur between species in fish farming as, to our knowledge, no instances of amensalism or parasitism have been observed among fish in aquaculture (Lecocq et al., 2024). Moreover, several piscivorous species (e.g., Percidae, Siluridae, Salmonidae, and Channidae) are often reared in aquaculture (FAO, 2024) due to their high market value and consumer demand (Kestemont et al., 2015; Ndobe et al., 2014; FAO, 2024). This means that developing fish polyculture systems may involve integrating one or more piscivorous species with other species. For example, polycultures based on piscivores like pikeperch (*Sander lucioperca*) (Kozłowski et al., 2014; Mihailov et al., 2017; Pěnka et al., 2024; Thomas et al., 2022), European perch (*Perca fluviatilis*) (Amoussou et al., 2022) or snakeheads (*Channa* sp.) (Saowakoon et al., 2021; Zhang et al., 2018) are also being increasingly considered in aquaculture (Thomas et al., 2021). Therefore, it is crucial to carefully assess the risk of predation when designing fish combinations to ensure the success of polyculture systems (Lecocq et al., 2024) and avoid losses for producers.

Estimating the risk of predation between fish can be approached in various ways. The simplest method is to rear the species together and empirically observe any predation acts (Baird et al., 2020). However, this approach is not recommended due to pragmatic reasons, such as the difficulty in detecting predation in some systems (e.g., ponds), and more importantly, ethical concerns such as predation-induced stress and mortality (Barcellos et al., 2007; Lennox et al., 2023; Slos and Stoks, 2008). Therefore, it is preferable to assess the risk of predation instead of conducting experimental assessments.

Two main methods for estimating predation risk without experimental trials are described in the literature (Lecocq et al., 2024). These methods use either a size relationship between predator and prey (Gaeta et al., 2018; Gill, 2003; Gravel et al., 2013; Vagnon et al., 2021) or a comparison of escape and capture strategies (Domenici, 2010; Krause and Godin, 1996; Weihs and Webb, 1984) to assess predation potential through match-mismatch analyses. For instance, if a piscivorous species forages its prey with the sit-and-wait strategy, it can be expected that any species hiding in cavity has less risk of predation. However, using escape and capture strategies as proxy to estimate fish predation risk may be unsuitable for aquaculture environments since, compared to wild ecosystems, many predator (anti-) strategies (e.g., mimicry, escape, freezing) cannot be effectively applied in all farming systems. Indeed, some systems lack the diversity of components found in the natural environment, which can make ineffective some behavioral strategies (e.g., species will not be able to hide in cavities if the latter are not present in the rearing environment) (Abrahams and Kattenfeld, 1997; Higham et al., 2015; Savino and Stein, 1989). Thus, we argue that predation risk should primarily be assessed based on a species' ability to capture and handle co-farmed taxa by comparing the actual ratios of prey size to predator size (i.e., where predation is known to occur) with the calculated size ratios of the co-farmed species (Gaeta et al., 2018; Gravel et al., 2013; Vagnon et al., 2021). Such an assessment probably overestimates the predation risk, as specific anti-predatory strategies could effectively work in certain farming systems (such as mimicry in ponds) and predator conditions can change based on available food resources. Nevertheless, it provides a cautious estimate that can help mitigate risks to fish welfare and survival.

Niche allometric models can be a relevant and efficient method to assess predation risk based on body size (Gaeta et al., 2018; Gravel et al., 2013; Vagnon et al., 2021). Originally, these models were designed to construct the structure of a community's food web by identifying interspecific trophic links based on the ability of one species to consume another, determined by their respective sizes (Gravel et al., 2013; Vagnon et al., 2021). This type of model can therefore be adapted to estimate the risk of predation specifically between fish. However, existing niche allometric models that include fish (Gaeta et al., 2018; Gravel et al., 2013; Vagnon et al., 2021) are not well-suited for accurately predicting fish-on-fish predation risk. Indeed, the existing calibrated models are designed to consider all organisms (e.g., plankton, arthropods, fish) in aquatic ecosystems (Gravel et al., 2013; Vagnon et al., 2021) or to focus on one specific piscivorous species (Gaeta et al., 2018), thus limiting their relevance for fish-only polyculture systems. Moreover, these models typically include only a small number of fish species in their initial calibration (i.e., one model includes 7 species across 5 fish families (Vagnon et al., 2021), while another includes 7 species across 3 families (Gaeta et al., 2018)) and are not focused solely on fish consumption by piscivorous species (Gravel et al., 2013; Vagnon et al., 2021). As a result, their predictive accuracy for fish predation risk is limited. Consequently, there is a need for an adapted tool based on the allometric model that can predict predation risk for all fish based on a large dataset of piscivorous species and families.

In this paper, we introduce Predish, a new decision support tool as an open-source R-interface. Predish is designed to facilitate development of new polycultures considering fish predation risk. Predish is based on an allometric model (Gaeta et al., 2018; Gravel et al., 2013; Vagnon et al., 2021) calibrated with over 2000 data points from fish predation events.

Predish introduces several innovations over previous models (Gaeta et al., 2018; Gravel et al., 2013; Vagnon et al., 2021). It utilizes a larger dataset of piscivorous fish species and evaluates predator–prey interactions at the individual level, rather than inferring trophic links solely at the species level. Furthermore, it explicitly captures intraspecific variability and computes a "likelihood of predation" based on the proportion within vulnerable size ranges in contrast to earlier approaches that relied on a single representative size per species. In addition, Predish can integrate functional trait data from the TOFF (Traits OF Fish) database (Lecocq et al., 2019), ensuring that it remains operational even when detailed dietary or length-frequency information is unavailable. By addressing these limitations, Predish enables users to design fish polycultures with minimized predation risk, even under data-poor conditions, thereby contributing to more sustainable aquaculture practices.

2. Method

2.1. *Overview of Predish development*

Predish was developed using the fish total length (i.e., distance between the end of the snout and the end of the caudal fin) (mm) since it is a common measurement (Kahn et al., 2004). Other morphological traits such as the mouth gape, standard length or body depth could have been used (Mihalitsis and Bellwood, 2017). However, this type of morphological trait is more difficult to find in the literature for a large number of fish (Lecocq et al., 2019).

Predish was developed in two stages: first, the development of the underlying allometric model, followed by the design of the decision support tool itself.

First, an allometric model was developed in two key steps: calibration and validation. Calibration is essential for understanding the relationship between predator and prey sizes. This process relies on a set of calibration data: known cases of predation from the literature where both predator and prey sizes are documented (Gaeta et al., 2018; Gravel et al., 2013; Vagnon et al., 2021). During calibration, parameters were derived and used in subsequent analyses. This results in a parameterized model. Subsequently, validation ensures the accuracy of the parameterized model by comparing the model's predictions with additional predation data from the literature that were not used in the calibration phase. Keeping calibration and validation data separate ensures the results are unbiased (Witten and Eibe, 1999).

Second, the validated allometric model was implemented as a user-friendly decision support tool. This allows a wide range of users to predict the risk of predation between any fish species using just their sizes as input. This stage transforms the model into a practical and operational tool for users interested in assessing predation risks.

2.2. *Development of the allometric model*

2.2.1. *Dataset acquisition*

The development of the allometric model requires predation datasets (Gaeta et al., 2018; Gravel et al., 2013; Vagnon et al., 2021). We therefore compiled cases of predation by piscivorous fish reported in peer-reviewed articles where the total length of predator and prey fish are given. Papers were sourced from literature searches on Google Scholar and Web of Science using the search terms "fish" and "prey size". We considered freshwater, brackish, and marine species. The literature search was carried out repeatedly (i.e., several searches on the same search engine to detect new publications) between April and July 2024. Beside interspecific predation, we also considered instances of cannibalism as predation. When prey and predator size information is given in graphic form (see Lévy et al., 2024a), we used Plot digitizer (https://plotdigitizer.com/) to extract it from the figures.

Of all the predation cases reported in the literature, we excluded those that (i) did not involve juvenile or adult piscivorous fish and (ii) where the total length of the prey was greater than or equal to the total length of the predator. The first criterion is justified by the fact that polyculture fish farming primarily occurs during the grow-out phase, involving juveniles and/or adults (Amoussou et al., 2022; Biswas et al., 2020; Kozłowski et al., 2014; Papoutsoglou et al., 2001; Thomas et al., 2020). Therefore, the predation capacity of piscivorous larvae is not considered relevant for estimating predation risk in polyculture. The second criterion is based on the definition of predation used here, which implies that the predator, commonly larger than its prey, swallow all of it. In addition, we also excluded cases of predation involving Chondrichthyes, as these species are rarely used in aquaculture (FAO, 2024).

The resulting dataset was then randomly divided in two parts, one for calibration and the other for the validation (see Lévy et al., 2024a). For each species, approximately half of the data was attributed to the calibration dataset and the rest to the validation dataset.

In addition to positive predation controls, the validation dataset also included studies where piscivorous species were associated with potential prey (including from the same species) with total lengths provided, but no predation events were recorded (i.e., negative validation). All these studies were conducted in recirculating aquaculture systems with no enrichment that could prevent predation, and where the absence of predation (i.e., a 100 % survival rate or another known cause of mortality) could be established with certainty. We considered each fish smaller than the piscivore (including from the same species) living in the same system as a potential prey.

The calibration dataset comprised 2106 data points only with predation instances. The validation dataset comprised 2101 data points where predation occurred and 13,707 data points where predation did not occur. The calibration and validation dataset where predation occurred include the same 24 piscivorous species encompassing 19 families. The validation dataset where predation did not occur includes two species encompassing two different families. All of the datasets are available in the supporting information (Lévy et al., 2024a).

2.2.2. *Calibration*

The calibration step involved calculating regression parameters using the calibration dataset. These parameters were then used to define the upper and lower boundaries of prey total length that predators can ingest based on their own total length. Following the previous calibration approaches (Gravel et al., 2013; Vagnon et al., 2021), we computed the regression parameters as the slope and intercept at the 5 % and 95 % quantiles using a quantile regression model. In this model, the $\log_{10}$ of the prey's total length serves as the response variable, while the $\log_{10}$ of the predator's total length serves as the explanatory variable (Gravel et al., 2013). The calculation was performed using the "rq" function from R-package "quantreg" (Koenker, 2005). The parameters can then be used to calculate the prey size boundaries based on the total length of the piscivorous species using Eq. 1.

Equation 1: Estimation of the prey size boundaries. The equation is based from Gravel et al., 2013 and Vagnon et al., 2021.

$$log_{10}\left(Prey_{TL_{max}}\right) = \left(A_{95\%}*log_{10}\left(Piscivore_{TL}\right)\right) + Y_{95\%}$$

$$log_{10}\left(Prey_{TL_{min}}\right) = \left(A_{5\%}*log_{10}\left(Piscivore_{TL}\right)\right) + Y_{5\%}$$

$A_{95\%}$= Slope at quantile 95% $Prey_{TL_{max}}$= Maximal total length of the prey

$A_{5\%}$= Slope at quantile 5% $Prey_{TL_{min}}$= Minimal total length of the prey

$Y_{95\%}$= Intercept at quantile 95% $Piscivore_{TL}$ = Total length of the piscivore

$Y_{5\%}$= Intercept at quantile 5%.

2.2.3. *Validation*

We conducted a validation process by calculating the sensitivity (i.e., the proportion of observed cases of predation that are correctly predicted) and specificity (i.e., the proportion of observed absence of predation that is correctly predicted) of our model using the validation datasets (Yerushalmy, 1947).

To calculate the sensitivity, we used the validation dataset where predation is occurring. First, we calculated the range of prey size for each piscivore total length of the validation dataset using our regression parameter (Eq. 1). Second, we compared the model output with the validation dataset. If the prey size indicated in the validation dataset fell within the calculated range, it was considered a true positive, and if not, a false positive. Finally, the sensitivity is calculated as the number of true positives divided by the total amount of data (Yerushalmy, 1947).

To calculate the specificity, we used the validation dataset where no predation is occurring. First, we calculated the upper and lower boundaries of prey size for each piscivore of the negative validation dataset using our regression parameter (Eq. 1). We considered all fish smaller than the piscivore (including from the same species) as a potential prey and therefore we compared the model output with the total length of these individuals. Second, we compared the model output with the negative validation dataset. If the potential prey size indicated in the negative validation dataset fell within the calculated range, it was considered a false negative, and if not, a true negative. Finally, the specificity is calculated as the number of true negatives divided by the total amount of data (Yerushalmy, 1947). A sensitivity and/or specificity between 0.9 and 1 indicates good to excellent model, while a value between 0.8 and 0.89 indicates a fair model (Plante and Vance, 1994).

By implementing these two criteria, the True Skill Statistics (TSS) of our model can be calculated (Allouche et al., 2006) as follows: sensitivity + specificity – 1. TSS ranges between −1 and 1. A value between 0.4 and 0.75 indicates a good model, while a value greater than 0.75

indicates an excellent model (Allouche et al., 2006; Landis and Koch, 1977; Li et al., 2024).

Finally, we calculated the area under the Receiver Operating Characteristic curve (AUC), which illustrates the relationship between the true positive rate and the false positive rate using the “roc” and “auc” functions from R-package “pROC” (Robin et al., 2011). In this case, a true positive can refer to either a true positive (for sensitivity) or a true negative (for specificity). AUC ranges between 0.5 and 1. The model can be categorized as follows: poor ($AUC < 0.8$), acceptable ($0.8 \leq AUC < 0.9$), good ($0.9 \leq AUC < 0.95$), or excellent ($0.95 \leq AUC \leq 1$) (Resquin et al., 2020).

To evaluate whether the model performs less effectively for certain types of piscivorous fish (e.g., species groups or morphological types), we also calculated the sensitivity for each species (see Lévy et al., 2024a). Additionally, we investigated the correlation between sensitivity and the absolute difference in size variability between the piscivore and its prey using a Spearman rank correlation test (Spearman, 1904). Size variability was determined using the relative standard deviation (RSD) of the $\log_{10}$-transformed size measurements, incorporating both calibration and validation data where predation occurred. The absolute size variability difference was thus calculated as the absolute value of the RSD of the piscivore size minus the RSD of the prey size. Regarding specificity, we were unable to calculate species-specific values due to the limited number of species in our dataset with negative control cases.

The R-script of the calibration and validation process is available in Lévy et al., 2024b.

2.3. *Development of the decision support tool*

The decision support tool is in the form of a graphical interface using the open-access R software, making it accessible to those unfamiliar with informatic scripts and freely available. This section explains the necessary inputs, outputs, and the operation process (Fig. 1).

2.3.1. *Inputs*

The inputs are: the fish’s scientific name, the development stage, the minimum and maximum size or the mean and the standard deviation of the size (i.e., total length in mm), and whether the species is piscivorous or not (yes/no). The input should be loaded in a .xlsx or a .csv (comma-separated) file. The size metric choice (i.e., mean size and standard deviation or minimum and maximum size) must be defined before running the decision support tool and depends on the wish of the user. If the user wishes to estimate an averaged predation risk, the mean and standard deviation of total length are recommended. If the user wishes to determine the extreme value of the predation risk, the minimum and maximum size are recommended. The user must at least fill correctly the species name column, but the other columns can be left blank if the information is not known to the user.

2.3.1.1. Assumptions. The inputs need to respect certain assumptions to ensure the most accurate estimation of predation risk. First, the column

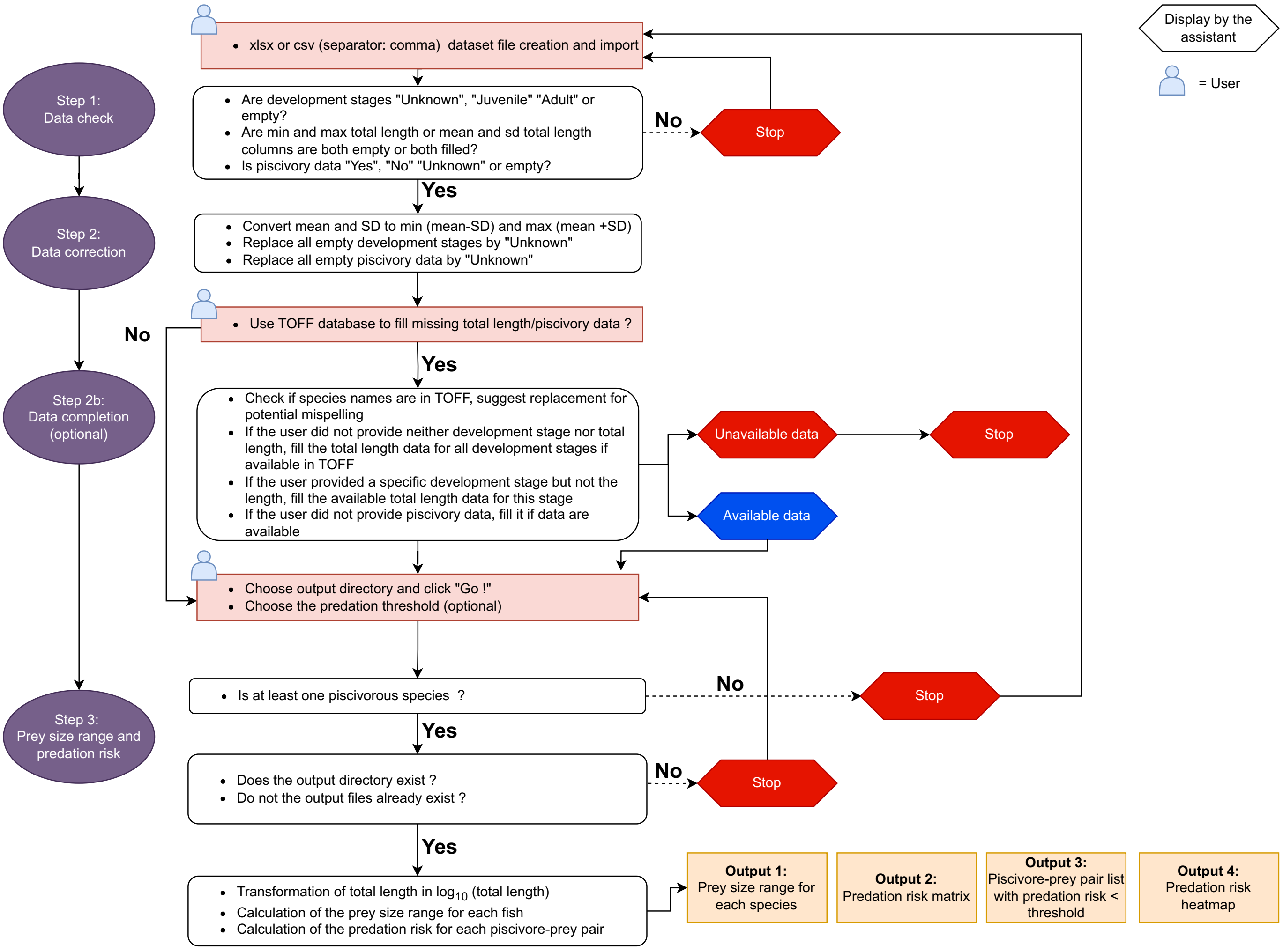

Fig. 1. Workflow of the decision support tool, Predish. SD is the standard deviation.

order and name must follow a specific format indicated in the Predish documentation following this link: https://github.com/thlecocq/Predish. Second, the user cannot indicate the larval development stage, as this is not used in the calibration process. Third, the user is not allowed to fill only one size column (e.g., only the mean size). Fourth, the list of species must contain at least one piscivorous species. The decision support tool will then check whether the first three assumptions are met when the user upload the file. If any assumptions are violated, an error message will be displayed to the user, and no further step can be performed.

2.3.2. *Flow of the decision support tool with outputs*

2.3.2.1. Completion of missing data. As previously mentioned, the user is not required to provide information on development stage, sizes, and piscivorous diet if they provide at least the scientific name of the species. This is made possible by the inclusion of the dataset from the TOFF database within the decision support tool (Lecocq et al., 2019). TOFF is a comprehensive compilation of functional traits, including total length and diet, sourced from scientific literature for fish species (Lecocq et al., 2019). The decision to use this database stems from its diversity range of total length measurements (i.e., mean, standard deviation, minimum, and maximum) for different species, and its accuracy compared to other available database (e.g., TOFF includes developmental stages while FishBase does not) (Lecocq et al., 2019). By using the TOFF database, the decision support tool can complete any missing information by matching the species name provided by the user with relevant data in TOFF, if data on the specified species are available in the database. Additionally, in case of mistakes in spelling of the scientific names the user will be alerted with potential corresponding species from the FishBase database integrated into TOFF (Lecocq et al., 2019).

Regarding piscivorous diet, if at least one record in TOFF indicates a piscivorous diet for a species, that species will be classified as piscivorous. Conversely, if no piscivorous diet data are available, the species will be automatically categorized as non-piscivorous. For each piscivorous species, the assistant provides the number of records indicating a piscivorous diet and the total number of records with at least one diet entry, allowing the user to assess the extent to which each species is piscivorous.

For total length, the minimum value is calculated as the median of the mean, minus the median of the standard deviation. On another hand, the maximum value is the median of the mean, plus the median of the standard deviation. The decision support tool displays all available and unavailable information on the total length after the user choose to use TOFF database to fill in missing information. If no available information is found for a species, it will be removed for the rest of the process.

Regarding developmental stages, if the user leaves the cells blank, the assistant considers three stages from TOFF: (i) juvenile, (ii) adult, and (iii) unknown (i.e., the development stage is not specified in TOFF, but is likely not a larva). If the user indicates one of these three categories, only that stage will be considered in TOFF.

2.3.2.2. Check of the number of piscivores. The decision support tool then checks whether the list of species provided by the user includes at least one piscivorous species. If no piscivorous species are present, the tool displays a message indicating that all species combinations are safe, and no further steps are necessary.

2.3.2.3. Calculation of the prey range size. If at least one piscivorous species is included in the list provided by the user, the next step is to calculate the prey range size for each piscivorous species using the calibration parameters (see eq. 1). The maximum prey size is determined by the 95 % quantiles of the maximum total length (or alternatively the mean plus the standard deviation), while the minimum prey size is calculated using the 5 % quantiles of the minimum total length (or the mean minus standard deviation). The quantiles were selected based on the method of Vagnon et al., 2021. The first output consists on the list of species and their corresponding prey size range. This output is useful if the user simply wants to identify the minimum and maximum sizes of species that can be associated with each piscivorous species.

2.3.2.4. Predation risk estimation. Once the prey size range is calculated for each piscivorous species, the last step consists to estimate the risk of predation between each piscivore and potential prey (i.e., all of the other species). For each pair, the predation risk is determined by the proportion of the prey size that falls within the piscivore prey size range. For example, if the predator's prey size range is between 2 and 3 and the prey's size range is between 1 and 3, the predation risk would be 0.5. The risk is thus expressed as a value between 0 and 1 (where 0 indicates no predation risk, and 1 means a high likelihood of predation). The final output is a matrix where each column represents the piscivorous species, and each row corresponds to a potential prey species (i.e., all of the species indicated by the user). To enhance clarity, a heatmap illustrating the level of predation risk is also generated if there is at least two piscivorous species. Additionally, a list of piscivore-prey pairs with a predation risk below a user-defined threshold is created. Before using the tool, the user must specify the directory for saving the outputs. Once the analysis is complete, all results are automatically saved to the designated directory allowing the user to review the outputs and determine the safest species combinations in terms of predation risk.

2.4. *Case studies*

To demonstrate the application of Predish, we present two case studies. The datasets of the two case studies are available in supporting information (Lévy et al., 2024a).

For the first case study, the goal is to develop new fish polyculture in Cambodian ponds, where species combinations are currently unmanaged. The initial dataset includes 33 freshwater fish species, both native and introduced in Cambodia, and commonly used in aquaculture across Asia. It provides the total length for each species, along with its mean and standard deviation values. Since the user already has all the relevant information, including total length and dietary details, the TOFF tool is not required. The total length data was sourced from peer-reviewed papers identified using the search term "total length" on Google Scholar between February and June 2024. Similarly, diet data was collected from peer-reviewed papers found using the search term "feeding habit" on Google Scholar over the same period.

For the second case study, the goal is to develop new fish polyculture in recirculating aquaculture systems in Belgium, France, Germany, and Luxembourg using temperate freshwater fish species already used in European aquaculture (PolyRAS project; https://interreg-gr.eu/project/polyras-fr/#:~:text=Le%20projet%20Interreg%20Grande%20Région). The initial dataset includes 44 species but lacks information on their total length and diet. Therefore, the missing total length and diet data were obtained using the TOFF database.

Table 1
Value of validation metrics and their evaluation.

Validation metric	Value	Evaluation
Sensitivity	0.88	Fair (Plante and Vance, 1994)
Specificity	0.95	Good to excellent (Plante and Vance, 1994)
Area Under the Curve (AUC)	0.92	Good (Landis and Koch, 1977)
True Skill Statistic (TSS)	0.84	Excellent (Allouche et al., 2006; Landis and Koch, 1977; Li et al., 2024)

3. Results

3.1. Validation of the model

The validation metrics are shown in Table 1. Additionally, Fig. 2A presents the distribution of true positives and false positives (i.e., specificity), while Fig. 2B shows the distribution of true negatives and false negatives (i.e., sensitivity). In evaluating of species-specific sensitivity, values ranged from 0.33 to 1, with the 1st quartile at 0.78, the median at 0.91, and the 3rd quartile at 0.95 (Lévy et al., 2024a). A significant negative correlation was observed between sensitivity and the absolute difference in size variability between piscivorous fish and their prey (Spearman rank correlation test: $\rho = -0.58$; p-value <0.003) (Fig. 3).

3.2. Case studies

The detailed results of Predish applied to the two case studies are presented in Figs. 4 and 5, as well as in the supporting information (Lévy et al., 2024a). It is worth noting that the result accounts only for predation and is therefore insufficient for designing new polycultures, which requires considering many other factors (e.g., abiotic requirements (Butruille et al., 2022; Lecocq et al., 2024)).

In the first case study, focusing on the fish polyculture in Cambodia, *Wallago attu* and *Channa micropeltes* are identified as the least suitable piscivorous species for polyculture due to their higher predation risks. In fact, 63 % of species cannot be associated with *Wallago attu*, and 71 % cannot be paired with *Channa micropeltes* without facing a predation risk >0 (Fig. 4). In contrast, *Anabas testudineus* appears to pose the lowest predation risk since the predation risk is >0 for only six species (Fig. 4). According to the model, *Trichopodus trichopterus*, and *Esomus metallicus* cannot be safely associated with any piscivores without a predation risk >0.9 (Fig. 4). An example of practical recommendation based on these results is that if a fish farmer aims to develop a polyculture with *Channa micropeltes* but is hesitant to combine it with *Labeo rohita* or *Trichopodus trichopterus*, it would be preferable to pair *C. micropeltes* with L. *rohita* to minimize predation risk within the rearing system.

In the second case study focusing on the development of polyculture of European species in RAS, missing information in the TOFF database prevents the calculation of predation risk for six species. Of the initial 44 species, only 38, each with at least one developmental stage, had sufficient data in TOFF to be processed by the decision support tool. Adults of *Acipenser transmontanus* (Mean Total length = 1108.5 ± 169.5 mm) are identified as the least suitable piscivorous species for polyculture due to their higher predation risks. In fact, 76.2 % of species cannot be associated with adults of *A. transmontanus*, without facing a non-zero predation risk 0 (Fig. 5). In contrast, juveniles of *Oreochromis mossambicus* (Mean Total length = 25.4 ± 6.4 mm) appear to pose the lowest predation risk since the predation risk is >0 for only six species. According to the model, juveniles of *Sander lucioperca* (Mean Total length = 76.1 ± 8.1 mm) can be safely associated with only 3 piscivores without a predation risk >0.9 (Fig. 5). An example of practical recommendation based on these results is that if a fish farmer aims to develop a polyculture with adults of *A. transmontanus* but is hesitant to combine it with *Gobio gobio* (Mean Total length = 12.2 ± 0.3 mm) or *S. lucioperca*, it would be preferable to pair adults of *A. transmontanus* with *G. gobio* to minimize predation risk within the rearing system since according to the model this species is too small to be consumed by *A. transmontanus*.

4. Discussion

4.1. Model performances

In this study, we introduce Predish, a decision-support tool that predicts fish predation in aquaculture systems using a niche-allometric framework (Gaeta et al., 2018; Gravel et al., 2013; Vagnon et al., 2021). According to the validation metrics (Table 1), the developed model demonstrates high predictive accuracy and is suitable for use with various freshwater, seawater and brackish fish. With the exception of sensitivity, all metrics are rated as good to excellent (Table 1).

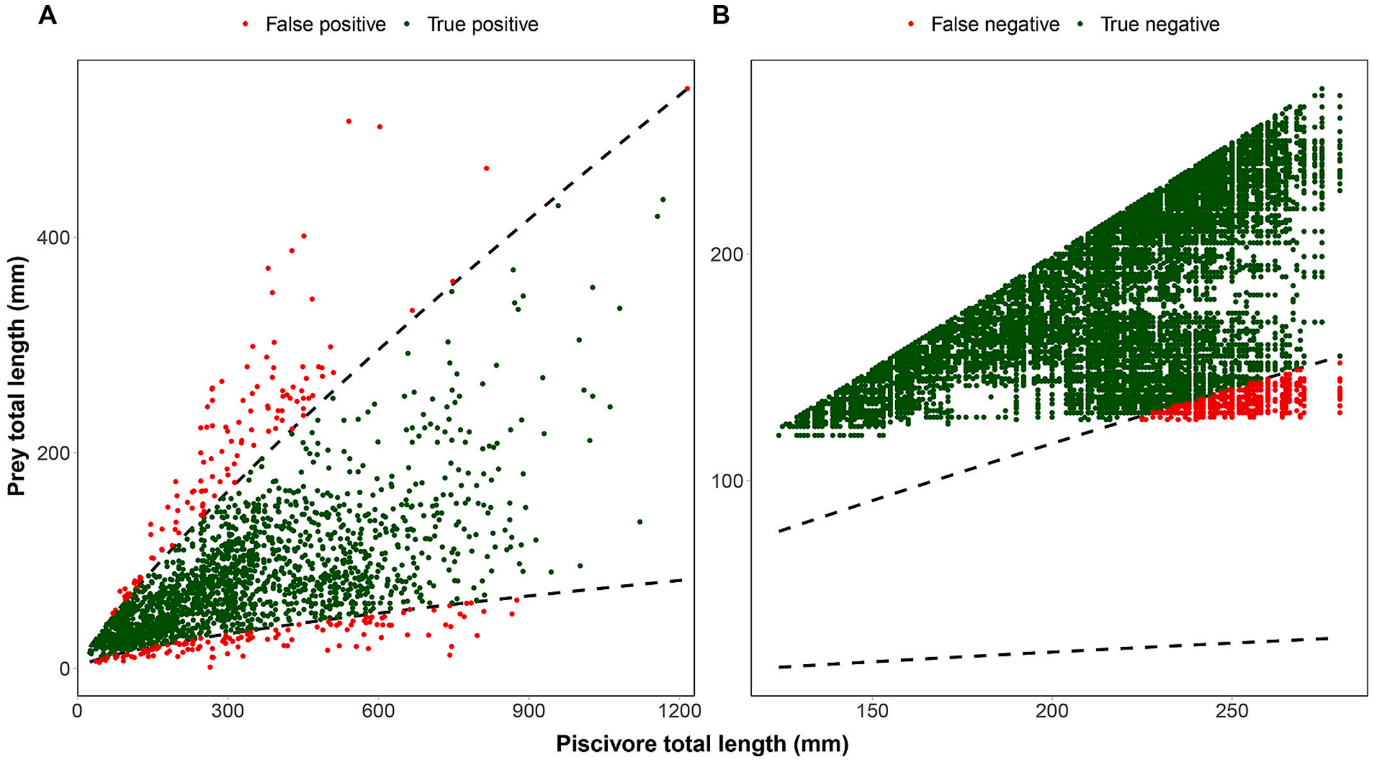

Fig. 2. Sensitivity (A) and specificity (B) of the predation model. Each point represents the piscivore and prey size from the validation dataset. The dashed lines indicate the lower and upper limit of prey size. The script used to generate the graph is available in the supporting information (Lévy et al., 2024b).

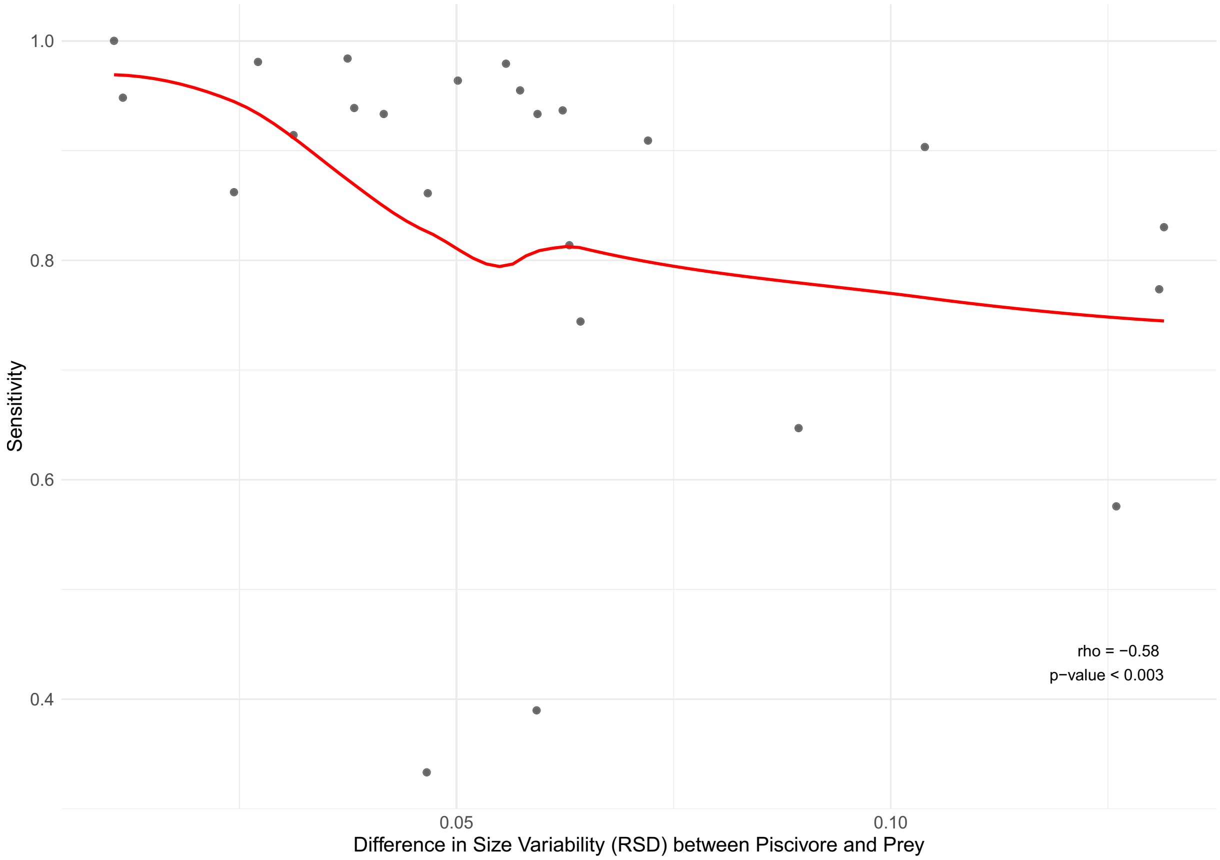

Fig. 3. Relationship between sensitivity and the absolute difference in size relative standard deviation (RSD) between piscivore and prey. Each point represents one species. The red curve represents the data trend, fitted with a Loess smoother. The script used to generate the graph is available in the supporting information (Lévy et al., 2024b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

For species with a sensitivity below 0.8 (i.e., where the predation prediction is considered poor (Plante and Vance, 1994)), no consistent pattern emerges regarding morphology, origin, environment, and the number of data points of the piscivore (see Lévy et al., 2024a). However, sensitivity appears to correlate with the absolute difference in size variability between piscivore and prey. Specifically, sensitivity significantly decreases as this variability difference increases, suggesting that prediction errors are more likely when prey sizes are more variable than those of the piscivores. For instance, a homogeneous piscivorous population preying on more size-diverse prey is logically more prone to errors compared to a homogeneous population feeding on prey of similar size. Nonetheless, certain species defy this trend: for example, *Urophycis regia*, maintains high sensitivity (≥ 0.8) despite a substantial difference in size variability, while *Hemitripterus americanus* has low sensitivity (< 0.8) even with relatively small size variability differences (see Lévy et al., 2024a). This suggests that the correlation between sensitivity and size variability reflects a trend rather than an absolute rule.

4.2. How can Predish results be put to practical use?

Predish quantifies predation risk solely from predator and prey total length distributions and a piscivorous diet profile, yielding a probability that a given prey-size cohort will be consumed. While this metric provides a clear, size-based indicator for species combination decisions, it does not account for other biotic or abiotic factors, such as habitat complexity, system design, or fish density, that can strongly modulate encounter rates and predation outcomes (Gerritsen and Strickler, 1977; Gill, 2003; Griffiths, 1975; Hart and Gill, 1992; Hartman and Margraf, 1992; Rawlings, 1994). Consequently, users must set their own acceptable risk-threshold in light of their specific context.

First, users need to adapt the threshold according to their specific feeding practices. In systems where fish are fed ad libitum, users may increase the threshold up to 1 or even bypass Predish recommendation assuming that the piscivorous fish will prefer pellets over potential fish prey species due to a more favorable energy cost-benefit trade-off (Hart and Gill, 1992). In contrast, under starvation or minimal feeding, predators are more likely to consume fish rather than other natural sources which offers lower energetic benefits, suggesting a much lower threshold (Goldstein, 1993; Griffiths, 1975; Hart and Gill, 1992).

Second, the threshold needs to consider the rearing system and fish density. Indeed, creating a complex rearing environment (e.g., with cavities, shelters or plants to hide) or farming fish extensively in large systems can decrease the probability of encounters between species (Beukers and Jones, 1998; Gerritsen and Strickler, 1977; Hebblewhite et al., 2005; Savino and Stein, 1989; Vagnon et al., 2021; Walters and Juanes, 1993) and thus impact the threshold. As practical recommendation, in open system such as pond, we recommend to increase the threshold (e.g., 0.5) compared to closed system such as RAS (e.g., 0). These recommendations can vary in function of the fish density and the number of refuges (Walters and Juanes, 1993) in addition to the feeding practices.

Third, species ecology should also be considered to define threshold. Predation is less likely when predator and prey occupy different zones (e.g., pelagic *vs.* benthic) (Lecocq et al., 2024; Vagnon et al., 2021). Therefore, users raising bottom-dwelling prey alongside surface-oriented piscivores can safely adopt higher thresholds.

Fourth, although ethical issues cannot be disregarded, users should consider management goals and the economic risk-tolerance when selecting the threshold. For instance, if a high-value piscivore drives

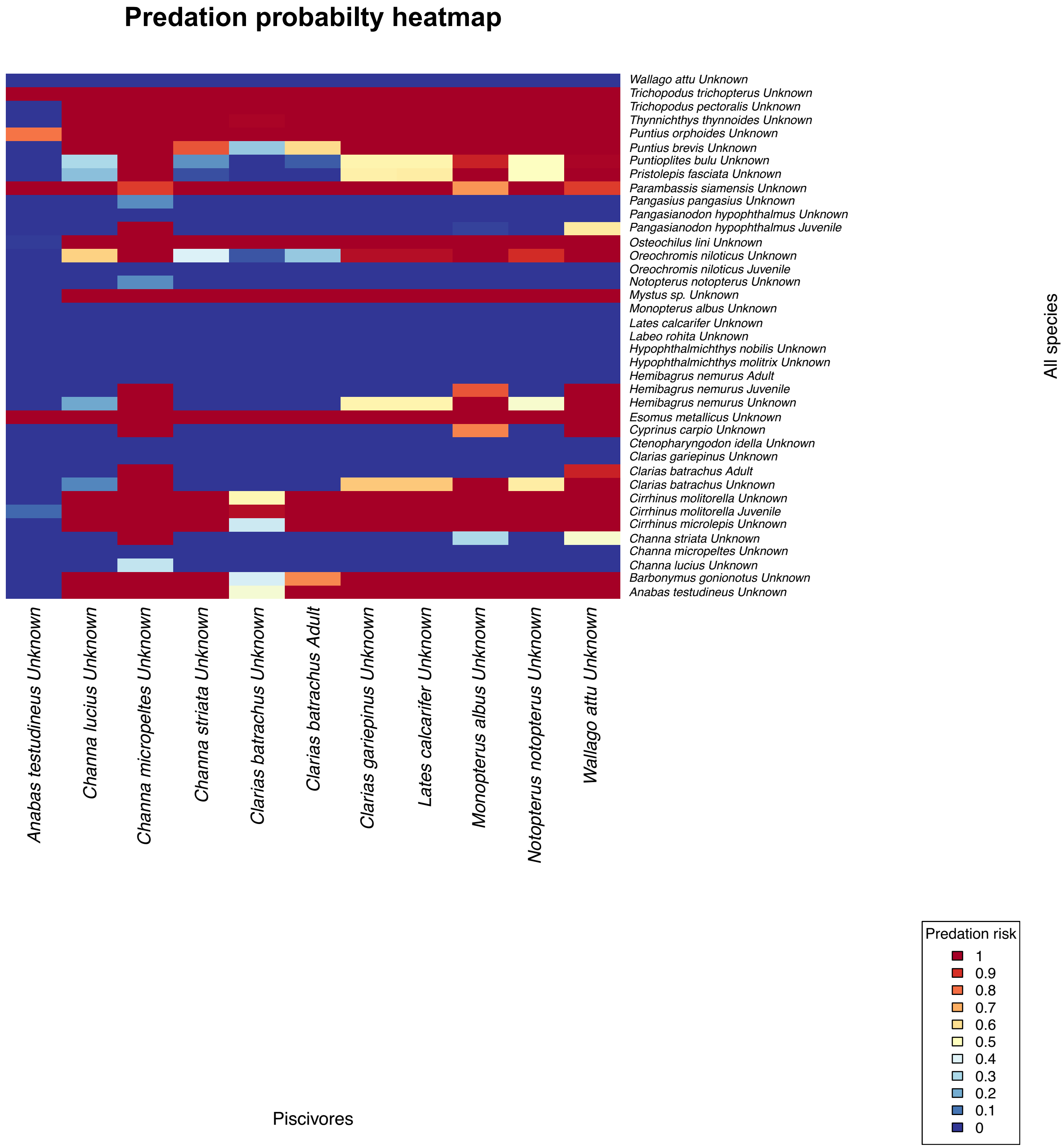

Fig. 4. Heatmap of the case study using the minimum and maximum total length of 33 freshwater fish considered for the development of fish polyculture in Cambodia. The development stage (i.e., juvenile, adult, or unknown) is indicated after the species name. The total length data used as the input, along with the range of prey size, the predation matrix, and the list of predation probability of piscivore-prey pair are available in the supporting information (Lévy et al., 2024a).

profitability, operators may tolerate higher risk. Conversely, when prey species command premium prices or when survival below ~50 % is unacceptable, thresholds should be set conservatively (e.g., < 0.5).

Finally, a predation risk probability lower than 1 indicates that certain fish of specific sizes will not be predated. This allows the user to mitigate or prevent predation risk by carefully selecting the size of fish to be stocked.

In summary, Predish serves as a cautionary decision support tool, enabling users to adjust their breeding practices if they wish to combine species with a non-zero predation risk.

Users must also be aware that the accuracy of the model's predictions depends on the quality of the data provided to Predish. If the input data is sourced from a database, the number and diversity of data sources must be considered to assess whether the intraspecific variability of the species and the quality of the information are sufficient to ensure confidence in the predictions. For example, users should recognize that the

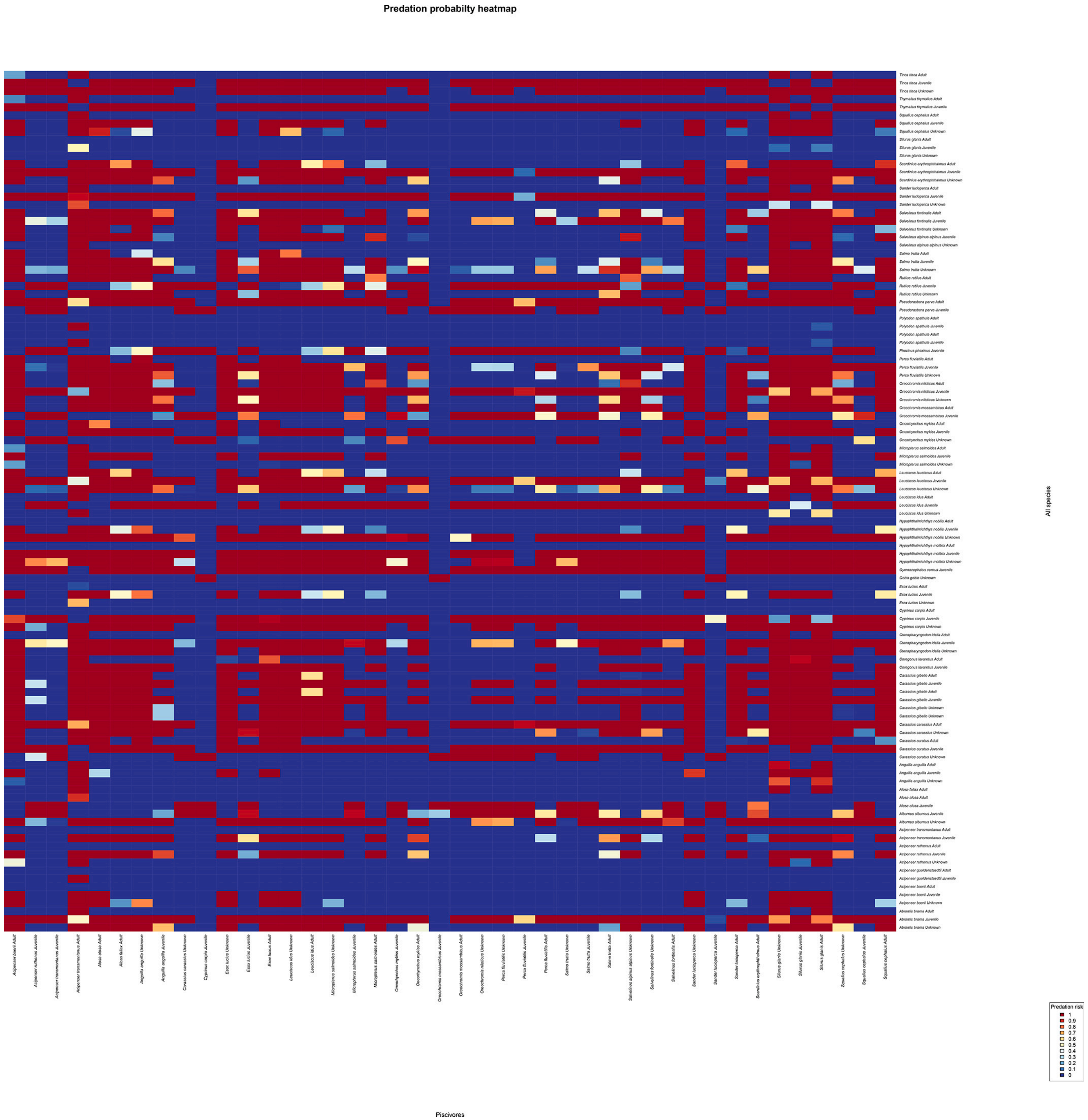

Fig. 5. Heatmap of the case study using the mean and standard deviation of total length of 44 freshwater fish already used in European aquaculture. The development stage (i.e., juvenile, adult, or unknown) is indicated after the species name. The total lengths were filled by TOFF database. The range of prey size, the predation matrix and the list of predation probability of piscivore-prey pair are available in the supporting information (Lévy et al., 2024a).

piscivorous diet data provided by TOFF may be misleading if it is based on a single source indicating fish consumption (e.g., juveniles of *Cyprinus carpio* in case study 2) or if there is insufficient data, which may cause a piscivorous species to be incorrectly classified as non-piscivorous (e.g., adults of *Anguilla anguilla* in case study 2). Moreover, the total length reported in TOFF is context-dependent (Lecocq et al., 2019), meaning that the actual size of the fish may vary according to the specific conditions of the targeted farming system, which could in turn affect the risk of predation. Therefore, it is crucial for users to verify the accuracy and relevance of the input data both before and after using the decision support tool to ensure reliable results.

In addition to interspecific predation, Predish can also be used to estimate the risk of cannibalism within a single fish stock. To do this, users can enter the total length for all individuals with a standard deviation of 0. The tool will then assess the predation risk among conspecifics, provided the species is known to exhibit cannibalistic behavior.

4.3. Limitations and perspective

The main limitation of Predish is its definition of predation, which relies on the swallowing of the whole living prey. Some fish, such as bluefish (*Pomatomus saltatrix*) (Scharf et al., 1997) and certain Anguilliformes (Helfman and Clark, 1986; Miller, 1989), can partially ingest other fish, allowing them to consume prey larger than their total length. In these cases, the prey is not entirely found in the digestive tract, making it difficult to measure the prey's total length (Scharf et al., 1997). However, in one study (Scharf et al., 2000), larger prey than the predator was found whole in the digestive tract of one piscivorous species (*Hemitripterus americanus*). As mentioned, these data were excluded from the calibration and validation datasets because swallowing whole living prey commonly means that the prey should be smaller than the predator. In fact, on the total of 4224 validation and calibration points only 17 points were excluded (i.e., 0.4 %). This might be due to an error by the authors or a unique ability of the species to swallow whole prey larger than its total length, which was not mentioned in the article. As a result, the decision support tool should only be used when the piscivore's feeding strategy is known to involve the swallowing of the whole living prey. For example, the species of genus *Anguilla* should not have been included in our two case studies (Helfman and Clark, 1986). Developing a model to account for species that utilize alternative feeding strategies, such as partial ingestion of prey, would be challenging due to the difficulty of obtaining accurate data on the characteristics of prey that are found in pieces within the digestive tracts of piscivores (Scharf et al., 1997).

Another limitation of Predish is that its estimate of predation risk is not dynamic and does not account for the growth of each species over the production cycle. Since fish growth rates vary by species (Kumolu-Johnson, 2010), this can influence the risk of predation during polyculture. For example, if the piscivore grows faster than the other species, a predation risk may emerge later in the cycle, even if it was absent initially according to the tool's output. In such cases, if farmers know the initial and final total lengths of their fish, they can use the decision support tool twice (i.e. once with the initial total length and again with the final total length) to assess whether the predation risk changes throughout the production cycle. The tool's interface could be improved in the future by incorporating growth rates based on length, although in aquaculture, growth rates are typically expressed in terms of weight (Lecocq et al., 2019).

Finally, Predish would benefit from an empirical validation of its model, using morphological traits to infer predation risk, by comparing its predicted probabilities to those obtained in dedicated predation trials rather than relying solely on literature data. For instance, one could test whether prey–predator combinations that Predish flags as high-risk indeed results in higher predation rates than combinations deemed low-risk. Such experiments are most feasible in closed system such as RAS and under low feeding rate which help control confounding factors such as refuge availability (Walters and Juanes, 1993), spatial niche partitioning (Lecocq et al., 2024; Vagnon et al., 2021), or feeding preferences (Hart and Gill, 1992). However, this kind of trials pose significant ethical challenges, as they involve exposing live prey to predators.

5. Conclusion

The predictive model of fish predation based on total length presented in this paper offers a valuable tool for stakeholders aiming to develop fish polycultures involving piscivorous species. With a demonstrated accuracy (i.e., evidenced by a TSS of 0.84 and an AUC of 0.92), this model can be applied across a wide range of fish species using the R-based decision support tool. Missing data can also be supplemented through the TOFF database (Lecocq et al., 2019). While the primary application of Predish is in designing new polycultures, it can also be used in public aquaria or to assess the risk of predation by an invasive species.

However, further improvements are possible by incorporating additional factors, such as the rearing environment, growth rate, and species behavior. It is also important to note that this model is not suitable for piscivorous species that do not swallow whole live prey.

Looking ahead, in addition to Aquadesign (Butruille et al., 2022) and Predish, new tools that account for other ecological interactions, such as competition, could offer a more comprehensive assessment of fish compatibility and complementarity. This would facilitate the development of new polyculture systems and further enhance the sustainability of aquaculture (Lecocq et al., 2024).

CRediT authorship contribution statement

S.A. Lévy: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **M. Thomas:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Conceptualization. **F. Pétronin:** Writing – review & editing, Visualization, Validation, Software, Resources, Formal analysis, Data curation. **M. Lecomte:** Resources, Methodology, Investigation, Conceptualization. **J.M. Mortillaro:** Validation, Writing - Review & Editing, Supervision, Funding acquisition. **D. Carval:** Writing – review & editing, Validation, Supervision. **T. Lecocq:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

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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Data availability

Data and script have been publicly made available at the attach file step

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