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A Leslie matrix model for *Sicyopterus lagocephalus* in La Réunion: sensitivity, uncertainty and research prioritization

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Abstract

We propose a Leslie matrix model for the population dynamics of *S. lagocephalus* in La Réunion. In order to capture both the amphidromous and the seasonal natures of the species' life history the model has four stages (sea + three river sites) and is periodic. Baseline parameters (age-specific fecundity, spatial dispersion patterns and survival rates) were chosen in such a way that the dominant eigenvalue of the year-on-year projection matrix is 1. Large uncertainties on the parameter values preclude the use of the model for management purpose. A sensitivity/uncertainty analysis sheds light on the parameters that cause much of the output to vary and that are poorly known: the life expectancy in rivers and the mortality both at river mouths and during the drift of larvae to sea. This work should help researchers understand which factors and parameters need to be better known and estimated before the model can be developed as an accurate management tool.

Keywords: Leslie matrix, *Sicyopterus lagocephalus*, population dynamics, sensitivity, uncertainty.

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1 Introduction

In La Réunion island the fry of juvenile red-tailed goby (*Sicyopterus lagocephalus*, Pallas 1770) is a much appreciated delicacy, although an expensive one. Known locally as "bichiques" the 3cm long juveniles are captured in very high numbers at river mouths as they swim upstream to grow and reproduce [1, 44]. As a result their numbers have dwindled over the years and the stakes are high [3, 18]. Although *S. lagocephalus* is widely distributed throughout the Indo-Pacific region, the population of the Mascarene Islands (Mauritius, La Réunion and Rodrigues) largely self-recruits [30]. This highlights the need for local management.

We propose here a population dynamics model of *S. lagocephalus* which aims to shed light on the factors and parameters that influence the species' persistence. The ultimate goal is to provide policymakers with management actions that could help them prevent the decline of the local stock.

Sicyopterus lagocephalus is an amphidromous migratory species [34, 36]. It has a singular life cycle adapted to the precarious hydrological conditions of rivers where they spawn large number of eggs [25, 31, 50]. Immediately after hatching, larvae drift down to the sea and become "pelagic" as they disperse in the sea [33, 35, 51]. After a few months, the pelagic larvae recruit into river mouths as they move back in freshwater and complete their growth and sexual maturation. They settle in various parts of rivers thanks to their strong climbing abilities which allow them to pass waterfalls up to several meters high, as described in Hawaiian gobies [6, 7].

In addition to living in a challenging natural environment *S. lagocephalus* are subjected to heavy anthropogenic pressures that often impact on aquatic species of tropical islands [24, 39]. Free movement between freshwater and the marine environment is a key factor for the completion of the life cycle [41]. River mouth closures caused by inadequate river flow management can lead to long-term fish extirpation [32]. A lack of recruitment at the river mouth causes a rapid decrease of adult population in the catchment. The presence of dams along the rivers further limits both the upstream colonization of fish and the

chances of larvae reaching the sea. In addition, after the marine larval phase, post-larvae are subject to massive fisheries at the river mouths [1, 14, 44].

In Section 2 we detail the Leslie matrix model which describes the population dynamic of the species. Survival, recruitment and fecundity rates are detailed in Section 3. Section 4 discusses the results obtained with a baseline set of parameters. A variance-based sensitivity analysis sheds light on the factors that need further study and helps us prioritize the acquisition of biological knowledge. Results are summarized in the concluding Section 5.

2 Leslie matrix model

2.1 The life cycle

We capture the population dynamics outlined above in a stylized manner by using a multi-stage cyclical Leslie matrix model for the female population only (Figure 1). Modeling only the female population is standard practice and assumes that the number of males does not affect the females' reproductive ability [10, 38]. The stages correspond to the different ecological sites inhabited during the life-cycle. There are four stages: the sea and three river sites.

A one-month time step is chosen because females spawn approximately once a month with a pause during the cooler periods [14, 31, 50]. The eggs hatch about 48 hours after fertilization. As with other Sicydiinae [2, 31], free embryos then drift toward the sea in less than a day or two [51]. Because this duration is negligible compared to the one-month time-step, we consider that larvae begin their life at sea. Our data shows that the Pelagic Larval Duration (PLD) extends from 96 to 296 days ($\approx$ 10 months) depending on the time of year the larva hatched [19, 29, 48]. During this period, larvae are subjected to the competing risks of mortality and recruitment: each month a larva can die or survive, with or without recruitment in river mouth.

After recruiting into river mouths post-larvae and juveniles adopt a benthic lifestyle

and colonize the watershed [25, 26]. They face competition for habitats as well as added risks of mortality through fishing and predation [25, 26]. If they survive, juveniles settle for their adult period anywhere from the mouth to the upper reaches of the rivers. The exact location and subsequent movements depend on accessibility and the availability of food, reproductive territories and others poorly known factors [18, 26, 49]. We capture these complex migratory patterns in a highly stylized manner by assuming that upon recruitment juveniles settle in one of three defined "river-sites" (indexed 1 to 3): downstream, midstream or upstream. Although recently recruited fish spend a short time in a lower site on the way to their final destination we simplify the migratory movements by assuming that at recruitment they are instantly dispatched to one of the three river-sites. In the absence of detailed information on migrations between sites we also assume that once a fish has reached its settlement site at recruitment it stays there.

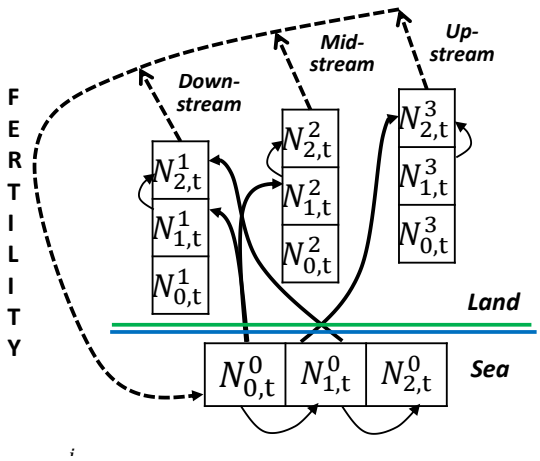

Figure 1: Stylized depiction of the four-site population structure (sea and down-, mid- and up-stream river destinations). The population of *Sicyopterus lagocephalus* is assumed for this illustrative example to have only three-age group. After their birth in rivers larvae drift rapidly towards the sea (dotted "fertility" line). They stay a few months at sea and recruit into the next age group (thick arrows) in one of three river sites where juveniles then stay, mature and reproduce. In $N^k_{i,t}$ the river sites are indexed by the superscripts $k = 1, 2, 3$ and age groups by the first subscript i. Thin arrows represent survival with a transition to the next age group.

2.2 The abundance vector

We let $\mathbf{N_t^0}$ be the age-structured larval abundance vector (population at sea with m_0 *larval* age groups) at the end of month t. The sea is the site indexed 0. Similarly $\mathbf{N_t^k}$ ($k = 1, 2, 3$) are the adult abundance vectors in the three rivers sites, each with m_k age groups (theoretically there could be different numbers of age groups in different river sites - if for example survival rates differed drastically). Each site-specific abundance vector is of the form

$$\mathbf{N_t^k} = (N_{0,t}^k, N_{1,t}^k, \ldots N_{m_k-1,t}^k),\ k = 0, 1, 2, 3. \tag{1}$$

When at time t a larva aged i at sea recruits and settle into the kth river site it has "migrated" from the $(i+1)$st component of $\mathbf{N_t^0}$ into the $(i+2)$nd component of $\mathbf{N_{t+1}^k}$[1]. The overall abundance vector

$$\mathbf{N_t} \stackrel{\text{def.}}{=} (\mathbf{N_t^0}, \mathbf{N_t^1}, \mathbf{N_t^2}, \mathbf{N_t^3}) \tag{2}$$

is obtained by stacking the site-specific vectors and has $\sum_{k=0}^{k=3} m_k$ components.

2.3 Twelve month-specific Leslie matrices

We will first give the structure of the twelve month-specific Leslie matrices which are used to obtain $\mathbf{N_{t+1}}$ on the basis of $\mathbf{N_t}$. These matrices contain survival, recruitment and fecundity rates. The modelling of these rates is detailed in Section 3.

In what follows τ will represent a month between 1 and 12 and $\mathbf{M}_\tau$ is the Leslie matrix with the survival, recruitment and fecundity rates prevailing during month τ. This matrix will be applied to a population vector at the end of the previous month to produce the population at the end of month τ.

[1] This means that the first components of the river sites have zero populations. However having these vectors start at age 0 simplifies notations

2.3.1 Site specific survival matrices

For each month $\tau = 1, 2, ..., 12$ the within-site matrices of survival rates in site k are

$$\mathbf{S}_{\tau}^{\mathbf{k}} \stackrel{\text{def.}}{=} \begin{pmatrix} 0 & 0 & . & . & 0 \\ s_{1,\tau}^{k} & 0 & . & . & 0 \\ 0 & s_{2,\tau}^{k} & 0 & . & 0 \\ . & . & . & . & . \\ 0 & 0 & . & s_{m_k-1,\tau}^{k} & 0 \end{pmatrix}, \; k = 0, 1, 2, 3. \tag{3}$$

The survival rate $s_{i,\tau}^{k}$ is thus the proportion of fish who at month τ are aged $i-1$ months and survive within site k to the next month. At sea ($k = 0$) the larvae are subjected to the competing risks of death (or dispersion) and recruitment, which means a possible migration to one of the river sites. In Section 3 we will therefore express these rates $s_{i,\tau}^{0}$ as products of a survival rate multiplied by a probability of absence of recruitment - both of which will depend on the current month τ.

The within river-sites survival rates $s_{i,\tau}^{k}$ for $k > 0$ are pure survival rates (no risk of migration) and will not be month-dependent (in this case the τ is superfluous).

2.3.2 Site-specific recruitment rates matrices

The matrices of site-specific recruitment rates from the sea into each one of the river-sites are

$$\mathbf{R}_\tau^{\mathbf{k}} \stackrel{\text{def.}}{=} \begin{pmatrix} 0 & 0 & . & 0 \\ r_{1,\tau}^k & 0 & . & 0 \\ 0 & r_{2,\tau}^k & . & \\ . & . & . & . \\ 0 & 0 & . & r_{m_0,\tau}^k \\ 0 & 0 & . & 0 \\ . & . & . & . \\ 0 & 0 & . & 0 \end{pmatrix}, \; k = 1, 2, 3. \tag{4}$$

The recruitment rate $r_{i,\tau}^k$ is the proportion of larvae at sea aged $i-1$ during the month τ who will survive an extra month at the end of which they will recruit in mouth and settle into site k - if they have also survived the hazards encountered at the river mouth (fishing, predation, etc.). Both the survival and recruitment rates will depend on τ. Each $\mathbf{R}_\tau^{\mathbf{k}}$ thus has m_k rows (the number of age groups in the k-th site) and m_0 columns (number of age groups in 0-th site (sea)). Equation (4) assumes that $m_k > m_0$ which is the case in our application. Indeed the maximum number of months m_0 spent in the sea is 10 months, whereas the maximum number of months m_k a fish lives in the rivers is of the order of one hundred months, as suggested for other Sicydiinae [3, 7, 23].

2.3.3 Fecundity rates

The m_0 by m_k matrices with a first row containing the fecundity rates are

$$\mathbf{F}_\tau^{\mathbf{k}} \stackrel{\text{def.}}{=} \begin{pmatrix} \overbrace{0 \quad 0 \quad \dots \quad 0}^{\xi \text{ times}} & f_{\xi+1,\tau}^k & . & f_{m_k,\tau}^k \\ 0 \quad 0 \quad \dots \quad . & . & . & 0 \\ 0 \quad . \quad \dots \quad . & . & . & . \\ . \quad . \quad \dots \quad . & . & . & . \\ 0 \quad . \quad \dots \quad . & . & . & 0 \end{pmatrix} \; k = 1, 2, 3 \tag{5}$$

where $f_{i,\tau}^{k}$ is the number of larvae produced in site k the month τ by a female aged i months. Females do not reproduce before roughly the third month spent in rivers [48]. Because the age in rivers is counted from birth (and not recruitment) we approximate this early period of infertility by specifying an age ξ (from birth) up to which fecundity is 0 (Eq. (5)).

If $\mathbf{0_{i,j}}$ denotes the zero matrix with i rows and j columns the 12 month-specific Leslie matrices are obtained by putting together the survival, recruitment, fecundity and zero matrices:

$$\mathbf{M}_\tau \stackrel{\text{def.}}{=} \begin{pmatrix} \mathbf{S}_\tau^{\mathbf{0}} & \mathbf{F}_\tau^{\mathbf{1}} & \mathbf{F}_\tau^{\mathbf{2}} & \mathbf{F}_\tau^{\mathbf{3}} \\ \mathbf{R}_\tau^{\mathbf{1}} & \mathbf{S}_\tau^{\mathbf{1}} & \mathbf{0_{m_1,m_2}} & \mathbf{0_{m_1,m_3}} \\ \mathbf{R}_\tau^{\mathbf{2}} & \mathbf{0_{m_2,m_1}} & \mathbf{S}_\tau^{\mathbf{2}} & \mathbf{0_{m_2,m_3}} \\ \mathbf{R}_\tau^{\mathbf{3}} & \mathbf{0_{m_3,m_1}} & \mathbf{0_{m_3,m_2}} & \mathbf{S}_\tau^{\mathbf{3}} \end{pmatrix}, \tau = 1, 2, ..., 12. \tag{6}$$

2.4 Leslie cyclical recurrence equation

The cyclical pattern in the Leslie matrices used for the projections will have at its core the (backward) product of the 12 month-specific Leslie matrices from January to December. This product is

$$\mathbf{M} \stackrel{\text{def.}}{=} \mathbf{M_{12}M_{11}} \cdots \mathbf{M_1}. \tag{7}$$

Because of the seasonalities we need to know the month m^* at which we start a projection with an initial population vector $\mathbf{N_0}$ at the end of month m^*. The Leslie matrix used to obtain the population $\mathbf{N_1}$ at the end of month $m^* + 1$ will be the one prevailing during month $m^* + 1$. Therefore the population vector $\mathbf{N_1}$ at month 1 will be $\mathbf{M_{m^*+1}N_0}$. Similarly at month 2 the vector $\mathbf{N_2}$ is $\mathbf{M_{m^*+2}M_{m^*+1}N_0}$ - at least if $m^* + 2 \leq 12$. More generally, we write any month t as $t = 12t_1 + t_2$ with $0 \leq t_2 < 12$, i.e. t_2 is $\mod (t, 12)$, the remainder of the division of t by 12. If $t_2 > 12 - m^*$ the population vector $\mathbf{N_t}$ is obtained by first multiplying $\mathbf{N_0}$ on the left by the matrices $\mathbf{M_k}$ for k from $m^* + 1$ to 12; then the result is multiplied by t_1 times the product of all 12 Leslie matrices ($\mathbf{M}$ of Eq. (7)), and finally by the matrices $\mathbf{M_k}$ for k from 1 to $t_2 - 12 + m^*$. Recalling that t is

written as $t = 12t_1 + t_2$ we have

$$\mathbf{N_t} = \mathbf{N_{12t_1+t_2}} = \mathbf{M_{t_2-12+m^*}M_{t_2-11+m^*}} \cdots \mathbf{M_1} \underbrace{\left(\prod_{i=0}^{i=11} \mathbf{M_{12-i}}\right) \ldots \left(\prod_{i=0}^{i=11} \mathbf{M_{12-i}}\right)}_{t_1 \text{ times}}$$

$$\times \mathbf{M_{12}M_{11}} \cdots \mathbf{M_{m^*+1}N_0}$$

$$= \mathbf{M_{t_2-12+m^*}M_{t_2-11+m^*}} \cdots \mathbf{M_1} \times \mathbf{M^{t_1}} \times \mathbf{M_{12}M_{11}} \cdots \mathbf{M_{m^*+1}N_0}. \tag{8}$$

If $m^* = 12$ then $\mathbf{N_0}$ is multiplied directly by the t_1 products of 12 matrices then by the remaining t_2 matrices. If $t_2 \leq 12 - m^*$ we obtain in a similar fashion

$$\mathbf{N_t} = \mathbf{N_{12t_1+t_2}} = \mathbf{M_{t_2+m^*}M_{t_2-1+m^*}} \cdots \mathbf{M_1} \times \mathbf{M^{t_1}} \times \mathbf{M_{12}M_{11}} \cdots \mathbf{M_{m^*+1}N_0}. \tag{9}$$

If the matrix $\mathbf{M}$ is primitive (i.e. there exists p such that $\mathbf{M^p} > \mathbf{0}$) then for a large t_1 we have by Perron-Frobenius that $\mathbf{M^{t_1}} \sim \lambda^{t_1}$ where λ is the (positive) dominant eigenvalue of $\mathbf{M}$. For a fixed remainder t_2, initial population and months $\mathbf{N_0}$ and m^* there exists a vector $\mathbf{V}(\mathbf{N_0}, t_2, m^*)$ such that for a large t_1 we have

$$\mathbf{N_{12t_1+t_2}} \sim \lambda^{t_1}\mathbf{V}(\mathbf{N_0}, t_2, m^*). \tag{10}$$

This expression shows that year-on-year all age groups grow at the same annual rate $\lambda - 1$, although with a λ^{t_1} that is a multiplied by a vector $\mathbf{V}(\mathbf{N_0}, t_2, m^*)$ which depends on the month being considered (as well as the initial population).

3 Survival, recruitment and fertility models

3.1 Pelagic survival without recruitment

3.1.1 Model

Before deriving the pelagic survival rates $s^0_{i,\tau}$ of Eq. (3) which take into account the risk of recruitment, we need to specify a survival model in the absence of this risk. This survival

at sea depend on age and the current month τ.

We will capture both aspects multiplicatively by assuming that month-to-month survival rates are the product of a baseline age-specific value multiplied by a seasonal factor depending on the month.

1. *Baseline survival.* Very little is known on mortality at sea, other than the fact of an extremely low survival by the time of recruitment (which we conflate with dispersion at sea: a larva that either dies or disappears has no chance of making it to shore) [35]. This survival rate at the end of larval duration is of the order of 10^{-5} or less as commonly observed for small pelagic larvae [20, 21]. We also assume that the hazard rate is extremely high initially and decreases as larvae grow [21]. A Weibull distribution with a shape parameter γ less than 1 captures this pattern because its hazard rate is of the form $x^{\gamma-1}$ where x is age (An "extremely high" initial hazard rate is thus modelled as a hazard rate approaching $+\infty$ for an age $x \approx 0$).

Because the standard parameters for the Weibull distribution are difficult to interpret, we will parametrize the distribution with survival rates σ_1 and σ_2 specified at two points in time t_1 and t_2. If we define

$$\gamma \stackrel{\text{def.}}{=} \frac{\ln\left(\dfrac{\ln(\sigma_2)}{\ln(\sigma_1)}\right)}{\ln\left(\dfrac{t_2}{t_1}\right)}; \; \alpha \stackrel{\text{def.}}{=} \frac{t_2}{\ln(1/\sigma_2)^{1/\gamma}} \tag{11}$$

then the Weibull survival rate with the required properties is

$$S(x) \stackrel{\text{def.}}{=} e^{-(x/\alpha)^{\gamma}}. \tag{12}$$

The baseline survival rate from age $i-1$ to i is then $S(i)/S(i-1)$. For the hazard rate

$$h(x) \stackrel{\text{def.}}{=} \frac{\gamma}{\alpha}\left(\frac{x}{\alpha}\right)^{\gamma-1} \tag{13}$$

to be a decreasing function of age x the shape parameter γ of Eq. (11) must be less than 1.

2. *Seasonal adjustment.* The dependence on the month τ comes from the fact that survival rates are higher with lower temperature, as demonstrated in marine larvae [20]. The temperature depends on the month with a fairly simple seasonal pattern. A periodic annual pattern for the temperature $T(\tau)$ at month τ is well captured by a periodic regression [5] of the form

$$T(\tau) \stackrel{\text{def.}}{=} b_0 + b_1 \sin\left(\frac{2\pi \times \tau}{12}\right) + b_2 \cos\left(\frac{2\pi \times \tau}{12}\right). \tag{14}$$

In order to model the effect of temperature we will need the minimum and maximum temperatures over the 12 months:

$$t_{min} = \min_{1 \leq m \leq 12} T(m),\ t_{max} = \max_{1 \leq m \leq 12} T(m). \tag{15}$$

We next define the parameter κ equal to the fraction by which the survival $S(i)/S(i-1)$ rate increases (or decreases) when the temperature reaches its minimum t_{min} (or maximum t_{max}). The survival rate $\sigma(i, \tau)$ of a larva aged i months at month τ is now the baseline survival rate $S(i)/S(i-1)$ multiplied by an affine function of $T(\tau)$ with the right properties:

$$\sigma(i, \tau) \stackrel{\text{def.}}{=} \frac{S(i)}{S(i-1)} \times \left(1 - \kappa - \frac{2t_{max}\kappa}{t_{min} - t_{max}} + \frac{2\kappa}{t_{min} - t_{max}} T(\tau)\right). \tag{16}$$

Indeed one easily checks that the minimum (or maximum) survival rate $S(i)/S(i-1) \times (1-\kappa)$ (or $S(i)/S(i-1) \times (1+\kappa)$) are obtained at the warmest (or coolest) month when the temperature $T(\tau)$ is t_{max} (or t_{min}).

3.1.2 Baseline parameter values

Numerical values for the parameters b_0, b_1 and b_2 of the modelled temperature of Eq. (14) are found by routine least square minimization (Table 1 brings together these and all other parameter values). Data were Sea Surface Temperature (SST, in Celsius degree) between 2001 and 2011 from an analysis of NOAA satellite images (0.5 degree resolution)

on the Reunion station, France (21°5'S, 55°E) [37]. The fraction κ is taken equal to 0.2 which reflects a 40% decrease from the coldest to the warmest months. With this value the modelled peak recruitment months coincided with the known periods of maximum larvae abundance at the river mouths (i.e. from September to December). The survival parameters σ_1 and σ_2 used to specify the baseline Weibull were chosen at times $t_1 = 2$ months (roughly the highest mortality period) and $t_2 = 7$ months (roughly the longest pelagic duration). More on the choice of these survival rates in the Discussion section.

3.2 Recruitment and site-dispersion models

3.2.1 Model

In the absence of the risk of mortality/dispersion at sea the time until a larva moves back into freshwater is a random variable R_{mb} which depends on the month of birth mb[2] [48], as observed in others Sicydiinae [4, 45]. For a larva aged i months at month τ the month of birth is a simple arithmetic function $mb(i, \tau)$ of i and τ:

$$mb(i,\tau) = \begin{cases} \mathrm{mod}(\tau - i - 1, 12) + 1 & \text{if } \tau - i - 1 \geq 0 \\ 12 - \mathrm{mod}(i - \tau, 12) & \text{otherwise} \end{cases} . \tag{17}$$

For each one of the 12 possible months of births mb we define the cumulative distribution function $F_{mb}(x)$ of R_{mb}. We will need the discretized hazard of reaching a river mouth for a fish aged i at month τ. This hazard is the probability $\rho_{i,\tau}$ of the event occurring during the next month conditionally on it not having occurred yet:

$$\rho_{i,\tau} \stackrel{\text{def.}}{=} \frac{F_{mb(i,\tau)}(i+1) - F_{mb(i,\tau)}(i)}{1 - F_{mb(i,\tau)}(i)}. \tag{18}$$

The pelagic survival (at sea) $s^0_{i,\tau}$ of Eq. (3) for $k = 0$ must incorporate the probability

[2] "Recruitment", formulated through the recruitment rates $r^k_{i,\tau}$ of Eq. (4) will occur when a larva reaches a river mouth *and* survives the various risks of predation and fishing during that event *and* chooses a river-site.

$1 - \rho_{i,\tau}$ that the larva does not reach a river mouth that month:

$$s^0_{i,\tau} \stackrel{\text{def.}}{=} \frac{\sigma(i+1,\tau)}{\sigma(i,\tau)}(1-\rho_{i,\tau}) \tag{19}$$

where the σ's are those of Eq. (16).

The rates at which larvae return in freshwater are $\rho_{i,\tau}\sigma(i+1,\tau)/\sigma(i,\tau)$. In order to have the desired recruitment rates we incorporate the risk of mortality at recruitment (through fishing, predation or competition): φ_τ is the survival rate at month τ from those combined threats at recruitment. This dependence on the month τ can reflect seasonal changes in the intensity of fishing - although in our numerical application the φ_τ's will be equal. We also define the vector $\theta = (\theta_1, \theta_2, \theta_3)$ of probabilities of larvae choosing each one of the three river-sites ($\Sigma\theta_i = 1$).

The recruitment rate $r^k_{i,t}$ into site $k \geq 1$ for a fish aged i at time t (Eq. (4)) is now obtained by combining the return rate in freshwater with survival at the river mouth and the choice of river site:

$$r^k_{i,\tau} \stackrel{\text{def.}}{=} \frac{\sigma(i+1,\tau)}{\sigma(i,\tau)}\rho_{i,\tau}\varphi_\tau\theta_k, k = 1,2,3. \tag{20}$$

3.2.2 Baseline parameter values

The distribution of the age-at-recruitment R_{mb} conditionally on the month of birth mb was obtained by measuring the number of growth rings in the otoliths (i.e. structure of the inner ear of fish) of 396 post-larvae sampled at river mouths on 14 days between November 2006 and March 2009 [48]. Although sample sizes for each month of birth were small, the distributions were roughly normal, i.e.

$$R_{mb} \sim \mathcal{N}(\mu_{mb},\, \sigma_{mb})\; mb = 1, 2, \ldots, 12. \tag{21}$$

with the 12 estimated mean and standard deviations given in Table 1.

The survival rates φ_τ when recruitment takes place the month τ are all taken equal

to 0.05. This value is consistent with survival rate at settlement observed in recruits of marine reef species, such as *Epinephelus merra* (Serranidae) in La Réunion coral reefs [13, 28]. We did not include seasonal effect of fisheries pressure due to the lack of reliable data. The spatial distribution of *S. lagocephalus* is strongly influenced by the river gradient [18, 49]. Data from the Ichthyological Monitoring Network of the Reunion Island (online data[3]) shows that around 55% of settled populations were found downstream, whereas 35% and 10% were observed respectively in the midstream and upstream sites [40]. The probabilities of river-site choice θ_i were thus taken equal to 0.55, 0.35 and 0.10.

3.3 River survival (adult period)

3.3.1 Model

In the absence of precise information we will assume constant death rates in each one of the three sites (exponential survival times, which depend on the river-site). We will parametrize the distribution with life expectancies after recruitment e_1, e_2, e_3 months, for each one of the three river-sites. One-month survival rates thus depend only on the site:

$$s_{i,\tau}^{k} \stackrel{\text{def.}}{=} \exp(-e_k^{-1}) \approx 1 - e_k^{-1}, k = 1, 2, 3. \tag{22}$$

3.3.2 Baseline parameter values

Survival in rivers is known as poorly as larval pelagic survival. In the absence of more precise information we took a life expectancies e_i of 24 months for all three sites. This is consistent with the 2 to 4 years of river life observed for *Sicyopterus stimpsoni* in Hawaiian Islands [7] and the 6 to 7 years of *Sicyopterus japonicus* in Japan [23].

[3]http://banquededonnees.eaureunion.fr/bdd/

3.4 Fecundity

3.4.1 Model

Fecundity rates are the numbers of female eggs produced each month by a female fish. As observed for others Sicydiinae, these rates drop to 0 during colder months of the year [15, 23, 31]. These months depend on the altitude of each one of the river-sites [14, 50]. We thus define three vectors Z_1, Z_2, Z_3 containing the zero fertility months for each site. For example $Z_1 = (8, 9, 10)$ means that in the downstream river-site fertility falls to 0 from August to October.

Fecundity rates increase then level off as fish age. A logistic ("S-shaped") function $F(i)$ captures this pattern. We parametrize $F(i)$ with i) the minimum and maximum values of these fecundity rates f_{min} (for $x \to -\infty$) and f_{max} (for $x \to +\infty$), ii) the age a_{inf} at which the fecundity has its point of inflection; and iii) the value d_{inf} of the derivative of the fecundity at the point of inflection. The logistic function parametrize in this way is

$$F(i) \stackrel{\text{def.}}{=} f_{min} + \frac{f_{max} - f_{min}}{1 + \exp\left(\dfrac{4d_{inf}(i - a_{inf})}{f_{min} - f_{max}}\right)}. \tag{23}$$

After hatching, larvae are subjected to a risk of mortality as they drift toward the sea. In order to capture this effect we will multiply the logistic function by site-specific drift survival rates η_k. The site-specific fecundity rates of Eq. (5) in the three sites are then

$$f_\tau^k = \begin{cases} 0 & \text{if } \tau \in Z_k \text{ or } \tau \leq \xi \\ F(\tau)\eta_k & \text{otherwise} \end{cases}, k = 1, 2, 3; \tau = 1, 2, \ldots, m_k \tag{24}$$

where Z_k is the set of months during which fertility falls to zero in site k and ξ is the age up to which fecundity is 0, as discussed in Section 2.3.3. Given the absence of major obstacles on the river-ocean corridor we consider that mortality is negligible during the rapid downward drift of larvae toward the sea. In the absence of precise information we assume this to be the case regardless of the river-site of birth. We thus assume a survival rate η_k equal to 1 for each river site. The f_τ^k's are *effective fecundity rates* in the sense

that they give numbers of larvae that make it to sea.

3.4.2 Baseline parameter values

The logistic model was fitted using a relationship between age and size [14] then a relationship between size and fertility [50]. The function $F(x)$ becomes positive at age $x > 3.763$ months and fits the data well. The negative values for ages below 3.763 mo. are not a problem because there is no fertility before ξ months and we are setting $\xi = 9$. The months during which fertility fall to zero Z_1, Z_2 and Z_3 are given in Table 1 [50].

4 Results

4.1 Dynamics

Our goal is not to reproduce a plausible trajectory or projection of the age-specific population of *S. lagocephalus*. This is because the real population is not in any sort of stable state - i.e. not even in the year-on-year sense of the annualized Leslie matrix model represented by the product $\mathbf{M}$ of the 12 monthly matrices (Eq.(7)). Indeed there are stochastic environmental changes which affect fecundity and survival rates, thus precluding any form of stability. We believe there may also be density-dependent mechanisms by which the survival rate at recruitment φ_τ decreases during the months when large numbers of juveniles arrive at the river-mouths. This negative feedback reflects larger natural mortality in high density conditions and enhanced opportunistic fishing efforts at work when there are more juveniles to be caught. Even if we were to envisage a stochastic model with these feedbacks such a model would be difficult to calibrate because there is little data on these processes.

Despite environmental and other fluctuations and hazards the population of *S. lagocephalus* has maintained itself over the decades and centuries. For this reason the numerical values given above for the survival rates both at sea and in the rivers (which are the parameters with the largest uncertainties) were chosen in such a way that they produced

a dominant eigenvalue 1 - which is a stylized expression of a population in a long-term equilibrium. Implausible values for survival rates chosen in this way would have alerted us to problems in the model specifications. Still, we do not claim that "plausible" means "accurate". For example a life expectancy of 24 months in rivers may be too small, although it does not contradict the fact that a few relatively old fish have been observed. Indeed an exponential distribution with a 24-month average still means that 8 % of fish live more than 5 years after entered in river ($\exp(-60/24) = 0.082$).

Having specified the model with plausible parameters (Table 1) leading to a λ equal to 1, we took an arbitrary (and wholly unrealistic) initial population of 1 for the first five age groups and 0 for others. We started the projection in January.

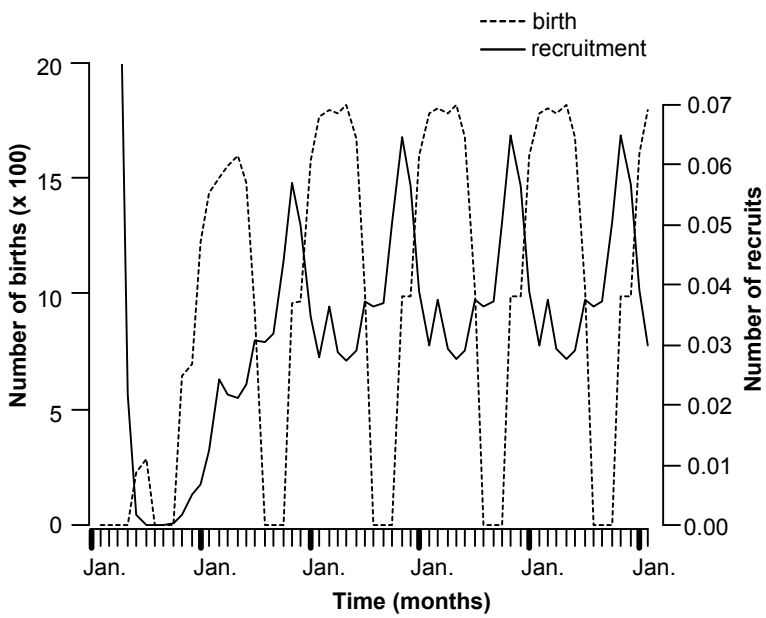

Figure 2: Projection of the population dynamics model of *Sicyopterus lagocephalus* showing the number of births and the number of recruits at the river mouth.

In order for the matrix $\mathbf{M}$ of (7) to be primitive we need to delete the components of the river-sites population vectors that remain 0 (see footnote in Section 2.2) as well as the corresponding columns of $\mathbf{M}$. Notwithstanding the unrealistic initial population as well as the size and complexity of the model, the population then converged in only two years (24 iterations) to its stationary state (Figure 2). The model reproduces seasonal patterns in good agreement with the periods of high recruitment between September and

December. These periods are well known locally because they coincide with high levels of fishing at the river mouths [44]. Known smaller recruitment "bursts" between March and July also appear in the model. Zero births between August and September reflect the fact that during those months fertility rates are zero in all three sites (Figure 2).

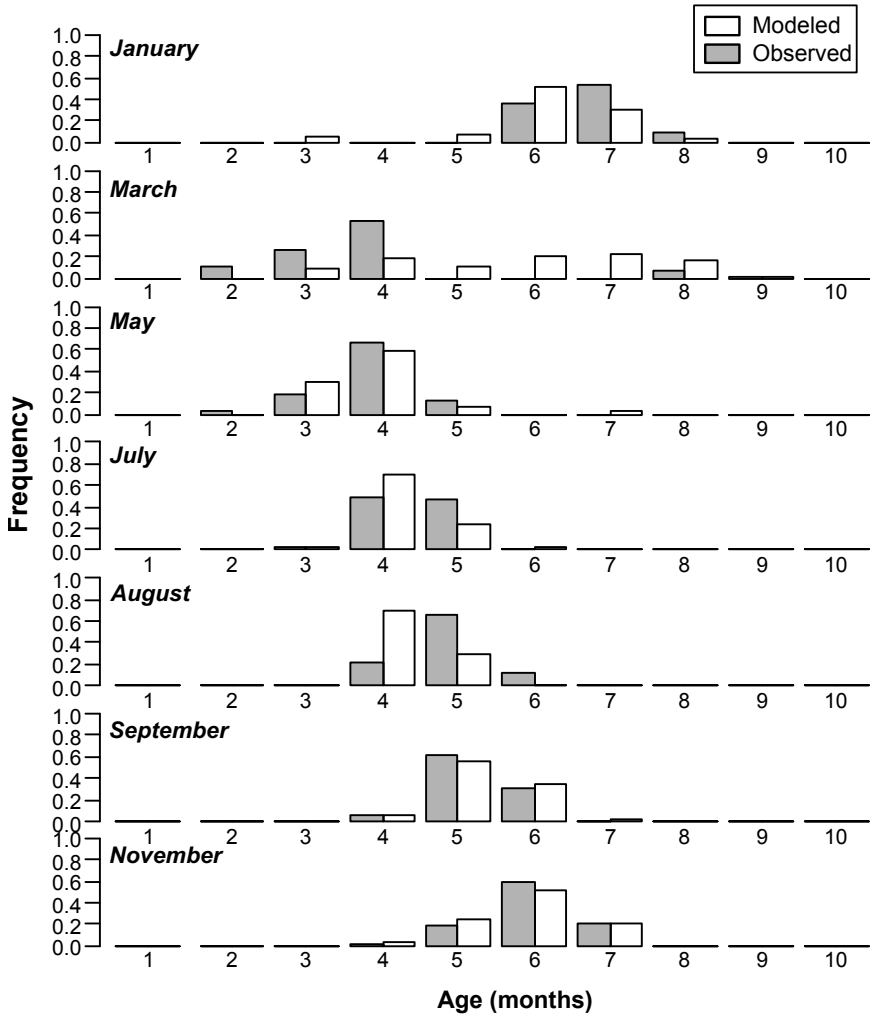

Figure 3: Distribution of pelagic larval duration (duration at sea) by month of recruitment(modeled and observed). Except for March and August the model approximates observed patterns at least crudely.

Field work has produced data on the distribution of Pelagic Larval Duration (PLD, duration at sea) by month of recruitment, for seven of the 12 months in the year [48]. These data can be compared with the model's corresponding outputs (Figure 3). The figure shows a good agreement between modelled and observed values, except in March and August. In March the observed durations are in the 2 to 4 and 8 to 9 months

range while the modelled ones are more spread out. In August there is a one-month shift between the two distributions. We can see in Figure 3 that starting in March the distribution of PLD shifts to the right with each month of recruitment. This increasing duration is caused by the decreasing temperature encountered by larvae in the marine environment.

We have achieved a first goal of devising a model with plausible parameter values compatible with a λ equal to 1. Our second goal is to assess the sensitivity of the model to the various parameters. This information will help biologists identify the parameters that need to be estimated more accurately.

4.2 Sensitivity analysis

4.2.1 The linear approximation

There are considerable uncertainties concerning the values of the model's parameters and their impact on the model. Before the model can be used with some confidence as a management/planning tool we therefore need to perform a sensitivity analysis of the model's output. In Leslie matrix models the output is the dominant eigenvalue λ of the projection matrix. In the simple situation of an unchanging Leslie matrix and a single site there are detailed results on the sensitivity of λ to the *entries* of the matrix, considered the model's parameters [10]. Sensitivity results are also available for density-dependent models [11], periodic models [27] and in situations where populations are classified by age and state [11]. These results rest on the linear nature of the models and ignore interaction between parameters in addition to being mostly local.

The present situation is more complex with a stage (or state)-classified model and periodically changing matrices. In addition we want a sensitivity analysis not in terms of the entries of the matrices but in terms of the biological parameters used to define these entries. This entails non-linear relationships from the parameters $\mathbf{p}$ to the product $\mathbf{M}$ of 12 Leslie matrices (Eq. (7)) and to the dominant eigenvalue $\lambda(\mathbf{p})$ of $\mathbf{M}$. We thus have a complex non-linear system and choose to use variance-based methods by which we can

assess more globally the relative contribution of each parameter to the output's variance [8, 17, 46]. These variance-based methods have been used extensively by physicists and engineers [43, 47] but less so by life scientists (see however [9, 16] and references therein).

In order to reflect the uncertainty concerning their values the model's parameters $\mathbf{p} = (p_i)$ are considered random variables. They can for example be normally or uniformly distributed with the baseline values used above as expected values. The goal is to write the variance of $\lambda(\mathbf{p})$ as a sum of terms that can be interpreted and can shed light on the relative contribution of each parameter to the variance.

We start off with the Sobol decomposition of the function $\lambda(\mathbf{p})$ written as a sum of square integrable functions of an increasing number of the parameters [46]:

$$\lambda(\mathbf{p}) = \lambda_0 + \sum_{i=1}^{i=k} \lambda_i(p_i) + \sum_{j>i} \lambda_{ij}(p_i, p_j) + \cdots + \lambda_{1\ldots k}(p_1, p_2, \ldots, p_k) \tag{25}$$

Although $\lambda(\mathbf{p})$ is not a linear function of the parameters it is customary to test whether the model might be approximately linear, at least when parameters do not vary too much. In this case the calculations are simpler. A linear approximation can be justified for biological models if parameters are not allowed to vary too much and have unambiguously monotone effects, e.g. an increase in fertility rates or survival rates both increase $\lambda(\mathbf{p})$. A linear model means that the Sobol decomposition is of the form

$$\lambda(\mathbf{p}) = a_0 + \sum_{j=1}^{j=k} a_j \times (p_j - E(p_j)). \tag{26}$$

Because the p_j's are independent we have

$$\mathrm{Var}(\lambda(\mathbf{p})) = \sum_{j=1}^{j=k} a_j^2 \mathrm{Var}(p_j). \tag{27}$$

The first-order variance-based sensitivity index is then defined as

$$S_j \stackrel{\text{def.}}{=} \frac{a_j^2 \mathrm{Var}(p_j)}{\mathrm{Var}(\lambda(\mathbf{p}))}, j = 1, 2, \ldots, k \tag{28}$$

which is the fractional contribution of the jth parameter to the overall variance $\mathrm{Var}(\lambda(\mathbf{p}))$. The sum $\sum_i S_i$ is then 1 or approximately 1 if the model is approximately linear. We can interpret S_i as the expected amount by which the variance of λ will be reduced if we know the true value of p_i. This is of particular interest for our purpose as we wish to prioritize future research in order to improve the reliability of our model. Such an approach is called *Factor Prioritization* [42].

Given that

$$\mathrm{Cov}(\lambda(\mathbf{p}), p_i) = \mathrm{Cov}\left(a_0 + \sum_{j=1}^{j=k} a_j \times (p_j - E(p_j)), p_i\right) = a_i \mathrm{Var}(p_i), \tag{29}$$

we have

$$S_i = \frac{a_i^2 \mathrm{Var}(p_i)}{\mathrm{Var}(\lambda(\mathbf{p}))} \tag{30}$$

$$= \frac{\mathrm{Cov}(\lambda(\mathbf{p}), p_i)^2}{\mathrm{Var}(\lambda(\mathbf{p}))\mathrm{Var}(p_i)} = \rho_i^2 \tag{31}$$

where ρ_i is the coefficient of correlation between the output $\lambda(\mathbf{p})$ and the i-th parameter p_i.

The squared value of the Pearson correlation coefficient (CC) is therefore an estimator $\hat{S}_i$ of S_i when the model is linear. We then consider a sample of n values of each parameter, i.e. $\mathbf{p_i} = (p_{1i}, p_{2i}, \ldots, p_{ni})$ for i going from 1 to k, the number of parameters. We let $\boldsymbol{\lambda} = (\lambda_1, \lambda_2, \ldots, \lambda_n)$ be the corresponding n-dimensional vector of outputs, i.e. the dominant eigenvalues. We then have

$$\hat{S}_i = \hat{\rho}_i^2 = \frac{\left(\sum_{j=1}^n (p_{ji} - \bar{\mathbf{p}}_i)(\lambda_j - \bar{\boldsymbol{\lambda}})\right)^2}{\sum_{j=1}^n (p_{ji} - \bar{\mathbf{p}}_i)^2 \times \sum_{j=1}^n (\lambda_j - \bar{\boldsymbol{\lambda}})^2} \tag{32}$$

where the horizontal bars indicate empirical means of the corresponding samples.

4.2.2 Numerical results

The $k = 43$ parameters listed in Table 1 are assumed to be uniformly distributed with a range of $\pm 20\%$ around their baseline values. This way no parameter is favoured. Because the *scale* in the seasonal variations in pelagic survival is not well known we include in the sensitivity analysis the fractional seasonal increase (or decrease) in survival κ. Because the seasonal variations in pelagic survival are *qualitatively* well known the parameters of the periodic regression of temperature are considered fixed. The discrete-value parameters (i.e. the beginning and ending months of the reproductive periods) are taken equal to their baseline value minus 1, their baseline values, and the baseline value plus 1 with equal probabilities 1/3.

A latin hypercube sample of size $n = 256$ is employed to generate the sample. For each trial $\mathbf{p_j} = (p_{j1}, \ldots, p_{jk})$, $j = 1, \ldots, n$, the model is run and $\lambda(\mathbf{p_j})$ computed. The Pearson correlation coefficients are then estimated from Eq. (32). The Pearson correlation coefficients between the outputs $\lambda(\mathbf{p})$ and the parameters are given in Table 1 and range from -0.19 to 0.58. The signs of the CCs are consistent with the expected effects of the parameters. For example the life expectancy e, the maximum fertility f_{max}, the probability of reaching the sea η and the survival rate at recruitment φ_τ are positively correlated with the output. Conversely, the age at fertility inflection a_{inf} and the durations of non-reproductive periods Z_k are negatively correlated with $\lambda(\mathbf{p})$. The linear approximation is justified *a posteriori* because $\sum_i \hat{\rho}_i^2 = 0.982$ is close to 1 and the square values of the CCs can then be used as estimators of S_i.

4.2.3 Pooled sensitivity

Given the quasi-linear behaviour of our model, it is of interest to pool (i.e. sum) squared CCs within biologically meaningful groups - specifically the seven parameter groups defined in bold letters in Table 1. The sum of squared CCs within each group is

$$\rho^2_{group} \stackrel{\text{def.}}{=} \sum_{i \in group} \hat{\rho}_i^2 \tag{33}$$

and represents the percentage in λ's variation that is due to the parameters in the group. The life expectancy of fish within rivers ("River Survival group" - RSG) is the most important group and explains $\rho^2_{RSG} = 34.1\%$ of the output variations. The "Age-specific fecundity" group explains $\rho^2_{ASF} = 17.8\%$ of the variation. The "Recruitment Survival and Site Dispersion" comes in third at $\rho^2_{RSSD} = 12.8\%$. These three groups capture almost two thirds of the total variation (64.7%). More surprisingly and despite the extremely high larval mortality, the pelagic survival (6.5%) and pelagic duration at sea (3.4%) are the least influential parameter groups. Three parameter groups are in the 10 to 20 % range (Figure 4 incorporates the uncertainty on the parameters and has these percentages on the x-axis). In the next section we argue that a sensitivity analysis goes hand in hand with an uncertainty analysis.

4.3 Uncertainty vs. sensitivity analysis

An Uncertainty Analysis (UA) usually complements a Sensitivity Analysis (SA). Indeed there is a relatively recent consensus that UA "quantifies the variability of the output caused by the incomplete knowledge or misspecification of the modeller" while SA "aims at establishing the relative importance of the input factors involved in the model" ([9] pp. 168-169). Both analyses dovetail however. Indeed, our concern until now has been with a sensitivity analysis aimed at prioritizing future research in terms of identifying the parameters that have the greatest impact on the output variability - with a view toward improving the precision of the corresponding parameter. But the need for this improvement depends on the level of "certainty" on the parameters. If a parameter has a great influence on the variance but is already well known, there is no need to improve its estimate. The same holds if a parameter is very "uncertain" but contributes little to the variance.

A detailed quantified uncertainty analysis is beyond the scope of this paper. However some parameters (or groups thereof) are better known than others. For example fecundity rates and pelagic durations are known fairly accurately whereas we do not even know

orders of magnitudes for survival rates, both at sea and in the rivers. It is then of interest to cross-classify, however crudely, the groups of parameters according to levels of uncertainty and levels of sensitivity. Uncertainty is assessed through our own subjective "expert opinion" as being low, medium or high. Sensitivity for each one of the seven parameter groups is measured by the pooled ρ^2_{group}'s discussed in Section 4.2.3.

Through river survival and fecundity, Figure 4 shows that it is the river life stage that has the most influence on the model. Perhaps this is because these factors are at play during years, as opposed to recruitment which is a one-off, instantaneous event, or pelagic duration which affects only the first few months of the life cycle. River survival (i.e. life-expectancy in river) is thus the single most critical parameter in view of its large influence on the model and large uncertainty - this parameter should therefore be a priority for future research.

Both the sensitivity and uncertainty on fecundity is substantially smaller than that on river survival, but is still far from negligible. A logistic function is a highly simplified model for a fecundity that increases with age. The timing and steepness of the inflection rely on delicate relationships between size, age and fecundity which can also depend on the river site due to differences of environmental conditions - a dependence not accounted for in our model. More generally fecundity, as well as drift and recruitment survival rates depend on environmental and anthropomorphic factors that are both poorly understood and documented.

If the river parameters are the most sensitive and uncertain, Figure 4 shows that the pelagic duration and survival are the least sensitive factors, but have very different uncertainties: it is low for pelagic duration (in the absence of mortality) while the pelagic survival is extremely uncertain.

5 Conclusion

Modelling the population dynamics of species subjected to fluctuating conditions in a multi-stage environment is a challenge - particularly when little data is available. The

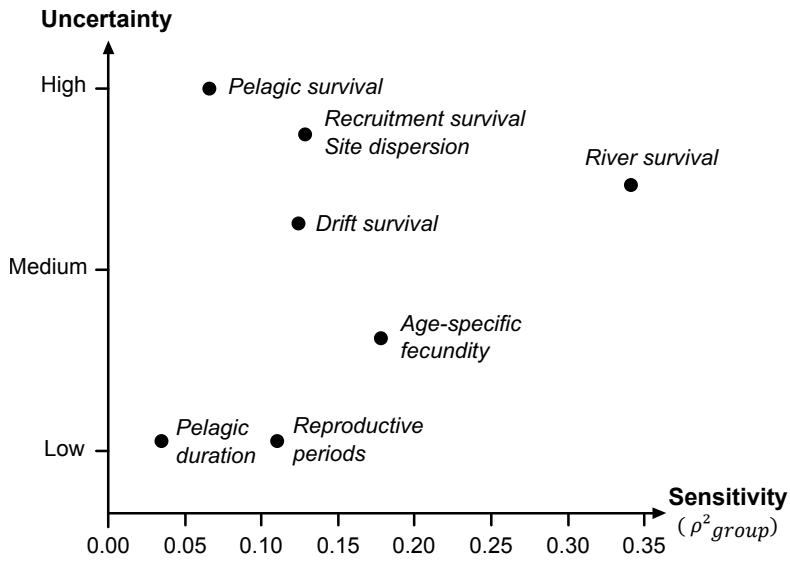

Figure 4: Rough cross-classification of the seven parameter groups by their pooled sensitivity ρ^2_{group} (Eq. (33)) and our "expert opinion" estimates of the uncertainty on each group.

challenge is enhanced by the extreme nature of the fecundity rates (tens of thousands a month) and of the survival rates (one in a hundred thousand reaches the age of reproduction). These extreme rates reflect challenging natural conditions of tropical islands which affect food availability, competition for habitat, predation etc. To these natural hazards one has to add anthropogenic factors such as the intensive fishing at river mouths and poaching. Dams and weirs can affect the movement of migratory species and compromise habitats diversity.

Our model aggregates many natural and anthropogenic factors which have a large influence on the growth potential of the population. For example, an assessment of fisheries efficiency and productivity are preliminary requirements in order to evaluate the importance of this human activity on the population and distinguish its effect from the natural causes of mortality at settlement. Unfortunately, the quantities/weight of post-larvae caught by fisheries are not subject to official declarations in La Réunion, which complicates the task of data-hungry biologists.

Despite the many pitfalls and "blind data spots" we were able to reproduce the dynamics of *S. lagocephalus* in good general agreement with our knowledge on survival,

fecundity and seasonal patterns (i.e. the model captures age and peaks of recruitment in river mouths). The large uncertainties that remain concerning the parameter values still preclude the use of our model for projection/management purposes. Such a model would ideally lead to recommendations on preservation and conservation measures that would insure the subsistence of the local stock of *S. lagocephalus*. Although not mature enough to be used as a projection tool, our model has shed light on the components of the life history that are critical to the completion of the life cycle: more precise estimates of the fish's life expectancy in river and mortality at recruitment and survival during the drift of larvae toward the sea would bring the model closer to being a workable management tool.

Parameter	Definition	Value	Source	Corr. coeff.
Reproductive periods				
Downstream	Begin-End months	Nov.-July	[50]	(0.20, -0.19)
Midstream	Begin-End months	Jan.-June	[50]	(0.15, -0.10)
Upstream	Begin-End months	Fev.-May	[50]	(0.01, -0.10)
Age-specific fecundity				
ρ	Time before sexual maturation	9 mo.	[48]	-0.05
f_{max}	Max fertility	73989.71 eggs	[50, 14]	0.38
f_{min}	Min fertility	-31583.25 eggs	[50, 14]	-0.03
a_{inf}	Age at fertility inflection	11.80 mo.	[50, 14]	-0.16
d_{inf}	Deriv. fertility at inflection	3.49 eggs/mo.	[50, 14]	0.07
Drift survival				
η	Probability of reaching the sea	1	[51]	0.35
Pelagic survival				
σ_1	Larval survival rate at 2 mo.	10^{-4}	[20, 21]*	0.13
σ_2	Larval survival rate at 7 mo.	2×10^{-5}	[20, 21]*	0.21
κ	Seasonal effect of temperature	0.2	[20]*	0.06
b_0	Mesor of the periodic regression	25.73	[37]	
b_1	Periodic regression coefficient	2.24	[37]	
b_2	Periodic regression coefficient	0.80	[37]	
Pelagic duration				
(μ_1, σ_1)	(mean, std. dev)	(4.37, 0.76)	[48]	(-0.10, 0.00)
(μ_2, σ_2)	(mean, std. dev)	(5.14, 0.78)	[48]	(-0.01, 0.04)
(μ_3, σ_3)	(mean, std. dev)	(5.38, 0.91)	[48]	(-0.05, 0.02)
(μ_4, σ_4)	(mean, std. dev)	(6.31, 1.00)	[48]	(-0.05, 0.01)
(μ_5, σ_5)	(mean, std. dev)	(6.71, 0.86)	[48]	(-0.08, -0.04)
(μ_6, σ_6)	(mean, std. dev)	(7.09, 1.01)	[48]	(-0.04, -0.01)
(μ_7, σ_7)	(mean, std. dev)	(7.08, 0.88)	[48]	(-0.02, 0.01)
(μ_8, σ_8)	(mean, std. dev)	(6.80, 0.84)	[48]	(0.04, 0.01)
(μ_9, σ_9)	(mean, std. dev)	(6.05, 0.65)	[48]	(-0.01, 0.00)
(μ_{10}, σ_{10})	(mean, std. dev)	(4.79, 1.01)	[48]	(0.02, -0.02)
(μ_{11}, σ_{11})	(mean, std. dev)	(4.28, 0.35)	[48]	(0.00, 0.04)
(μ_{12}, σ_{12})	(mean, std. dev)	(4.48, 0.78)	[48]	(-0.05, 0.01)
Recruitment survival and site-dispersion				
φ_τ	Survival rate at recruitment	0.05	[13, 28]*	0.35
(θ_1, θ_2)	Probabilities of river-site choice ($\theta_3 = 1 - (\theta_1 + \theta_2)$)	$(0.55, 0.35)$	[40]	(0.07, 0.03)
River survival				
e	Life expectancy	24 mo.	[7, 23]*	0.58

Table 1: Parameter descriptions, their baseline values and sources (*: studies dealing with species close to *Sicyopterus lagocephalus*). The last column has the estimated Pearson correlation coefficients.

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