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A reproductive resilience index for pelagic fish in the southern Humboldt Current Large Marine Ecosystem

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Abstract

Efforts to manage small and medium-sized pelagic fishes (SMPF) using traditional stock assessment methods are hampered by the elusive relationship between spawning stock biomass and recruitment. We propose to compute a reproductive resilience index (RRI) in three steps: (*i*) we selected 16 biological traits related to distinct aspects of SMPF reproductive biology and characterized by a continuous (e.g., growth rate) or ordinal variable (e.g., spawning site fidelity) scored from 1 to 5 (1 representing a low contribution of the trait to reproductive resilience); (*ii*) an expert panel assigned the traits' scores to five exploited species in the southern Humboldt Current Large Marine Ecosystem; (*iii*) a Bayesian Belief Network (BBN) model was used to estimate an RRI based on the combination of the traits' scores. The BBN was used to explore environmental effects on the species' RRI, as some reproductive traits can show intraspecies variability under external forces (e.g., fishing pressure). Through proving the RRI application to detect variability in species' resilience at local time series, we show how the resulting RRI can be interpreted by fishery managers to improve the current management of SMPF.

Key words: trait-based approach, expert knowledge, Bayesian Belief Network, ecological indicator, fishery management

Résumé

Les efforts de gestion des petits et moyens poissons pélagiques (PMPP) par des méthodes traditionnelles d'évaluation des stocks sont limités par la mauvaise définition de la relation entre la biomasse du stock reproducteur et le recrutement. Nous proposons d'établir un indice de résilience reproductive (IRR) par les trois étapes suivantes : (*i*) nous avons choisi 16 caractères biologiques reliés à différents aspects de la biologie de reproduction des PMPP et caractérisés par une variable continue (p. ex., taux de croissance) ou ordinale (p. ex. fidélité au lieu de frai) notée de 1 à 5 (1 représentant une faible contribution du caractère à la résilience reproductive), (*ii*) un panel d'experts a assigné les notes pour ces caractères pour cinq espèces exploitées dans le grand écosystème marin du courant de Humboldt méridional, (*iii*) un modèle de réseau de croyances bayésien (RCB) a été utilisé pour estimer un IRR basé sur la combinaison des notes des caractères. Le RCB a été utilisé pour explorer les effets environnementaux sur l'IRR des espèces, certains caractères reproductifs pouvant présenter une variabilité intraspécifique sous l'effet de forçages externes (p. ex. la pression de pêche). En démontrant l'application de l'IRR pour détecter la variabilité de la résilience d'espèces pour des séries chronologiques locales, nous illustrons comment l'IRR résultant peut être interprété par les gestionnaires de pêches pour améliorer la gestion actuelle des PMPP. [Traduit par la Rédaction]

Mots-clés : approche basée sur les caractères, connaissances d'experts, réseaux de croyances bayésiens, indicateur écologique, gestion des pêches

1. Introduction

In fisheries science, the term productivity refers to those factors that affect both adult biomass and our ability to sustainably capture wild fish stocks (Lowerre-Barbieri et al. 2017). However, in many marine species, reproductive success may be less affected by the spawning stock biomass (SSB) than by the life-cycle spatial patterns, especially those that link adult reproduction to early life stage survival (Lowerre-

Barbieri et al. 2017). For example, stock–recruitment relationships are hard to identify in small and medium-sized pelagic fish (SMPF), whose populations can fluctuate by up to 100-fold in a brief time (Vert-Pre et al. 2013; Szuwalski et al. 2015). These changes in productivity pose a major challenge for the management of SMPF stocks where the use of reference points such as maximum sustainable yield (MSY) rely on simplifying stock stationarity assumptions (Mace 2001). On the other hand, most exploited marine fish are highly fecund and reproductive success does not have the same relationship to fecundity as seen in many harvested terrestrial species (Hedgecock 1994; Christie et al. 2010). Consequently, a clear stock–recruitment relationship is often lacking, especially in the presence of stochasticity, suggesting that adult abundance and fecundity are often poor predictors of fish recruitment (Canales et al. 2020; Caputi et al. 2021). In fact, less than 20% of the stocks have shown a pattern of productivity consistently driven by adult abundance (Vert-Pre et al. 2013) and only 39% have shown a positive relationship between recruitment and spawning biomass (Szuwalski et al. 2015).

The reproductive strategies of exploited marine fish vary widely in spatio-temporal scales, and so do factors that affect offspring survival. Fisheries science focused on SMPF has shown that we are still far from providing robust yet straightforward monitoring tools or stock assessment metrics that are easily understood and applied by fisheries managers. Despite significant advances in the scientific understanding of complex spawner–recruit ecology (e.g., the behaviour of target species (Queiroga et al. 2007; Ospina-Alvarez et al. 2012), larval transport and dispersion processes (Chen and Chiu 2003; Parada et al. 2003; Brochier et al. 2008; Ospina-Alvarez et al. 2015), and larval connectivity between subpopulations (Catalán et al. 2013; Silva et al. 2019; McGrath et al. 2020), etc.), the generated scientific knowledge has not, in general, been up-taken by decision-makers. The reproductive resilience paradigm was recently introduced to help address this problem (Lowerre-Barbieri et al. 2017). The authors defined reproductive resilience as "the capacity of a population to maintain the reproductive success needed to result in long-term population stability despite disturbances such as environmental perturbations and fishing" (Lowerre-Barbieri et al. 2017). A novelty of this eco-evolutionary framework is that it develops the concept of multidimensional spawner–recruit systems, through which the authors reviewed the commonality and diversity of biological traits affecting reproductive success and productivity in marine fishes.

Ecological resilience is the magnitude of disturbance that a system can tolerate before it shifts into a different state (stability basin) with different controls on structure and function (Holling 1973; Folke 2006; Scheffer et al. 2009). The concept of resilience can be applied to different biological and ecological scales: the resilience of an ecosystem (e.g., the resilience of a coral reef to the disruption of extractive fisheries) or the resilience of a population (e.g., the resilience of individuals of a tropical fish species that are displaced from the coral reef by a natural catastrophic event such as a storm; Bellwood et al. 2006; Hughes et al. 2010). The resilience of a community, population, or species to external drivers depends to a large extend on the biological traits exhibited by the species and their mediating role on the survival of the species, populations, or communities under changing environmental conditions (Bremner et al. 2006). A biological-traits approach to the assessment of species' vulnerability or resilience to external pressures has thus become popular in marine ecology over the past decades (Hinz et al. 2021; de Juan et al. 2022), and it is widely applied to understand species' distributions in relation with environmental variability and to develop ecological indicators as part of monitoring programs (Beauchard et al. 2017; de Juan et al. 2020).

The concept of resilience, addressed by biological-traits indicators, is attractive for fisheries management because it provides a means to quantify ecosystem and species' plasticity to natural (e.g., natural variability of the climate system) or anthropogenic stressors (e.g., fishing pressure). To maintain the resilience of fish stocks, particularly when they also face other pressures such as climate change, their geographical extent and age structure should be preserved rather than relying solely on biomass management. In consequence, a paradigm shift is expected in fisheries sciences that moves from an oversimplification of spawner–recruit relationships and management, based on harvest rules and factors that affect production, to a better understanding of complex systems and ecological conservation, based on biological traits that impact reproductive success, increasing the number of individuals reaching reproductive age. This approach does not imply leaving behind useful stock assessment techniques, for example egg production surveys (Lo 1985; Bernal et al. 2012; Dickey-Collas et al. 2012; Ospina-Alvarez et al. 2013), but the shift to a reproductive resilience approach has the advantage of a direct link to the concept of ecosystem-based management through trait-based analysis. Based on this link, changes in fishing pressure, food availability (including competition) or larval connectivity may switch-on alarm signals that could elicit proper management responses at different scales.

The coupling of fisheries science and reproductive resilience has been recently addressed for single species (*Lutjanus campechanus* (Lowerre-Barbieri et al. 2015), *Sciaenops ocellatus* (Lowerre-Barbieri et al. 2016)) and limited areas. A multiple species approach applied at regional scales could have enormous potential for fisheries management because, based on biological (reproductive) traits exhibited by the species, it can provide a simple and integrative index that allows identification of vulnerable species or reproductive resilience erosion. By merging approaches taken in SMPF and other areas of marine ecology, we propose to use the concept of reproductive resilience to select a relevant set of biological traits that, in combination, can explain the vulnerability of SMPF species to external forces, including, but not exclusively, fishing. Importantly, the nature of these species (e.g., rapid growth and boom/bust patterns) implies that some traits exhibit plasticity and may vary over short to medium time scales, with important implications for management.

The proposed approach includes the development of a species-specific reproductive resilience index (RRI) for five SMPF species in the Humboldt Current Large Marine Ecosystem (HCLME). The index is based on 16 biological traits related to variability in reproductive success for the populations of these five species. The within-trait variability was represented by a score, ranging from 1 to 5, where 1 represents the lowest contribution to reproductive resilience of the species. A panel of experts reviewed the exploited stocks of the five SMPF species in the HCLME and assigned to each species the scores for the 16 biological traits affecting their reproductive resilience. With the aim to define the reproductive vulnerability of SMPF in the HCLME, the traits' scores exhibited by the species were used to construct a Bayesian Belief Network (BBN) model to estimate an overall RRI for each species. We show how the RRI can provide managers a tool to compare reproductive resilience across species and time, and how this can help improve the management of SMPF by identifying key traits to be monitored as risk indicators of changes in population productivity.

2. Materials and methods

The first step was the selection of a set of reproductive traits relevant to SMPF. Sixteen reproductive resilience traits (see Section 2.2), occurring over ordinal or continuous scales, were ranked from 1 to 5, with 5 representing values of the trait that imply high contribution to the species' reproductive resilience. Scores for the 16 traits assigned to each species were combined to develop a species-specific RRI. These indices were evaluated for a selection of SMPF species from the HCLME (see Section 2.3). Due to the fishery and environmental characteristics prevailing in this region, the southern portion of the HCLME is an ideal scenario to introduce an RRI (see Section 2.1). A panel of 27 experts on HCLME species completed a survey to assign the 16 traits' scores to each species (see Section 2.4) and the median of the 27 experts' responses was obtained. In a third step (see Section 2.5), a BBN model was constructed to evaluate the most important traits impacting reproductive success in these species and to assess the effects of variable environmental conditions on the RRI. Lastly, we evaluated RRI temporal variability for two selected species under different population size scenarios (see Section 2.6). We selected two example species to exemplify how the information obtained through the RRI temporal dimension can complement the existing management schemes (see Supplementary material, Section B, also available in the Figshare Digital Repository (https://doi.org/10.6084/m9.figshare.16661344) for an explanation of the methods).

2.1. Case study

In its southern zone in the Pacific Ocean, the HCLME is one of the most productive regions of the world's oceans (Arcos et al. 2001; FAO 2005) (Fig. 1). In the Humboldt region, marine fisheries landings (FAO 2020) reached nine million tons in 2018, representing 11% of global production. Recent investigations have shown that bottom-up mechanisms controlling the spatial distribution of small pelagic fish in the area are more complex than temperature responses (Peck et al. 2021). It was previously suggested that environmental forcing is a major driver of regional reproductive success resulting in synchronized recruitment patterns across species (Vert-Pre et al. 2013). However, there has been little evidence of this, and recent research indicated several SMPF species did not exhibit the recruitment success (sensu transitioning to a harvestable size) expected based on remote climate drivers in the HCLME (Valdés et al. 1987; Gutiérrez et al. 2009; Salvatteci et al. 2018). Despite the diversity of species and potential underlying mechanisms controlling the populations, the fishery's management in the HCLME is based on simple single-species models, with the only fishery-independent indicator based on scientific surveys of abundance (e.g., acoustic, and egg-production method surveys).

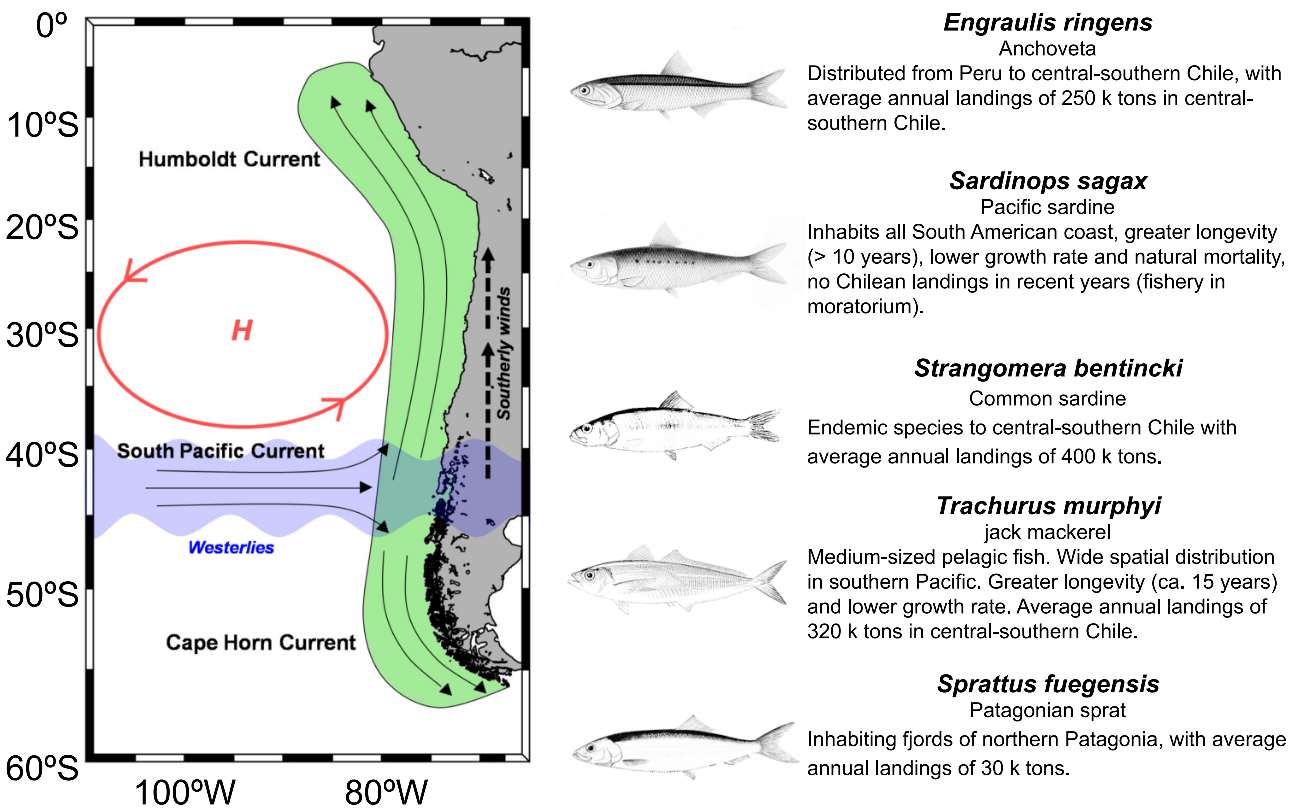
2.2. Reproductive resilience traits

Biological traits affecting reproductive resilience are those traits within a species-specific spawner–recruit system that impact reproductive success. These include traits associated with reproductive effort, demographic trends, reproductive timing (on both annual and lifetime scales), spawning site distribution and selection, larval dispersal, and recruitment variability (Lowerre-Barbieri et al. 2017). The classification of the 16 reproductive traits into these 8 broader categories facilitated the biological interpretation of the traits' scores and reproductive properties of a species that mostly contribute to increase/decrease resilience to external stressors. The traits were characterized by either continuous (e.g., growth rate) or ordinal (e.g., spawning site fidelity) variables (Table 1). To produce metrics that follow the same scale to be later integrated into an index, each reproductive trait variable, including continuous and ordinal variables, was categorized in a score scale related to the reproductive resilience of the species (Table 1). The score scale ranged from 1 to 5, where 5 represents the value of the trait with the most contribution to the reproductive resilience of the species (Table 1). The rationalization of the scoring system was as follows: "If anchoveta (evaluated species) has a high growth rate (a reproductive trait), how resilient is the species in reproductive terms?". In this example, the growth rate is determined using the coefficient of individual body growth (K) obtained from the von Bertalanffy function.

2.3. Case study species: biological surveys

Five SMPF species were chosen according to their role in the ecosystem (low and mid trophic level species), their fishing importance (over 80% of annual landings in HCLME in the last 10 years), and the amount of available biological and fishery information: (*i*) *Strangomera bentincki*, (*ii*) *Engraulis ringens*, (*iii*) *Sprattus fuegensis*, (*iv*) *Sardinops sagax*, and (*v*) *Trachurus murphyi* (Fig. 1). Most of these species have supported fisheries for decades, which has led to the development of highly informative monitoring programs and long-term data that allowed us to analyse the variability of biological and demographic indicators associated with population productivity and reproductive success. Consequently, a panel of 27 experts on the case study species could be gathered to assign the 16 reproductive traits' scores (Table 1) to the 5 SMPF (see Section 2.4). For the traits' scores assignation, we provided experts with example RRIs for two species with quite different reproductive traits. The two reference species were lightfish (*Vinciguerria lucetia*), a mesopelagic fish that inhabits the entire eastern Pacific, does not support Chilean fisheries and has a short reproduc-

Fig. 1. Location of the Humboldt Current Large Marine Ecosystem (HCLME) and the five most important small and medium-sized pelagic fish (SMPF) species for fisheries in the region. Red line and "H" represent the mean location of high-pressure South-east Pacific Anticyclone which controls the meridional wind dynamics. Blue region represents the belt of southern westerly wind. The characterisation of the HCLME was based on the works of Thiel et al. (2007), Chavez and Messié (2009), and FAO (2020). All fishery data were derived from Chile's National Fisheries and Aquaculture Service web portal (www.sernapesca.cl). The base map was made using terrain shapes from "A Global Self-consistent, Hierarchical, High-resolution Geography Database" GSHHG v.2.3.7 Released June 15, 2017. The map projection used was Mercator. *Engraulis ringens* and *Sardinops sagax* images are from the public domain work available on Wikimedia Commons (https://commons.wikimedia.org). The other fish images were created by the authors. [Colour online.]



tive life span and rapid growth ($K > 2.00$ year^{-1}), resulting in high reproductive resilience (i.e., score of 4.06); and orange roughy (*Hoplostethus atlanticus*), a deep-sea species that inhabits seamount regions and in Chile has sustained a short duration fishery (ca. 5 years) with no landings in the last 15 years. This species has slow growth ($K < 0.10$ year^{-1}), extremely late maturity, long reproductive life span, synchronous spawning and low relative fecundity, and high endemism, resulting in low reproductive resilience (i.e., score of 1.94; Fig. 2). It is interesting to note that these species are not related to SMPF and represent the extremes for the traits' ranking in scores. Consequently, the methods to estimate the RRI could be applied to any other system (e.g., pelagic and benthic).

2.4. Local expert surveys

Twenty-seven experts on the case study species' biology and fisheries completed a questionnaire launched through Survey Monkey during March to June 2019. The study was performed following the Declaration of Helsinki and was prepared under the H2020 Co-tRiP project approved by the Research Ethics Committee of European Research Council. All participants gave informed consent and participation was on a voluntary basis. Answers were anonymized so there is no way to link the statements back to individual subjects. The survey was designed to allow respondents to score each of the 16 reproductive traits from 1 to 5 (Table 1) and scores for the reference species outlined above were provided as guidance (Fig. 2). Respondents were also asked to score the level of confidence they felt with their answers on a scale from 0 to 100, where 100 represents high confidence in their response. Survey data was prepared and analysed using "plyr" (Wickham 2011) and "dplyr" (Wickham et al. 2021) packages in R language and environment for statistical computing (version 4.1.2, released 2021-11-01; R Core Team 2021).

2.5. Bayesian Belief Network development

A BBN model was constructed to estimate an overall RRI based on the combination of the eight trait categories (Table 1) for the five SMPF species. Developed as essentially qualitative graphical models, BBNs are especially powerful in explaining the causal relationships between variables (nodes) via conditional probability distributions (CPDs) (Jordan 1998).

Table 1. Reproductive traits of small and mid-sized pelagic species used for the reproductive resilience index.

Category	Trait	Type	Very low (1)	Low (2)	Medium (3)	High (4)	Very high (5)	Unit	Definition
Demographic trends	Growth rate	Continuous	<0.10	0.10–0.30	0.30–0.60	0.60–2.00	>2.00	$year^{-1}$	Coefficient of individual body growth (*K*) obtained from von Bertalanffy function.
	Natural mortality	Continuous	<0.05	0.05–0.20	0.20–0.70	0.70–1.50	>1.50	$year^{-1}$	Relative instantaneous rate of decreased abundance due to causes other than fishing.
Larval dispersal potential	Predation in early life stages	Discrete	Discrete variable—expert opinion from Very low (1) to Very high (5)						Level of impact of interspecific predator–prey relationships on survival of eggs, larvae, and juveniles.
	Distance between spawning and nursery habitats	Continuous	>80%	60%–80%	40%–60%	20%–40%	0%–20%	%	Proportion of the total distribution of the stock that constitutes the separation between spawning and nursery areas.
Recruitment variability	Variability in spawning stock biomass (SSB)	Discrete	Discrete variable—expert opinion from Very low (1) to Very high (5)						Breaks in the SSB from historical time series.
	Relationship between stocks and recruits	Discrete	Discrete variable—expert opinion from Very low (1) to Very high (5)						Relationship between SSB and the subsequent recruitment in numbers or the year class strength.
Reproductive effort	Energy devoted to reproductive processes affecting spawning	Continuous	<50	50–200	200–400	400–600	>600	$eggs \cdot g^{-1}$	Relative fecundity, defined as the number of eggs produced per gram of body weight.
	Reproductive migration	Continuous	>80%	60%–80%	40%–60%	20%–40%	0%–20%	%	Proportion of the total spatial distribution of stock that constitutes a displacement for reproductive purposes.

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Table 1. (*concluded*).

Category	Trait	Type	Very low (1)	Low (2)	Medium (3)	High (4)	Very high (5)	Unit	Definition
Reproductive timing (annual scale)	Spawning interval	Continuous	>20	15–20	10–15	5–10	<5	days	Estimated time between spawning batches of an average female within the spawning season.
	Spawning season duration	Continuous	Total spawners	<1	1–3	3–6	>6	months	Duration of spawning season within an annual reproduction cycle.
Reproductive timing (lifetime scale)	Sexual maturity	Continuous	>10	5–10	3–5	1–3	<1	years	Age/length at which 50% of the individuals are sexually mature and contribute to reproduction.
	Reproductive life span	Continuous	0%–20%	20%–40%	40%–60%	60%–80%	>80%	%	Proportion of life span reproductively active.
Spawning site distribution	Size of the spawning area	Continuous	0%–20%	20%–40%	40%–60%	60%–80%	>80%	%	Proportion of the total stock distribution that constitutes a spawning area.
	Spawning site diversity	Discrete	Discrete variable—expert opinion from Very low (1) to Very high (5)						Number of spawning areas identified within the stock distribution area.
Spawning site selection (life-cycle scale)	Distance between nursery and adult foraging habitats	Continuous	>80%	60%–80%	40%–60%	20%–40%	0%–20%	%	Proportion of the total distribution of the stock constituting the separation between adults feeding and juvenile nursery grounds.
	Consistent use of spawning habitats	Discrete	Discrete variable—expert opinion from Very low (1) to Very high (5)						Consistent use of spawning grounds over time (i.e., multiple spawning seasons) for the stock.

Note: Traits are scored according to their contribution to the reproductive resilience of the species, with a 5 indicating high resilience (e.g., 5 = fast growth) and 1 indicating low resilience (e.g., 1 = slow growth).

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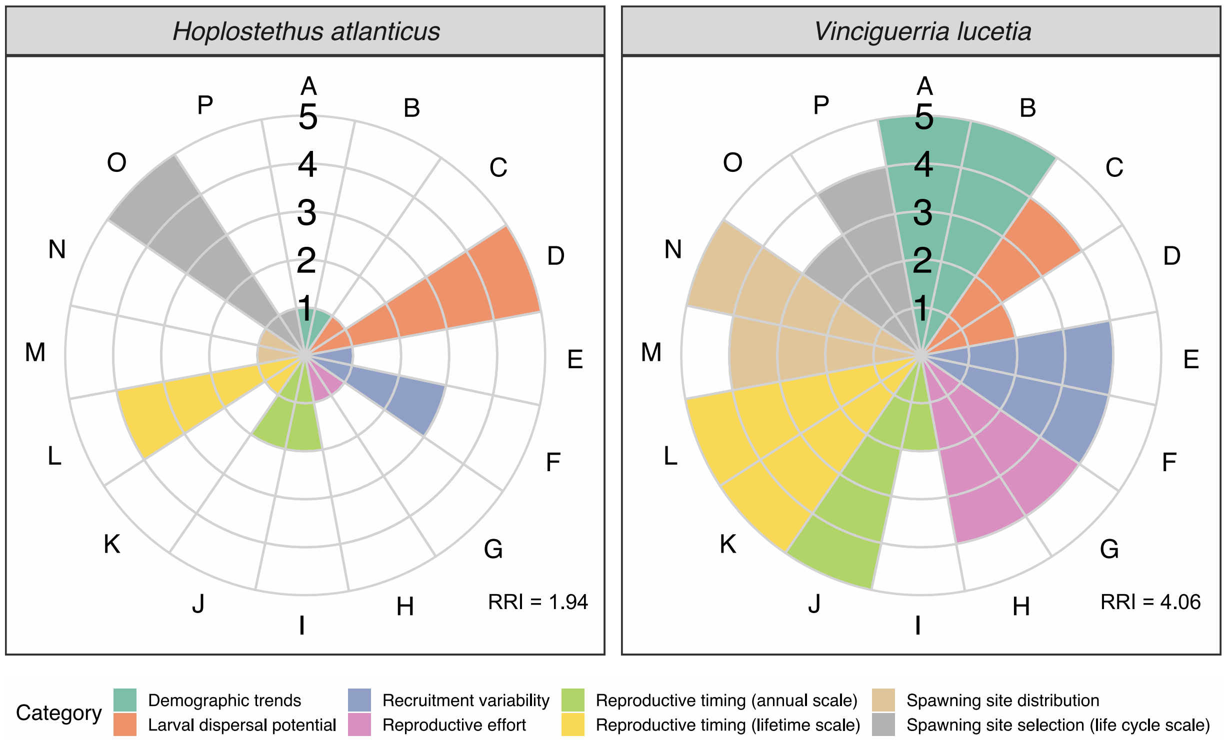
Fig. 2. Reproductive resilience index scores for orange roughy (*Hoplostethus atlanticus*) and the lightfish (*Vinciguerria lucetia*), provided as a reference for trait scoring for the small and medium-sized pelagic fish (SMPF) panel. The graph shows radial plots for each species and the eight categories (colours) of traits. Letters from A to P represent the traits. Legend: (A) growth rate; (B) natural mortality; (C) predation in early life stages; (D) distance between spawning and nursery habitats; (E) variability in the spawning stock biomass (SSB); (F) relationship between stock and recruits; (G) energy devoted to reproductive processes affecting spawning; (H) reproductive migration; (I) spawning interval; (J) spawning season duration; (K) sexual maturity; (L) reproductive life span; (M) size of spawning area; (N) spawning site diversity; (O) distance between nursery and adult foraging habitats; and (P) consistent use of spawning habitats. [Colour online.]



In BBNs, the processes are not necessarily explicitly captured; on the contrary, the expected probabilities of the outcomes are based on combinations of events (Gelman et al. 2013). Moreover, the probabilities coming from the combination of qualitative and quantitative data can be assigned to the BBN nodes and could come from combinations of expert opinions, empirical field data, or previous experiences cited in the literature. Since BBNs provide a probability of an outcome rather than a discrete (deterministic) one, a mean (expected) outcome and a confidence interval can be determined (Ellison 2004). How each input is combined to report the probability of an outcome is determined by a weighting combination rather than by a numerical estimation process. In other words, although possible, it is not necessary to develop formal structural relationships linking the different components of the model, allowing for nonlinear or discontinuous results if deemed appropriate (McCann et al. 2006).

BBNs consist of two structural models: (*i*) a conceptual model (directed acyclic graph, DAG) that represents the best available knowledge about the functioning of the system and representing the links between the model variables (called nodes) and (*ii*) conditional probability tables (CPTs) and CPDs, which determine the strength of the links in the DAG (Jensen 2001). Directed arrows representing presumed cause–effect relationships between system variables indicate the statistical dependence between nodes. Each arrow starts in a parent node and ends in a child node. Feedback arrows from child nodes to parent nodes are not allowed. Experts can develop the DAG based on an understanding of the system or based on empirical observations (Jensen 2001). This initial structure of the DAG is the basis for an operational BBN. The probabilistic relationships between the model nodes are specified in the CPTs and CPDs (Rohmer 2020). The CPTs and CPDs can be parameterized based on expert opinion, derived from mathematical or logical equations, or learned from the relevant empirical data structure. The nodes are restricted to a limited number of states that describe the probability distribution of system variables (e.g., a node can be based on discrete data, with incremental or decremental states or levels, or continuous data) (Rohmer 2020). Probability distributions in the CPT or CPD fall between 0 and 1, so that the sum of the state values adds up to 1 (100%).

In our study, the DAG was developed iteratively based on the system understanding of the research team based on the responses from the local experts' survey. Then, based on the mean of each of the 16 reproductive traits' scores assigned by 27 experts, a model was constructed by BBN to estimate an overall RRI for each of the five study species. A causal map, as a DAG, is brought out via the results of weighted means and experts' opinions (Fig. 4). To ease a quick inspection of the traits, and trait categories, contributing to a greater or lesser extent to the RRI for each species, radial plots were constructed with the means of each trait present in the DAG. Radial plots summarizing the results were designed using "ggplot2" package (Wickham 2016) in R language. However, the DAG remains the most complete and appropriate representation for selecting critical traits contributing to the RRI due to the probabilistic information it provides. A sensitivity analysis was performed to identify to what degree the variability in its posterior probability distribution was explained by other variables (i.e., rank order) (Marcot et al. 2006). This was achieved by calculating the entropy reduction for the model node "RRI". In other words, sensitivity analysis identified the reproductive traits that have the most significant impact on the RRI for each species. The highest variance and entropy reduction scores correspond to the reproductive traits that have the greatest impact on the RRI. The BBN modelling and sensitivity analysis were conducted using the commercial software Netica (Norsys, version 5.24).

To compare the RRI and place it in the context of other extensively used indices based on stock management, we extracted information from Fishbase. For comparative purposes, we tabulated the RRI and the Fishbase indices of intrinsic vulnerability and resilience to fishing pressure for the five species studied and the two species used as reference. For more information on the Fishbase indices, see the Supplementary material, also available in the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.16661344.

2.6. Temporal analysis of the RRI

To analyse the RRI response to changes in stock size, the research team evaluated reproductive traits and assigned scores based on literature review for contrasting periods in stock size for two selected data-rich species: anchoveta (*Engraulis ringens*) and common sardine (*Strangomera bentincki*) for the periods 2001–2007 and 2009–2016. These two periods represent contrasting population status of these species (Supplementary material, Section B), as in the first period anchoveta was the dominant species with spawning biomass levels that far exceeded the MSY, while the common sardine reached levels close to collapse. During the second period, the anchoveta steadily declined until collapsing, while the common sardine increased its spawning biomass above MSY.

3. Results

3.1. Reproductive resilience scores

Confidence in respondents' values were high with less than 10%–15% of participants assigning less than 50 to a score. The mean, median, standard deviation, interquartile range (IQR), and the 80% and 90% confidence levels from the 27 experts' responses were obtained for each trait per species. The standard deviation was below 1. The highest standard deviations were observed for the questions: (*i*) predation in early life stages, (*ii*) reproductive migration, (*iii*) distance between nursery and adult foraging habitats, (*iv*) spawning site diversity, and (*v*) variability in the SSB. The most uncertain species are *Engraulis ringens*, *Strangomera bentincki*, and *Sardinops sagax*. Results did not vary when responses with certainty below 50 were removed. Consequently, all the data were included in the later analysis to embrace the diversity of experts' opinions.

Target SMPF species exhibited moderate variability in reproductive traits, compared to the reference species. Those species with the highest scores (i.e., highest reproductive resilience) were *Engraulis ringens* and *Strangomera bentincki*, and the species with lowest scores was *Trachurus murphyi*. Variability in specific traits was observed among species, particularly in reproductive timing and frequency. Overall, scores for most traits fell between two and four (Fig. 3). The high reproductive resilience scores in *Engraulis ringens* and *Strangomera bentincki* were driven by reproductive timing traits (both at the annual and life-scales); demographic trends traits also scored high for *Engraulis ringens,* while the distance between spawning and nursery and nursery and foraging contributed to high scores in *Strangomera bentincki.* The lowest scores exhibited by *Trachurus murphyi* were driven by spawning site selection-related traits and by reproductive migration and distance between spawning and nursery (Fig. 3).

The derived BBNs represented the reproductive resilience traits, categorization, and RRI, including the posterior probability distributions of the compiled models (Fig. 4). These distributions reflect the current beliefs of each node and the resulting RRI score. The most resilient species was *Engraulis ringens* (RRI = 3.68) and the least resilient species, also showing the most parsimonious RRI, was *Trachurus murphyi* (RRI = 2.97). In other words, *Trachurus murphyi* had the least variability in experts' responses and derived RRI. On the other hand, the RRI of *Engraulis ringens* was characterized by high variability between the categories' scores. The orange roughy (*Hoplostethus atlanticus*, with low reproductive resilience, RRI = 1.94) and the lightfish (*Vinciguerria lucetia*, with high reproductive resilience, RRI = 4.06) provide context for the results (Fig. 5 and Table 2).

For comparison, we tabulated the RRI next to Fishbase's intrinsic vulnerability and resilience to fishing pressure indices for the five species under study and the two species used as reference (for a more in-depth explanation of the FishBase index, see Supplementary material, Section A). The ranking between the Fishbase vulnerability and resilience indices is similar. However, the RRI differs in the position of *Sprattus fuegensis*, which drops two positions, from being the most resilient species to position 3 (out of 5) among the species under study. It is interesting to note that *Sprattus fuegensis* was identified in southern Chile in 2006, while previously it was recorded as *Strangomera bentincki*. Because of this, there may be misinterpretation of the scores in the survey or there may be uncertainty in the Fishbase index (see Supplementary material, Section A: Table S1, also available in the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.16661344).

3.2. Sensitivity analysis

In a sensitive analysis of a BBN, the highest variance and entropy reduction percentages correspond to the reproduc-

Fig. 3. Reproductive traits for small and medium-sized pelagic fishes in the Humboldt Current Large Marine Ecosystem (HCLME). Radial plots for each species and each of the eight categories used; letters from A to P to represent the traits. Legend: (A) growth rate; (B) natural mortality; (C) predation in early life stages; (D) distance between spawning and nursery habitats; (E) variability in the spawning stock biomass (SSB); (F) relationship between stock and recruits; (G) energy devoted to reproductive processes affecting spawning; (H) reproductive migration; (I) spawning interval; (J) spawning season duration; (K) sexual maturity; (L) reproductive life span; (M) size of spawning area; (N) spawning site diversity; (O) distance between nursery and adult foraging habitats; and (P) consistent use of spawning habitats. [Colour online.]

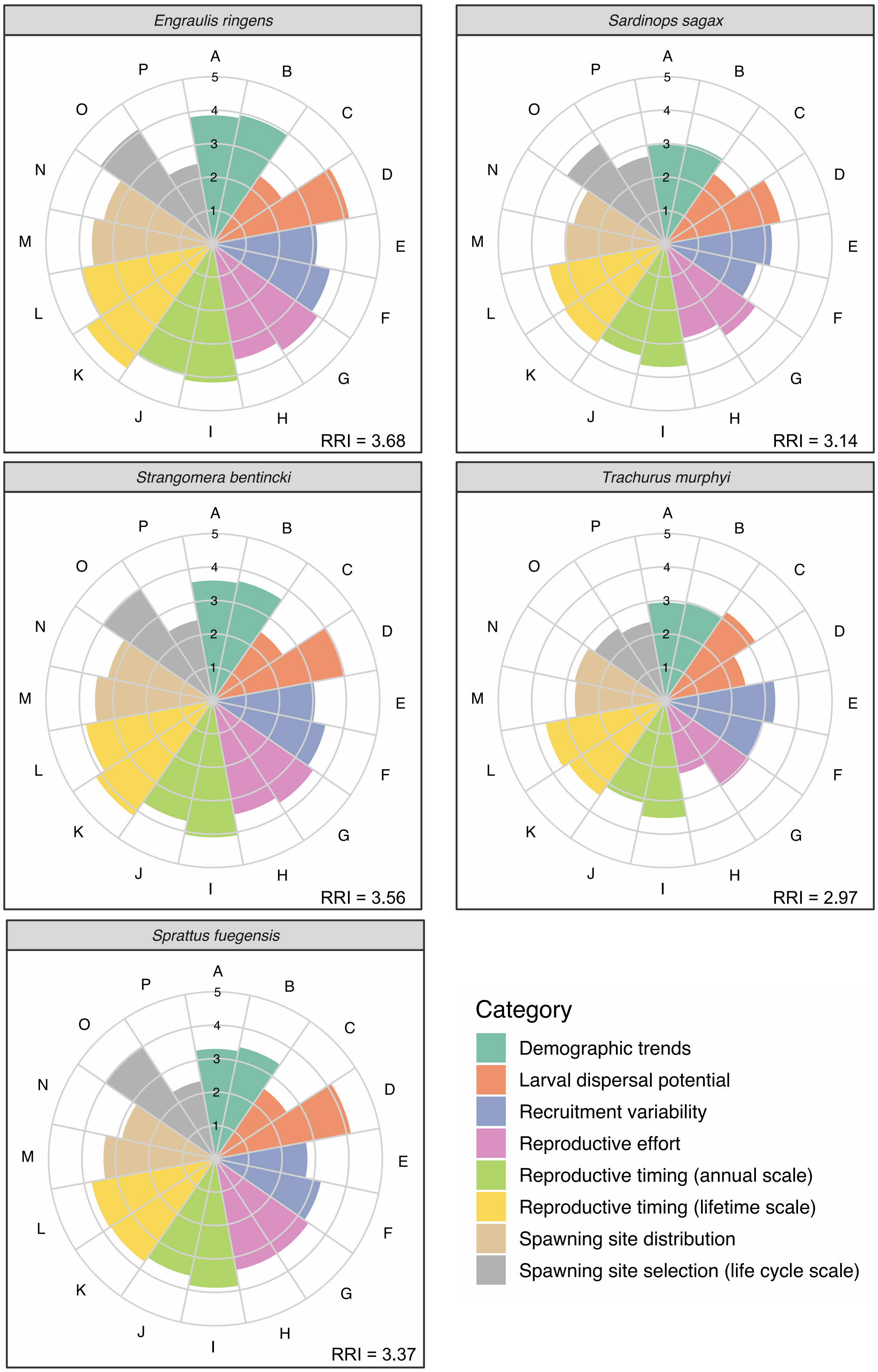


Fig. 4. Bayesian Belief Network model for *Engraulis ringens*, describing the influence of the 16 reproductive traits (outer boxes) on the eight reproductive categories (inner boxes) and reproductive resilience index (RRI) score (centre). Posterior probability distributions of the compiled net are shown for all nodes. The BBN results for the other species can be found in Appendix Figs. A1–A4; also available in the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.16661344. [Colour online.]

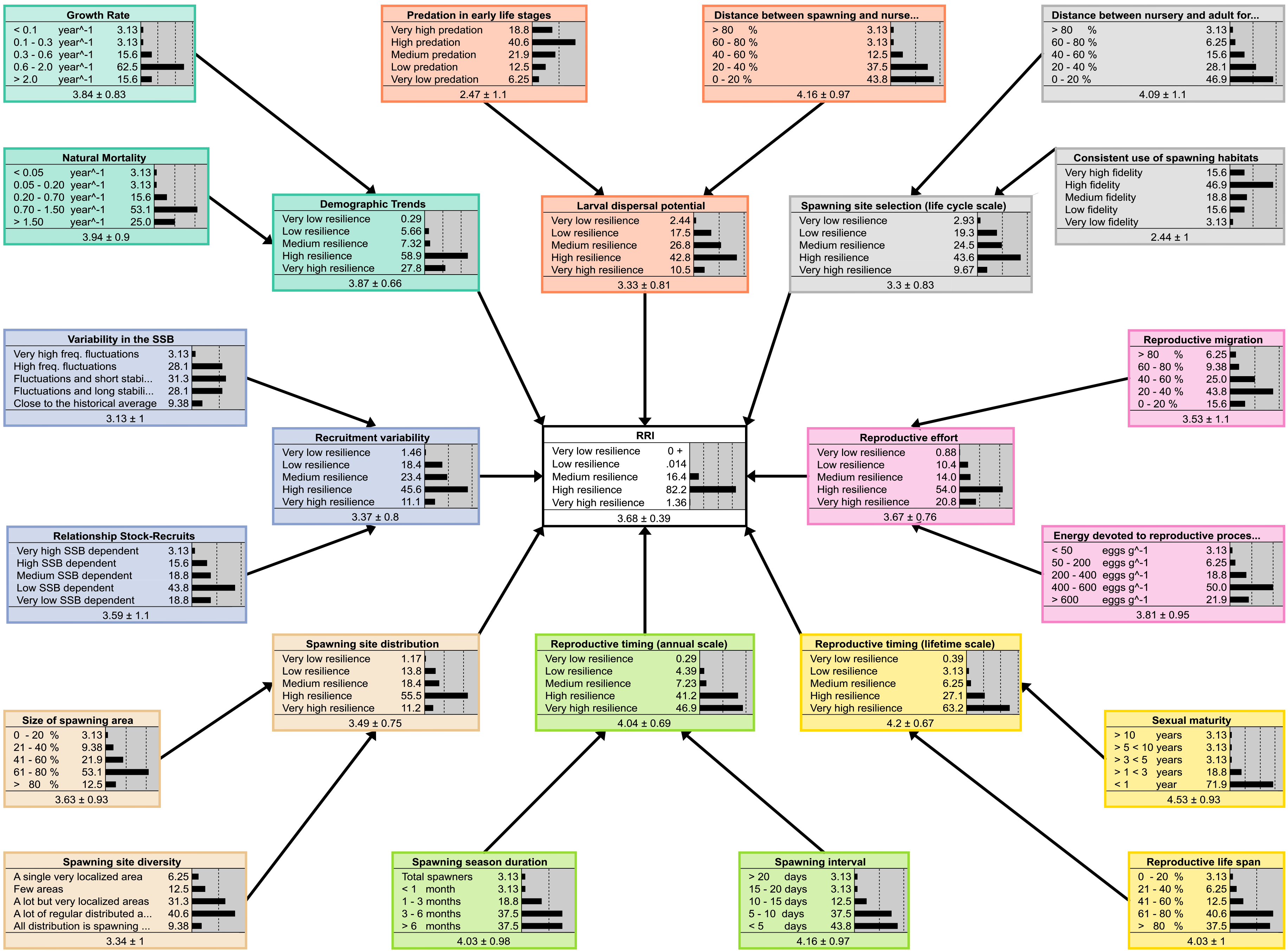


Fig. 5. Distribution of reproductive resilience index (RRI) values, as determined from score statistics for the five study species and the two reference species. The uncertainty distribution results from the use of BBN (see Fig. 4 and Appendix Figs. A1–A4) integrates information based on quantitative data and expert opinion into probability distributions for each variable, which are appropriately combined into a single RRI measure. [Colour online.]

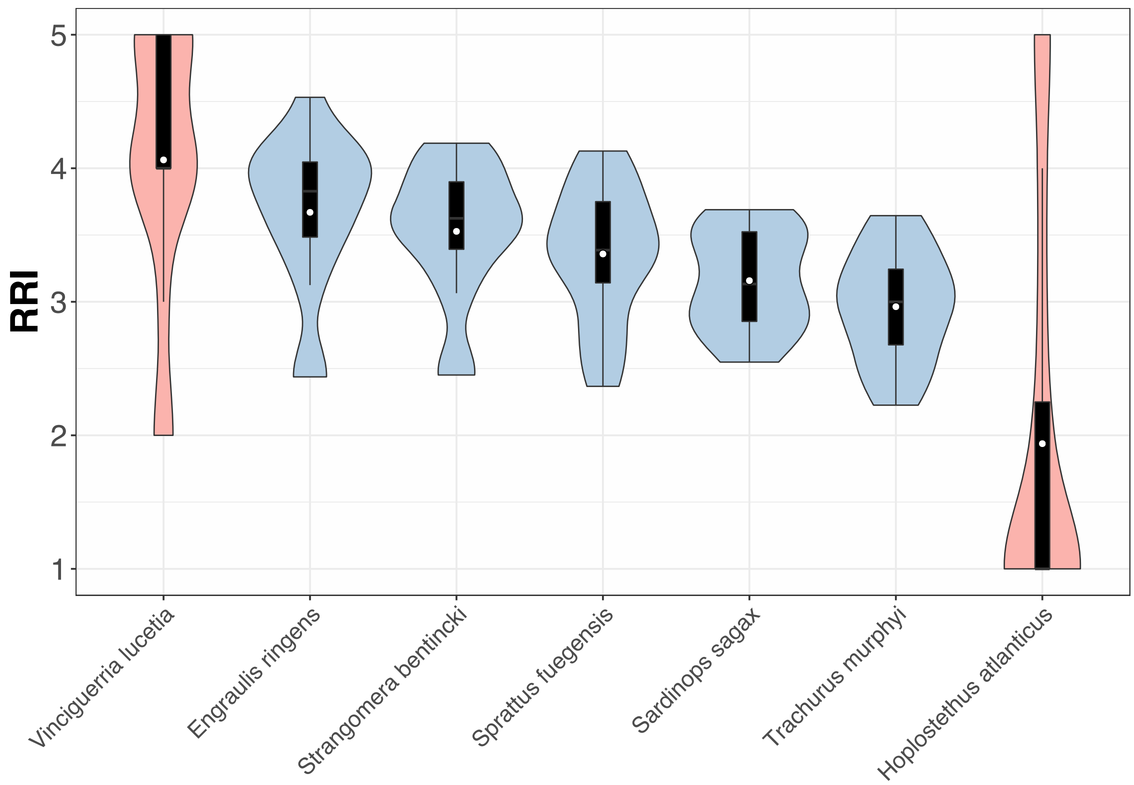


Table 2. Reproductive resilience index (RRI) mean, standard deviation (SD), median, interquartile range (IQR), 80% and 90% confidence levels for the five study species and the two reference species, denoted with an asterisk, to illustrate the extremes of species-specific RRI statistics.

					80% conf. level		90% conf. level	
Species	RRI mean	RRI SD	RRI median	IQR	Lower	Upper	Lower	Upper
Vinciguerria lucetia∗	4.06	—	4.06	—	—	—	—	—
Engraulis ringens	3.68	0.39	3.73	0.49	3.08	4.12	2.72	4.19
Strangomera bentincki	3.56	0.44	3.63	0.65	2.87	4.09	2.67	4.17
Sprattus fuegensis	3.37	0.47	3.35	0.80	2.75	4.03	2.63	4.16
Sardinops sagax	3.14	0.41	3.09	0.51	2.69	3.79	2.61	4.10
Trachurus murphyi	2.97	0.37	2.99	0.46	2.62	3.36	2.04	3.83
Hoplostethus atlanticus∗	1.94	—	1.94	—	—	—	—	—

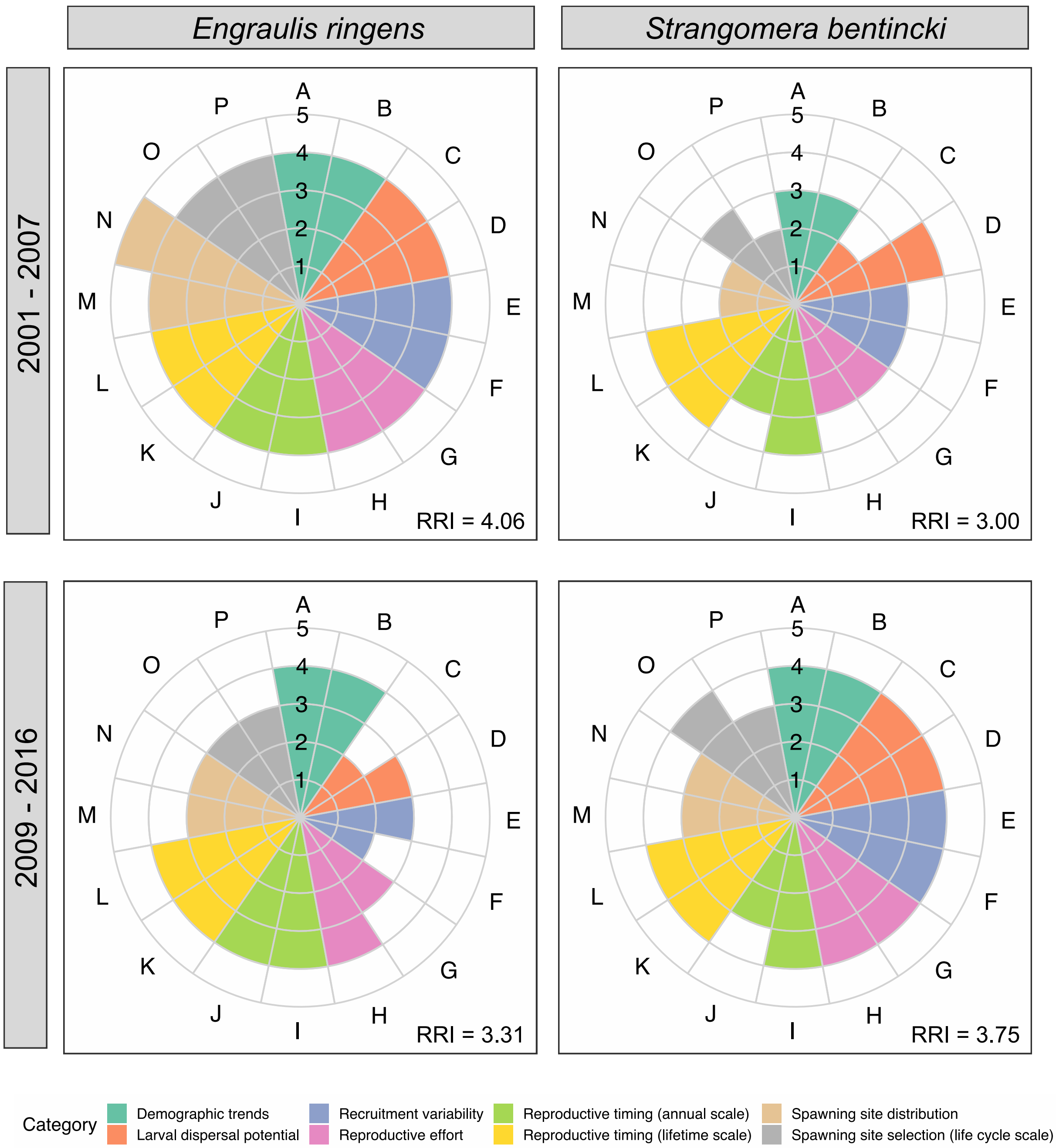
Note: The species are listed from highest to lowest mean RRI value.

tive traits that have the greatest impact on RRI. In the present study, the traits with higher contribution to variance reduction were "Distance between nursery and adult foraging habitats"; "Relationship between stocks and recruits"; "Reproductive migration"; "Distance between spawning and nursery areas" and "Spawning site diversity", while the categories that most contributed to the variance reduction were "Spawning site selection (life-cycle scale)" (4.8%); "Larval dispersal potential" (4.5%); and "Recruitment variability" (4.4%). All reproductive traits and category nodes showed a percentage of variance reduction greater than 1% for the five species. For detailed information on sensitivity analysis, see Supplementary material, Section C: Tables S3–S8, also available in the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.16661344).

3.3. RRI temporal variability under variable population size scenarios

Anchoveta and common sardine have evidenced temporal variability in the RRI linked to the fish stock state (see Fig. 6 and the Supplementary material: Section B, Table S2, and Fig. S1, also available in the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.16661344). For ex-

Fig. 6. Reproductive traits and radial plots for reproductive resilience index (RRI) for anchoveta (*Engraulis ringens*) and common sardine (*Strangomera bentincki*) in the Humboldt Current Large Marine Ecosystem (HCLME) under two contrasting time periods: 2001–2007 (upper panel) and 2009–2016 (lower panel). A to P represent the traits and values go from low (1) to high (5) resilience for each trait: (A) growth rate; (B) natural mortality; (C) predation in early life stages; (D) distance between spawning and nursery habitats; (E) variability in the spawning stock biomass (SSB); (F) relationship between stock and recruits; (G) energy devoted to reproductive processes affecting spawning; (H) reproductive migration; (I) spawning interval; (J) spawning season duration; (K) sexual maturity; (L) reproductive life span; (M) size of spawning area; (N) spawning site diversity; (O) distance between nursery and adult foraging habitats; and (P) consistent use of spawning habitats. [Colour online.]



ample, anchoveta exhibited an RRI of 4.06 for the high population size scenario (2001–2007), which contrasted with an RRI of 3.31 for a smaller population size (2009–2016) (Fig. 6). These differences were driven by changes in the categories “Spawning site distribution, “Spawning site selection (life-cycle scale)”, “Larval dispersal potential”, and Recruitment variability”, which had lower resilience scores during the 2009–2016 period (Fig. 6). On the other hand, the common sardine showed a similar response to population size changes with an RRI of 3.00 during the 2001–2007 period (low abundance) and an RRI of 3.75 during the 2009–2016 period (high abundance) (Fig. 6). The main sources of differences were attributed to the categories "Recruitment variability", "Reproductive effort", and "Larval dispersal potential", which were given higher resilience scores during the 2009–2016 period (Fig. 6).

3.4. Application of the RRI in the management of SMPF

A simplified example of the application of the RRI in the management of SMPF is summarized in Fig. 7. The baseline RRI for a species was estimated from an experts' survey (see Section 2.4 for details), and it can be annually updated and compared with the baseline RRI. If the new RRI is equal or higher than the baseline RRI, the current fishery management is considered adequate. However, if the RRI decreases with respect to the baseline RRI, the critical reproductive traits (i.e., traits that cause the decrease) are identified and management actions are implemented in two ways. The first way is through the incorporation of the RRI in the harvest control rule (HCR) (Fig. 7). Threshold values for the species' RRI must be previously defined to establish target or limit levels. If the RRI is below these thresholds, the HCR activates a management action such as a total allowable catch (TAC) reduction or fishing effort control. The second way is connected to the monitoring of the fishery, where changes in the critical reproductive traits, along with the indices usually used (e.g., GSI, sexual maturity), are identified in a timely manner to activate fishing bans or temporary closures of fishing zones (Fig. 7). Therefore, the RRI (with its components, the reproductive traits) can function as a performance indicator of the stock reproductive status. The estimated RRI, against the relevant reference points, could inform of effective management actions to be incorporated in the broader management strategy currently in place in Chile (Fig. 7).

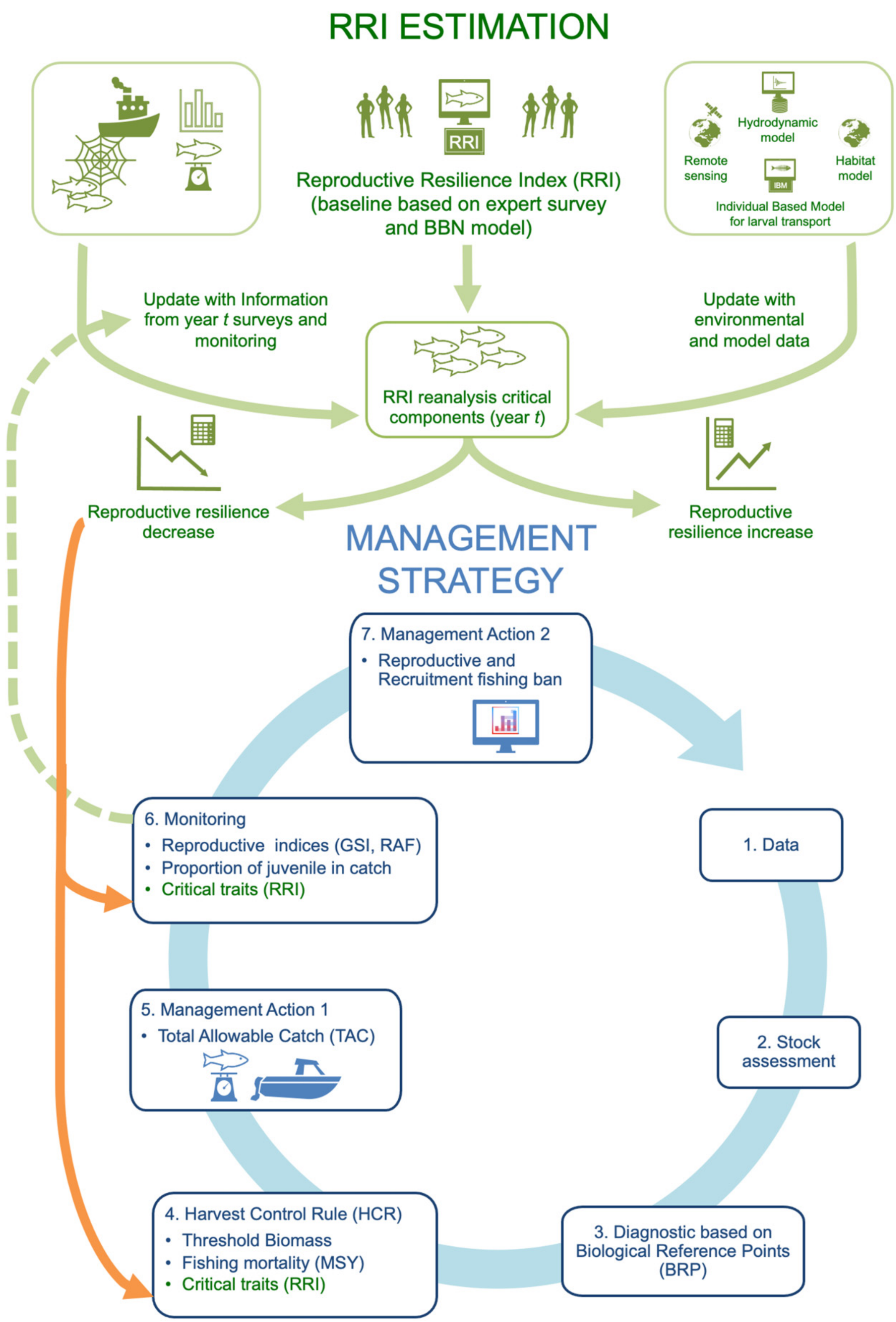
4. Discussion

Trait-based analyses are widely applied to understand species' distribution in relation to environmental variability; therefore, applied marine ecology has traditionally focussed on these approaches for the development of ecological indicators as part of monitoring programs (Beauchard et al. 2017; de Juan et al. 2020). However, to our knowledge, no study has used a trait-based approach to produce an index of reproductive resilience for pelagic fish (see Section A of Supplementary material). The RRI is based on 16 continuous or discrete traits having a species-specific score that represents the contribution of the trait to the reproductive resilience of the species. The RRI can be illustrated in a DAG (Fig. 4) or simply in a radial plot that groups traits into eight main reproductive categories (e.g., demographic trends, larval dispersal potential, recruitment variability), similar to other trait-based indices developed to assess the environmental status of marine ecosystems (e.g., Rice et al. 2012), including the vulnerability of demersal fish assemblages (de Juan et al. 2020). An average of all scores is calculated to obtain an RRI for each species; the RRI can allow decision-makers to rank the species from a fished assemblage in terms of their reproductive resilience and vulnerability to external forces. This index provides easy-to-communicate information for managers and makes it possible to measure erosion in reproductive resilience from a "virgin" stock or over time, as this work illustrates with two commercially important small pelagic fish. Despite the assumed high resilience of small and medium pelagic fish, the large fluctuations in their abundance over time suggest they do not meet equilibrium assumptions and may be sensitive to a changing climate (Peck et al. 2021). These species are also particularly well suited for the analysis of changing reproductive-related traits, because in many cases large spatial and temporal data sets on reproductive components exist (e.g., Daily Egg Production Methods (DEPMs) surveys).

The five species exploited in the HCLME have high reproductive resilience levels compared to the low resilience reference species (*Vinciguerria lucetia*). However, reproductive resilience traits associated with greater vulnerability were identified: the selection of spawning sites, variability in the spawning stock, and high environmental influence on early survival. These traits were also the most sensitive in the temporal analysis (see Supplementary material, Section B). Changes in these traits may trigger a decline in abundance and alterations in the synchrony of some biological processes such as the size-dependent spawning season duration (Cubillos and Claramunt 2009), the coupling of the reproductive cycle with favourable environmental conditions for recruitment (Cubillos 2001), or the spatial distribution patterns (Aedo et al. 2020). Among the species analysed in this study, small coastal pelagic fishes (*Engraulis ringens* and *Strangomera bentincki*) showed the highest estimated RRI values (Table 2) due to traits such as rapid growth, high fecundity, early maturity, and long reproductive span. In the case of *Sprattus fueguensis*, an endemic species from northern Patagonia, where there are environmental conditions associated with the influence of estuarine zones (low temperatures, high influence of fresh water, etc.), the RRI was slightly lower than the most resilient species *Engraulis ringens* and *Strangomera bentincki* (Table 2), and the differences were mainly associated with demographic trends such as lower growth rate and higher natural mortality. The species with the lowest estimated RRI was *Trachurus murphyi* (Table 2), a medium-sized pelagic fish, whose life history and spatial distribution differ from the other species. The traits driving this RRI were a shorter spawning season (Leal et al. 2013), long migrations, with up to 1500 km between feeding and spawning areas (Arcos et al. 2001) and up to 2000 km between spawning and nursery grounds, resulting in connectivity tied to large-scale oceanographic processes (Vásquez et al. 2013). All these characteristics, which involve the interaction between fisheries and a species' biology, can lead to dynamic instability in populations due to negative effects on their life history, abundance, and ecological traits (Hsieh et al. 2006).

Fishing can cause significant alterations in the demography and status of fish stocks, however, even in regions where scientific advice has contributed to sustainable exploitation, caution must be exercised. A meta-analysis on 38 species on the northeast Atlantic coast reported that the exploitation of the juvenile fraction has a negative effect on the current condition of the stocks, placing the fishing activity at levels below the precautionary limits (Vasilakopoulos et al. 2011).

Fig. 7. A proposal for the application of the reproductive resilience index (RRI) in the management of small and medium pelagic fisheries in Chile. The RRI estimation is shown in green and the management strategy in blue. The baseline RRI is based on a survey of experts. Each year, critical reproductive traits (i.e., traits that may be changing significantly) are identified using information from continuous monitoring (box 6, green dashed line) and environmental and modelling data. A revised RRI is then calculated and compared with the baseline RRI. If it decreases, the critical traits identified can be incorporated (orange lines) as additional information in the Harvest control Rule and Monitoring steps (boxes 4 and 6) and management action decisions can be adapted (boxes 5 and 7). If the RRI increases or remains unchanged, the management strategy begins with the data collection (box 1) from the commercial fishery and scientific surveys for year *t* – 1. All icons and shapes are royalty-free available on Microsoft 365. [Colour online.]



Similarly, it has been proposed that age truncation from fisheries can alter the dynamics and basic processes of exploited populations and reduce natural buffers to adverse environmental conditions (Anderson et al. 2008), leading to fluctuations that precede a systematic decline in stock abundance (Anderson et al. 2008). The traits linked to reproductive resilience can change rapidly due to fishing and environmental effects and, therefore, must be periodically reviewed in relation to the context of the analysed stock. SMPF suffer large fluctuations at several scales (Alheit and Niquen 2004). The causes of these fluctuations can be attributed to different links between the environment and life-cycle spatio-temporal components, which are often not integrated into traditional stock assessments. The RRI supplies a means to do so. High variability in SMPF recruitment imposes a major challenge for traditional stock assessment where early indicators of change are needed for tactical decisions such as the adoption of HCRs for catch quota allocation or management decisions such as determining of biological reference points. Thus, the ability of the RRI to show which traits most strongly influence the reproductive success of species becomes a useful tool to establish indicators that can be monitored and tracked over time in a pragmatic way to complement the traditional stock assessment, strengthening the advisory capacity for the fisheries management system.

Fisheries management involves developing recovery plans when stocks are being depleted due to fishing pressure. This implies determining the time horizon for the recovery, through the development and application of recovery plans. Using an RRI provides additional information for the execution of recovery plans by allowing for a measure of reproductive resilience erosion and a more holistic accounting of traits that affect productivity and need to be protected. Stock recovery plans have focused on reaching the level of SSB that generates the recovery of stocks. However, the relationship between stocks and recruitment has not been explained in its strictest sense. Consequently, more detailed behavioural and biological characteristics that define reproductive success of the species should be included in such analyses, and a way to do it could be by incorporating the RRI and the species-specific components most important to productivity. For example, in the case of anchoveta, by establishing early warning systems based on potential interruptions of larval flow, or on the spatial structure of spawning sites. Note, for example, that the sensitivity analysis consistently highlights five reproductive traits as having the most significant impact on the RRI of SMPF: "Distance between nursery and adult foraging habitats", "Distance between spawning and nursery habitats", "Reproductive migration", "Stock–Recruit Relationship", and "Spawning site diversity". This highlights that in addition to stock–recruit relationships in SMPF, other spatially explicit factors related to the geographical location of spawning and nursery areas and their diversity affect reproductive resilience and productivity of these species.

A fisheries manager has three primary objectives related to economic productivity: (*i*) Increase, maintain, or recover the population size of target species (Cochrane and Garcia 2009); (*ii*) set HCRs that maximize the sustainable yield (Cochrane and Garcia 2009); and, more recently, (*iii*) minimize the monetary cost of environmentally responsible search, harvest, and landing operations. If these objectives are supported by sound science (e.g., adapting the goals at timescales that account for interannual fluctuations due to environmental constraints), it is possible to fish SMPF species sustainably. The bottleneck remains in the uptake of scientific advice by decision-makers. Decision-makers may or may not have an education focused on biological sciences, ecology, or statistics, so it is necessary for fisheries researchers to provide them with monitoring tools, such as an easy to implement RRI. As proposed in this study, the approach of the RRI as a product of a BBN model, provides an interface easily interpreted by nonscientific stakeholders, with an overall RRI that can be decomposed into eight broad categories associated with a species' biology and spatial ecology, and 16 more detailed traits that affect a species' vulnerability to external pressures. The BBN is constructed on probabilistic principles, and its interpretation is therefore also probabilistic, considering the variability of the traits that condition the RRI. In consequence, the BBN can provide insight into the conditional dependence and independence relationships between variables through a hypothetical observation. Furthermore, expert knowledge can be integrated together with empirical data in a graphical model that is easily understandable and interpretable by managers (Rambo et al. 2022).

Decision-makers might (*i*) categorize the species according to their RRI; (*ii*) identify the traits with the greatest impact on the RRI; and (*iii*) identify those reproductive resilience traits which are invariant over time and key contributors to changes in resilience with external forces such as climate change or changing fishing pressure. These three characteristics are an advance from earlier traits-based indicators, as these indicators were generally static: a species has a score within a vulnerability scale, and the species composition changes in different scenarios (de Juan et al. 2020). One of the principal current limitations of the approach is that threshold values at which the RRI operates safely for each species still need to be determined. The RRIs proposed here for five SMPF species correspond to the survey responses of a group of experts on the HCLME system in its current state. Consequently, we do not know at which minimum values the RRI of each species can fall to before observing a decline in their adult populations. To overcome these limitations, our proposed index allows capturing physiological and behavioural changes of the species with changing environmental scenarios. This property has two main advantages: first, it reflects the adaptive capacity of the species, and second, it provides a means to assess if the reproductive resilience of the species increases or decreases over time under variable conditions (including effects of projected climatic scenarios). In the temporal analysis of the RRI for two of the selected species in the area, the results suggest that there is temporal variability in the reproductive traits analysed, and moreover, these changes are related to variability in the reproductive success and ultimately to the population size of two coexisting species. Indeed, small pelagic fish are characterized by highly plastic biological processes (Hunter et al. 2015), making it likely that the species have adapted their reproductive traits simultaneously to environmental conditions and to fishing pressure. In the applied example, the variability in the RRI was caused by changes in reproductive traits associated with the early survival of the species analysed, confirming that processes occurring during this stage of the life cycle largely determine the reproductive resilience of SMPF.

The proposed multidimensional RRI can be applied to multispecies assessments, providing an integrative perspective to regional fisheries management (see Fig. 7). Nevertheless, despite the RRI being feasible to apply to species with markedly different life histories (e.g., small pelagic, demersal, freshwater fishes), this characteristic may challenge the detection of temporal differences in reproductive traits of a particular species. The scoring scale was designed to accommodate an ample expression of the traits (e.g., from slow to fast growth rates), and thus, its capacity to detect interspecific variability is limited. Future versions of the RRI could include scales adjusted for species with similar life histories to highlight possible differences that determine temporal changes in reproductive resilience. A multidimensional RRI could accommodate widely differing life history parameters from various species, including deep-sea fish (e.g., Patagonian toothfish) to SMPF (e.g., sardines and anchovies). At the same time, under a broader perspective, the RRI could be used for an analysis of the species vulnerability among different ecological systems (i.e., upwelling system vs. oceanic system), allowing for the discussion of the options of fishing management related to spatio-temporal environmental variability.

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Data availability

Survey data from the panel of 27 local experts that support the findings of this study are available on request from the corresponding author, AO. The data are not publicly available because they contain information that could compromise the privacy of research participants. The script codes used in this study are available from the corresponding author, AO, upon reasonable request. The remaining research data are available within the article and (or) its supplementary materials, also available in the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.16661344.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2021-0263.

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Appendix A

Appendix Figs. A1–A4 appear on the following pages.

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Fig. A1. Bayesian Belief Network model for *Sardinops sagax*, describing the influence of the 16 reproductive traits (outer boxes) on the eight reproductive categories (inner boxes) and RRI score (centre). Posterior probability distributions of the compiled net are shown for all nodes. [Colour online.]

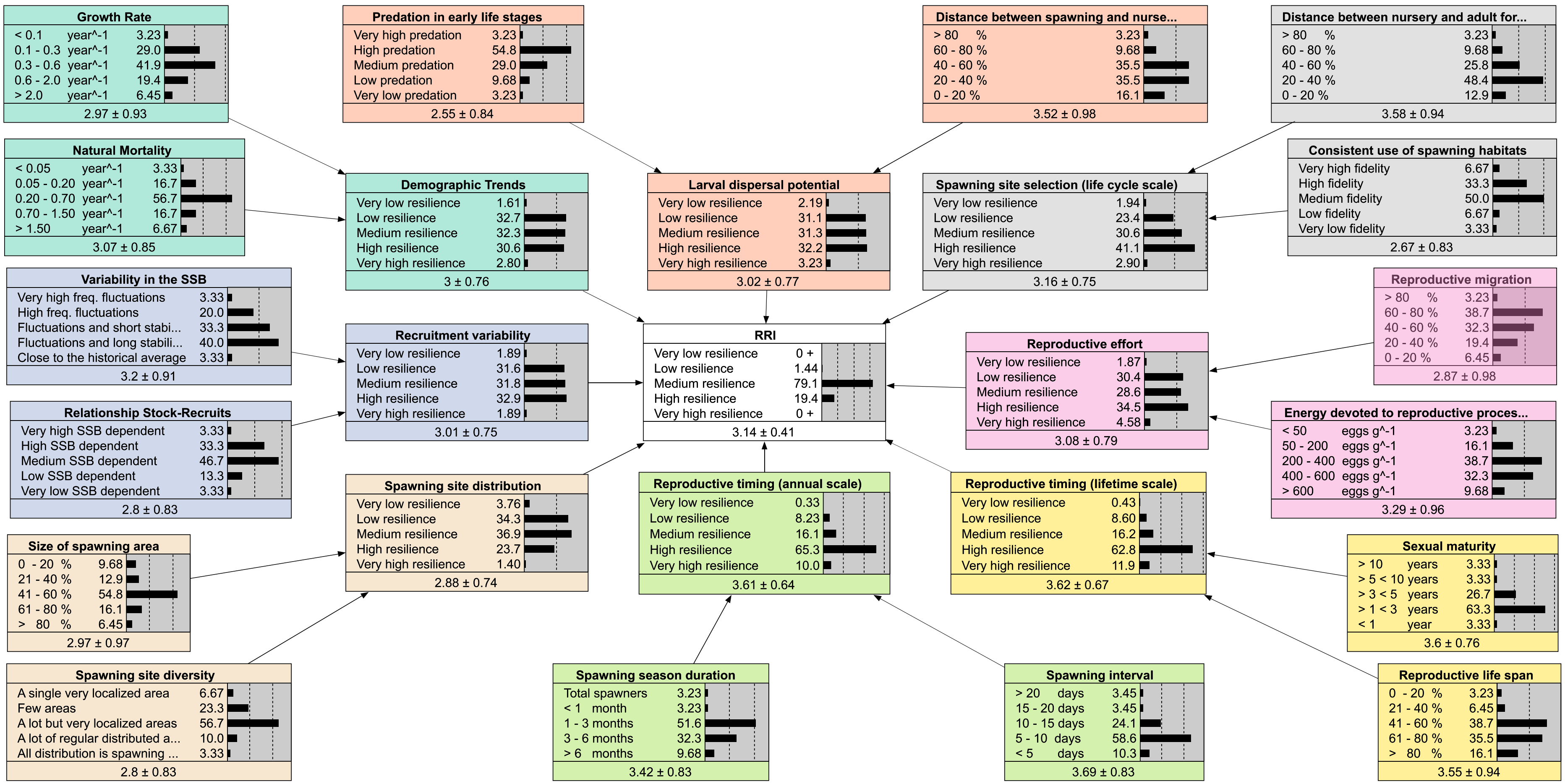

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Fig. A2. Bayesian Belief Network model for *Sprattus fueguensis*, describing the influence of the 16 reproductive traits (outer boxes) on the eight reproductive categories (inner boxes) and RRI score (centre). Posterior probability distributions of the compiled net are shown for all nodes. [Colour online.]

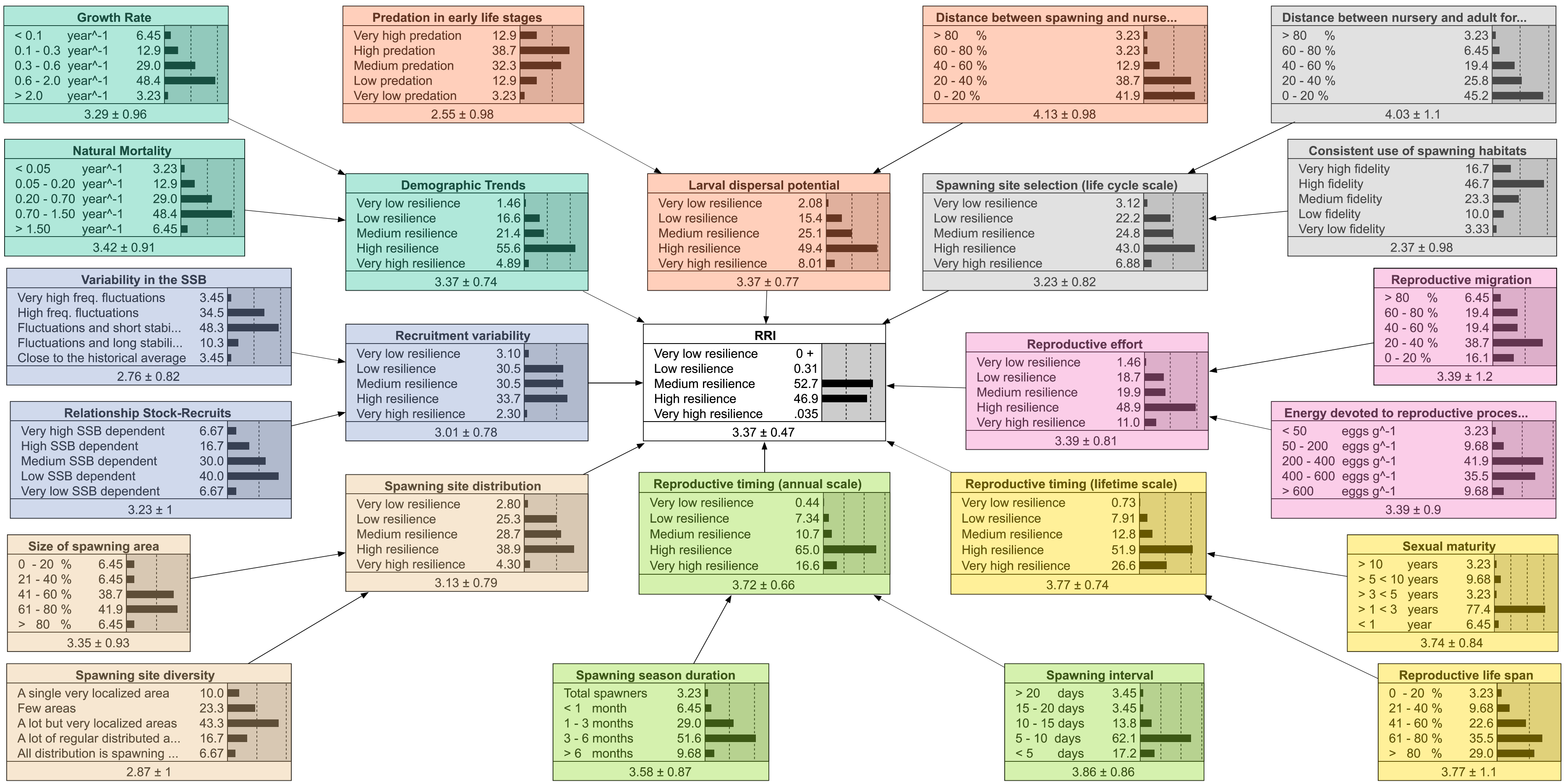

Fig. A3. Bayesian Belief Network model for *Strangomera bentincki*, describing the influence of the 16 reproductive traits (outer boxes) on the eight reproductive categories (inner boxes) and RRI score (centre). Posterior probability distributions of the compiled net are shown for all nodes. [Colour online.]

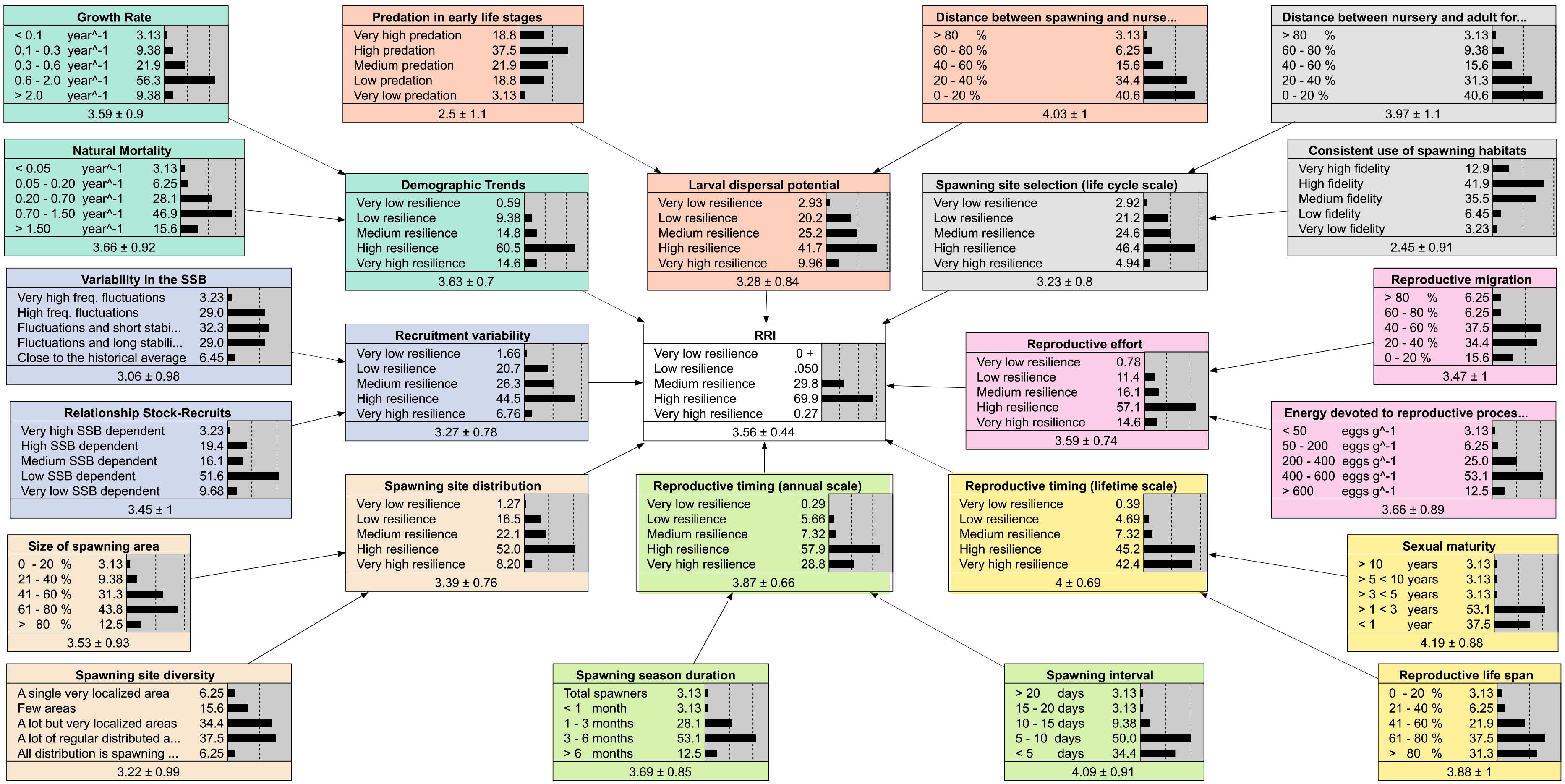

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Fig. A4. Bayesian Belief Network model for *Trachurus murphyi*, describing the influence of the 16 reproductive traits (outer boxes) on the eight reproductive categories (inner boxes) and RRI score (centre). Posterior probability distributions of the compiled net are shown for all nodes. [Colour online.]