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Assessing management scenarios for the river shrimp *Cryphiops caementarius* in the semi-arid region of Chile: Based on semi-quantitative ecological network approach

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ABSTRACT

The conservation of native amphidromous freshwater shrimp in semi-arid basins is challenged by habitat fragmentation, prolonged droughts, and unregulated artisanal fisheries. We evaluated alternative management scenarios for *Cryphiops caementarius* in the semi-arid Choapa River basin (north-central Chile) using semi-quantitative ecological and eco-social models based on Loop Analysis. Three limnetic zones (River Mouth, Potamon, and Rhithron) were modeled according to their dominant life stages and key ecological drivers. Four management strategies: Fisheries Regulation, Water Management, Restocking, and an Integrated Approach, were simulated to assess local stability, resilience, and component sensitivity. All models were locally stable and resilient, but responses varied spatially: the Potamon exhibited the highest stability, whereas the Rhithron showed the lowest. Integrated management enhanced resilience in upstream zones but had more constrained effects downstream, reflecting differences in structural complexity. Sensitivity patterns highlighted Detritus, Water flow, and Adult shrimp as critical variables shaping system behavior. Restocking alone provided limited benefits and was strongly dependent on habitat quality and hydrological conditions. These findings underscore the need for basin-scale, spatially explicit, and adaptive governance frameworks that integrate fisheries, water, and habitat management. Loop Analysis proved to be a valuable tool for informing decision-making in drought-prone freshwater systems under ecological uncertainty.

1. Introduction

The river shrimp *Cryphiops caementarius* is a palaemonid native to the arid and semi-arid basins of northern Chile. In these areas, its populations support a small-scale artisanal fishery carried out by local fishing communities (Velásquez et al., 2022a). Harvesting is typically conducted manually, with or without simple fishing gear (e.g., small hand-held dip nets, locally known as “chinguillos”), either by free diving or by targeted hand collection in shallow river sections (Fig. 1). This species is heterosexual and polygamous, and exhibits an amphidromous life cycle in which adults inhabit rivers while larvae develop in estuarine mixing zones (e.g., Bahamonde and Vila, 1971; Norambuena, 1977; Zuñiga and Ramos, 1990). Sexual maturity is generally attained during the first year of life, although size at maturity varies geographically; ovigerous females have been reported at cephalothorax lengths (CL) as small as 7–10 mm CL, while larger mature females may reach 33–36 mm CL. Fecundity increases with body size and may exceed 30,000 eggs in large individuals. Spawning occurs mainly between September and May, with peak reproductive activity during austral spring-summer, and eggs incubate for approximately 25–30 days (Morales and Meruane, 2013a; Moreno-Reyes et al., 2021). Larval development includes at least 18 stages under cultured conditions, progressing through multiple zoeal stages before reaching the first juvenile stage (Morales et al., 2006). After completing development in estuarine environments, juveniles migrate upstream into freshwater habitats, where adults can reach up to approximately 180 mm total length (Meruane et al., 2006; Morales and

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Fig. 1. Manual harvesting by free diving or targeted hand collection in shallow river sections for the capture of *Cryphiops caementarius*.

Meruane, 2013b). This dependence on estuarine-river connectivity, together with geographically variable size at maturity, underpins the relevance of management measures such as seasonal closures, minimum size limits, and the protection of ovigerous females.

The fishery operates under an open-access regime, although it is not formally recognized as such under the General Fisheries and Aquaculture Law (LGPA), as it is not included in the official list of Chilean artisanal fisheries. This lack of formal recognition is linked to the small-scale and geographically dispersed nature of the activity, which takes place in isolated continental basins and involves relatively low landing volumes that do not reach economically significant thresholds at the national level. Historically, the fishery has operated without formally registered fishers' organizations or a legally constituted administrative unit, limiting its institutional visibility. The absence of systematic landing records since 1994 has further reduced statistical continuity, hindering its formal incorporation into the regulatory framework. In addition, the LGPA has traditionally prioritized marine resources, leaving certain inland fisheries in a regulatory "grey area" between national fisheries legislation and regional management responsibilities (Velásquez et al., 2022a, b). Consequently, the activity persists under a de facto open-access regime, with limited monitoring, enforcement, and structured governance instruments to support sustainable management. Basic fisheries information, such as up-to-date landings data, remain incomplete. The only historical landing data available correspond to official records from the National Fisheries and Aquaculture Service (Sernapesca) between 1984 and 1994, with reported landings fluctuating between 2 and 6 tons; no official updates have been reported since then. Nevertheless, since 1986, several regulations have been established to protect the species, including a biological closure during the reproductive period (December 1 to April 30), a minimum legal size (30 mm CL) and a permanent prohibition on the extraction of ovigerous females (Morales and Meruane, 2013b; Velásquez et al., 2022a, b). Although these regulations are formally in place, their practical effectiveness is constrained by limited enforcement capacity and low compliance. As a result, populations are subjected to intense extractive pressure for human consumption. The relatively high market value of the species (13–20 USD kg^{-1}) creates strong economic incentives that may further undermine regulatory compliance, increasing fishing pressure despite the existing management measures (Velásquez et al., 2022b).

The fisheries of this species are carried out in highly fragmented habitats with prolonged periods of drought, intensive use of water resources, and the presence of invasive fish, such as cyprinids and salmonids, which compete with shrimp for habitat (especially for adult stages) or predators (especially of juvenile stages), all of which pose a severe threat to the conservation of *C. caementarius*, leading to massive mortalities and local extinctions (Avilés et al., 2018; Velásquez et al., 2020; 2022c). In 2013, the Ministry of the Environment of Chile (MMA) classified *C. caementarius* as a Vulnerable (VU) species, reflecting its high risk of extinction in the wild. This designation was based on documented population declines over the previous decade, a geographically restricted distribution, and extensive habitat fragmentation. Recently, several initiatives have been proposed to conserve wild populations, including restocking actions through the release of hatchery-reared juveniles (Velásquez et al., 2024), mitigation measures addressing physical disturbances in their habitat (Velásquez et al., 2023), and proposals for fisheries management and regulation (Velásquez et al., 2022a, b). All of these initiatives were carried out in the Choapa River basin (semi-arid region of north-central Chile), constituting the first documented conservation and restocking efforts for a freshwater crustacean in the country, and one of the few implemented worldwide in semi-arid ecosystems. Among these initiatives, restocking with hatchery-reared juveniles has emerged as a complementary tool to support population recovery in basins where recruitment is constrained by drought, habitat fragmentation, or intense fishing pressure. Although restocking is not a stand-alone solution and its long-term effectiveness remains uncertain, it represents one of the few active interventions currently implemented for *C. caementarius* (Velásquez et al., 2024). For this reason, it is important to evaluate its potential ecological consequences alongside other management measures within an integrated, basin-scale framework.

In this context, ecological qualitative or semi-quantitative modeling has been proposed as a useful tool to evaluate potential changes in natural systems resulting from the implementation of management measures (including those aimed at improving fishery productivity) in both marine (e.g., Ortiz and Ayala, 2024; Berrios and Ortiz, 2025) and freshwater ecosystems (e.g., Marcot et al., 2001; Mantyka-Pringle et al., 2016). This type of modeling integrates digraphs with interaction community matrices, allowing the estimation of local stability and resilience, through which it is possible to address the main challenges facing this species (i.e., poorly regulated fishing exploitation and high conservation risk during drought), and understand the biophysical variables affecting *C. caementarius* along the river. Local stability refers to the tendency of a system to return to its equilibrium or average value after small disturbances, whereas the definition of resilience used in this work is that related to the ability to resist perturbations. Therefore, the aim of this study was to evaluate management scenarios using semi-quantitative modeling approach known as Loop Analysis (Levins, 1998; Ortiz and Levins, 2011) to guide and improve decision-making processes aimed at enhancing *C. caementarius* populations in the semi-arid Choapa River basin. For this purpose, three eco-social models were built that represent different limnetic zones along the river. These approaches will assist in simulating the behavior of the eco-social system (Ortiz and Levins, 2017) interacting with *C. caementarius*, providing the necessary information to guide appropriate management actions while considering the challenges faced by the species, and offering insights into how system stability and resilience may shift under alternative management strategies.

2. Methods

2.1. Semi-arid Choapa River basin

The Choapa River basin (ca. 32°S) (Fig. 2), located in the semi-arid region of central-northern Chile, is characterized by a mixed hydrological regime with both pluvial and nival inputs. It is strongly influenced

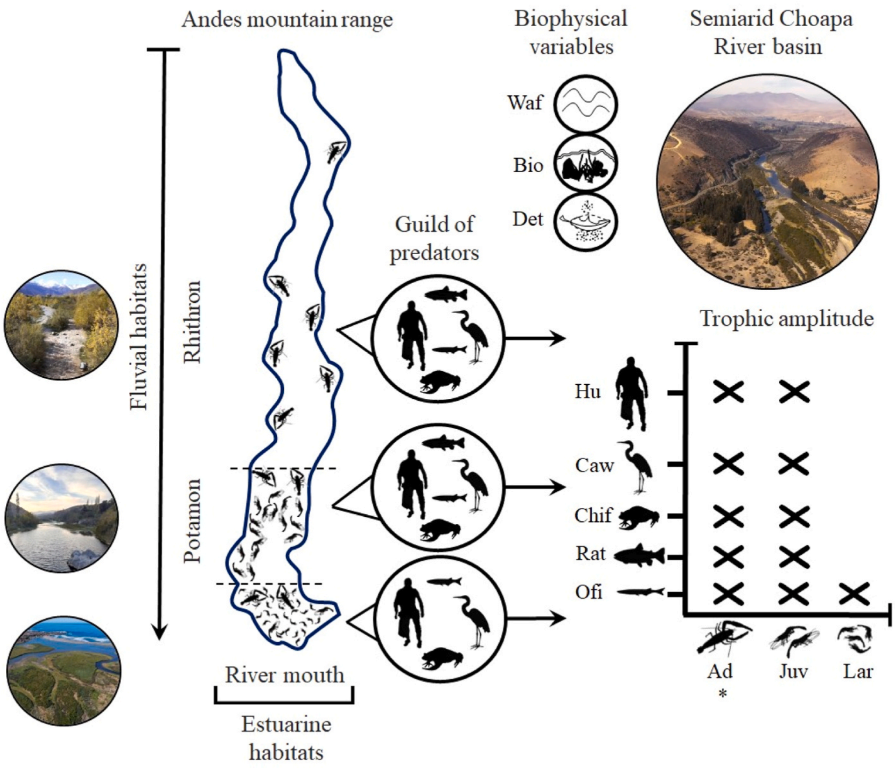

Fig. 2. Schematic representation of the limnetic zones in the semi-arid Choapa River basin (River mouth, Potamon, and Rhithron). For each zone, the occurrence of ontogenetic stages of *Cryphiops caementarius* is indicated (Lar: Larvae; Juv: Juvenile; Ad: Adult), along with predator guilds (Hu: Humans; Caw: Carnivorous waterbirds; Chif: Chilean giant frog; Rat: Rainbow trout; Ofi: Omnivorous fish) and key biophysical variables (Waf: Water flow; Bio: Biophysical refuges; Det: Detritus). The trophic amplitude diagram shows that predation pressure varies depending on the ontogenetic stage of *C. caementarius*. *Indicates cannibalistic behavior of adults toward juveniles.

by prolonged droughts during summer and autumn, followed by a short but intense rainy season in winter (Souvignet et al., 2012). This sharp seasonal contrast generates high interseasonal variability in average monthly water flows. Annual precipitation in the basin is low (approximately 80–300 mm·yr^{-1}) and exhibits a marked orographic gradient from the coastal zone to the Andes (Favier et al., 2009). Most rainfall occurs during late autumn and winter, while the nival contribution originates mainly from the Andes mountain range. Together, these pluvial and nival inputs reinforce the strong seasonality of water availability characteristic of semi-arid systems.

Since 2010, the Choapa River basin has been affected by a persistent mega drought, part of a broader climatic phenomenon impacting much of central-northern Chile (Garreaud et al., 2020; Alamos et al., 2024). This prolonged dry period has severely reduced water availability for domestic and agricultural use. In response, the Ministry of Public Works of Chile (MOP) declared the basin a "zone of water scarcity", authorizing emergency interventions such as river channelization and surface water extraction. These emergency actions have reduced habitat connectivity, directly impacting the viability of *C. caementarius* populations (Velásquez et al., 2022c).

In recent years, climate change and other large-scale environmental changes have altered the hydrological regime of the basin. These include the upward shift of the zero-isotherm, which has reduced snow accumulation in the Andes mountain range, and increasing irregularity in precipitation patterns (Araya-Osses et al., 2020). Together, these factors have negatively impacted basin recharge processes and, consequently, the availability and quality of aquatic habitats critical to native species (Velásquez et al., 2023).

2.2. *Natural history of Cryphiops caementarius in the semi-arid Choapa River basin*

Within this increasingly constrained hydrological and habitat context, *C. caementarius* follows an amphidromous migratory cycle in which reproduction occurs in freshwater, whereas larval development takes place in estuarine mixing zones. After completing larval development, juveniles migrate upstream and settle in freshwater habitats, where they grow and reach the adult stage. This migratory pattern generates a spatial segregation of larvae, juveniles, and adults along the basin’s limnetic zones (Fig. 2). Although the spatial structure of this cycle is well documented, precise information on longevity, age at maturity, and the duration of each ontogenetic stage within specific zones of the basin remains unknown. The species is detritivorous/omnivorous and exhibits cannibalistic behavior, with adults preying on juveniles. Consequently, juveniles tend to concentrate near riversides, whereas adults are more frequently found along the central axis of the river (Velásquez et al., 2024).

This basin provides favorable ecological conditions for *C. caementarius* due to its diverse benthic habitats (e.g., riffles, pools, and riversides) shaped by river hydrodynamics (e.g., slope and water flow velocity) and the availability of biophysical refuges. Among these, water flow velocity is particularly relevant, influencing the altitudinal distribution of juveniles and adults, with the latter better adapted to turbulent upstream zones (Fig. 2). Biophysical refuges, such as aquatic macrophyte banks, submerged riparian roots, and sedimentary substrates, serve as essential feeding and reproductive sites (Velásquez et al., 2023, 2024). Detritus, the primary food resource for this species, also plays a key role in nutrient cycling, a process strongly influenced by local hydrodynamic conditions (López et al., 1986; Velásquez et al., 2020).

Across the Choapa River basin, the amphidromous cycle is expressed through a clear spatial organization of life stages within three major limnetic zones (River mouth, Potamon, and Rhithron), each characterized by distinct ecological conditions and eco-social interactions. In the River mouth, larvae, juveniles, and adults coexist (Fig. 2), although this zone is particularly important for larval development due to the transitional conditions created by the mixing of seawater and freshwater (Velásquez et al., 2024). Fishing occurs here but is less intensive than in upstream reaches.

In the Potamon zone, juveniles dominate the population structure (Fig. 2), reflecting their preference for reaches with gentle slopes, laminar flow, and sandy-gravel or fine sediment substrates (Velásquez et al., 2024). This zone supports the highest fishing intensity in the basin and is also the most vulnerable to drought and physical habitat alterations (Velásquez et al., 2023), which have repeatedly triggered mass mortality events (Velásquez et al., 2022c). Catch numbers follow a clear altitudinal pattern, peaking in the Potamon and progressively decreasing upstream (Velásquez et al., 2022a).

In the Rhithron zone, the population is composed mainly of reproductive adults (both males and females) (Fig. 2). This upstream section is defined by steep slopes, turbulent flows, and boulder-type substrates (Velásquez et al., 2024). Although fishing also occurs here, the Rhithron benefits from a more stable year-round water supply due to snowmelt contributions from the Andean mountain range. In contrast to catch abundance patterns, total prawn biomass increases from the Potamon to the Rhithron, reflecting the predominance of larger adults in these upstream reaches (Velásquez et al., 2022a).

Thanks to its trophic versatility, *C. caementarius* occupies a key position in the riverine food web, whereas its extensive migratory movements expose it to a wider range of predator guilds, including humans. It is preyed upon by five main predator groups: Humans (Hu; fishers); Carnivorous waterbirds (Caw; *Ardea cocoi*, *Ardea alba*, *Egretta thula*, *Nycticorax nycticorax*, *Nannopterum brasilianus*, *Larus dominicanus*); the Chilean giant frog (Chif; *Calyptocephalella gayi*); the Rainbow trout (Rat; *Oncorhynchus mykiss*); and Omnivorous fish (Ofi; *Mugil cephalus*, *Basilichthys microlepidotus*, *Cyprinus carpio*) (Velásquez et al., 2020). Predation pressure differs among limnetic zones because each ontogenetic stage occupies distinct habitats and is exposed to different Predator guilds (Fig. 2).

2.3. Loop analysis theoretical framework: quantification of local stability, resilience, and transient stable states

To translate the ecological structure described in Section 2.2. into a formal analytical framework, we applied the semi-quantitative Loop Analysis to quantify the stability and resilience of the model-system under different management scenarios. This approach enables us to simulate the dynamic response of *C. caementarius* to internal ecological interactions and external perturbations (e.g., Ortiz and Levins, 2011; 2017). Loop Analysis enables the integration of interactions among variables within a Jacob–Levins community matrix. This approach accommodates both quantifiable and non-quantifiable variables, interactions, and the relationships between ecological and social field and the propagated effects of anthropogenic impacts to the systems (Giavelli and Bodini, 1990; Levins, 1998; Ramsey and Veltman, 2005; Dambacher et al., 2007; Ortiz and Levins, 2011; 2017; Bodini et al., 2018; Reum et al., 2020; Ortiz and Ayala, 2024), showing a high degree of predictability (after disturbances) of natural phenomena (Briand and McCauley, 1978; Lane, 1986; Hulot et al., 2001; Ortiz, 2008).

Based on this theoretical framework, it is possible to determine the local stability and resilience of different model networks, and how direct and indirect effects propagate in response to perturbations (i.e., management scenarios). Variable relationships are represented using semi-quantitative signed digraphs, where each variable is denoted as a node (solid circle) and the interactions are depicted as directed links. Arrows indicate positive effects; small circles represent negative effects; and absence of symbols denotes neutral effects. It is important to note that this technique only captures the nominal effect between the interacting variables not quantifying its magnitude or weight. Furthermore, the other parameters and constants of the equations that describe the interactions are not included, and in predictive terms only estimates the direction of change (positive, null or negative) in the system variables. In this sense, the standard ecological predator–prey relationship is captured with a positive effect ($+1$) towards the predator and a negative (-1) towards the prey. In the case of competition, both have a mutual negative effect (-1, -1), mutualism, both positive ($+1$, $+1$), commensalism ($+1$, 0), and amensalism (-1, 0). Each variable can also exhibit self-regulation through feedback loops: self-negative (-1), self-null (0), or self-positive ($+1$). These self-feedbacks describe the fluctuations that local populations exhibit around their equilibrium values (i.e., average values), driven by density-dependent or independent processes, biotic interactions (e.g., predation, competition), and environmental changes (Lewontin and Levins, 2007). Likewise, the changes among negative, null, and positive self-feedback would be related to density-dependent, density-null, and density-independent dynamics of any population that exhibits a unimodal shape in the sense of the logistic equation (Levins et al., 2013). It is relevant to mention that loop models promote generality and realism rather than precision (Levins, 1998).

A dynamical system can be represented by the correspondence of differential equations at equilibrium, matrices, and their digraphs. Therefore, in any system, the a_{ij} element of the Jacob–Levins interaction matrix and the digraph represent the effect of variable j on the growth of variable i when the equation:

$$dX_i/d_t = F_i\ (X_1, X_2, X_3, \ldots, X_n; C_1, C_2, C_3, \ldots, C_n),$$

where the dynamical change of the variable X_i is a function of F_i of other interconnected variables X_n and parameters C_n and is solved at equilibrium. The link from X_j to X_i is like the α_{ij} in Levins (Levins, 1968), as follows:

$$\propto_{ij} = \partial F_i\ (X) X^* / \ \partial X_j$$

where X^* is evaluated at equilibrium. The α_{ij} is the element of the digraph representing the link from j to i. The semi-quantitative function sign of X is $+1$ when $X > 0$, 0 when $X = 0$ and -1 when $X < 0$.

The Routh–Hurwitz criteria for local stability translate into loop terms as Condition 1 (RH1) when $Fs < 0$ for all s. Fs corresponds to the negative feedback on every level of complexity (s) that must exceed the positive feedback. Condition 2 (RH2) indicates that negative feedback on higher levels of complexity cannot be too great compared with the negative feedback on lower levels to conserve the qualitative stability properties of the systems. This second condition can be calculated by using the expansion of the Hurwitz determinants in terms of feedback or loops (Puccia and Levins, 1985). In this case, stability (using Fs) is defined as the ability of a system to return to the initial state after being disturbed. The feedback for each level (s) (Fs) can also be calculated by estimating the characteristic polynomial related to the Jacob–Levins community matrix, in which the polynomial now can be written in terms of the feedback (Fs) notation as follows:

$$F_0\lambda^n + F_1\lambda^{n-1} + F_2\lambda^{n-2} + \cdots + F_{n-1}\lambda^1 + F_n\lambda^0 = 0,$$

where $F_0 = -1$ and F_n is the feedback of the entire system (n = total number of variables in the system) (Puccia and Levins, 1985). Because the stronger the negative Fn is, the greater the resistance of the system to external changes (Levins, 1998), this feedback can be used as a quantification of resilience according to the definition given by Holling (Holling, 1973). In this work, stability and resilience will be quantified by Fs and Fn, respectively, which are related attributes in the polynomial equation. In short, it would be possible to quantify local stability (Fs) and resilience (Fn) of any system and explore strategies that increase or decrease them.

To determine the total number of transient states related to the Jacob–Levins matrices, the main diagonal was filled with unknowns (?), through which the three self-feedbacks (positive, null, and negative) for each variable were explored using combinations. Once the matrices were set, their characteristic polynomials, the Routh–Hurwitz's local stability criterion 1 (*Fs*) and Levins' criterion (*Fn*) were determined using Loop Analysis software. In terms of sensitivity, variables showing $<$ 5% stable transient states under any self-feedback configuration were considered the most vulnerable to external perturbations. In this context, we refer to "sensitive components" as those variables that exhibit a lower than 5% of stable transient states across all possible self-feedback (positive, null and negative) configurations. Such variables are therefore more vulnerable to external perturbations and have a greater influence on the stability of the system. Identifying these sensitive components allows us to determine which elements of the eco-social network are most likely to drive system-wide responses under management interventions.

c) Eco-social Model 3 - Rhithron

Variables	Caw	Ofi	Chif	Rat	Ad	Juv	Lar	Hu	Waf	Bio	Det
Caw	?	1	1	1	1			0	0	-1	0
Ofi	-1	?	0	-1	-1			-1	1	1	1
Chif	-1	0	?	0	1			-1	1	1	0
Rat	-1	1	0	?	1			-1	1	-1	1
Ad	-1	-1	-1	-1	?			-1	1	1	1
Juv											
Lar											
Hu	0	1	1	1	1			?	0	-1	0
Waf	0	0	0	0	0			0	?	-1	0
Bio	0	0	0	0	0			0	1	?	1
Det	1	1	1	1	1			1	1	1	?

b) Eco-social Model 2 - Potamon

Variables	Caw	Ofi	Chif	Rat	Ad	Juv	Lar	Hu	Waf	Bio	Det
Caw	?	1	1	1	1	1		0	0	-1	0
Ofi	-1	?	0	-1	-1	1		-1	1	1	1
Chif	-1	0	?	0	1	1		-1	1	1	0
Rat	-1	1	0	?	1	1		-1	1	-1	1
Ad	-1	-1	-1	-1	?	1		-1	1	1	1
Juv	-1	-1	-1	-1	-1	?		-1	1	1	1
Lar											
Hu	0	1	1	1	1	1		?	0	-1	0
Waf	0	0	0	0	0	0		0	?	-1	0
Bio	0	0	0	0	0	0		0	1	?	1
Det	1	1	1	1	1	1		1	1	1	?

a) Eco-social Model 1 - River mouth

Variables	Caw	Ofi	Chif	Rat	Ad	Juv	Lar	Hu	Waf	Bio	Det
Caw	?	1	1		1	1	0	0	0	-1	0
Ofi	-1	?	0		-1	1	-1	-1	1	1	1
Chif	-1	0	?		1	1	0	-1	1	1	0
Rat											
Ad	-1	-1	-1		?	1	0	-1	1	1	1
Juv	-1	-1	-1		-1	?	1	-1	1	1	1
Lar	0	-1	0		0	-1	?	0	1	0	0
Hu	0	1	1		1	1	0	?	0	-1	0
Waf	0	0	0		0	0	0	0	?	-1	0
Bio	0	0	0		0	0	0	0	1	?	1
Det	1	1	1		1	1	1	1	1	1	?

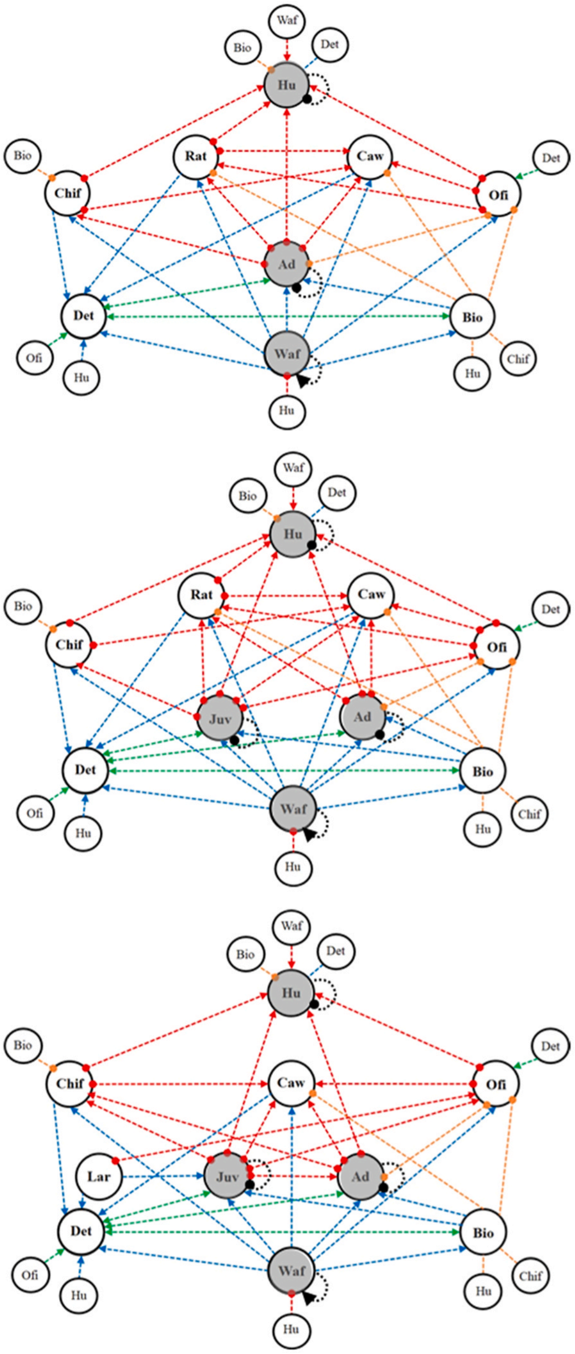

Fig. 3. Signed digraphs for the initial Eco-social Model for the River Mouth (a), Potamon (b), and Rhithron (c). Variables: Carnivorous waterbirds (Caw); Omnivorous fish (Ofi); Chilean giant frog (Chif); Rainbow trout (Rat); Adult shrimp (Ad); Juvenile shrimp (Juv); Larvae (Lar); Humans (fishers) (Hu); Water flow (Waf); Biophysical refuges (Bio); Detritus (Det). The relationships are shown as edges: arrows represent positive effects, small circles represent negative effects, and the absence of either symbol indicates a null effect. The Jacob–Levins community matrices associated with each eco-social model are also shown. The unknown (?) on the main diagonal indicates that the three self-feedbacks of each variable will be simulated. Empty cells indicate that no variables are available for that zone. The grey circles highlight the variables with negative self-feedback (Hu, Ad, and Juv) and the variable with positive self-feedback (Waf). The grey-circled variables represent the key components whose self-feedback were modified to simulate the different management scenarios.

2.4. Eco-social model and management scenarios

Building upon the theoretical framework described in Section 2.3, and using the ecological patterns described in Section 2.2 as structural inputs, we constructed eco-social models that represent the *C. caementarius* system and allow the evaluation of management scenarios. Four key variables, Predator guilds, Detritus (Det), Biophysical refuges (Bio), and Water flow (Waf), were identified as the main drivers influencing the habitability and population dynamics of *C. caementarius* (Fig. 2). These variables were incorporated into a conceptual model that served as the foundation for the Loop Analysis. Given the amphidromous life cycle of *C. caementarius* and the spatial segregation of its ontogenetic stages across the basin, three zone-specific eco-social models were constructed to represent the River mouth, Potamon, and Rhithron. Each model retained the same core variables but differed in the presence of life stages (Larvae, Juvenile, and Adult) and in the sign of specific interactions, reflecting the ecological conditions and fishing pressures characteristic of each zone (Fig. 3). This structure allowed us to evaluate how management interventions may differentially affect system stability and resilience across the basin.

For each eco-social model, four management scenarios were simulated by modifying the self-feedback of key variables within the Jacob–Levins community matrix:

a) Shrimp Fishery Regulation (FR): Enforcement of the regulatory framework governing shrimp extraction was modeled as negative self-feedback on the Humans (Hu) variable (Fig. 3). In Loop Analysis, negative self-feedback represents internal constraints that limit the growth or intensity of a variable. In this context, increasing negative self-feedback on Hu reflects stricter compliance, monitoring, and enforcement, which reduce the effective fishing pressure exerted on shrimps.

b) Water Management (WaM): Sustainable water use and the protection of environmental flows were represented as positive self-feedback on the Water flow (Waf) variable (Fig. 3). This reflects management actions that maintain or enhance hydrological conditions, such as securing minimum flows during drought or improving water allocation efficiency, thereby increasing the system’s capacity to sustain suitable habitat conditions for *C. caementarius*.

c) Shrimp Restocking (Res): Restocking was modeled as negative self-feedback on the Juvenile (Juv) or Adult (Ad) variables, depending on the dominant life stage in each zone (Fig. 3). In Loop Analysis, negative self-feedback on a biological variable represents density-dependent regulation. By increasing this self-feedback, the model incorporates the idea that restocking elevates local densities and intensifies density-dependent processes such as competition, cannibalism, or habitat limitation.

d) Integrated Management (FR + WaM + Res): A combined strategy that incorporates all three interventions.

In the context of Loop Analysis, this formulation does not simulate the numerical magnitude, timing, or spatial precision of releases; instead, it captures the general ecological consequence of adding individuals to the system-namely, the intensification of density-dependent processes. Therefore, the modeled scenario corresponds to a generic, recurrent restocking program that increases local densities within each zone, rather than a specific operational protocol. This approach is consistent with the qualitative nature of Loop Analysis, which evaluates the direction and propagation of effects within the system rather than predicting quantitative population trajectories. Because Loop Analysis is a semi-quantitative framework, it does not incorporate quantitative attributes such as release size, frequency, or spatial targeting. These factors influence the magnitude of population responses but do not alter the qualitative structure of the system or the sign of interactions among variables. For this reason, the model focuses on the ecological direction of change generated by restocking, an increase in local density and its associated feedbacks, rather than on the operational details of specific release programs.

3. Results

All eco-social models and management scenarios were locally stable (*Fs*), resilient (*Fn*), and exhibited at least some stable transient states. Among the three initial models, the Potamon showed the highest local stability, resilience, and proportion of stable transient states, whereas the Rhithron displayed the lowest values (Table 1). Sensitivity analysis revealed consistent patterns across zones. Detritus (Det) emerged as a sensitive variable in all models, while Water flow (Waf) was sensitive in the River Mouth and Potamon, and Adult shrimp (Ad) in the River Mouth and Rhithron. Additional zone-specific sensitivities included Omnivorous fish (Ofi) in the River Mouth and Carnivorous waterbirds (Caw) in the Potamon, whereas Biophysical refuges (Bio) were sensitive only in the Potamon (Fig. 4). As defined in the Methods, these sensitive components represent the most vulnerable elements of each model, as they exhibit low proportions of stable transient states.

3.1. Eco-social Model 1. River mouth

Shrimp Restocking (Res) produced the highest average local stability (*Fs*), while both Res and Water Management (WaM) generated the strongest resilience (*Fn*). However, these interventions also reduced the proportion of stable transient states, in contrast to Shrimp Fisheries Regulation (FR), which achieved the highest percentage of stable transient states (Table 1). Fig. 4a show that WaM increased the number of sensitive components relative to the initial model, indicating that hydrological interventions make system stability more dependent on specific self-feedback configurations. FR, by contrast, did not alter sensitivity patterns, while Res partially counteracted the sensitivity induced by WaM. Combined interventions (WaM+Res and FR+WaM+Res) produced the broadest sensitivity across variables, reflecting a more constrained stability landscape.

3.2. Eco-social Model 2. Potamon

The simultaneous application of FR, WaM, and Res yielded the highest stability, resilience, and proportion of stable transient states (Table 1). Individual interventions produced only minor deviations from the initial model. As shown in Fig. 4b, combinations of management actions generally reduced the number of sensitive components, suggesting that integrated management broadens the range of self-feedback configurations compatible with transient stability. This pattern contrasts with the River Mouth, highlighting the Potamon’s greater structural robustness and its capacity to absorb management interventions without increasing vulnerability.

3.3. Eco-social Model 3. Rhithron

This zone exhibited a pattern similar to the Potamon; combined management interventions increased stability, resilience, and stable transient states more than any individual action (Table 1). Fig. 4c shows that both individual and combined interventions tended to reduce sensitivity relative to the initial model, indicating that management actions generally enhance the system’s tolerance to perturbations in this upstream zone. This contrasts with the River Mouth, where combined interventions increased sensitivity, likely reflecting the higher ecological complexity and multi-stage overlap characteristic of the estuarine transition zone.

4. Discussion

The semi-quantitative modeling approach revealed clear spatial differences in the structural stability of the eco-social system across the longitudinal gradient of the Choapa River basin. All modeled zones were locally stable and resilient, but the magnitude of this stability varied considerably along the river continuum. Among the three modeled

Table 1
Average and standard deviation (SD) of local stability (*Fs*), resilience (*Fn*), and percentage of locally stable transient states for each management scenario (Shrimp Fisheries Regulation, FR; Water Management, WaM; Shrimp Restocking, Res; and combined scenarios) across the three Eco-social Models (River Mouth, Potamon, and Rhithron). Stability (*Fs*) is based on the Routh–Hurwitz criterion 1 (RH1), and resilience (*Fn*) corresponds to the highest-order feedback of the system.

Eco-social Model	Management scenarios	Average *Fs*	SD	Average *Fn*	SD	Transient states	Stable transient states	%
River mouth	Initial model	-45.09	50.55	-7.79	6.56	59049	218	0.37
	FR	-47.35	53.14	-9.01	7.08	19683	164	0.83
	WaM	-43.27	51.53	-4.50	4.95	19683	2	0.01
	Res	-82.76	79.67	-11.33	8.14	19683	24	0.12
	FR+Res	-53.43	60.78	-11.51	8.34	6561	57	0.87
	FR+WaM	-43.27	51.53	-4.50	4.95	6561	2	0.03
	WaM+Res	-50.18	59.74	-8		6561	1	0.02
	FR+WaM+Res	-50.18	59.74	-8		2187	1	0.05
Potamon	Initial model	-67.82	97.22	-9.72	10.11	59049	404	0.68
	FR	-69.13	99.16	-11.67	11.74	19683	247	1.25
	WaM	-75.84	103.6	-12.36	11.83	19683	182	0.92
	Res	-78.78	111.1	-12.40	11.99	19683	212	1.08
	FR+Res	-80.39	113.1	-14.82	13.91	6561	130	1.98
	FR+WaM	-75.76	103.8	-14.10	13.08	6561	126	1.92
	WaM+Res	-85.84	116.5	-15.10	13.77	6561	100	1.52
	FR+WaM+Res	-86.06	116.7	-17.16	15.28	2187	69	3.16
Rhithron	Initial model	-28.14	29.14	-6.81	5.81	19683	42	0.21
	FR	-32.72	42.62	-7.43	6.75	6561	107	1.63
	WaM	-33.21	43.28	-7.09	6.81	6561	88	1.34
	Res	-33.36	43.50	-6.05	5.88	6561	157	2.39
	FR+Res	-34.55	44.77	-7.77	6.91	2187	91	4.16
	FR+WaM	-35.08	44.32	-8.79	7.73	2187	56	2.56
	WaM+Res	-33.55	43.70	-7.15	6.79	2187	84	3.84
	FR+WaM+Res	-35.78	45.04	-9.02	7.73	729	52	7.13

zones, the Potamon exhibited the highest resilience values, whereas the River Mouth and Rhithron zones showed lower stability (see Table 1). These results suggest that intermediate river reaches may play a key role in buffering ecological and socio-economic disturbances affecting populations of *C. caementarius*. The higher resilience observed in the Potamon likely reflects the greater structural complexity and ecological connectivity typically found in middle river sections, where habitat heterogeneity and resource availability tend to support more diversified trophic interactions and stable benthic communities (e.g., Vannote et al., 1980). In contrast, the River Mouth is exposed to stronger environmental variability and anthropogenic pressure, including fishing activities and sediment dynamics associated with coastal processes. Similarly, the Rhithron zone, characterized by steep gradients and variable discharge, may be more sensitive to perturbations affecting habitat structure and water availability (e.g., Vannote et al., 1980). Together, these results indicate that resilience within the basin is not evenly distributed along the river continuum, and that certain sections may function as ecological buffers capable of stabilizing population dynamics under environmental or anthropogenic disturbances (Van Looy et al., 2019; Pelletier et al., 2020; Ward et al., 2023).

This spatial perspective is particularly relevant for amphidromous species like *C. caementarius*, which rely on connectivity between freshwater and marine environments (de Mazancourt and Ravaux, 2024). Disruptions along the longitudinal gradient can affect multiple life stages, influencing overall population persistence (Bauer, 2013; Jarvis and Closs, 2019; Franklin and Gee, 2019). The relatively high resilience of the Potamon suggests that intermediate reaches are crucial for maintaining ecological connectivity, providing feeding, growth, and migratory habitats that stabilize the broader eco-social network (e.g., Pusey and Arthington, 2003; Darwall and Vié, 2005). These patterns reinforce the value of an eco-social modeling perspective, as human pressures and ecological processes jointly shape system stability across the basin.

Water Management (WaM) emerged as a key driver of system stability. Variations in water availability influenced habitat structure, food resources, and restoration effectiveness, consistent with the recognized role of hydrological regimes in river ecosystems (Pringle, 2001; Bunn and Arthington, 2002; Lake, 2003). In semi-arid basins like north-central Chile, drought and water extraction have reduced habitat connectivity and altered sediment and nutrient dynamics (Álamos et al., 2024). For amphidromous species, flow reductions may limit larval transport and disrupt migration, highlighting the fundamental importance of maintaining adequate water flows to sustain populations and management interventions (Augspurger et al., 2017; Harris et al., 2017; Novak et al., 2017). Sensitivity analyses further identified Water flow (Waf), Detritus (Det), and Adult shrimp (Ad) as key variables influencing system responses, underscoring their central role in maintaining ecological function under fluctuating hydrological conditions.

Fisheries pressure also shaped system responses. Scenarios with Fisheries Regulation (FR) produced more stable outcomes than open-access exploitation, suggesting that uncontrolled harvesting amplifies instability (Arlinghaus et al., 2015). In semi-arid regions, small-scale fisheries are often critical for local livelihoods but operate under limited regulation (e.g., Lopes et al., 2018; Velásquez et al., 2022b). FR stabilizes the system by reducing direct pressure on shrimp populations and allowing recruitment and habitat recovery (e.g., Price and Humphries, 2010; Williams et al., 2021).

Restocking (Res) scenarios had limited effectiveness when applied in isolation. While they could increase local shrimp abundance, long-term stability depended on suitable environmental conditions and the underlying ecological network. This aligns with broader trends in fisheries enhancement, where stock augmentation fails if habitat degradation or altered hydrology remain unresolved (Loneragan et al., 2006, 2013). For *C. caementarius*, restocking is further constrained by the need for functional connectivity during early life stages (e.g., Kikkert et al., 2009; Franklin and Gee, 2019; de Mazancourt and Ravaux, 2024). Thus, habitat protection and hydrological management remain more fundamental conservation measures (Verástegui et al., 2017; Jarvis and Closs, 2019; Velásquez et al., 2023).

Overall, the results emphasize the importance of viewing inland fisheries as components of broader socio-ecological systems. Interventions targeting a single component are unlikely to produce stable outcomes. Combined strategies, including WaM, FR, and habitat restoration, generated the most resilient responses, particularly in semi-arid basins where water scarcity and competing demands create complex management challenges. Basin-scale planning integrating ecological knowledge with fisheries management is essential to sustain biodiversity and support livelihoods (Barletta et al., 2009; Gawne et al., 2018). While

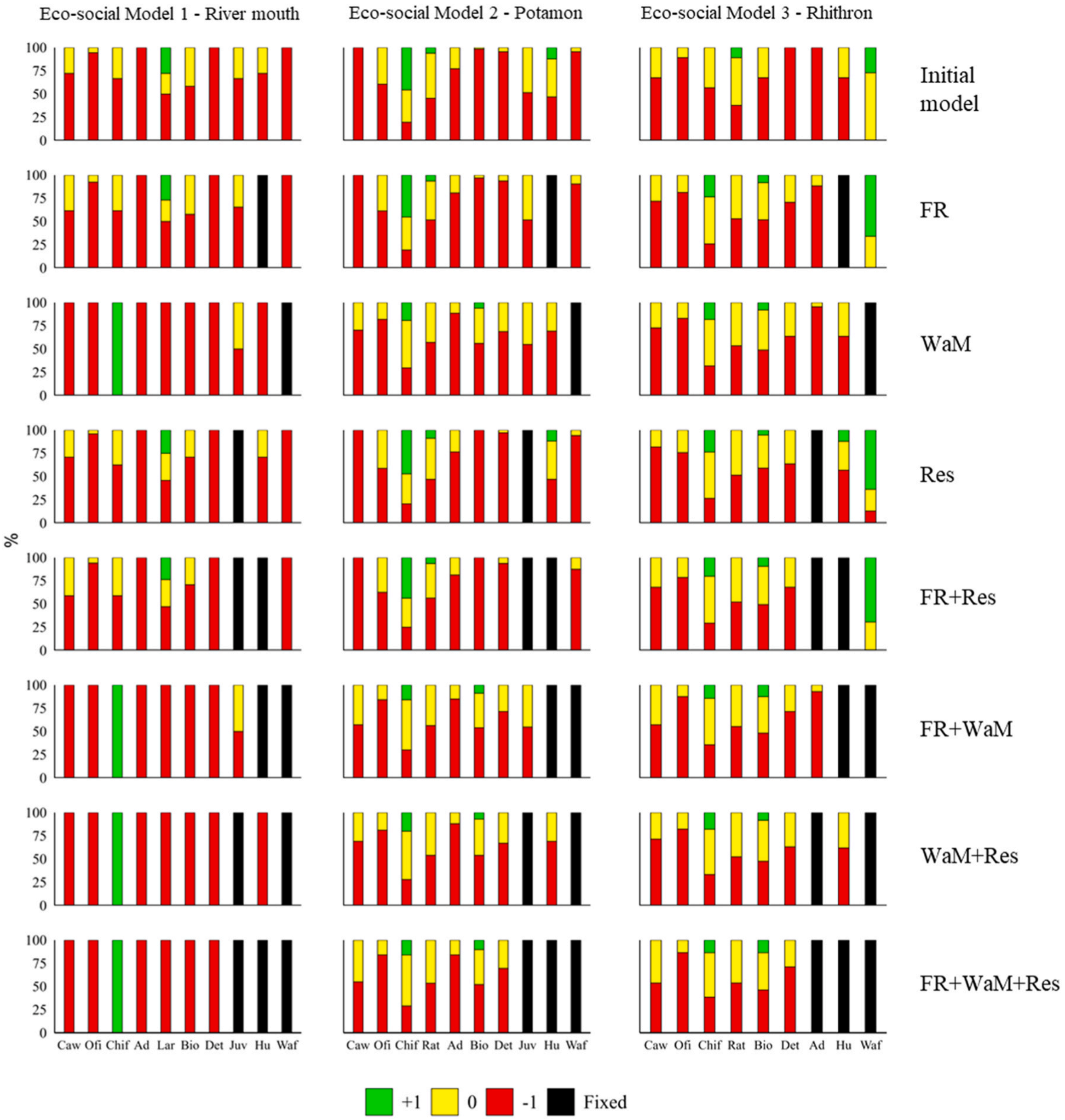

Fig. 4. Percentage of negative (red), null (yellow), positive (green), and fixed (black) self-feedbacks associated with stable transient states for each management scenario (Shrimp Fisheries Regulation, FR; Water Management, WaM; Shrimp Restocking, Res; and Integrated Management) in each Eco-social Model (River Mouth, Potamon, and Rhithron). Acronyms for all variables are provided in Fig. 3.

semi-quantitative ecological network modeling provides insights where empirical data are limited, several caveats apply. Likewise, the current work should be considered as a general modelling strategy since it captures the direction of interactions rather than their magnitude, allowing us to predict the system's putative responses rather than predicting quantitative changes in variables (local populations). Ultimately, it promotes generality and realism over precision (Puccia and Levins, 1985; Levins, 1998). Network structure relies on conceptual relationships from literature and species knowledge. Despite these limitations, qualitative models offer valuable exploratory tools to identify key stability drivers and guide research and management. Notably, integrated management produced spatially divergent outcomes, increasing resilience in upstream zones while slightly reducing it downstream, likely due to higher structural complexity and interaction density in lower reaches. This spatial heterogeneity highlights the need for geographically differentiated management strategies.

From a fisheries management perspective, conserving *C. caementarius* in the Choapa River basin requires addressing ecological drivers and human pressures simultaneously. WaM is critical for sustaining habitat connectivity and the amphidromous life cycle (Velásquez et al., 2022c; 2023). FR is essential to prevent destabilization from open-access harvesting and to allow positive population responses (Velásquez et al., 2022a, b). Restocking should be applied cautiously and only with habitat protection and hydrological management (Velásquez et al., 2024). Spatial differences in resilience suggest interventions may need to be targeted, with special attention to intermediate river reaches that disproportionately contribute to stability. In sum, integrated basin-scale management combining WaM, FR, and habitat restoration is crucial to support the long-term sustainability of shrimp fisheries in semi-arid rivers. Model patterns align with *C. caementarius* ecological traits and Choapa River dynamics, reinforcing the approach's ecological plausibility.

CRediT authorship contribution statement

Denisse Torres-Avilés: Software, Data curation. **Yeriko Alanís:** Conceptualization. **Carlos Velásquez:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Marco Ortiz:** Writing – review & editing, Supervision, Methodology. **Luis Henríquez-Antipa:** Writing – review & editing, Formal analysis.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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