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Evaluating the Efficacy of Approaches to Control Invasive Populations: A Conceptual Model Development for the Signal Crayfish

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Abstract: Invasive crayfish are among the major threats to freshwater ecosystems, with the signal crayfish, *Pacifastacus leniusculus*, being one of the most successful crayfish invaders in Europe. Approaches to invasive crayfish control range from manual and physical to biological and biocidal control methods. However, all of these approaches have their drawbacks and have limited efficacy. Among traditional approaches with minimal impacts on environment and non-target species, manual control via trapping is the most frequently applied. More innovative approaches comprise, among others, usage of sterile male release technique, whose efficacy in the field is yet to be fully tested, especially how it combines with more traditional approaches. A good alternative to costly and logistically challenging field comparisons of these approaches and their combinations is population modeling. Population models can integrate all relevant species-specific biological and ecological information and can be applied to identify management scenarios of highest impact on invasive crayfish abundances. In this study, we developed a conceptual population model of the invasive *P. leniusculus* following the Pop-GUIDE framework. In addition, we expanded on the framework to increase its applicability to other fields beyond environmental risk assessment. Finally, we discuss potential application of the model and its future use as a management tool.

Keywords: Pop-GUIDE; invasive crayfish management; trapping; sterile male release technique; *Pacifastacus leniusculus*



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1. Introduction

Invasive crayfish are one of the major threats to freshwater ecosystems. There is a high number of documented negative impacts of invasive crayfish on native crayfish diversity, abundance, and freshwater biodiversity and ecosystem structure globally [1–3]. The signal crayfish, *Pacifastacus leniusculus* (Dana, 1852), is among the most successful crayfish invaders and one of the most widespread invaders in Europe [1]. It is responsible for the decimation of numerous native European crayfish species, primarily through transmission of crayfish plague, to which causative agent, *Aphanomyces astaci*, it is relatively tolerant [4,5]. Moreover, in crayfish plague-free populations, it can outcompete native crayfish [6] due to its advantageous life history traits, such as faster growth, earlier maturation, higher fecundity, and aggression [7–10]. In Europe, it is listed as the Invasive Alien Species of Union concern (the Union list) pursuant to the EU Regulation on invasive alien species No. 1143/2014. According to the IAS regulation, for the species listed on the Union list, member states have to provide efficient management strategies aimed at controlling invader's dispersal and population growth.

To date, no standard methodology for the control of invasive crayfish has been established [11,12]. Traditional techniques for control of invasive crayfish have relied upon

a set of measures ranging from manual and physical control methods (intensive trapping activities, structural barriers, and drainage interventions) to biological and biocidal control [13–19]. However, all these approaches had limited success, especially in open ecosystems such as rivers and streams, and in long-established and highly abundant invasive crayfish populations [15]. Furthermore, some of them may have a high impact on habitat and other species (i.e., physical control via migration barriers and drainage interventions, chemical control, and biocontrol). Among traditional approaches, manual control via intensive trapping is the most frequently applied method—on the one hand, it has been shown that it could help reduce adult crayfish populations and minimize some of their impacts (cf. [20]), but on the other hand, it could lead to reduction of intraspecific competition which would consequently allow rapid growth of smaller individuals [15]. Innovative approaches for control of invasive crayfish of lower environmental impact include a range of techniques whose applicability have been/are being tested in the field. These comprise, among others, the use of pheromones, hormones, and sterile male release technique (SMRT) [15]. SMRT is a highly species-specific technique which is based on a release of sterile males (after mechanical removal of gonopods or X-ray exposure) into the environment, where they compete with non-treated males. This approach has the potential to achieve sterility in 57% of treated males and reduce reproduction output, without significant effects on mating behavior of treated males [11]. Manual removal of gonopods has been shown to interfere partly with mating behavior and duration, but had no effects on male readiness to engage in copulation and also resulted in reduced reproductive output in females [11]. However, the majority of studies were performed in controlled laboratory conditions; therefore, the applicability of SMRT in the field remains to be further tested. A recent field trial in Italy yielded an 87% reduction in population size in two years of SMRT application, which shows that this is a potentially promising and applicable field approach [21]. Finally, both trapping and application of SMRT need to be executed continuously for extended time-periods in order to be effective; thus, they are labor-intensive and may incur significant costs [22].

Just how effective these different approaches would be on long-term population persistence and reduction has not been fully explored. Testing these in isolation and in combination may prove to be logistically too challenging to address with empirical (field) studies. Population modeling could potentially be used to test the efficacy of different management methods and to support field studies. Population models that integrate the relevant information on species biology and ecology, as well as any relevant external drivers, can be applied to evaluate multiple management scenarios [23]. To date, models have not been extensively used to inform crayfish management. The majority of models representing crayfish populations focus on different aspects related to aquaculture [24,25] or are more focused on conservation objectives [26,27]. Several modeling studies explored the impact of spatial spread and various management options on the rusty crayfish, *Faxonius rusticus* (Girard, 1852), control [28,29]. However, there are currently only a couple of published models representing populations of the invasive *P. leniusculus*, i.e., a deterministic model by [14] and stochastic model by [30]. Both models include components of signal crayfish biology important for advising management, but some crucial aspects are lacking. For instance, the existing models do not include seasonality driven by temperature dependency of physiology, which can inform about the temporal windows when management is the most efficacious. Furthermore, the model presented by [14] does not explicitly represent individual sizes; rather, it simulates only abundances of different life stages. However, size structure is a relevant determinant of crayfish population dynamics, including density-dependent regulation.

To develop a model suitable for evaluating management efficacy, we need to clearly define the model objectives, identify the core model processes required in the context of the defined objectives, and identify relevant available empirical data for model parameterization and testing. This process results in a conceptual model that can be implemented and fully realized as a tool addressing the relevant objectives [31]. In this study, we develop such

a conceptual model based on [30], following the Pop-GUIDE framework, and in the process, we also provide concrete suggestions on how to expand the Pop-GUIDE framework to become more applicable for developing population control and management models.

2. Methods and Results

The conceptual model development closely follows the phases and decision steps laid out in the Pop-GUIDE framework [31].

2.1. Phase I—Model Objectives

As invasive crayfish threaten the existence of native fauna in many freshwater systems, many management approaches targeting the control of the size and spread of their populations were designed. However, many of these have yet to be fully tested to establish their long-term efficacy. Especially relevant is the understanding of the interplay between core mechanisms regulating invasive crayfish populations and different population control approaches. Invasive crayfish are known to be regulated by population density—they establish dominance hierarchies through frequent direct agonistic interactions, which affect their priority of access to limited resources, such as shelters, and affect their distribution patterns within a habitat [32,33]. Shelter is a resource of higher perceived value than food [34] since its ownership directly lowers the risk of predation and cannibalism, and also since shelter is more likely to be a limited resource than food due to omnivorous diet of crayfish [32]. In populations of high crayfish density, usually found in nature, competition intensity for limited resources is high, and since body size is an important predictor of success in such agonistic interactions [33], larger/dominant individuals will exhibit increased control over space and shelters [35]. This means that crayfish management by intensive trapping through the use of size-selective traps could actually boost, instead of reduce, population growth, since it will remove the competitive effects of the larger dominant individuals within a population which regulate spatial dynamics and resource use. Previous studies have recorded that with reduced density of larger adult signal crayfish individuals, juveniles may show compensatory growth, and remaining individuals exhibited an improved body condition [9,20,36]. Thus, the effects of manual crayfish removal by trapping may be impeded at least partially by density-dependent compensation, which improves the body condition of remaining individuals and enable their earlier maturation and higher fecundity [9].

The aim of this model is to integrate the relevant information about the signal crayfish biology, specifically in the context of the size-dependent population regulation, and to evaluate the following options and their combinations for population control: (1) Traditional approach of crayfish removal via trapping—but with application of different trap types in order to target different ontogenetic stages, (2) The application of SMRT technique, and (3) the combination of SMRT with trapping aimed at reduction of female density. The model will further be applied to explore the impact of dispersal on different population control options, as well as evaluate control efficacy under various dispersal scenarios.

The objectives of our model fit the general-realistic or general-precise category, according to the decision tree of the Pop-GUIDE framework [31] based on conceptual framework described in detail in [37] because the model aims to evaluate management options for a general invasive signal crayfish population. To achieve that, general biology and behavior of the signal crayfish is being captured. However, data that support the crayfish properties that the model captures are based on specific locations and habitats which puts it into the realistic/precise category, based on [31,37].

2.2. Phase II—Data Compilation

Data were compiled by an extensive literature research and were classified according to the Pop-GUIDE tables provided in [31], with some modifications, however. For example, table which collects information on chemical exposure and effects characteristics (Table 4 in [31]) was assessed as not relevant for the assessment of population control/management

options conceptualized within this study. All collected data can be viewed in the Supplement S1 (Tables S1–S3).

Broadly, we found that information on life history (Table S1) exists for the three categories (general, realistic, and precise) and these were the most important data to feed our conceptual model. Data on population and spatial characteristics (Table S2) and data on external factors (Table S3) were also dominated by realistic-precise data. In addition to data required for the development of this conceptual model (Tables S1–S3), we collected information for the specific characteristics which were not included in the current model (highlighted in gray in Tables S2–S3), but which may be added in further iterations.

2.3. Phases III and IV—Decision Steps and Conceptual Model

Descriptions of all decision steps relevant for crayfish management are presented within this section, while the chosen decisions for the signal crayfish management and control according to the [31] are highlighted in yellow in the Supplement S2. Some of the questions within the original decision steps [31] have been modified to make the framework more applicable to model development beyond chemical risk assessment (in red font color in the Supplement S2).

2.3.1. Step 1: Life History Representation

Life history of the signal crayfish is most similar to 1.5.D. Invertebrates for which adults reproduce more than once, with reproduction rates varying with age of adults (Figure 1). Survival rates within life stages are relatively well known.

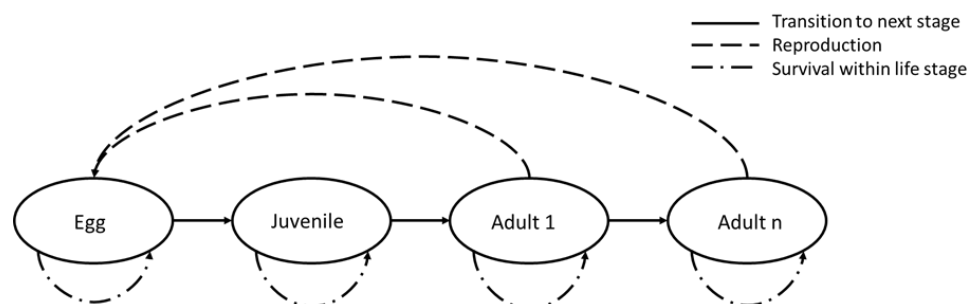


Figure 1. Life history representation for the signal crayfish (*Pacifastacus leniusculus*). The general life cycle includes eggs (embryos) which remain at that stage until they hatch into juveniles. Juveniles remain in the juvenile stage until they mature into the adult life stage. Only adults can reproduce, and reproductive output is size/age dependent. Adult life stage can be separated to multiple stages (n) due to the size/age dependent reproductive output as well as data availability for survival rates of different life stages.

2.3.2. Step 2: Organism-Level Processes

Growth and Development

As with all crayfish species, signal crayfish grow periodically through molting [38]. These molts are quite frequent in juvenile crayfish occurring approximately 11 times during their first year, reducing to 2 molts in their third year, and then, after the age of four, they occur once a year [39]. Growth rates vary between the sexes, with males frequently having faster growth rates compared to females [40]. Furthermore, growth is isometric in juveniles, but becomes allometric as individuals reach sexual maturity [40]. Finally, signal crayfish weight is positively correlated to their length; maximum carapace length (CL) of 50 to 70 mm corresponds to weight of 60 to 110 g [38]. Population density affects growth in signal crayfish, with slower growth rates in populations of high density—thus, the largest crayfish are not necessarily the oldest [40]. Signal crayfish growth is faster in newly introduced populations where they encounter little or no competition [9]. Typically, this species will reach maximally 50–70 mm CL, while the increment per molt for a crayfish of 35 mm CL crayfish ranges from 2.9 mm to 4.5 mm [38]. Moreover, growth is affected by season (mainly

water temperature) and year-cycle: molting in the population is synchronized in adults (crayfish older than circa 3 years), and males molt in early spring (when water temperature rises over 14 °C), while berried females molt after egg hatching (in May or June) [41]. Both sexes may again grow/molt in autumn before the mating period [41].

In the population model, individual growth and development are represented in the context of the Dynamic Energy Budget (DEB) theory [42]. A DEB model for this species exists in the Add-my-Pet database (https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/entries_web/Pacifastacus_leniusculus/Pacifastacus_leniusculus_res.html; accessed on 10 March 2022) [42,43]. DEB models describe the processes of energy acquisition by individual crayfish and energy allocation to metabolic endpoints. The standard model assumed that a certain fraction of acquired food is assimilated to reserve which is then mobilized to cover the costs of metabolic functioning, growth, and reproduction. A fraction κ of the reserve is allocated to somatic maintenance and to growth, whereas the $1-\kappa$ fraction is allocated to maturity maintenance and maturity in juveniles or reproduction in adults. Growth and reproduction patterns of individuals emerge from the described processes. Processes in DEB models are driven by temperature and resource availability, allowing for the effects of seasonality and competition processes on growth and development to drive growth and development in the model. Explicit growth and development of relevant life stages of males and females are included in the population model via the existing DEB model. Even though crayfish are known to grow allometrically, we simplify this by assuming isometric growth in both sexes where males differ from females based on several parameters, which ultimately results in their larger overall size.

Maturation and Reproduction

Signal crayfish reach maturity at the age of 2–3 years, when they are around 60 to 90 mm total length (TL), but they could reach it earlier, even during their first year of life, if the biotic and abiotic conditions in the environment are optimal [39]. The most common age at maturity is 2 years. Frequently, *P. leniusculus* males grow faster than females, and, consequently, males mature one year earlier [38]. Different populations show significant variation in size at maturity (size at maturity from 25 to 47 mm CL) [38]. Numerous factors and their interactions influence size and age at maturity, such as, crayfish density, quality and temperature of water, food supply [9]. Fecundity in crayfish is species-specific and, within species, body-size dependent [44]. Signal crayfish have been shown to carry from as few as 3 to as many as 548 pleopodal eggs [38,45]. The number of eggs is positively correlated with female's size, and larger females also carry eggs more successfully until hatching compared to smaller females [38] (Table S1). Spawning is triggered by mating, which occurs seasonally (once a year, in autumn) [40]. Both mating and spawning are triggered by the same environmental conditions (changes in photoperiod and temperature: in the signal crayfish, mating occurs when temperatures drop approximately below 15 °C and spawning at temperatures below 12 °C) [40,46]. Almost all reproductively active females mate, but 40–60% are successfully fertilized and ovigerous [47–49], while large males mate more often and with a higher number of females (cf. [40]). Incubation success increases with female size [40] and it takes from 166 to 280 days until hatching [38]. Hatching is also temperature-dependent (increase in temperature in spring) and synchronized [40] and involves growth in two stages: stage 1 when hatchlings are immobile and feed on yolk reserves, and stage 2 when hatchlings resemble adults and start foraging independently. During this stage juveniles gradually start becoming independent (i.e., gradually leave the female) and become fully independent by stage 3. This stage typically occurs when juveniles grow to 12–13 mm total length (TL) [50].

Both males and females are represented in the population model, and the sex-specific differences in maturation and reproduction are captured by the existing DEB model for the signal crayfish. Parameters governing the resource intake as well as the maturity threshold differ between the sexes, resulting in males attaining larger sizes and reaching maturity earlier than females. Once females reach maturity, they invest into reproduction, i.e., they

allocate energy into their reproductive buffers. Release (creating) of the eggs from the reproductive buffer is triggered by temperature which corresponds to the observations in the field. In the model, spawning will occur in autumn, when water temperatures fall consistently below 15 °C for at least 7 days in a row. We assume that 50–60% of all adult females are successfully fertilized; this is not dependent on female age or size. Juveniles have a certain probability of hatching, which increases with the size of the female. Once juveniles grow to 12–13 mm TL, they completely detach from their mother and become fully independent entities in the model. This means that the potential death of their mother does not affect them anymore.

Once juvenile males become adults, which is typically earlier than females of the same cohort, the reserve previously allocated to maturation is assumed to be invested in developing sexual dimorphism (e.g., allometric growth of claws). In standard DEB theory, sexual dimorphism is rarely discussed and the std model does not specify processes in males that would be parallel to the allocation to the reproduction buffer and egg production in females. The population model does not include processes where explicitly representing sexual dimorphisms is required, therefore, this will be ignored in the model. The adult males will continue allocating energy to reproduction, but in the model, this will not result in any measurable effect on growth or survival of male adults.

2.3.3. Step 3: Population and Spatial Factors

Population Status

Established crayfish populations, and especially populations of invasive crayfish such as the signal crayfish, often exhibit high densities in introduced areas (i.e., reports for signal crayfish up to 110.4 individuals/m²) [51] and abundances differ significantly between long-established populations and those newly established at invasion fronts in open ecosystems such as rivers (i.e., 5–37 times differences) [52,53]. Different stressors, including pollution, predation, interspecific competition, or disease outbreaks may affect population dynamics and growth (i.e., [53–55]), especially in newly establishing populations at invasion fronts. Populations of the signal crayfish may be present in the wild at different stages of the invasion process (i.e., newly introduced population in establishment phase vs. long-established population) and population viability may be affected by the above-mentioned stressors present, which may significantly affect the potential success of the chosen management strategy.

In the population model described here, the population status will be a factor driving the strength of density dependence and its influence on the chosen management strategy. Density dependent mechanisms are described in the following section.

Density Dependence

Management efficacy will strongly depend upon crayfish density. Consequently, management activities will also strongly impact population density and may induce density-dependent effects on growth, reproduction and other physiological and behavioral traits [9,36]. Therefore, this information is essential in examining the effects of different management scenarios and their effectiveness in controlling invader's population growth and dispersal.

Invasive crayfish are known to be regulated by population density—they establish dominance hierarchies through frequent direct agonistic interactions, which affect their priority of access to limited resources [32,33]. As already mentioned, shelter is a resource of higher perceived value than food for crayfish [34] and more likely to be a limited resource [32]. In populations of high crayfish density, there is competition intensity for limited resources and as already mentioned, larger/dominant individuals will exhibit increased control over space and shelters [35], resulting in their higher survival and fitness [33]. Thus, the competitive effects of the larger dominant individuals within a population will regulate spatial dynamics and resource access and use within a population. This has also been observed in the field (i.e., larger signal crayfish often found in lentic locations while

smaller sized individuals and juveniles in riffles) [56–58]. Existing research has recorded density-dependent effects on a number of signal crayfish life history traits, including growth, reproduction, behavior, and physiology. As already mentioned in Section 2.3.2, subsections *Growth and Development* and *Maturation and Reproduction*, and here, crayfish growth is density-dependent [40,59] and since fecundity is positively correlated with crayfish size, density will affect reproduction rates as well. Additionally, individuals in populations of higher abundance at invasion cores were found to be more aggressive and with a lower body condition and lower organosomatic indices (a proxy for physiological condition) compared to individuals in recently established populations of lower abundance at invasion fronts [60,61], showing that density affects individual behavior and condition. Finally, density significantly affects signal crayfish survival, which is especially evident in juveniles [59,62] which are also cannibalized by larger (adult) crayfish [63,64]. Density-dependent effects on signal crayfish survival are much less pronounced in adults since rates of mortality, similar to growth, decline with size, and age (cf. [65]).

In the model, we assume that higher densities negatively impact growth and survival of all crayfish, but males are more impacted than females; impacts on survival represent a proxy for known cannibalistic interactions. Based on the available information described above, density-dependent effects are assumed to be size-dependent, where smaller individuals are more affected by population biomass than larger individuals. Both growth and survival are impacted by population density and biomass. Density-dependent survival in juveniles is implemented as size-dependent mortality, which is a function of the biomass of the total population. In addition, as shelter availability is crucial to individual survival, we assume that the strength of the density-dependent function is dependent on shelter availability. Shelter availability is modeled as a scale between 0 and 1 where 1 represents highly complex habitats with an abundance of good quality shelters. As no reliable quantitative evidence exists for the relationship between the number of shelters and organismal condition, this implementation ensures that the qualitative observations are accounted for. Ultimately, density-dependent impact on survival will depend on individual sizes and will be a function of both population biomass and shelter availability. The influence of these assumptions will be explored in model analysis.

As it is observed that individuals from dense populations also have smaller body sizes and lower overall condition, most likely due to numerous antagonistic interactions that are energetically costly, we assume that there is a density effect on the somatic maintenance in individual crayfish. Somatic maintenance is a process defined within the DEB theory, in which the acquired energy is allocated to maintaining the basal organismal functioning. Somatic maintenance costs can increase due to, for instance, exposure to chemicals [66], and due to other stressors in the environment. Increased costs for maintenance result in less energy that is allocated to growth and thus ultimately result in smaller body size in individual organisms. In the model, we assume that both the biomass of the total population, as well as shelter availability represent a stressor increasing the costs of somatic maintenance. The implementation follows the well-established implementations of impacted somatic maintenance due to chemical exposure [66,67]. Briefly, the amount of stress that both densities and shelter availability impose on the individual is calculated by accounting for current population biomass and population biomass below which we assume there are no adverse impacts. This difference is scaled based on shelter availability, where at the lower part of the range (closer to 0) the effects of stress will be increased relative to when more shelters are assumed to be available. The influence of proposed drivers for density-dependent effects on crayfish growth will be explored in model analysis.

Movement

Management measures aimed at invasive crayfish control will seek to control population size and growth. Immigration or emigration of individuals can significantly affect population size in open ecosystems such as rivers; therefore, data regarding the movement of the individuals across the habitat will be very important in river ecosystems,

and less important in closed ecosystems such as lakes. With the exception of migration barriers [15,18], the vast majority of available management techniques are aimed at reducing crayfish population size and/or crayfish eradication. Reduction of population size presumes reduction in further dispersal, since it has been previously suggested that dispersal is also density-dependent (i.e., [68–71]; but see also [72]). High population density increases competition intensity for progressively more limited resources, leading to spatial displacement of subdominant individuals [60,73].

Crayfish have a patchy distribution in respect to the shelter availability, habitat structure, and substrate composition [74]. Moreover, there might be an ontogenetic shift in habitat usage, with juveniles occupying habitat less favorable for adults [40,75]. Furthermore, while their home range is relatively small (around 40 m) [74,76], they may disperse both upstream and downstream in a river system. Crayfish density and competition intensity might be a trigger for dispersal as discussed above, while dispersal (downstream direction in the rivers) may also partially occur through drift, especially during extreme events (i.e., flooding events) [77]. Therefore, while the probability of dispersal may constitute an important component in application of the population model to invasive species management, dispersal data from the populations in the wild may not be readily available. In addition, in some countries, the signal crayfish is predominantly established in closed ecosystems (i.e., lakes; prevailing in Scandinavian countries) [78], where dispersal is very limited and will have a limited effect on the model application. Moreover, links between population size and dispersal rates in both upstream and downstream directions are not well understood, can often be site-specific, and dependent upon other hydrological events (i.e., floods, droughts), and, thus, are very variable (recorded dispersal rates in the literature for the signal crayfish varies between 0.35 to 24.4. km/year) [77,79].

We decided not to include dispersal as an integral part of the model due to several factors. Firstly, the already-mentioned increase of dispersal with increasing density and limited shelter availability, which has been repeatedly demonstrated [80], indicates that the control of population growth should also lead to control of further dispersal. Secondly, detailed dispersal data availability is currently lacking for many populations, and its ranges will be site-specific. Thirdly, dispersal is not of the same relevance for all types of freshwater ecosystems (i.e., important in rivers but not as much for lakes). Finally, dispersal is not a primary focus of management measures selected in this study (i.e., different types of physical control of population size, through which effects on dispersal should be achieved as indirect result of control of population growth). However, we will implement a relatively simple process where individuals will be dispersing from the population by different probabilities and distances, which will be determined at a later stage. The influence of dispersal rate assumptions and consequences of implemented management actions on dispersal rates will be explored in model analysis.

Behavior

Behavior is an important component of crayfish population dynamics, since crayfish form strong dominance hierarchies in both the field and laboratory, which regulate priority of access to limited resources [33]. While some of the applied management approaches may target specific sex (i.e., pheromone traps) or may potentially affect crayfish behavior during mating (i.e., male sterilization), or behavior may affect the success of different trapping methods (i.e., some traps may be sex-biased towards dominant males) [81], behavior will be a less prominent feature in the success of applied management strategies in comparison to density-dependent effects and the effects of dispersal of individuals.

Currently, the relationship between dominance and its effects on individual fitness (survival, growth, and reproduction) is mostly inferred hypothetically, but not quantified in the field. However, since crayfish size is one of the most important determinants of their dominance (cf. [33]), in the model, the survival and growth of smaller signal crayfish is assumed to be adversely affected by their subdominant status via density-dependent effects on growth and survival.

Habitat Features

In the case of crayfish management, habitat features have an important role in shaping crayfish distribution patterns and crayfish density. As already mentioned, crayfish distribution in the habitat is patchy. It is dependent upon the availability of shelters and established dominance hierarchies, as well as upon other habitat features (i.e., substrate composition, water velocity, shading). Moreover, as mentioned, there might be an ontogenetic shift in habitat usage, with juveniles occupying habitat less favorable for adults [40,75]. Finally, it has been demonstrated that higher habitat complexity increases the recruitment of juvenile signal crayfish, since it decreases the competition intensity for food and shelter [63]. In terms of crayfish management, habitat features are an important component of fieldwork, since experienced researchers will select appropriate habitat features for conducting management activities (i.e., in terms of presence of riffles, pools, and shading, selecting those where crayfish might be aggregated).

In the conceptual model, we do not represent habitat explicitly since such data are not readily available. The crayfish distribution in the habitat is patchy and related to the resource (shelter) availability and habitat structure, which will affect population density through resource limitation (i.e., shelter availability). In the model, we represent the habitat features and complexity implicitly by assuming there is a certain number of shelters available, since shelters are a limited resource in nature that will shape crayfish abundance and population dynamics at a given location. Influence of shelter availability on individual growth and survival is implemented as a scale of density-dependent functions for survival and growth (more detail in Section 2.3.3, subsection *Density Dependence*). This will allow us to quantify the effects of changes in this limiting resource for population growth and management efficacy.

2.3.4. Step 4: External Factors

Diet

Crayfish are omnivores and food is not likely to represent a limited resource [32], but food consumption and feeding activity can be affected by density-dependent interactions (i.e., increased competition intensity due to high population density may reduce time spent in feeding, or may limit access to specific food resource to subdominant individuals).

In terms of crayfish management, diet will not be as important for crayfish population dynamics as shelter availability and density; therefore, the role of diet has not been taken into account in this conceptual model, but could be added in future iterations as data are available (Table S2). In the DEB model, food will be assumed to be constant and ad libitum, i.e., $f = 1$.

Other Interspecific Interactions

The success of management interventions can be highly increased if a predator or an interspecific competitor is present. It has been previously shown that a combination of trapping approaches with an increase in fish predation of crayfish juveniles may lead to a significant and long-term reduction of invasive crayfish population size [82] and the subsequent significant changes in the food-web structure in a closed ecosystem [83]. However, it may be difficult to assess the contribution of predation to crayfish control in open ecosystems such as rivers. Similarly, interspecific competition may lead to slower population establishment and growth and may also affect invasive crayfish dispersal (i.e., as in [53], where signal crayfish dispersal rate was similar at both upstream and downstream direction due to the presence of an abundant population of native narrow-clawed crayfish). Thus, both predation and interspecific competition may contribute to the planned intervention measures aimed at control of the signal crayfish; however, it may be difficult to quantify their contribution. Finally, presence of pathogens will have a major impact on the viability of population and may lead to declines and collapses of populations of invasive species (i.e., population collapses in the signal crayfish populations [54,55,84], as mentioned in Section 2.3.3, subsection *Population Status*). However, quantitative, dose-

response types of data are not available to support inclusion of impacts of pathogens in this population's model. Thus, the contribution of predation or pathogens has not been considered in this conceptual model, but could be included in next iterations when dose-response data become available (Table S3).

Furthermore, we do not expect that the management interventions aimed at reducing signal crayfish population densities potentially affect other species in the system (especially those that are critical for habitat integrity), since, within this model, we are only taking into account manual removal approaches and are not considering the effects of chemical/biological control or control by physical barriers to crayfish movement. We assume that the use of crayfish traps will not produce significant bycatch, and that non-target animals (i.e., fish, turtles, or small mammals) will be released on the site.

Abiotic Factors

The signal crayfish is a species with a life cycle adapted to cool temperate zones, with optimal growth at 22.8 °C and tolerance up to 33 °C and a wide optimal thermal range (18–26 °C) compared to native European crayfish [85]. It reaches greater sizes and grows faster in temperate zones than its counterparts [39]. Temperature is an important driver of signal crayfish year cycle—a drop in the temperature is a trigger for egg spawning, while winter diapause is required for egg development [39]. Spawning occurs during October in the majority of populations, regardless of latitude differences, which indicates that colder temperatures at higher latitudes act as compensation for longer photoperiod preceding spawning [38]. As discussed in Section 2.3.2, subsection *Maturation and Reproduction*, the incubation of eggs is primarily regulated by water temperature. Estimated thermal units required for incubation range from 1500 to 2200 [38]. While egg spawning is less variable, the incubation period is more variable among different latitudes, and higher temperatures shorten it [38].

Similarly, flood events, water flow, and depth will also influence population dynamics and crayfish distribution—habitat suitability models have identified temperature range and seasonality, temperature maxima, as well as precipitation extremes and seasonality and altitude, as the most important parameters driving signal crayfish habitat suitability [86–88]. Among these, temperature appears to be a major factor influencing the timing and extent of movements of crayfish between tracking periods, and is also a key factor setting the limits to physiological tolerance reflected in growth of individuals, time to maturation, fecundity, and distribution patterns [43,88]. Crayfish exhibit seasonal differences in activity according to changes in environmental conditions (primarily temperature). The highest activity of signal crayfish occurs from late summer to late autumn, when both sexes are equally active due to preparation for reproduction [40]. During winter, when temperatures drop below 10 °C, activity of both sexes significantly decreases and their growth/molting stops [41].

The influence of temperature in the population model is described in Section 2.3.2, subsections *Growth and Development* and *Maturation and Reproduction*. Briefly, external temperatures are the main driving factor of processes described with the DEB model where the temperature correction of relevant parameters follows the Arrhenius temperature function [42]. This means that the growth and development of all individuals—from embryo to adult—in the model is driven by temperature. Temperature triggers for spawning are additionally implemented in the population model.

Besides anthropogenic changes in temperature and the resulting changes in the hydrology, many additional stressors may affect the success of management interventions. These stressors are likely to be similar as for the native crayfish species (i.e., pollution, damming, or water management) [89,90], but their effects on management interventions involving invasive crayfish have not been studied so far. Thus, additional abiotic effects will not be directly included in the model, as described in Section 2.3.4, subsection *Other Interspecific Interactions*.

2.3.5. Step 5: Exposure and Effects Characteristics

Exposure

Since we are not considering any form of chemical control of invasive crayfish species, exposure routes and toxicity data are not included in this conceptual model. Therefore, this whole section of decision steps is not applicable to analysis of approaches to signal crayfish management chosen within this study.

Mortality Effects

As in Section 2.3.5, subsection *Exposure*, since we are not considering any form of chemical control of invasive crayfish species, mortality effects related to exposure, their endpoints, and survival rates are not included in this conceptual model. We are only considering the mortality/survival data already elaborated in Section 2.3.3., subsection *Density Dependence*: all crayfish life stages are subject to density-dependent survival/mortality, with juveniles having lower survival rates than adults.

Sublethal Effects

As in the sections above, since we are not considering any form of chemical control of invasive crayfish species, sublethal effects on growth, reproduction, metabolism, and survival are not included in this conceptual model.

Temporal Representation

Due to the importance of seasonal changes in crayfish biology and population dynamics, as well as the inclusion of DEB processes which operate at a relatively fine scale, the temporal resolution of the model is set to a day.

2.4. Model Application—Management Actions

Conceptual model development, as described above and presented in Figure 2, is the fourth phase of the Pop-GUIDE framework [31], beyond which model implementation and evaluation are conducted. Model application typically follows once a model is fully developed, implemented, analyzed (e.g., sensitivity and uncertainty analyses), and validated. Model application to evaluate various management strategies for control of invasive populations was a major driver of the conceptual model here described. Therefore, here, we briefly lay out the management strategies that will be evaluated and conceptualize their implementation in the model.

Here, we consider the single and joint effects of management approaches that are applicable in all freshwater ecosystem types, have no environmental impacts and no impacts on other non-target species, but that potentially need to be performed in the long-term and are labor-intensive. The first management approach (manual removal via trapping) assumes the use of different trap types: those targeting adults only and those targeting different size classes (i.e., artificial refuge traps or ‘Pritchard traps’ versus baited funnel traps) [81,91]. However, we still assume that the majority of removed individuals will be adults, and that only up to 5% of juveniles will be removed (based on [81]). The model will be applied to analyze the effects of increasing number of trapped juveniles on efficacy of this management action. We will assume that all adult crayfish have an equal chance of being caught, irrespective of the size and sex, but depending on their sex-specific year cycle activity. Even though baited funnel traps are usually biased towards large and active (dominant) males [81,91], here, we assume that the use of different trap types (i.e., sex and size biased baited funnel traps and less biased traps such as artificial refuge traps or ‘Pritchard traps’) will overcome this bias. Finally, we assume that trapping is performed continuously in the period of high crayfish activity (approximately May to December). With the model we will test different periods to identify those time windows when trapping is most efficacious.

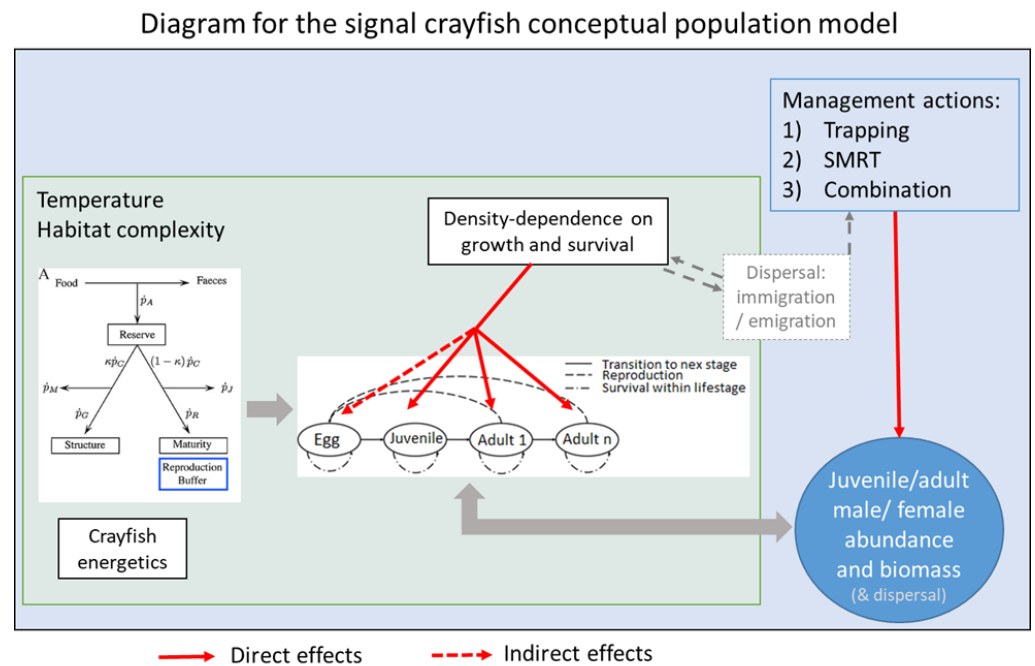


Figure 2. Diagram of the signal crayfish conceptual model. Crayfish life history and life cycle result from underlying DEB processes which are driven by external temperature. Density-dependence is based on population size and habitat complexity, i.e., shelter availability, and its impacts are size-dependent, but not stage-specific. Several management actions will impact the age- and size structure of the population, as well as the overall abundance and biomass. These changes feed back to the population model, mainly through the density-dependent functions. Density-dependent effects and the efficacy of different management options will be affected by dispersal. Even though dispersal is not the integral part of the model, consequences of implemented management actions on dispersal rates will be explored in model analysis.

The second management approach (SMRT technique) tests the impact of sterilization of adult males and their return into the population. We assume that all caught males are sterilized and released back into the population: both dominant large males and smaller subdominant males are predicted to be sterilized at equal rates due to the use of different trap types here as well. Furthermore, we assume that sterilized males have an equal chance for mating as non-sterilized males. The number of sterilized males in the population will increase over time, as SMRT technique will also be used continuously as in the first approach. The impact of sterilized males on the brood production by females will be modeled as a reduction in percentage of fertilized females. A fertilization success parameter will be introduced, which will be at 100% if all males in the population are fertile. This number will be multiplied with the percentage of females that are fertilized in unmanaged populations (50% to 60%, see Section 2.3.2, subsection *Maturation and Reproduction*). If, for instance, we assume that 50% of males in the population are sterilized, this will result in only 25% of females to be fertilized. With this approach we can test how efficacious management could be relative to the effort put into trapping and sterilizing. We will also test management effectiveness under different fertilization success rates (i.e., higher than the 50–60% inferred from the literature).

The third management approach involves a combination of both SMRT technique and trapping and removal of females from the population. A combination of SMRT with trapping females only could potentially decrease the reproduction potential in a population while additionally increasing the intraspecific reproductive competition. The assumptions here will be the same as for the second management approach, with the additional effect that the trapped females of all sizes will be removed from the population at the same time as sterile males are released back into the population.

For all management approaches, we will compare the changes in population sex and size structure and population growth over time, as well as the time and trapping effort required for a population size to be reduced by 50 and by 80%.

3. Discussion

Although predictive models are widely considered as excellent tools for risk-assessment and decision-making in the context of invasive species management in general and invasive crayfish in particular [15], they have not yet been extensively used or frequently applied to guide invasive crayfish management planning. Most often, predictive models based on species distribution and habitat suitability modeling have been applied in the context of invasive crayfish risk-assessments and identification of species likely to become successful invaders if translocated into the new environment [15,90,92]. Spatially explicit models, including individual-based models, have been developed for different crayfish invaders, including the signal crayfish (reviewed in [14,15,30]); however, so far, they have neither been widely applied nor applied to inform specific management decisions related to invasive crayfish. The only exceptions are an individual based model exploring the applicability of trapping in (manual) control of population growth and dispersal of the signal crayfish [30] and one deterministic model exploring the general efficacy of different control approaches for the signal crayfish in Great Britain [14]. Finally, some models based on harvesting of invasive crayfish in agri-systems of rice production have been developed [24] with the objective of identifying methods to minimize damage on rice production while investigating options to harvest crayfish for consumption. Application of models to assess the feasibility and efficacy of specific crayfish management combinations is lacking. We advocate that population modeling could be used to test the effectiveness of different management approaches to invasive crayfish control and evaluate the single and joint effects of multiple management scenarios. As such, models can support logistically demanding field studies, which are constrained by the number of management approach combinations and too lengthy timeframes required to adequately assess their efficacy. This is especially important since some of the management approaches for invasive species control must be performed over long time periods and may require continuous input of manpower and resources or maintenance. Thus, prioritization of these limited resources towards the most effective management option is of paramount importance (e.g., [93]), and models can serve as a much-needed tool in such decision-making.

In this study, we followed the steps outlined in Pop-GUIDE to develop a conceptual model for application to invasive species, specifically the management of one of the most successful aquatic invaders, the signal crayfish. Briefly, the conceptual model captures the life history of the signal crayfish, as well as implicitly capturing the spatial and dominance behaviors of individuals that result in population density regulation mechanisms. Physiology and life history of individual crayfish are described within the context of the DEB theory where growth, maturation, and reproduction are functions of underlying physiological processes and are driven by food availability and thermal conditions. Crayfish are mostly omnivorous, and food is usually not the limiting factor for their growth and survival, which are typically more limited by the availability of shelters from predators and competitors. In this model, we, therefore, did not assume any food limitation, but assumed density effects on size-dependent survival as smaller individuals are more at risk from cannibalism and predation. The larger the individual gets, the higher probability that it will manage to occupy a shelter and increase its survival probability. We did not include explicit territoriality and dominance hierarchies as quantitative evidence for their effects on individual survival, growth and reproduction is currently missing. However, as a proxy, we included density-dependent functions—driven by population density and shelter availability—on individual condition and growth. Model conceptualization conducted in this study will be followed by implementation and testing, and ultimately application to address and support management actions geared towards signal crayfish population control.

The model will further be applied to explore the impact of dispersal on different population control options, as well as evaluate control efficacy under various dispersal scenarios.

Through this process, we also modified the decision steps in Phase III and attempted to streamline the Pop-GUIDE vocabulary to make the framework more applicable to model development beyond chemical risk assessment. We have modified several decision steps by changing the term ‘exposure’ with ‘action’ as a broader and more general term and have further modified questions within the decision steps outlined in Supplement S2. Moreover, the vast majority of steps and questions related to exposure risk assessment (Section 2.3.5) and the required data (Table S4) were not applicable to species management and were not included in the conceptual model. Finally, we suggest that the model objective category determination should be reconsidered for its usefulness and applicability in fields beyond ERA. Currently, these are driven by specific regulatory statutes in the US which are not applicable to invasive species management or other possible model objectives. Re-defining those to consider the temporal and spatial scales more than legal statute may be an approach to determine whether a model objective is general, realistic, and/or precise. If, for instance, the model is geared towards managing a population in a specific location, then the objective could fall more into the realistic/precise category. If the objective is to provide a broader understanding of how management would affect growth of a generic population, then the objective would be defined as general. The current decision tree contains the main elements for such determinations but could benefit from defining those more explicitly.

Here, we demonstrated that Pop-GUIDE, with some modifications, can be a multifaceted tool for conceptualizing models with application to areas other than chemical risk assessment. Specifically, in this study, following the steps outlined in the framework facilitated a development of a conceptual model aimed at invasive species management. Given that we face an increased need to solve complex ecological challenges, such as invasive species management or management of endangered native populations affected jointly by biological invasions and climate change, we anticipate that population models will be one of the few tools able to integrate all relevant species and habitat information to evaluate appropriate actions. Thus, they should be at the core of adaptive management and decision-making in nature conservation and ecosystem restoration. In order to become more widely applicable, the development of such models should follow a well-defined and clear framework, which then ensures their transparency, consistency, and reproducibility.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/ecologies3020008/s1>: Supplement S1: Phase 2 data tables for signal crayfish—Table S1: Life-history characteristics that should be targeted to inform a population model for signal crayfish management; Table S2: Population and spatial characteristics that should be targeted to inform population model for signal crayfish management.; Table S3: External factors that should be targeted to inform population model for signal crayfish management; Supplement S2: Phase 3 decision steps for signal crayfish.

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