

The Regulation of Populations Featuring Non-Breeder Pools

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*A model analysis with implications for management
strategy design for the Great Cormorant*

Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften (Dr. rer. nat.)

am Fachbereich Mathematik/Informatik der Universität Osnabrück

vorgelegt von *Sten Zeibig* aus Riesa

Osnabrück 2009

Cover Picture: Fisherman on the Li River in the Chinese Guangxi Zhuang Autonomous Region
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Deutsche Zusammenfassung

Ausgangspunkt dieser Arbeit sind Konflikte, die zwischen Naturschutz und wirtschaftlichen Interessen entstehen können, wenn Populationen geschützter Arten aufgrund ihrer Größe deutliche wirtschaftliche Schäden verursachen. Dies ist zum Beispiel beim Kormoran oder der Kanadagans der Fall. Eine Möglichkeit solche Konflikte zu lösen besteht darin, die Größe der betreffenden Population direkt zu regulieren. Dabei muss die Regulation verschiedenen ökologischen und ökonomischen Zielen gerecht werden: **1)** die Populationsgröße und damit der von der Population verursachte Schaden soll reduziert werden; **2)** die Population muss überlebensfähig gehalten werden, da es sich in den hier betrachteten Fällen um geschützte Arten handelt; und **3)** die Regulationskosten dürfen das zur Verfügung stehende Budget nicht übersteigen.

Die vorliegende Arbeit konzentriert sich auf Populationen, in denen Gruppen geschlechtsreifer aber nicht brütender Individuen vorkommen. Bei diesen Arten ist zu vermuten, dass der *Vorrat an Nichtbrütern* Regulationsversuchen Widerstand leisten und diese so unwirksam machen kann. Andererseits gibt es, z.B. beim Spanischen Kaiseradler, auch Hinweise, dass der Nichtbrütervorrat eine zentrale Rolle für die Überlebensfähigkeit von Populationen spielen kann, so dass dies von Regulationsstrategien berücksichtigt werden müsste. Diese Fragen der Dynamik solcher Populationen und der Auswirkungen von Regulationsversuchen auf sie sind bisher kaum untersucht und verstanden.

Beispielhaft für solch eine geschützte Art mit einem Nichtbrütervorrat ist in Europa der Kormoran (*Phalacrocorax carbo sinensis*). Die wachsende Zahl dieser Fisch fressenden Vögel verursacht einen europaweiten Konflikt zwischen Fischereiwirtschaft und Naturschutz. Die vorliegende Arbeit möchte auch einen Beitrag zur Lösung dieses Konfliktes leisten.

Die Arbeit verfolgt drei Hauptziele **1)** die Entwicklung eines Modellieransatzes und eines *konzeptionellen Modells* um die grundsätzliche Funktionsweise und Auswirkungen der Populationsstruktur zu verstehen, die durch die Nichtbrüter erzeugt wird, **2)** das Aufdecken des Verhältnisses zwischen den Eigenschaften der Nichtbrüter und der Leistungsfähigkeit von Regulationsstrategien und **3)** die Anwendung des Modellieransatzes mit der Entwicklung eines *biologisch realistischeren Modells* der Kormoranpopulation auf der Basis empirischer Daten, um die Ergebnisse des konzeptionellen Modells zu prüfen und um Aussagen treffen zu können, die die Entwicklung konkreter Regulationsstrategien für den Kormoran unterstützen.

Auf beide Modelle werden verschiedene Arten von Regulationsstrategien angewandt. Diese entsprechen im Falle des Kormorans bereits durchgeführten Maßnahmen: dem Abschuss von Individuen, der Verringerung der Umweltkapazität für die Brüter und dem Einölen von Eiern. Alle betrachteten Regulationsstrategien besitzen, analog dem so genannten *threshold harvesting* biologischer Ressourcen, einen Schwellwert für die Populationsgröße, unterhalb dessen

keine Regulationsmaßnahmen durchgeführt werden. Die Leistungsfähigkeit der Strategien wird beurteilt nach dem Aussterberisiko, welches sie für die Regulation mit sich bringen, dem Aufwand, den sie verursachen, und der Reduktion des Schadens, die sie erzielen.

Die Ergebnisse der Arbeit bereiten ein Grundverständnis der Rolle der Nichtbrüter und zeigen unter welchen Umständen sie bei der Regulation explizit berücksichtigt werden müssen. Sie ermöglichen weiterhin eine vergleichende Bewertung der Arten von Regulationsmaßnahmen abhängig von den ökonomischen Rahmenbedingungen. Insgesamt stellt diese Arbeit einen ökologisch-ökonomischen Modellieransatz vor, mittels dessen geeignete Regulationsstrategien zur Lösung der eingangs geschilderten Probleme gefunden werden können.

Contents

1	Introduction	3
	I Conceptual Model Analysis	9
2	The Modeling Framework	11
2.1	Population Processes	11
2.2	Environment	14
2.3	Regulation Strategies	14
2.4	Measures and Thresholds of Performance	15
2.5	Assessment of Regulation Strategies and Targets	17
3	Non-Breeder Pool and Population Dynamics	19
3.1	Deterministic Environmental Fluctuations	19
3.2	Stochastic Environmental Fluctuations	30
3.3	Interdependence of Breeders and Non-Breeders	41
3.4	Discussion and Hypotheses for Management	47
4	Non-Breeder Pool and Regulation	51
4.1	Reference Scenarios	52
4.2	Non-Breeders and Catastrophic Events	52
4.3	Non-Breeders and Strong Variability	59
4.4	Discussion of Regulation Strategies	67
	II Regulation of the Great Cormorant	75
5	The Adapted Model Framework	77
5.1	Age-Structured Cormorant Model	77
5.2	Environment	80

5.3	Regulation Strategies	83
5.4	Modification of Criteria for Strategy Performance	84
5.5	Parameterization of the Cormorant Models	84
6	Population Dynamics	87
6.1	Sensitivity to Population Parameters	88
6.2	Importance of the Non-Breeder Pool	91
7	Performance of Regulation Strategies	95
7.1	Applying the Conceptual Cormorant Model	95
7.2	Applying the Age-Structured Cormorant Model	99
7.3	Sensitivity of Optimum to the Cost Function	102
7.4	Sensitivity to Breeder-Non-Breeder Interchange	107
7.5	Summary of Results for Cormorant Regulation	110
8	Discussion	113
8.1	Viability of the Cormorant Population	113
8.2	Performance of Regulation Strategies	114
8.3	General Methodological Remarks	118
8.4	Concluding Remarks	120
9	The Thesis in a Nutshell	123
	Acknowledgments	129
	List of figures	130
	List of tables	137
	Bibliography	140

Introduction

Nature conservation and economic interests are frequently at odds with each other. One such conflict emerges when populations of protected species grow to sizes that cause noticeable economic damage. Prominent examples can be found in fishing industry where losses are caused by ever-increasing numbers of the fish-consuming Great Cormorant (*Phalacrocorax carbo sinensis*) (Parrott et al. [2003]; Santoul et al. [2004]; Christensen et al. [2007]), or in agriculture where the Canada Goose (*Branta canadensis*) feeds on seed, causing a loss in farmers' profits (Hauser et al. [2007]).

To solve these problems, reconciliation strategies are needed. One possible approach is to regulate the size of the population in question. In doing so, regulation strategies have to meet multiple targets: first, population size has to be reduced to a predefined size; second, the viability of the population has to be maintained; and third, strategies have to adhere to the available budget.

To design strategies that fulfill these multi-criteria target settings, an understanding of the dynamics of the regulated population is required. This is particularly important as populations usually feature compensatory mechanisms that allow them to tolerate adverse environmental influences up to a certain degree (McLaughlin et al. [2002]; Walters et al. [2002]; Greene [2003]; Grimm et al. [2003]; Wichmann et al. [2003]; Grimm et al. [2005]; Bonesi and Palazon [2007]). These so-called buffer mechanisms may also resist regulation attempts. Uncertainty about the resistance potential may lead to ineffective or inefficient regulation attempts (if this potential is underestimated), or to an increased risk of population extinction (if the potential is overestimated). This was shown by Frederiksen (Frederiksen et al. [2001]) for the example of the Great Cormorant.

This study focuses on populations, that can be structured into two groups: breeders and mature non-breeders (Bosch et al. [2000]; Jackson et al. [2004]; Sarah et al. [2004]; Gunnarsson et al. [2005]; Soutullo et al. [2006]). The pool of non-breeders provides a reserve for the breeders, whereby they may enable the population to resist regulation attempts, as was observed by Frederiksen et al.

[2001] in the case of the Great Cormorant.

Several more studies exist that address the impact of non-breeders on the dynamics and stability properties of populations. The dynamical effect of non-breeders was investigated by Klomp and Furness [1992] based on the example of the Great Skua (*Catharacta skua*). They found that mature but non-breeding individuals have a smoothing effect on the dynamics of the breeder stock of the population. This result was confirmed by Sarah et al. [2004] in the case of British farmland bird populations featuring non-breeders. They used a population dynamical model including non-breeders to illustrate that there is a delay between the declines in total population size and breeder number. In this model the non-breeders were supplied by the surplus potential breeders, which do not find opportunities to breed. Penteriani et al. [2005] developed two individual-based models to investigate the population of the Spanish imperial eagle. Among other results they found that increasing mortality in non-breeders has a negative impact on the stability and dynamics of the breeder stock of the population.

While there are many other studies dealing with the effect of non-breeders (often also called *floaters*) on population dynamics (e.g. Bender et al. [1996], Schadt et al. [2002], or Walters et al. [2002]) the conditions under which non-breeders exert effects such as those described in these studies remain unclear. Is the pure existence of a pool of non-breeders sufficient to positively affect stability properties? The study of Penteriani et al. [2005] already points to the role of non-breeder mortality. But do other characteristics also influence stability properties of the populations? And finally, what are the implications of a non-breeder pool in the context of regulation? Non-breeders have seldom been explicitly considered in the design of regulation strategies and in the assessment of their performance. Hence, the interplay of non-breeders and regulation strategies has not yet been fully understood.

The requirement to maintain the viability of the target population leads to the need for adaptive regulation strategies. The definition of a threshold above which the population size is reduced by a certain rate is a suitable approach to meet this constraint (e.g. Lande et al. [1995]; Lande et al. [1997]; Enberg [2005]; Saether et al. [2005a]). As soon as population size declines below the threshold, the regulation strategy is suspended. Such approaches aim to conserve a certain portion of the population to prevent it from extinction.

However, Sarah et al. [2004] as well as Klomp and Furness [1992] indicate, that a decline in population size may be discovered late, because non-breeder numbers, which may be hard to measure, are the first to decrease. Again, it remains unclear whether this effect can threaten population survival despite the definition of a threshold.

The present study aims to overcome these problems by developing a conceptual ecological-economic modeling framework, which explicitly includes the pool of non-breeders. This allows the explicit assessment of its primary dynamical effects, which in turn permits to answer the questions raised above. Applying

threshold regulation strategies to this model also provides insight into the interplay between non-breeders, their characteristics, the performance of regulation strategies and achievability of regulation targets.

The conceptual model is based on the time-discrete logistic map for populations with overlapping generations. This allows a connection to classical, well understood ecological theory (Wissel [1990]). The logistic map is also widely used in classical resource economic theory (Clark [1990]). By adding a single structural property to the logistic map – namely the non-breeder pool – the importance of this property can be estimated, allowing direct assessment of whether lack of its inclusion in the model might lead to misleading results.

In addition to the conceptual model, a more realistic age-structured model of a population of the Great Cormorant is developed. For comparison, both models, the conceptual and the age-structured one, are parameterized with data from a Danish cormorant colony. The results of the conceptual model are taken as an initial hypothesis for the analysis of the age-structured model. This gives insight into the validity of the conceptual results in the face of more biological realism.

Finally, the assessment of the performance of regulation strategies applied to the cormorant model can support decisions regarding regulation strategies for the Great Cormorant. This issue is currently a highly debated conflict with which the European Commission is also concerned. The case of the Great Cormorant was chosen because it can be considered as a prime example for both a distinct population structure featuring non-breeders and for the conflict between nature conservation and economic interests as mentioned earlier (Rutschke [1998], Frederiksen and Bregnballe [2000], Frederiksen et al. [2002], Parrott et al. [2003]).

In light of these considerations the concrete objectives of this study are:

1. Development of a modeling approach to
 - a) understand the functioning and effect of the population structure induced by non-breeders on population dynamics in a fluctuating environment, and
 - b) uncover the relation between non-breeder characteristics and performance of management strategies, thus gaining a fundamental understanding of the role of non-breeders for management.
2. Application of the modeling approach to the regulation of the Great Cormorant in order to evaluate the results from the conceptual model.
3. Statements to support decisions on concrete management strategies for the Great Cormorant in Europe.

This study is structured as follows. After developing the modeling framework (Chapter 2), the influence of non-breeders on the dynamics of the entire, unregu-

lated population is investigated in Chapter 3. This allows for a systematic assessment of the impact of non-breeders on the performance of regulation strategies (Chapter 4). After that, the conclusions drawn from this assessment are taken as starting hypotheses for Part II and tested with a biologically more realistic age-structured model of the Great Cormorant developed in Chapter 5. The hypotheses are first tested without regulation (Chapter 6) and then with regulation (Chapter 7). Whereas in Chapter 7, the performance of regulation strategies is additionally judged from different economic perspectives. The thesis completes with general conclusions on the potentials and limitations of the approach and modeling framework developed and used in this study (Chapter 8).

PART I
CONCEPTUAL MODEL ANALYSIS

The first general aims of this study are to understand the primary effects of the non-breeder pool on population dynamics and the interplay between the non-breeder pool and the ecological-economic performance of regulation strategies. To achieve this a conceptual modeling framework is needed, which allows for both sufficient structure and simplicity (cf. Grimm [1994]). “Sufficient structure” means that the non-breeder pool should be modeled explicitly in order to allow for the assessment of the processes induced by it. Simplicity is required to allow for the explicit analysis of these processes and their interactions with regulation strategies. The model developed in the following meets these two conditions. It is based on the time-discrete logistic map and couples it with one further equation for the non-breeder pool. Basing the model on the time-discrete logistic map allows for the connection to classical, well understood ecological theory (Wissel [1990]) and to classical resource economic theory, where it is widely used (Clark [1990]). There are also examples, where the logistic mean field equation has been found to be a adequate approximation for population dynamics emerging from complex organismic interactions (e.g. Fahse et al. [1998]).

To gain an understanding of the processes and interactions between breeder stock and non-breeder pools, only deterministic environmental fluctuations are applied as a first step. This minimizes the complexity of the dynamics and allows systematic assessment of the influences and interactions of the parameters, not only on the level of population dynamics but also on the lower level of processes. This will later aid the understanding of the population dynamics when stochastic environmental fluctuations are applied. The systematic analysis of population dynamics under stochastic environmental fluctuations aims to assess the sensitivity of population stability properties (probability of extinction/time to extinction, variances, mean sizes) to changes in parameter values and thus in properties of the non-breeder pool.

Within this model, the effects of different regulation strategies can be better understood. The primary effects of regulation are exemplarily shown for fixed parameterizations of the population. To assess the possible interactions between the performance of regulation strategies and the characteristics of the non-breeder pool, the latter will be varied.

Finally, this procedure allows the generation of hypotheses concerning the regulation of populations featuring non-breeders. These hypotheses will then be used as a starting point for the analysis of the cormorant model presented in later chapters.

The Modeling Framework

To perform the above-mentioned tasks, the developed conceptual modeling framework has to allow the explicit assessment of the processes governing dynamics of breeders and non-breeders under deterministic and stochastic environmental conditions. Within the framework, different types of regulation strategies have to be implemented. Their performance is to be assessed according to population viability and regulation costs. This chapter introduces the framework and its components. It will also provide the starting point for the development of the more detailed cormorant model, which is introduced in Part II.

Below the conceptual population model is presented, followed by the assumed types of regulation strategies and the measures of their performance. Finally and to complete this chapter, an overview is given of the framework as a whole.

2.1 Population Processes

Following the reasoning outlined earlier, a stochastic and time-discrete population model with overlapping generations is developed. The model consists of two parts (see Figure 2.1). One represents the set of all reproductively active individuals (breeders) N_t , the other represents reproductively inactive individuals (non-breeders) P_t . For both, the dynamics are qualitatively different. Breeders are assumed to live longer than one generation and breed only in distinct breeding seasons. Thus, in the model the breeder stock N_t is assumed to follow a logistic growth dynamic $N_{t+1} = N_t + N_t(r(1 - N_t/K) + \xi_t)$, with environmental capacity K and reproduction rate r . Environmental fluctuations are assumed to affect reproductive success globally and thus enter via the effective reproduction rate $r_{eff} = r(1 - N_t/K) + \xi_t$ (see next section).

The non-breeder pool P_t is assumed not to feature reproduction, i.e. only death events occur. Its growth is assumed to be determined by the supply from the breeder stock and limited by the environment and thus is cut off at environmental capacity for non-breeders κ .

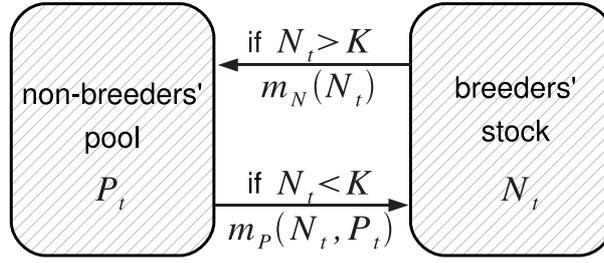


Figure 2.1: General model structure. If N_t (Equations 2.3 & 2.4) exceeds its capacity K , flux $m_N(N_t)$ (Equation 2.2) occurs. If N_t falls below K , flux $m_P(N_t, P_t)$ (Equation 2.1) takes place. In the non-breeder pool P_t no reproduction occurs (Equation 2.5).

Extending the logistic map by further processes implies a temporal order of these processes within one time step. For this model the order of processes in each time step is assumed as follows: first and before the breeding season, individual conversion between breeders and non-breeders takes place. Then breeding starts, influenced by breeder density.

Conversion of non-breeders into breeders. The conversion between breeders and non-breeders is different for both possible directions. It is assumed that non-breeder response to losses among breeders $m_P(N_t, P_t)$, i.e. the flux from the non-breeder pool into the breeder stock, depends on the non-breeder size P_t and the number of “free breeding opportunities”, i.e. the difference between breeder size N_t and its capacity K . Furthermore, it is assumed that the non-breeder response has a sigmoidal shape depending on the number of free breeding opportunities. This is based on the assumption that non-breeders have a limited ability to perceive opportunities to breed: if there are only few free breeding opportunities some non-breeders may fail to find them and non-breeder response is low. With increasing breeding opportunities the non-breeder response first increases exponentially, but this increase slows down as the number of free breeding opportunities approaches its maximum. Therefore, non-breeder response to loss of breeders is modeled in a similar way to a functional reaction of Holling type III (Holling [1959]).

$$m_P(N_t, P_t) = \beta((1 - \delta)P_t) \frac{\max(0, K - N_t)^2}{k^2 + (K - N_t)^2} \quad (2.1)$$

β denotes the maximum rate of this flux (and can also be interpreted as the disposition of non-breeders to convert to breeders), δ the mortality of non-breeders, and $(1 - \delta)P_t$ the number of non-breeders which have survived. The last term $\max(0, K - N_t)^2 / (k^2 + (K - N_t)^2)$ describes the per capita success of non-breeders of becoming a breeder depending on k , the medium saturation density of free breeding opportunities in the breeder stock (k can also be interpreted as non-

breeders' perception of free breeding opportunities). Thus, k determines the rapidity of the non-breeder response to the loss of breeders.

This approach adopts ideas from standard resource-consumer models, where the consumers' response to available resources (here: free breeding opportunities) can be modeled in the same way (Maynard Smith [1974]).

Conversion of breeders into non-breeders. In supplying the non-breeder pool $m_N(N_t)$, it is assumed that a fixed portion of surplus breeders becomes non-breeders. If there is no surplus, no flux into the pool of non-breeders takes place.

$$m_N(N_t) = \lambda \max(0, N_t - K) \quad (2.2)$$

λ represents the portion of surplus breeders converting into non-breeders. After the conversion from breeders into non-breeders and vice versa, breeding starts.

Breeders dynamics. To compute the breeder dynamics, a gross growth $N_{g,t}$ of breeders (i.e., size of breeder stock after fluxes between the two parts have taken place) is calculated first.

$$N_{g,t} = N_t - m_N(N_t) + m_P(N_t, P_t) \quad (2.3)$$

It is assumed that reproduction only takes place during breeding season and that breeder size is density regulated. Environmental fluctuations are assumed to affect the reproductive success. Thus, the gross growth is used in the equation for the logistic growth dynamics of the breeders where environmental fluctuations affect the effective reproduction rate $r(1 - N_{g,t}/K)$. The resulting equation for dynamics of breeders reads:

$$N_{t+1} = N_{g,t} + N_{g,t} \left(r \left(1 - \frac{N_{g,t}}{K} \right) + \xi_t \right) \quad (2.4)$$

The way, how environmental stochasticity is introduced is the same as in standard models for fluctuating population dynamics (Gurney and Nisbet [1985]).

Non-breeder dynamics. For the non-breeders, it is assumed that they are also limited by their environment. Among them no reproduction takes place and only death events occur. Therefore, their size P_{t+1} is modeled as the minimum between the result of the effect of mortality and conversion on the one hand and environmental capacity for non-breeders κ on the other hand:

$$P_{t+1} = \min(\kappa, (1 - \delta)P_t + m_N(N_t) - m_P(N_t, P_t)) \quad (2.5)$$

N_t and P_t are considered to be zero if they drop below $\Delta = 0.001$. The whole system is rescaled by setting $K = 1$. Thus, everything is measured in units of the environmental capacity K for the breeders.

2.2 Environment

Deterministic fluctuations. To get first insights into the primary dynamic interplay between breeders and non-breeders, simple deterministic environmental fluctuations are applied. They are defined by a sine $\xi_t = a_\xi \sin(2\pi f_\xi t)$ with frequency f and amplitude a . The amplitude of fluctuations will be set to $a_\xi = 0.2$ and frequency to $f_\xi = 1/20$.

Stochasticity and catastrophes Environmental stochasticity is modeled by a normally distributed random variable $\xi_t = \mathcal{N}(\mu_\xi, \sigma_\xi^2)$ with mean $\mu_\xi = 0$ and variance σ_ξ^2 . Furthermore it is assumed that rare but significant catastrophes occur. This is modeled by one pulse perturbation during 100 time steps, which only affects breeders. This is motivated by the assumption that breeders suffer higher stress during breeding and are less mobile and thus at greater risk of suffering heavy losses caused by adverse environmental conditions. The pulse at time t^* sets the size N_{t^*} of breeders to $0.02N_{t^*}$.

As the system is rescaled by $K = 1$, parameters of environmental fluctuations are also measured in units of K . Throughout the whole study, parameter μ_ξ is set to $\mu_\xi = 0$.

2.3 Regulation Strategies

The requirement of maintaining the viability of the target population leads to the need for adaptive regulation strategies. The definition of a threshold for population size is a suitable approach to meet this constraint: As soon as population size declines below the threshold no further regulation takes place (“stop-loss rule”) (Lande et al. [1995]; Lande et al. [1997]; Enberg [2005]; Saether et al. [2005a]). Instances of these “bang-bang” or threshold strategies are applied in this study. Different types of regulation strategies are assumed (Table 2.1): Regulation affects either the size of the breeder stock N_t , the size of the non-breeder pool P_t , the reproduction rate r_t or the environmental capacity for the breeders K_t (note: by making r and K subject to regulation they become time-dependent). Additionally, regulation strategies are considered (e.g. culling of individuals without differentiating between breeding and non-breeding individuals) which affect both N_t and P_t equally.

Regulation strategies are defined as pairs $S := (\iota, \theta)$, where $\iota \in [0, 1]$ stands for the rate of regulation; applied as long as the total population size $N_t + P_t$ exceeds the threshold $\theta \in [0, \infty]$. If $N_t + P_t \leq \theta$ no regulation takes place. If at the end of a time step $N_t + P_t > \theta$ holds, then depending on the strategy type either N_t , P_t , r_t or K_t are reduced to $N_t = N_t - \iota N_t$, $P_t = P_t - \iota P_t$, $r_t = r_t - \iota r_t$ or $K_t = K_t - \iota K_t$ respectively. In the r -reducing strategy, in the case of $N_t + P_t \leq \theta$, r_t is set back to the initial reproduction rate r . In the K -reducing strategy, whenever $N_t + P_t \leq \theta$

(i.e. when no regulation takes place) it is assumed that environmental capacity K recovers slowly with a rate of 0.05 (Table 2.1 first row). Note that θ is also expressed in units of the environmental capacity K .

Table 2.1: The four different types of regulation strategies (reducing N_t , P_t , N_t and P_t , r_t or K) affect different system components. Reduction takes place if $N_t + P_t > \theta$, which in case the term in the second column is subtracted from the respective component. Otherwise, if $N_t + P_t \leq \theta$ the reduced component recovers.

affected component	reduced by (if $N_t + P_t \leq \theta$)	recovery (if $N_t + P_t > \theta$)
N_t	$\imath N_t$	according to Eq. 2.4
P_t	$\imath P_t$	according to Eq. 2.5
r_t	$\imath r_t$	immediately to initial value r
K_t	$\imath K_t$	if $K_t < K = 1 : K_t = K_t + 0.05K$

2.4 Measures and Thresholds of Performance of Regulation Strategies

The performance of each regulation strategy under discussion has to be assessed according to the three requirements of conflict reconciliation mentioned above: reaching the given regulation target, keeping the regulated population viable, and adhering to the budget. In the following, measures will be defined that allow a systematic quantitative consideration of all three requirements.

Reaching the desired population size M . This can be assessed by taking the mean square deviation d^2 from the desired population size M as a measure, which is defined as follows:

$$d^2 := R^{-1} \sum_{i=1}^R \left[T_{s,i}^{-1} \sum_{t=1}^{T_{s,i}} ((N_t + P_t) - M)^2 \right] \quad (2.6)$$

with $N_t + P_t$ denoting the total population size, $T_{s,i}$ the time of survival in run i and R the total number of simulation runs. A strategy is said to *reach the desired population size* if $d^2 < \varepsilon_d$ where ε_d denotes the predefined Maximum Accepted Deviation from M .

Maintaining population viability. Here use can be made of standard conventions from population viability analysis (Shaffer [1981]). The population is said to be *viable* if the probability of extinction after 100 years $P_0(100)$, meets the following condition: $P_0(100) < \varepsilon_p$, with ε_p being the Maximum Accepted Extinction Risk.

Adhering to the budget. Costs of regulation are assumed to be linear with respect to regulation effort. The effort in one time step is measured by the product $\iota(N_t + P_t)$. The mean effort over the entire life-span of the population is measured by

$$e = R^{-1} \sum_{i=1}^R \left[T_{s,i}^{-1} \sum_{\{t:t \in [1, T_{s,i}] \wedge (N_t + P_t) > \theta\}} \iota(N_t + P_t) \right] \quad (2.7)$$

A strategy is said to be *effective and adhering to the budget*, if $P_0(100) < \epsilon_p$, $d^2 < \epsilon_d$ and $e < \epsilon_b$, with ϵ_b being the Mean Budget for regulation measurements in one time step. (Note, by the definition in Equation 2.7 $\iota(N_t + P_t) > \epsilon_b$ is allowed to happen. Only the mean effort e has to be less than the mean budget ϵ_b .)

Throughout this study the Maximum Accepted Extinction Risk will be set to $\epsilon_p = 0.05$, the Mean Budget to $\epsilon_b = 0.02$. M and the Maximum Accepted Deviation ϵ_d will be varied.

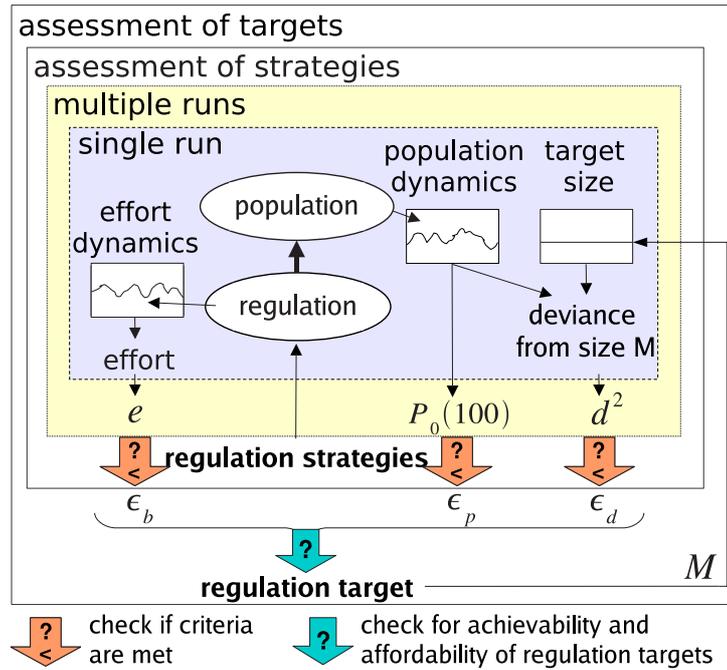


Figure 2.2: Modeling framework. Regulation strategies define regulation, which influences population dynamics and effort. Mean effort e , probability of extinction $P_0(100)$, and deviance d^2 from the desired population size M are calculated in multiple simulation runs. These are compared to the target values ϵ_b , ϵ_p and ϵ_d .

2.5 Assessment of Regulation Strategies and Targets

The last step missing is a convention for the assessment of the performance of the regulation strategies under consideration and the achievability of regulation targets. If the first and the second criteria are fulfilled ($d^2 < \varepsilon_d$ and $P_0(100) < \varepsilon_p$) and if the mean effort is less than a given mean budget ε_b , the strategy is considered to be *effective* while at the same time adhering to the budget. More formally, this represents a multi-criteria problem featuring three dimensions. Regulation targets are defined by a tuple $target = (M, \varepsilon_d, \varepsilon_p, \varepsilon_b)$ (note: these parameters are normative and therefore dependent on subjective preferences of stakeholders).

A *target* is said to be *achievable* if a certain strategy exists that fulfills the following two conditions: $d^2 < \varepsilon_d, P_0(100) < \varepsilon_p$. To go one step further, a target is referred to as *affordable* if a certain strategy exists that is effective and adheres to the budget, i.e. meets both of the aforementioned conditions and, additionally, the condition $e < \varepsilon_b$. The whole process of assessing strategy-specific effectiveness and adherence to budget, as well as achievability and affordability of targets is illustrated in Figure 2.2.

To summarize, the presented modeling framework allows regulation strategies to be assessed from the point of view of different ecological and economic targets and the role of the non-breeders to be systematically investigated.

2.5. Assessment of Regulation Strategies and Targets

Non-Breeder Pool and Population Dynamics

After the conceptual modeling framework is developed, the model is now applied to obtain a better primary understanding of the effects of the non-breeder pool on population dynamics and stability properties. Thus, in this chapter regulation is not taken into consideration.

Below, a qualitative analysis is given of how parameter variations influence population dynamics under *deterministic* environmental fluctuations. This will provide insight into the processes and interactions governing the population dynamics. After this, a sensitivity analysis is carried out for population behavior under *stochastic* environmental conditions. This enables to determine which processes are dominant under stochastic conditions and furthermore allows the generation of hypotheses concerning performance and design of regulation strategies.

3.1 Deterministic Environmental Fluctuations

This section it is examines how non-breeder characteristics influence stock dynamics. According to the literature cited earlier (Penteriani et al. [2005], Frederiksen et al. [2001], Sarah et al. [2004], Klomp and Furness [1992]), the starting hypothesis is that the presence of the non-breeder pool reduces fluctuations in breeder size. To test this hypothesis and to gain insight into the conditions (i.e. which characteristics of the non-breeder pool) under which it holds true, the focus here will lie on the qualitative assessment of breeder and non-breeder dynamics. The primary aim is to gain insight into the influences of the different parameters on population dynamics and interplays.

The non-breeder pool is characterized by parameters for interactions between breeders and non-breeders and vice versa (λ , β and k), maximum non-breeder size (κ) and non-breeder mortality (δ). Accordingly it is started with the assess-

ment of the influence of varying conversion rates from breeders to non-breeders. Following this, the conversion from non-breeders to breeders and the remaining two parameters will be systematically examined.

Conversion from breeders into non-breeders λ

In the first step of this analysis a reference parameter set is arbitrarily chosen as a starting point ($\lambda = 0.5, \beta = 0.5, k = 0.5, \delta = 0.1$ and $\kappa = 0.7$). Then parameter λ is varied individually while all others are held constant at their reference value. Reproduction rates are set at $r = 0.5, r = 2.5$ and $r = 3.0$. This choice is motivated by the behavior of the common time-discrete logistic map with overlapping generations: For $r = 0.5$ population size increases monotonically into capacity K . If reproduction is set to $r = 2.5$, the population size fluctuates regularly in a cycle of length 4. For $r = 3.0$, deterministic chaotic fluctuations occur. Figure 3.1 shows the corresponding population dynamics for varying λ for the three values of r . This comparison is done to cover the range of population dynamics in the deterministic case.

In the first row in Figure 3.1 the behavior of the population without a non-breeder pool is depicted. In the case of $r = 0.5$, breeder dynamics follow the environmental fluctuations. This corresponds to the behavior of an ordinary logistic map, which means that breeder size remains at the equilibrium, which changes according to the environmental fluctuations ($\xi_t = a_\xi \sin(2\pi f_\xi t)$). This can easily be calculated:

$$N_{t+1} = N_t + N_t \left(r \left(1 - \frac{N_t}{K} \right) + \xi_t \right) \quad (3.1)$$

At equilibrium $N_{t+1} = N_t$ holds. The nontrivial solution for N^* therefore is

$$r \left(1 - \frac{N^*}{K} \right) + \xi_t = 0 \quad (3.2)$$

$$\Rightarrow N^* = \frac{r + \xi_t}{r} K = \left(1 + \frac{\xi_t}{r} \right) K \quad (3.3)$$

For the case of $r = 2.5$, intrinsic fluctuations due to over-compensation and environmental fluctuations superimpose. Thus, the cycles can not be identified anymore. In the case of $r = 3.0$, fluctuations lead to extinction.

The column of $r = 0.5$ in Figure 3.1 shows that the presence of non-breeders does not alter population behavior considerably. The population simply does not “need” the non-breeder pool for stabilization -the dynamics simply continue to follow the extrinsic fluctuations. The size of the non-breeder pool increases with increasing λ and the amplitude of fluctuations in the breeder stock decreases slightly. While the dynamics of the breeder stock almost immediately follows

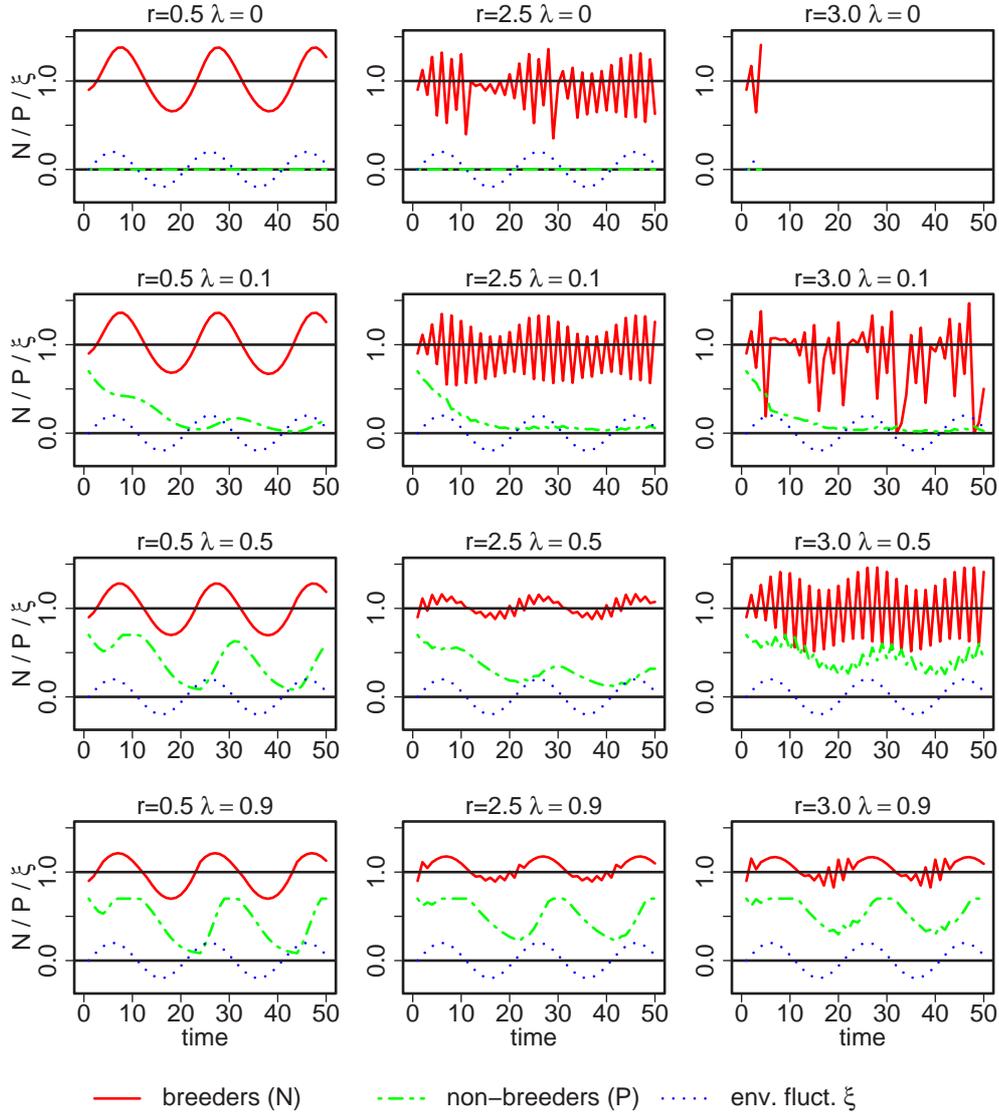


Figure 3.1: Variation of λ . All other parameters are set to their reference values ($\lambda = 0.5, \beta = 0.5, k = 0.5, \delta = 0.1$ and $\kappa = 0.7$). Environmental fluctuations are modeled deterministically $\xi_t = a_\xi \sin(2\pi f_\xi t)$, with $a_\xi = 0.2$ and $f_\xi = 1/20$.

the environmental fluctuations, the non-breeder dynamic follows with a certain delay.

For $r = 2.5$, the regular fluctuations induced by ξ_t are replaced by fluctuations with higher frequency, which are caused by over-compensation. For small λ , the amplitude of these short term fluctuations reaches its maximum at the same time as extrinsic fluctuations do. Increasing λ strongly decreases these fluctuations within the breeder stock. At the same time longterm fluctuations as in the case of $r = 0.5$ occur, but with a smaller amplitude. Further increasing λ again

increases non-breeder pool. The effect of reduced short term fluctuations is due to the *sink functionality* of the non-breeder pool: The higher the value of λ , the more surplus of breeders convert into non-breeders. Thus, over-compensation is reduced.

The picture does not alter qualitatively for $r = 3.0$ with the exception that, for this reproduction rate without any non-breeder pool, the population dies out. In any case, the higher λ is, the greater is the reduction in short-term fluctuations in the size of breeder stock and non-breeder pool. The pure existence of the non-breeder pool prevents the population from extinction. This is caused by the *source functionality* of the non-breeder pool. Even though the supply by non-breeders is only small, it suffices to lift the size of the breeder stock above zero, so that it can increase again (see Figure 3.1 second row third column).

Comparing the dynamics for fixed $\lambda = 0.5$ or $\lambda = 0.9$ but varying reproduction rate (last two rows of Figure 3.1), shows that increasing r from $r = 0.5$ to $r = 2.5$ leads to a considerable reduction of fluctuations in population dynamics. A further increase to $r = 3.0$ increases overall fluctuations again. Hence, there is a trade-off in r between reduction of fluctuation and over-compensation. This part of the analysis shows that the sink functionality has a smoothing effect on a small time scale. The condition for this smoothing is a high value of λ . For this value of λ , the source functionality has the greater smoothing effect on the larger time scale. In the following the reference value of λ is set to $\lambda = 0.9$.

The same kind of variation for the remaining four parameters shows for $r = 0.5$ roughly the same: population behavior is fairly insensitive to changes in these parameters. This can be interpreted as if there is no effect of non-breeders in the case of non-over-compensatory dynamics. Again, the case of $r = 3.0$ is qualitatively similar to $r = 2.5$. Therefore the following considerations are limited to $r = 2.5$ but hold also for $r = 3.0$.

Conversion from non-breeders into breeders k and β

Conversion from non-breeders into breeders is determined by the parameters k and β . The value of parameter k determines the sluggishness of the non-breeder response to losses among breeders. Figure 3.2 indicates that the smaller the value of k , the faster is the reaction of non-breeders. A small value of k also allows higher maximum fluxes. Analyzing the effect of variation of a single parameter, while holding the remaining parameters fixed at their respective reference value, shows that out of the four parameters β , k , δ and κ , k turns out to be the only one to which population behavior is sensitive.

The insensitivity of β , δ and κ is caused by the chosen reference value of $k = 0.5$. In this region of the parameter space, the effect of a more sluggish non-breeder response (determined by the relatively high value of k) dominates population behavior, so that changing other parameters does not influence the dynamics of the breeder stock.

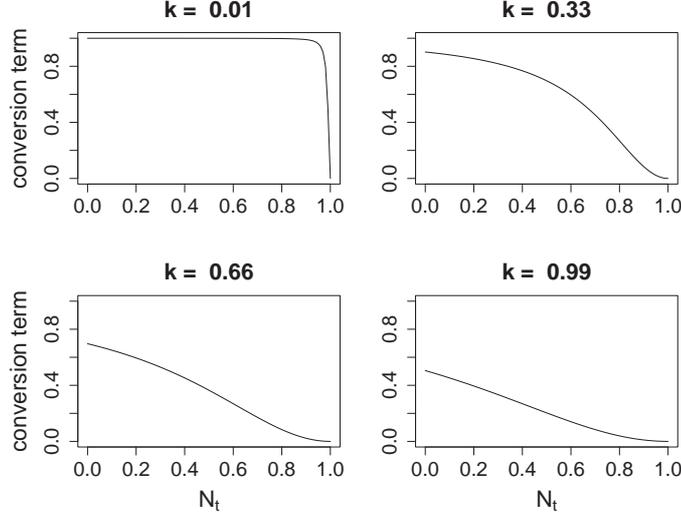


Figure 3.2: The term for conversion from non-breeders to breeders $\frac{(K-N)^2}{(k^2+(K-N)^2)}$ with $K = 1$ for different values of k . The value of k determines the “rapidity” respectively “sluggishness” of the non-breeder response to breeder loss.

After this first step, it cannot be stated, however, that population behavior is globally, over the entire parameter space, insensitive to the values of β , δ and κ . To examine this, the effect of β for different given k -values is assessed. Parameters are set to their reference values $\delta = 0.1$ and $\kappa = 0.7$, while λ was set to 0.9. Figure 3.3 shows nine exemplary plots of this analysis.

It reveals several effects. First, the effect of k on breeder dynamics depends on β : For low values of $\beta = 0.1$ and low $k = 0.1$, breeder dynamics show least fluctuations. If β is set to a higher value of $\beta = 0.9$, then k has to be set to a slightly higher value of $k = 0.25$ to achieve dynamics with low fluctuations.

Hence, depending on the value of β , there is a trade-off in k : If the maximum strength of non-breeder response is set to $\beta = 0.9$ and the sluggishness of non-breeder response to $k = 0.1$, then population dynamics becomes turbulent in periods where ξ_t is negative and the size of the non-breeder pool low. This can be explained by the abrupt ($k = 0.1$) and strong ($\beta = 0.9$) response of non-breeders to losses among the breeders. It allows for the pool of non-breeders to quickly be exhausted. This strong conversion of non-breeders into breeders can lead to an overshooting of breeders. The conditions for that effect can be calculated explicitly: Overshooting happens if $N_{b,t} > K$ (cf. Section 2.1). This can be written as

$$K - (K - N_t) + m_P(N_t, P_t) > K \quad (3.4)$$

$$\Leftrightarrow m_P(N_t, P_t) > K - N_t \quad (3.5)$$

$$\Leftrightarrow \beta(P_t - \delta P_t) \frac{(K - N_t)^2}{k^2 + (K - N_t)^2} > K - N_t \quad (3.6)$$

3.1. Deterministic Environmental Fluctuations

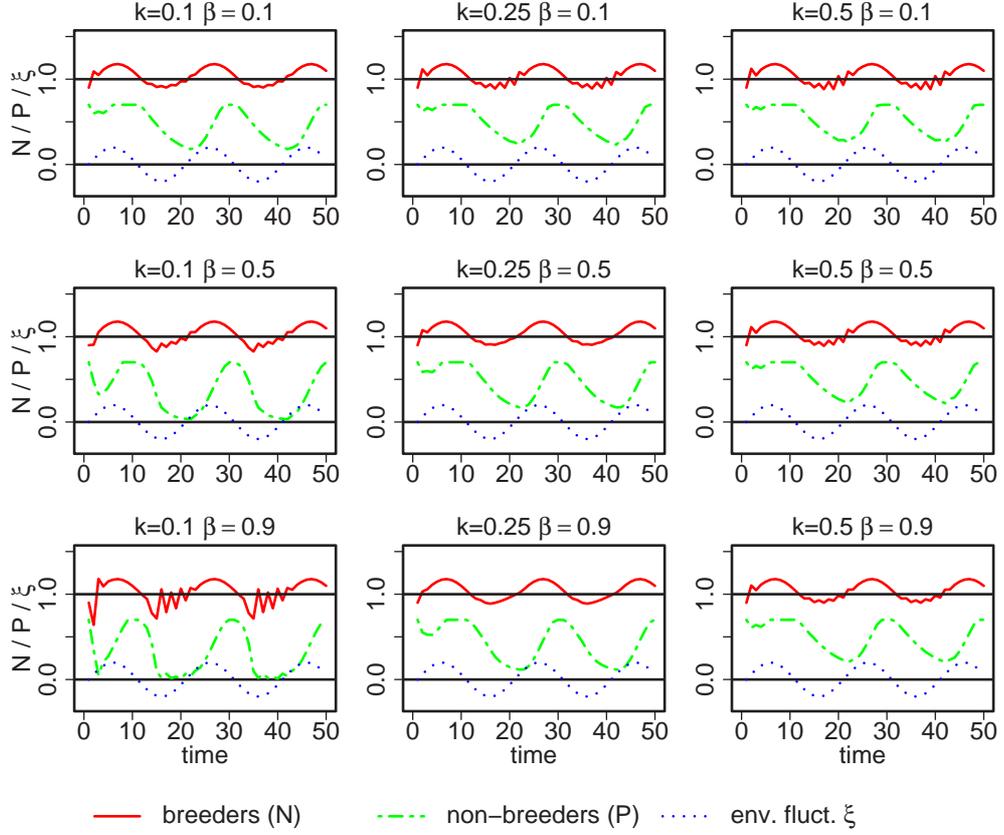


Figure 3.3: Interplay between k and β . Values of the other parameters are $\lambda = 0.9$, $\delta = 0.1$ and $\kappa = 0.7$.

$$\Leftrightarrow \beta(1 - \delta)P_t \frac{(K - N_t)}{k^2 + (K - N_t)^2} > 1 \quad (3.7)$$

Finally the condition for overshooting can be written as

$$P_t > \frac{k^2 + (K - N_t)^2}{(K - N_t)} \frac{1}{\beta(1 - \delta)} \quad (3.8)$$

Evidently, the lower k and δ and the higher β is, the larger is the range of P_t where the non-breeders can cause overshooting of the breeder stock. For the given parameters of $k = 0.1$, $\beta = 0.9$ and $\delta = 0.1$, $K = 1$ and non-breeder size P_t set to $\kappa = 0.7$, the capacity of the breeder stock is exceeded at $t + 1$ if $0.46 < N_t < 0.98$. For decreasing size P_t of the non-breeder pool the range of N_t where overshooting occurs diminishes (e.g. $P_t = 0.3$: $0.81 < N_t < 0.94$). For the two parameterizations with the greatest smoothing effect ($\beta = 0.1$, $k = 0.1$ and $\beta = 0.9$, $k = 0.25$ with $\kappa = 0.7$ and $\delta = 0.1$ in both) the inequality 3.8 can not be solved.

In contrast, being empty or having reached a very small size, the non-breeder pool is no longer able to compensate losses and starts losing its source functionality. In this case the conversion into breeders $m_P(N_t, P_t)$ cannot prevent decreases in the size of the breeder stock. Lower sizes of the breeder stock N_t in turn increase the effective reproduction rate $r(1 - N_t/K)$ (as long as $N_t > 0.5$ holds). Because of $r = 2.5$, overshooting of N_t over K occurs due to high reproduction, which is then over-compensated. This also makes the dynamics less smooth.

Increasing k makes the non-breeder response more sluggish such that overshooting due to non-breeder response is diminished. However, further increases in k lead to a more sluggish non-breeder response such that fluctuations caused by over-compensation are no longer fully compensated, which means source functionality is too weak and fluctuations start again.

Non-breeder mortality δ

Given these results, the qualitative influence of non-breeder mortality δ on the population dynamics is investigated. To gain further insight, the two parameterizations, which induce the most even dynamics are analyzed for different values of δ . Furthermore, a parameterization which leads to strong overshooting/over-compensation dynamics is also analyzed in the same way. Figure 3.4 shows the results.

Figure 3.4 shows that increasing δ can have two opposite effects. In the case of the two smoothing parameterizations (upper rows), increasing δ leads to more uneven dynamics. This is caused by the fact that increasing δ decreases the size of the non-breeder pool and thus the number of non-breeders converting into breeders. Therefore, non-breeders are not able to compensate for fluctuations induced by the reproduction rate of $r = 2.5$.

On the other hand, it is exactly this reduced conversion into breeders which leads to less bumpy dynamics in the third case (lower row). It reduces overshooting induced non-breeders converting into breeders. However, in this case (lower row) there is also a trade-off in δ : increasing δ further leads to a reduced conversion into breeders which is not able to compensate for fluctuations induced by the reproduction rate.

Figure 3.4 also shows that increasing non-breeder mortality not only influences the strength of the conversion into breeders, but also its timing. In other words, the higher δ is, the more non-breeder fluctuations are synchronized with breeder fluctuations. This synchronization can be explained as follows: If effective reproduction is high, the breeder stock increases and conversion into non-breeders becomes high as well. However, because of high non-breeder mortality, the non-breeder pool is “not able to store” the surplus. Hence for high δ -values, there are simply no non-breeders available in case of breeders’ loss and the non-breeder pool loses its “insurance effect”. To put it the other way around, low non-breeder mortality creates a delay in population dynamics which acts in a

3.1. Deterministic Environmental Fluctuations

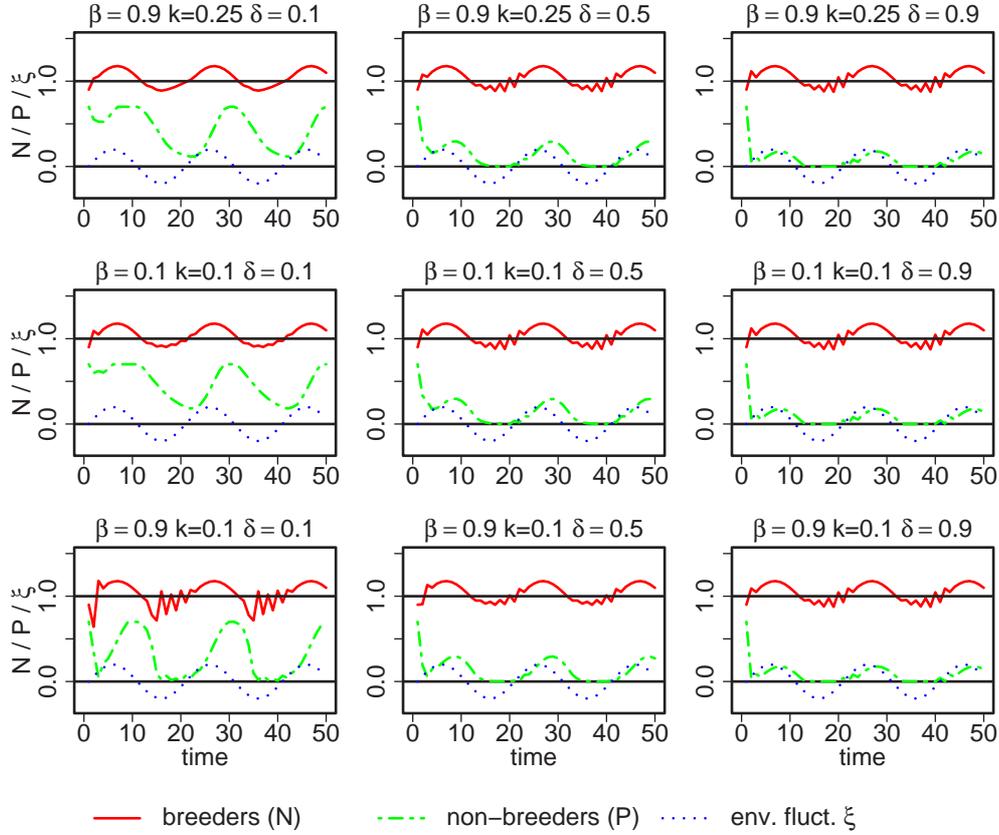


Figure 3.4: The role of δ . Values of the other parameters not shown are $\lambda = 0.9$ and $\kappa = 0.7$.

desynchronizing manner. For the next analysis steps δ is set to $\delta = 0.1$.

Non-breeder capacity κ

Now, the remaining parameter κ is taken into account (Figure 3.5). Decreasing non-breeder capacity κ from its reference value of $\kappa = 0.7$ to $\kappa = 0.3$ leads to slightly increased fluctuations in the size of the breeder stock on a short time scale. Increasing to $\kappa = 1.5$ in case of $\beta = 0.9$ and $k = 0.25$ also makes population dynamics slightly more uneven. Hence there is a slight trade-off in κ . This trade-off is again related to the conversion of non-breeders into breeders, which potentially increases with κ . In case of $\beta = 0.1$ and $k = 0.1$, increasing capacity for non-breeders leads to more even dynamics. In this case overshooting only occurs if non-breeder size exceeds $P_i = 2.23$ (cf. Equation 3.8), which is not reached in this example. Finally, Figure 3.5 shows that population dynamics are relatively insensitive to changes in κ .

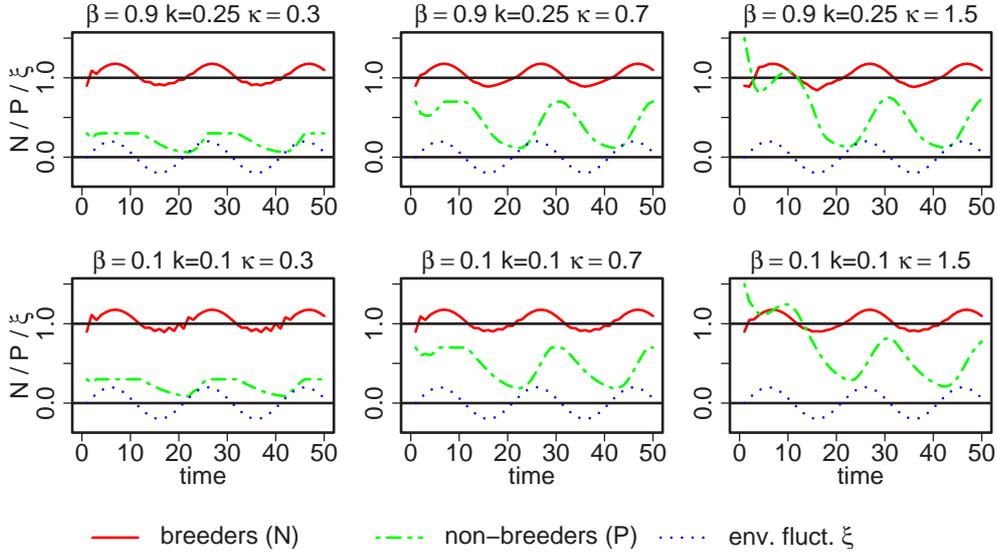


Figure 3.5: The role of non-breeder capacity κ . Values of parameters not shown are $\lambda = 0.9$ and $\delta = 0.1$

Discussion of non-breeders' role for dynamics

At the beginning of this section it was asked about the qualitative effects of the pool of non-breeders on population dynamics and especially on fluctuations in the breeder stock. It was hypothesized that the presence of non-breeders reduces these fluctuations. However, it was not clear under which conditions this hypothesis holds true. Now, at the end of this section non-breeder characteristics can be given, for which population dynamics, given the deterministic nature of environmental fluctuations, fluctuate less. Table 3.1 shows the corresponding parameter values. Each parameterization leads to a different type of non-breeder response. For the first, where the maximum strength of non-breeder response is set to $\beta = 0.9$, the conversion from breeders into non-breeders $m(N_t, P_t)$ tends to be very strong. To prevent overshooting/over-compensation dynamics induced by the strong conversion, this must be bounded. This is achieved by choosing a more “sluggish” mobilization of the non-breeders ($k = 0.25$, see Figure 3.2). Furthermore the non-breeders' environmental capacity κ is bounded to $\kappa = 0.7$. This also limits the maximum conversion into breeders. Because of the setting of k and β , in the following this type of non-breeder response is referred to as “*sluggish but strong*”.

The second possibility to characterize a non-breeder response such that it smoothes dynamics effectively is to set $\beta = 0.1$ and $k = 0.1$. This leads to a weak conversion, which already reaches its maximum with slight losses in the breeder stock. As the maximum strength of conversion into breeders β is set to a very low value, the maximum flux does not have to be bounded by the non-

3.1. Deterministic Environmental Fluctuations

breeder capacity. Therefore it is set arbitrarily to $\kappa = 1.5$, which in fact is never reached. This non-breeder response type is referred to as “*agile but weak*”. In both parameterizations, $\lambda = 0.9$ and $\delta = 0.1$ are set to the same value.

Table 3.1: Parameter sets for which the non-breeder pool has the greatest smoothing effect.

non-breeder response	λ	β	k	δ	κ
sluggish but strong	0.9	0.9	0.25	0.1	0.7
agile but weak	0.9	0.1	0.1	0.1	1.5

The previous analysis showed that sink functionality (determined by λ) and source functionality (determined by β , k , δ and κ) affect population behavior in different ways. To make this more explicit Figure 3.6 shows population dynamics without a non-breeder pool ($\lambda = 0$, $\kappa = 0$), with only sink functionality of the non-breeder pool ($\beta = 0$) and with full sink and source functionality. All parameters not mentioned are set exemplarily to the values of the sluggish but strong non-breeder response (Table 3.1).

Figure 3.6 shows that in cases where extrinsic fluctuations lead to higher effective reproduction rates ($r(1 - N_t/K) + \xi$), the sink functionality decreases fluctuations. However, for lower effective reproduction rates intrinsic fluctuations occur. This is because of the growing value of the term $N_t(r(1 - (N_t/K) + \xi))$ for lower values of N_t as long as $K/2 < N_t < K$ holds. In the case of $r = 2.5$ this leads to over-compensatory reactions of the population and thus to short frequent intrinsic fluctuations. These fluctuations are compensated by the source functionality of the non-breeder pool (see rightmost plot in Figure 3.6).

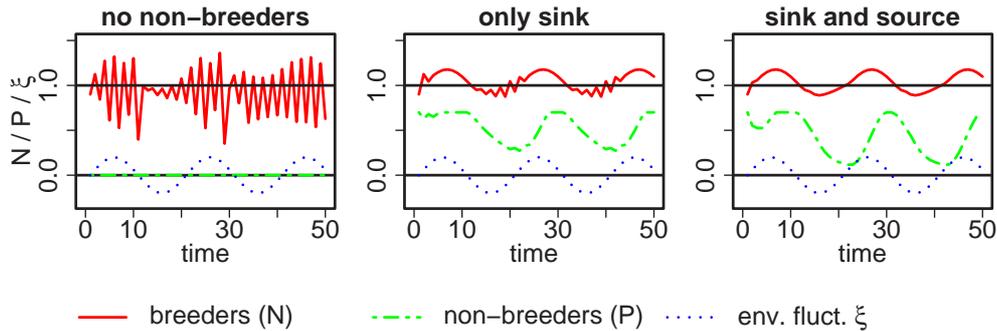


Figure 3.6: Effects of sink functionality and combination of source and sink functionality compared with dynamics of the population without non-breeder pool. Parameters are chosen as for the sluggish but strong non-breeder response to breeders’ loss (see Table 3.1).

As already stated, if N_t is decreasing, effective reproduction increases as long as $K/2 < N_t < K$ holds. In these cases a high reproduction rate r could be considered as a kind of buffering mechanism. The structure induced by non-breeders

acts in addition to this existing ability of the population to compensate individual losses. It can counterbalance the drawback of over-compensation at high reproduction rates.

In contrast to this, Figure 3.7 indicates that applying the parameterization of a sluggish but strong non-breeder response to populations with different reproduction rates ($r = 0.5$, $r = 2.5$, $r = 3.0$) shows that also for high reproduction rates, intrinsic fluctuations are smoothed. Furthermore, the total amplitude of fluctuations is reduced by increasing r . Thus the non-breeder pool enables the population to benefit from the advantages of high reproduction without suffering its disadvantages, namely over-compensation.

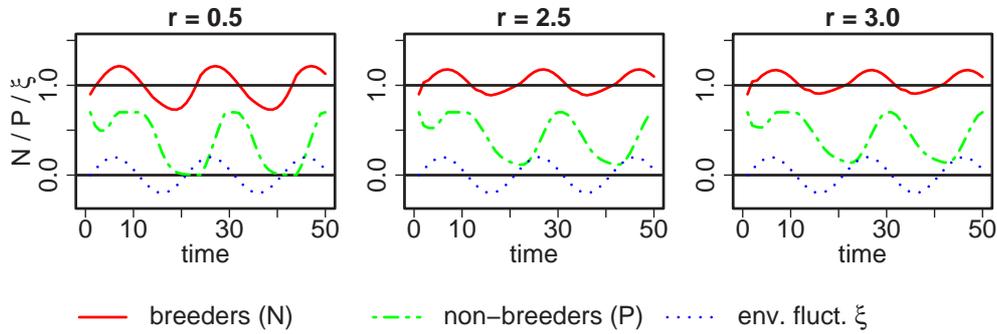


Figure 3.7: Effects of increasing reproduction rate r on a population with a sluggish but strong non-breeder response to breeders' loss. (see Table 3.1).

Figure 3.7 also shows that overall fluctuations decrease and the size of the non-breeder pool increases with increasing reproduction rate r . Nevertheless, in all shown plots the size of the breeder stock follows the extrinsic fluctuations ξ_t . This can be explained analytically by Equation 3.3 according to which, increasing r reduces the effects of extrinsic fluctuations.

The aim of this analysis was to gain an insight into the qualitative function of the non-breeder pool. It showed that there are parameterizations which best reduce intrinsic fluctuations of the breeder stock. These parameterizations maximize the rate of conversion into non-breeders in cases of breeder surplus by setting λ to a high value near one. This maximizes the sink functionality of the non-breeder pool and thus minimizes over-compensation.

The two parameters β , k , which determine the conversion from non-breeders into breeders, are set to values which either maximize the strength of conversion (high β) but do not let the non-breeders react too abruptly to losses among breeders (higher k), or which set the maximum strength of conversion to a low value but then let the non-breeders react in a very agile way.

The parameters κ and δ influence the size of the non-breeder pool. If δ is set to a low value, it desynchronizes the maxima of the size of the non-breeder pool

and the extrinsic fluctuations. κ on the other hand defines the maximum size of the non-breeder pool.

3.2 Stochastic Environmental Fluctuations

The analysis of population behavior thus far has shown that under deterministic environmental conditions, the presence of the non-breeder pool *can* reduce fluctuations in the size of the breeder stock, but does not necessarily have to. Whether or not fluctuations in breeder size are reduced by the non-breeder pool depends on its characteristics. The next step is to examine whether this also holds under stochastic environmental conditions and which parameters are most crucial for population dynamics. The introduction of stochasticity is a step towards more realistic assumptions, but the results from the preceding deterministic case will help to understand the following results.

In contrast to the preceding section, a sensitivity analysis of the parameters is now performed. Thus, the perspective is shifted towards quantitative measures, namely the *mean size of the breeder stock* \bar{N} , *variance in the size of the breeder stock* $var(N)$ and the *probability of extinction within 100 time steps* $P_0(100)$. Given the results of the previous section, the hypothesis now is that the presence of the non-breeder pool *may* have a stabilizing effect. More formally, the non-breeder pool can increase mean size of the breeder stock, reduce variances in breeder stock size and probability of extinction. As seen in the deterministic case the extent to which the non-breeder pool is able to do so depends on its characteristics, i.e. the parameterization of the population.

Setting of experiments

As environmental fluctuations are no longer a deterministic process, ξ_t becomes a random variable (cf. Section 2.2). Two sources of fluctuations can influence population dynamics: environmental fluctuations determined by ξ_t and intrinsic fluctuations determined by r . Therefore, all the calculations described in the following were made for six different settings of environmental fluctuations and reproduction rates, which are listed in Table 3.2.

Table 3.2: Settings of reproduction rate and environmental fluctuations in the investigated scenarios. (*w* stands for “weak” and *s* for “strong” fluctuations)

scenario name	05w	05s	25w	25s	30w	30s
variance var_{ξ}	0.05	0.4	0.05	0.4	0.05	0.4
reproduction rate r	0.5	0.5	2.5	2.5	3.0	3.0

For the following analyzes parameterizations $(\lambda, \beta, k, \delta, \kappa)$ contained in the sub-

set Θ of the parameter space are applied:

$$(\lambda, \beta, k, \delta, \kappa) \in \Theta = \Theta_1 \times \Theta_1 \times \Theta_1 \times \Theta_1 \times \Theta_2 \quad (3.9)$$

with

$$\lambda, \beta, k, \delta \in \Theta_1 = \{0.1, 0.25, 0.5, 0.75, 0.9\} \quad (3.10)$$

and

$$\kappa \in \Theta_2 = \{0.3, 0.7, 1.0, 1.5, 2.0\} \quad (3.11)$$

Population behavior is measured in terms of probability of extinction within 100 time steps $P_0(100)$, mean size of the breeder stock \bar{N} and variance in the size of the breeder stock var_N .

Non-breeder characteristics and population behavior

As a starting point, reference parameterizations for further analyzes are chosen. To avoid setting these reference parameterizations arbitrarily they are chosen according to the resulting population behavior. The criteria are in order of consideration: $P_0(100) < 0.05$, \bar{N} as high as possible and var_N as low as possible. These conditions are heuristic and normative. They lead to parameterizations with highest possible stability in any respect. Behind that, lies the assumption that populations feature mechanisms, which under “normal” environmental conditions increase their probability of survival. A high population size and low variance in population fluctuations might contribute to this. However, as the non-breeder characteristics gained from this estimation method are used only as reference values for further investigations, the analysis itself is less affected by these assumptions.

Analyzing the population behavior throughout the parameter space shows that only in the scenario of strong fluctuations and low reproduction rates (05s) no parameterizations can be found for which $P_0(100) < 0.05$ holds. Thus, in the case of 05s the ratio var_ξ/r (cf. Equation 3.3) is too large to enable the populations’ survival, even though the population features a pool of non-breeders. This is in agreement with the theory of stochastic populations, which states that var_ξ/r is a determinant for the intrinsic mean time to extinction T_m of a population (Grimm and Wissel [2004], Wissel and Stöcker [1991]). In 05s the effect of environmental variability is obviously such strong that population viability cannot be conserved by the non-breeder pool.

In nearly all scenarios all parameterizations with the highest \bar{N} and $P_0(100) < 0.05$ (the highest $P_0(100)$ is found in 05s) show $\delta = 0.1$ and $\lambda = 0.75$ or $\lambda = 0.9$. The only exception is the 05w-scenario where $\lambda = 0.5$ also occurs. Hence, low non-breeder mortality and a strong sink functionality tend to enhance population survival and increase the size of the breeder stock.

Parameterizations yielding the highest \bar{N} and $P_0(100) < 0.05$ in scenarios with weak fluctuations contain a strongly varying non-breeder capacity κ . In strong

fluctuation scenarios κ varies between 1.5 and 2.0. Thus, in low fluctuation scenarios, the non-breeder capacity κ does not seem to be crucial. However, if environmental fluctuations are high, a high κ -value allowing high sizes of the non-breeder pool becomes advantageous.

The most characteristic differences are observable for the values of β and k (both parameters determine conversion into breeders). In the 05w-scenario β is high (0.75 and 0.9) and k low (0.1) in the parameterizations leading to highest \bar{N} and $P_0(100) < 0.05$. In the 05s-scenario it is more or less the other way around: β is low (0.1 and 0.25) and k tends to high values (0.5 to 0.9). In all other scenarios both β and k have high values of 0.75 or 0.9. Table 3.3 shows parameterizations for all scenarios for which \bar{N} is highest and $P_0(100) < 0.05$ holds.

All parameterizations with the highest \bar{N} -values (except for the 05s-scenario) lead to $P_0(100) < 0.05$. This is different when considering var_N . For the strong fluctuation scenarios, parameterizations which lead to minimum var_N differ considerably from those leading to high \bar{N} . This is most significant for the 25s and 30s scenarios where minimum var_N is achieved with $\lambda = 0.1$ and $\delta = 0.9$. Furthermore, these parameterizations lead to very low $P_0(100)$ and \bar{N} values. The same holds the other way around: parameterizations with high \bar{N} and $P_0(100) < 0.05$ yield a considerably higher variance than the lower bound. Table 3.3 shows this in detail.

These findings indicate that there is no simple relationship between var_N , \bar{N} and $P_0(100) < 0.05$, as assumed at the beginning of this section. This issue will be examined in more depth later on. For now the aim is to get reference parameterizations from which further analysis can start. These reference parameterizations are shown in the gray shaded lines in Table 3.3.

Sensitivity of parameters

To gain more insight into the role of the single parameters, sensitivity for every parameter and measure is computed using the following formula (Saltelli et al. [2000])

$$S(X_i) = \frac{Var(E(X_j|X_i))}{Var(Y)} \quad (3.12)$$

X_i denotes the input parameter (e.g. λ) for which sensitivity is to be calculated. For every *fixed* X_i all other parameters X_j are varied and the mean output (e.g. $P_0(100)$) is calculated. First, a mean output is assigned to each X_i , and then the variance of the mean output for all X_i is calculated. This variation is divided by the total variation of the output Y (e.g. $P_0(100)$). Thus a measure is gained, which indicates how much of the output variation can be explained by the variation of one input parameter.

Looking at the results of this sensitivity analysis, it can be seen that concerning $P_0(100)$, λ is the most sensitive parameter, followed by δ , β , k and κ in weak fluctuation scenarios (05w, 25w, 30w). In strong fluctuation scenarios (05s, 25s,

Table 3.3: Comparison of parameter values which define a populations with minimum variance in breeder dynamics (min. var_N), maximum mean size of breeders (max. \bar{N}) and probability of extinction within 100 time steps ($P_0(100)$). Gray shaded lines indicate reference parameters.

scenario/measure	λ	β	k	δ	κ	\bar{N}	var_N	$P_0(100)$
05w/max. \bar{N}	0.75	0.75	0.10	0.10	2.0	0.95	0.06	<0.05
05w/min. var_N	0.90	0.90	0.75	0.10	1.5	0.93	0.05	<0.05
05s/max. $P_0(100)$	0.75	0.25	0.90	0.10	2.0	0.61	0.28	0.16
05s/max. \bar{N}	0.90	0.90	0.50	0.10	2.0	0.69	0.31	0.40
05s/min. var_N	0.90	0.10	0.50	0.90	1.0	0.48	0.19	0.89
25w/max. \bar{N}	0.90	0.90	0.90	0.25	1.5	1.04	0.05	<0.05
25w/min. var_N	0.90	0.75	0.25	0.10	0.7	1.03	0.05	<0.05
25s/max. \bar{N}	0.90	0.90	0.90	0.10	1.5	1.04	0.32	<0.05
25s/min. var_N	0.10	0.10	0.25	0.90	1.5	0.49	0.30	0.85
30w/max. \bar{N}	0.90	0.90	0.90	0.50	2.0	1.06	0.07	<0.05
30w/min. var_N	0.90	0.90	0.25	0.10	0.7	1.03	0.06	<0.05
30s/max. \bar{N}	0.90	0.90	0.90	0.10	1.5	1.07	0.34	<0.05
30s/min. var_N	0.10	0.10	0.10	0.90	0.3	0.49	0.31	0.84

30s) δ and λ change place in the ranking, and the sensitivity of δ is about one order of magnitude higher than that of the following parameters. Table 3.4 shows the sensitivities of $P_0(100)$ of all parameters for every scenario.

Table 3.4: Sensitivities $P_0(100)$

	05w	05s	25w	25s	30w	30s
λ	-	0.0617	0.0638	0.0768	0.0567	0.0822
β	-	0.0423	0.0511	0.0283	0.0456	0.0181
k	-	0.0207	0.0063	0.0212	0.0053	0.0178
δ	-	0.72380	0.0511	0.8301	0.0517	0.8476
κ	-	0.0081	0.0000	0.0001	0.0001	0.0001

For the measures \bar{N} and var_N , λ is most sensitive. Its sensitivity is one order of magnitude higher than the others. This holds for all scenarios except 05s, for which δ is the most sensitive, as shown in Tables 3.5 and 3.6.

Interactions between parameters

To get an understanding of the interactions between parameters, $P_0(100)$, \bar{N} and var_N are plotted for varying values of the two most sensitive parameters (λ and δ), the two which directly determine the size of the non-breeder pool (δ and κ), and the two which determine the conversion from breeders into non-breeders

3.2. Stochastic Environmental Fluctuations

Table 3.5: Sensitivities \bar{N}

	05 _w	05 _s	25 _w	25 _s	30 _w	30 _s
λ	0.5168	0.2128	1.0996	1.2268	1.2478	1.2469
β	0.0630	0.2442	0.0028	0.0537	0.0051	0.0507
k	0.0611	0.0322	0.0001	0.0024	0.0001	0.0023
δ	0.3262	0.3038	0.0054	0.1215	0.0095	0.1096
κ	0.0072	0.0838	0.0000	0.0018	0.0000	0.0016

Table 3.6: Sensitivities var_N

	05 _w	05 _s	25 _w	25 _s	30 _w	30 _s
λ	0.9094	0.2460	0.9442	0.1364	0.9591	0.1393
β	0.0016	0.0624	0.0028	0.0416	0.0023	0.0075
k	0.0005	0.0153	0.0001	0.0008	0.0002	0.0004
δ	0.0067	0.5594	0.0055	0.0049	0.0042	0.0041
κ	0.0004	0.0914	0.0000	0.0017	0.0000	0.0007

(β and k). The remaining three parameters are set to their respective reference values (see Table 3.3).

As the analyzes above showed, the differences between 25_w and 30_w as well as between 25_s and 30_s are marginal. As taking the two scenarios with $r = 3.0$ into account does not provide additional insights, they are left out in the following presentation of results.

For weak fluctuations (05_w and 25_w), the probability of extinction $P_0(100)$ is not affected by varying two parameters and setting the rest to reference values (not shown). Figure 3.8 (upper row) shows that in the 05_s-scenario $P_0(100)$ increases monotonically with λ and decreases with δ . $P_0(100)$ also decreases with increasing β . This is only weakly influenced by the value of k . The value of κ , has very little influence on $P_0(100)$, in this scenario.

In the 25_s-scenario (Figure 3.8 lower row), there are strong interactions between λ and δ . For high λ and low δ , $P_0(100) < 0.05$ holds. If $\delta > 0.25$ then $P_0(100)$ is always < 0.05 . The same holds for $\lambda = 0.1$. If $k \leq 0.25$, then $P_0(100) < 0.05$ also cannot be reached for high values of β . Again, κ has no influence on $P_0(100)$.

In the 05_w scenario, mean size of the breeder stock \bar{N} is only weakly affected by the variation of λ and δ (see Figure 3.9 top left). In all other scenarios an increase in λ leads to an increased \bar{N} . In the two scenarios with strong fluctuations (05_s and 25_s, Figure 3.9 right), this effect is strongly modified by non-breeder mortality: The lower δ , the higher \bar{N} can be. In the 05_s scenario in particular the *strength* of this modification also depends strongly on λ . This means that for low λ values a low non-breeder mortality does not increase \bar{N} , but for high λ it

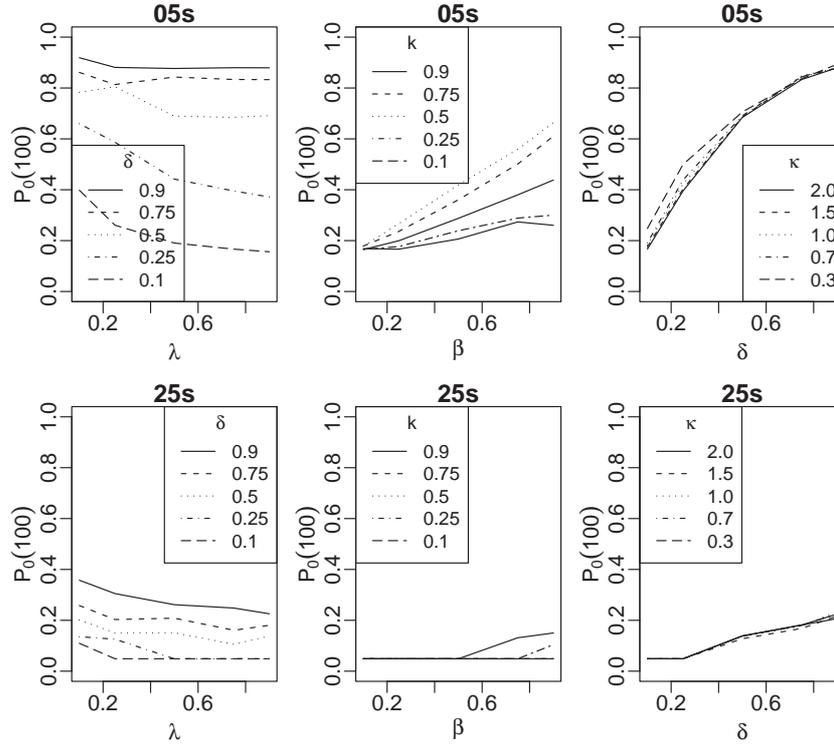


Figure 3.8: $P_0(100)$ vs. λ , β and δ for different values of δ , k and κ in scenarios with strong fluctuations (05s and 25s). All parameters, which are not varied are set to their respective reference values.

does.

Variations of β and k only affect in strong fluctuation scenarios (05s and 25s Figure 3.10 left). Depending on $k \leq 0.25$ there is a slight trade-off in β . If $k \leq 0.25$ holds, the highest \bar{N} -values occur for $\beta = 0.5$. If $k > 0.25$, \bar{N} increases with β . But in both scenarios the highest \bar{N} is reached for $\beta = 0.9$, whereas \bar{N} in the 25s scenario is considerably higher than in the 05s scenario.

In weak fluctuation scenarios (05w and 25w), altering the values δ and κ does not influence \bar{N} . In the two other scenarios it does (see Figure 3.10 right). There, it can be seen that increasing δ decreases \bar{N} . The strength of this effect is influenced by κ the capacity for non-breeders – the lower κ is, the weaker the effect.

Variance var_N is not changed by varying λ and δ in the 05w and the 25s scenario (Figure 3.11 top left and bottom right). In the other two scenarios, increasing λ decreases var_N (Figure 3.11 top right and bottom left). The strength of this is strongly influenced by δ in the 05s scenario. For $\delta = 0.1$ there is a slight trade-off in λ , in which case var_N is highest for $\lambda = 0.25$ and $\lambda = 0.5$.

For alterations in β and k , var_N is not influenced in the weak fluctuation sce-

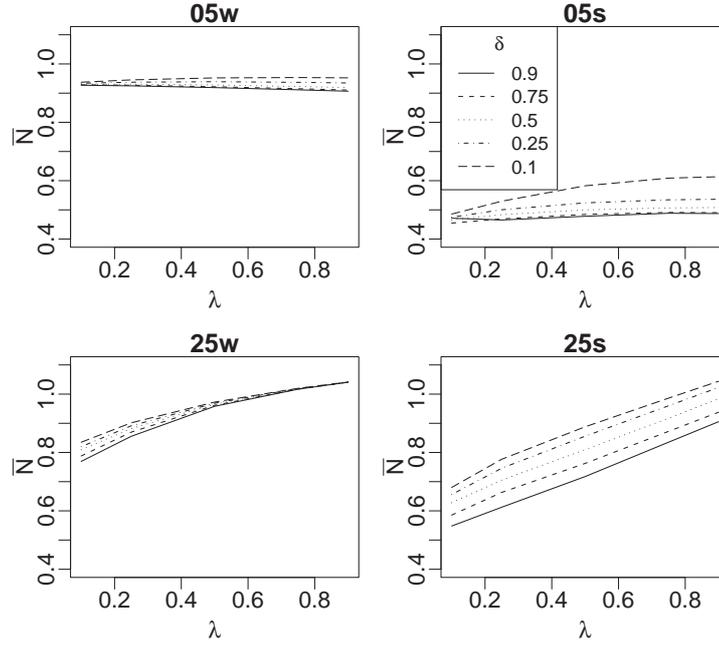


Figure 3.9: Mean size of breeder stock \bar{N} vs. λ for different values of δ in all scenarios. All parameters, which are not varied are set to their respective reference values.

narios 05 w and 25 w (Figure 3.12 left). For strong fluctuations there is a slight increase of var_N with increasing β and k .

When κ and δ are changed (Figure 3.12 right), there are again no changes in var_N under weak fluctuations. Under the 05 s fluctuation regime, var_N decreases with increasing non-breeder mortality. This is slightly amplified by increasing κ the capacity for non-breeders. In the 25 s -scenario the opposite effect is observable: Increasing δ increases var_N slightly. For high values of κ there is a slight trade-off in δ .

Discussion of parameter sensitivity

Depending on the measure ($P_0(100)$, \bar{N} , var_N), the roles and sensitivities of parameters differ. They depend also on the given situation, as determined by reproduction rate r and the environmental fluctuations ξ_t . Thus, the following discussion is ordered by scenarios. The analysis showed that results for scenarios with $r = 2.5$ and $r = 3.0$ do not differ broadly. Therefore, in the following $r = 3.0$ -scenarios are not considered, but statements about $r = 2.5$ also hold for $r = 3.0$.

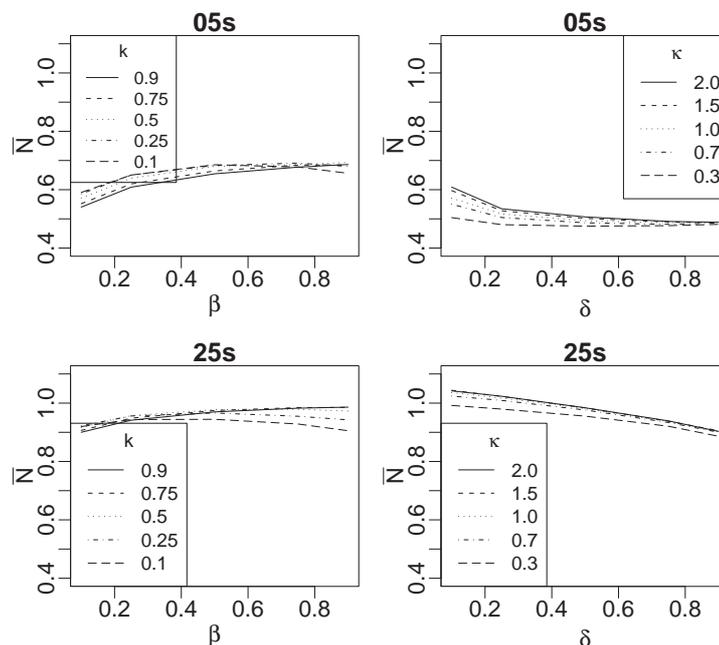


Figure 3.10: Mean size of breeder stock \bar{N} vs. β and δ for different values of k and κ in scenarios with strong fluctuations (05s and 25s). All parameters, which are not varied are set to their respective reference values.

Scenario 05_w. Reference parameters (Table 3.3) found for this scenario reflect a strong sink functionality ($\lambda = 0.75$) and a quickly and strongly reacting source functionality ($k = 0.1$, $\beta = 0.75$). The non-breeder pool itself is big and survives for a long time ($\kappa = 2.0$, $\delta = 0.1$).

Probability of extinction $P_0(100)$ is not sensitive to any changes in any parameter (Table 3.4). Thus any non-breeder characteristics allow for long-term survival. This is due to the weak environmental fluctuations and the low reproduction rate, for which over-compensation do not occur.

Nevertheless, \bar{N} and var_N are sensitive to the characteristics of the non-breeders (Table 3.5 and 3.6). For both, λ is the most decisive parameter and both are decreased by increasing λ . The reason for this is the under-compensatory behavior of the time-discrete logistic map with $r = 0.5$. As a result of this under-compensation, size of the breeder stock may stay above its capacity for several time steps and even may increase further in case of positive amplitudes of environmental fluctuations. This allows for relatively large sizes of the non-breeder pool. This effect is reduced by increasing λ because this reduces the amount of surplus breeders, and thus \bar{N} and var_N . Hence, a strong sink allows a lower variance var_N but also reduces size \bar{N} .

\bar{N} is relatively sensitive to changes in non-breeder mortality δ as well, because decreasing δ increases the number of available non-breeders, which in

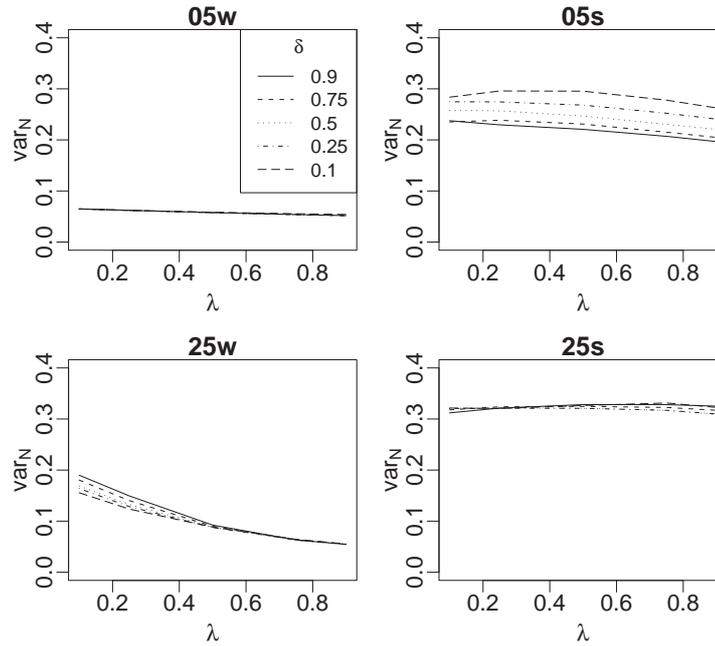


Figure 3.11: Variance of size of breeder stock var_N vs. λ for different values of δ in all scenarios. All parameters, which are not varied are set to their respective reference values.

turn increases the conversion from non-breeders into breeders and thus helps the breeder stock to recover faster after losses.

Interactions between parameters are low in this scenario (see Figures 3.9 and 3.11).

Scenario 05s. Here no parameterization can be found for which $P_0(100) < 0.05$ holds. The lowest probability of extinction after 100 time steps ($P_0(100) = 0.16$) can be found for the reference parameters. These parameters (see Table 3.3) characterize a population with a relatively strong sink functionality ($\lambda = 0.75$). The source functionality is sluggish ($k = 0.9$) and relatively weak ($\beta = 0.25$). The non-breeder pool itself is big ($\kappa = 2.0$) and long lasting ($\delta = 0.1$).

These characteristics can be explained by the strong fluctuations and low reproduction rate. The under-compensatory property of this population explains that λ is not as large as it possibly could be. As such, the storing effect of under-compensation is preserved to a certain degree. However, the fluctuation regime frequently causes negative effective reproduction rates. Hence the non-breeder pool is needed frequently. This means that in this scenario it is crucial that the non-breeder pool lasts as long as possible. This is reflected in the sluggish and weak source and the big non-breeder pool with low mortality.

As a result of the low reproduction rate, the breeders do not compensate losses

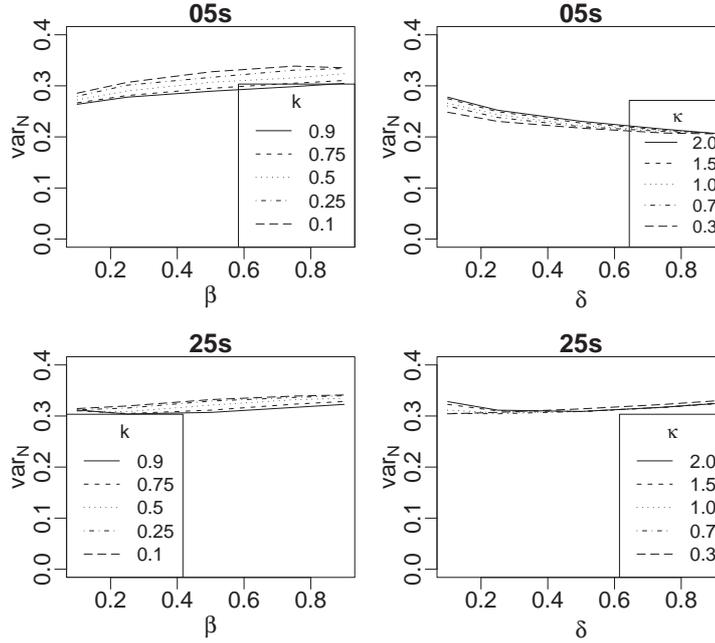


Figure 3.12: Variance of size of breeder stock var_N vs. β and δ for different values of k and κ in scenarios with strong fluctuations (05s and 25s). All parameters, which are not varied are set to their respective reference values.

quickly. Thus the regeneration mechanism – which could be procured by a high reproduction rate (see analysis of deterministic fluctuations 3.1) – is very weak in this scenario. Furthermore the breeder stock only exceeds its capacity (thus supplying the non-breeder pool) if environmental fluctuations have a sufficiently high positive amplitude. Because of these two points it is crucial that the non-breeder pool survives for as long as possible.

In general, $P_0(100)$ is mainly sensitive to non-breeder mortality δ : the lower δ the lower $P_0(100)$ can be (cf. Table 3.4 and Figure 3.8), which supports the reasoning about the reference parameters. Non-breeder mortality δ again is the most sensitive parameter for \bar{N} and var_N .

To summarize the findings for the two scenarios with $r = 05$, it can be stated that the population behavior becomes very sensitive to non-breeder characteristics, if environmental fluctuations become high. Under these conditions the population has to “save” non-breeders. This is possible in cases featuring a low response strength β and low mortality δ , as well as by high sluggishness k and high non-breeder capacity κ . On the other hand the non-breeder pool is supplied strongly but not as strong as it would be required to benefit from the storage effect of under-compensation.

Scenario 25_w. The reference parameterization characterizes a population with a very strong sink functionality ($\lambda = 0.9$). Source functionality is strong ($\beta = 0.9$) but sluggish ($k = 0.9$). The non-breeder pool itself is relatively big ($\kappa = 1.5$) and relatively long-lasting ($\delta = 0.25$). Sensitivity analysis showed (Table 3.4, 3.5 and 3.6) that for all measures ($P_0(100)$, \bar{N} and var_N), the only sensitive parameter is λ .

In this scenario, environmental fluctuations are weak, but fluctuations induced by the high reproduction rate are potentially high because of effects of over-compensation. As seen in the analysis of the deterministic fluctuation scenarios, the sink functionality reduces the effects of over-compensation. This in turn enables the population to benefit from two mechanisms: The non-breeder pool itself and the high reproduction rate. This is reflected by the high value of $\lambda = 0.9$ in the reference parameter set.

In contrast to the 05_s-scenario above, in 25_w, non-breeders do not have to be saved for as long as possible, because they are frequently supplied by breeders. To achieve high values of \bar{N} , the non-breeder pool has to be able to react strongly enough (high β , see Table 3.3) to heavy losses, which occur when over-compensation and negative amplitudes of environmental fluctuations occur at the same time.

Scenario 25_s. The reference parameters are quite similar to the 25_w-scenario, with a difference seen only in non-breeder mortality ($\delta = 0.1$). Hence the population is characterized by a strong sink functionality, a strong but sluggish source functionality and a large, long-lasting non-breeder pool. The most sensitive parameter for $P_0(100)$ is δ . For \bar{N} and var_N , sensitivity is, as above, highest for λ .

The lower value of $\delta = 0.1$ and the higher sensitivity of δ indicates that in this scenario the source functionality is more important than in the case of the 25_w-scenario. The heavy losses caused by over-compensation and negative amplitudes of environmental fluctuations are more likely to happen and thus occur more frequently. As these events can occur several times in short time intervals, there is a possibility that the non-breeder pool is not resupplied by the breeders. Therefore, it has to have few losses by mortality in order to make high values of $P_0(100)$ possible.

Non-breeder response strength β vs. response sluggishness k . In the analysis of the deterministic fluctuation regimes, the issue of non-breeder response to breeders' loss (i.e. conversion from non-breeders into breeders) has already been addressed (see Section 3.1). There, two different possibilities were identified, which under deterministic conditions equally reduce variations in size. First, non-breeders could respond to losses immediately (low k) but with low response strength β , or second, they could respond more sluggishly but with high response strength.

During the analysis of stochastic situations, which focused on the three measures $P_0(100)$, \bar{N} and var_N , these two possible non-breeder responses were found to be of minor relevance. In fact they arise in only an appropriated form in 25w and 25s. In both of these scenarios they lead to the lowest var_N -values, and it is only under weak fluctuations that low var_N and $P_0(100) < 0.05$ occur together. Hence, the simple classification of non-breeder responses from the deterministic situation can not be confirmed in stochastic ones.

Instead, distinct differences in response strength β for the 05s and 25s scenarios are found. While for 05s, saving non-breeders is crucial and, thus, low a response strength is advantageous. For 25s it is more important to compensate for heavy losses quickly and thus a high response strength is advantageous.

3.3 Interdependence of Breeders and Non-Breeders

After the influences of and sensitivities to parameter changes are investigated, the question arises if there are, regardless of the actual parameterization, conditions under which the non-breeder pool does increase population viability and reduce fluctuations. This section starts with two hypotheses. First, that for population viability non-breeders are only “needed” under certain conditions, and second that there is a minimum size of the non-breeder pool below which there is no increase in population viability or no reduction in breeders’ variance. If these hypotheses hold, consequences for regulation strategies immediately emerge. In cases where the non-breeder pool is not needed it probably could be more strongly reduced, but if on the other hand it is crucial for population viability it should be maintained. The next section begins with the first hypothesis.

The relevance of non-breeders for population viability

The differences between the scenarios shown here reflect the fact that the relative importance of the considered aspects of the non-breeder pool for the stabilization of a population depends on the given situation, i.e. on reproduction rate r and strength of environmental fluctuations ξ_t . If a non-breeder pool is said to be effective if $P_0(100) < 0.05$ holds, then in the scenarios investigated here, three different cases can be distinguished.

CASE I The population survives regardless of the characteristics of the non-breeder pool (05w), i.e. the population does not rely on the non-breeder pool;

CASE II The population does not survive regardless of the characteristics of the non-breeder pool (05s), i.e. the non-breeder pool cannot prevent the population from extinction;

CASE III The population survives depending on the characteristics of the non-

breeder pool (25w and 25s), i.e. the non-breeder pool can be a mechanism to foster population viability.

In the third case, the characterization of non-breeders which enables the population to survive depends on the given situation, which is determined by reproduction r and strength of environmental fluctuations var_{ξ} .

Now, the question arises regarding the conditions under which the survival of the population depends on non-breeder characteristics. In other words, is it possible to calculate borders or transitions between the three different cases enumerated above? To find these borders or transitions it must be considered, under which conditions fluctuations of the breeder stock exceed a critical variance and thus make the non-breeder pool necessary for population viability.

In a time-discrete logistic model without a non-breeder pool and without extrinsic stimulation, the population does not reach its environmental capacity at reproduction rates of $r > 2$ but fluctuates around it. If the reproduction rate exceeds $r = 3$, fluctuations lead to extinction. For the model with a non-breeder pool, however, the sink functionality of the non-breeder pool reduces over-compensation and thus extinction due to *intrinsic* fluctuations does not occur anymore (cf. Section 3.1). Thus, in the model presented in this study, the only source of extinction is *external* environmental fluctuations. To classify different stochastic fluctuation regimes, affecting the effective reproduction rate $r(1 - N_t/K)$ (cf. Equation 2.4), according to the risk of extinction $P_0(100)$, which they cause to the population, the phase space of breeder size is investigated.

As in the model, environmental fluctuations ξ_t are assumed to be normally distributed, they can potentially become very large or small. Thus, the range of amplitudes occurring in any given fluctuation regime will be limited by the 0.001-quantiles of the distribution of fluctuations. This is to say, only those amplitudes of ξ_t are considered which occur with a minimum probability $p_{occ} = 0.001$ in any time step. In the considered fluctuation regimes, amplitudes are normally distributed with $var_{\xi} = 0.05$ and $var_{\xi} = 0.4$. The corresponding quantiles are $\xi_t = q_{0.05}^{\pm} \approx \pm 0.69$ for $var_{\xi} = 0.05$ and $\xi_t = q_{0.4}^{\pm} \approx \pm 1.95$ for $var_{\xi} = 0.4$. These quantiles provide the extremes, with $p_{occ} = 0.001$.

Now, a population is considered with *only* a sink functionality of the non-breeder pool and *no* source functionality ($\beta = 0$). The sink functionality is determined by $\lambda = 0.75$. Using the 0.001-quantiles, it is possible to calculate a margin in the phase space which is not exceeded in any time step with a probability of $p_{ex} = 0.998$. This margin depends on $q_{0.05/0.4}^{\pm}$, r and λ . Figure 3.13 shows these margins for the above examined fluctuation scenarios (05w, 05s, 25w, and 25s, cf. Table 3.2). The upper solid curves always mark the trajectory for positive amplitudes of $\xi_t = q_{0.05/0.4}^+$, while the lower solid curves constitute the trajectory for negative amplitudes of $\xi_t = q_{0.05/0.4}^-$.

In the following the positions of two points are considered: the intersection L

of the lower curve with the N_t -axis and the maximum H of the upper curve, projected on the N_t -axis (cf. Figure 3.14). The maximum H of the corresponding upper curve denotes the maximum size of the breeder stock, which is not exceeded in 99.9% of the time steps. (Note: Because of the structure of the growth function, there is always a maximum.) The lower curve as well is not undershoot by the size of the breeder stock in 99.9% of all time steps. The size of the breeder stock N_{t+1} can be considered as zero (and the population as extinct) in the next time step, if the curves fall below zero.

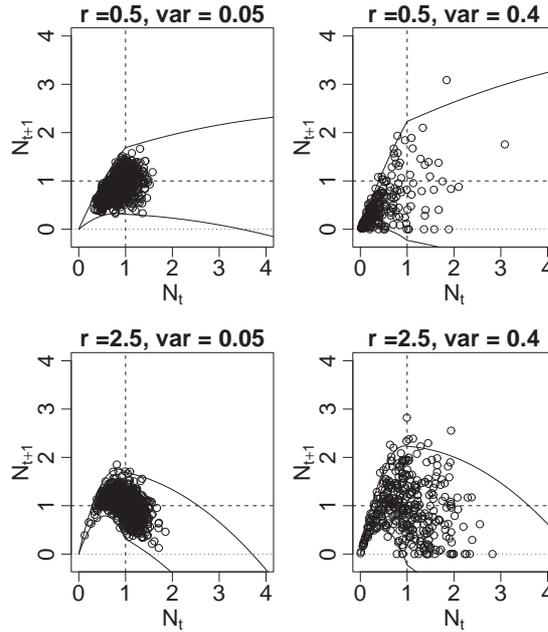


Figure 3.13: Curves in the N_t - N_{t+1} -phase space defined by 0.001-quantiles. Also depicted are points in the N_t - N_{t+1} -phase space. For the two strong-fluctuation scenarios, points are generated in several runs, because under these conditions the population becomes extinct very quickly. This explains the fact that there is more than one point on the N_t -axis. Strength of sink functionality is set to $\lambda = 0.75$. The dashed lines mark the environmental capacity K for breeders.

Due to the sink functionality of the non-breeder pool, the population will not become extinct in the absence of environmental fluctuations. This was already demonstrated in Section 3.1 and is now confirmed by Figure 3.14. There, for any curve C in the N_t - N_{t+1} -plane, the maximum N_{t+1} -value of C is lower than the N_t -value of the point $(N_t, 0)$ of C . Hence, extinction cannot occur by *intrinsic* fluctuations. Thus, in the given four scenarios, the population is only threatened by the strength of environmental fluctuations ξ_t . As every fluctuation can be seen as a jump from one curve C to another C^* , the potential difference between two subsequent curves C and C^* increases with the strength of environmental fluctuations and thus the risk of extinction as well. This is reflected by the distance

3.3. Interdependence of Breeders and Non-Breeders

between L and H . The relation between L and H gives a measure for how frequently the source functionality of the non-breeder pool is needed. Effectively, it reflects the worst case of two subsequent fluctuations within the given probability margin. The probability of this particular, or an even more extreme, event is very low.

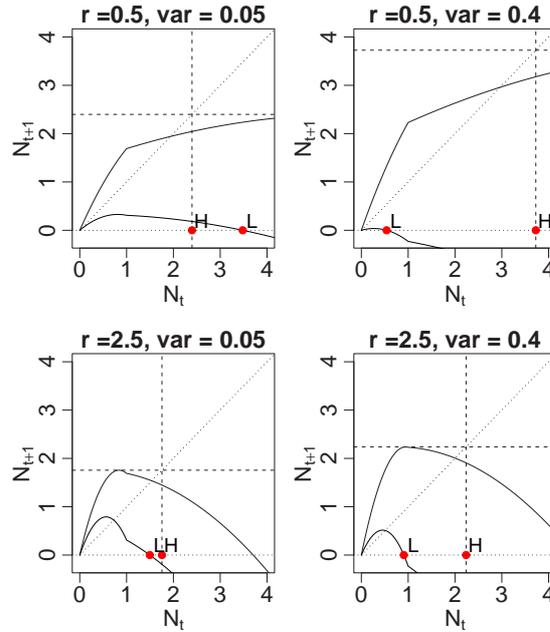


Figure 3.14: Curves in the N_t - N_{t+1} -phase space defined by 0.001-quantiles. Point L marks the null of the curve defined by the 0.001-quantile and thus the N_t -value for $\xi_t = q_{0.05/0.4}^-$ above which the population becomes extinct. H denotes the maximum N_{t+1} -value (dashed lines) which can be reached for $\xi_t = q_{0.05/0.4}^+$. Strength of sink functionality is set to $\lambda = 0.75$.

If $H < L$ holds, it is very unlikely that L is exceeded in the course of population dynamics. Hence, the population will not become extinct (regardless of the source functionality provided by the non-breeder pool). The higher the difference between these two values, the lower the probability of extinction. Such scenarios ($H < L$) belong to CASE I.

In the opposite case ($L < H$), there is a certain range of N_t -values that result in $N_{t+1} > L$, i.e. could – given ξ_t is sufficiently low – cause extinction in the case of a missing non-breeder pool. Thus, the dependence on the source functionality provided by the non-breeder pool increases. The larger the difference between L and H with $L < H$, the more likely are sequences of fluctuations which lead to $N_t = 0$, which in turn increases the dependence on the non-breeder pool. Such scenarios with $L < H$ belong to CASE II or CASE III depending on the distance between L and H .

Figure 3.14 shows that in the 05w-scenario ($r = 0.5$, $var = 0.05$), a sequence

of fluctuations which sets N_t to or below zero is extremely unlikely. Here, the non-breeder pool is not needed for preserving viability. For the 25w-scenario ($r = 2.5$, $var = 0.05$) it is also unlikely. For the two remaining scenarios, lethal sequences of fluctuations are likely. In these cases, the non-breeder pool becomes a key factor for population survival. This especially holds for the 05s-scenario ($r = 0.5$, $var = 0.4$). As already seen in the above sections, in the latter two the characteristics of the non-breeder pool are decisive for population survival. Figure 3.14 also underlines that the need for the non-breeder pool for population viability depends on the strength of environmental fluctuations ξ_t and the intrinsic reproduction rate r (see Equation 3.3) as well as on the strength of the sink functionality λ .

The presented plot provides insight into the *need* for the non-breeder pool for preserving population viability. Whether the non-breeder pool is *actually able* to meet the demand, requires additional analyzes.

Role of non-breeder pool size for population viability

Until now, the model has been analyzed in terms of the influence of different parameters and their interactions. The focus was on processes and the models' sensitivity to them. A still open question concerns the importance of the size of the non-breeder pool. In practice and especially in the context of regulation, which will be dealt with in the subsequent chapter, it might be of interest if the size of the non-breeder pool is correlated with the population viability. This would have direct implications for the design of regulation strategies, which aim to keep the population viable. Therefore, now the interdependence of breeder and non-breeder size with population viability is investigated.

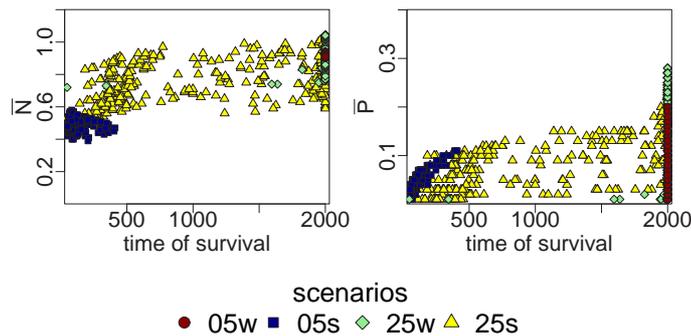


Figure 3.15: Relationship between risk of extinction $P_0(100)$ and the mean size of breeders \bar{N} resp. non-breeders \bar{P} . Plotted are all parameterizations as given in Equations 3.9 to 3.11.

In Figure 3.15 and also Table 3.7, the mean time to extinction T_m (Grimm and Wissel [2004]) is used as an alternative, equivalent measure for population viability. Figure 3.15 shows the relationship between mean time to extinction T_m

3.3. Interdependence of Breeders and Non-Breeders

and the mean size of the breeder stock \bar{N} , and the non-breeder pool \bar{P} over all parameterizations of the model. Table 3.7 shows the correlations for the different scenarios.

Table 3.7: Correlations between mean time to extinction T_m and the mean size of breeders \bar{N} , and non-breeders \bar{P} over all parameterizations of the model as given in Equations 3.9 to 3.11.

	05w	05s	25w	25s
\bar{N}	-0.05	0.03	0.22	0.50
\bar{P}	0.06	0.86	0.11	0.72

There it can be seen that for the scenarios of weak environmental fluctuations ξ (05w and 25w), only low correlations between mean time to extinction T_m and the mean size of the non-breeder pool \bar{P} exist. The correlations are considerably higher for the two scenarios with strong environmental fluctuations ξ . Whereas the correlations between T_m and \bar{P} increase for increased environmental fluctuations ξ , the correlations between T_m and \bar{N} are higher for the scenarios with high reproduction rate r . This indicates that the importance of the non-breeder pool P_t also depends on the *source of fluctuations*. This corresponds to the findings of the previous section, where it was shown that the non-breeder pool is more important in face of strong environmental fluctuations ξ . This also corresponds to the finding that in CASE I population viability is independent of the non-breeder pool.

Especially in the 25s-scenario, the points marking different parameterizations are rather scattered (Figure 3.15). Hence, it is not only the mean size of the non-breeder pool \bar{P} and breeder stock \bar{N} , which is crucial for T_m , and thus population viability, but also other processes which are observed in the preceding sections.

The main conclusions drawn from Figure 3.15 and Table 3.7 point towards the answer to the hypothesis concerning the non-breeder size and population viability: The size of the non-breeder part P_t has to be big enough to meet the demand of breeders for population survival. This is most important in scenarios with heavy environmental fluctuations, because there the source functionality of the non-breeder pool is needed extensively (cf. Figure 3.14). Thus, in general the pure existence of a non-breeder pool is not sufficient, but if the non-breeder pool is needed, it also has to have a certain size to enhance population viability.

The preceding analyzes showed that the non-breeder pool contributes only to population viability and is “only needed” in an intermediate range of environmental fluctuations (CASE III). This range depends on the relation between strength of environmental fluctuations and reproduction rate (see Equation 3.3). Here it has been shown that if the non-breeder pool is needed, its mean size influences population survival positively. This gains more importance, the stronger environmental fluctuations in relation to reproduction rate are.

3.4 Discussion and Hypotheses for Management

The aim of this chapter was to understand the primary effects a non-breeder pool can have on population dynamics. The simple structure of the population model (the two groups – breeders and non-breeders, are the only modeled structural property of the population) allows the explicit assessment and analysis of the processes requiring the presence of non-breeders. The analyzes, done in the last sections, provide a basis for the understanding of the more complex situation when regulation strategies are applied.

The starting hypothesis for this chapter was that the pool of non-breeders' influences the stability properties of the population in terms of \bar{N} , var_N and $P_0(100)$ such that the mean size of the breeder stock \bar{N} increases, variance var_N in it decreases as well as population viability $P_0(100)$ increases. This hypothesis holds true for a certain range of cases. The results indicate that the following three cases can be distinguished.

CASE I Population viability is independent from non-breeder characteristics, because environmental fluctuations are weak enough that the non-breeder pool is not “needed” to preserve population viability. Nevertheless, non-breeders can have an effect on mean breeder stock size and the stock-size variance. This first case is found for low reproduction rates and low environmental fluctuations.

CASE II Population viability is highly dependent on non-breeder characteristics, because environmental fluctuations are very strong. Here the population survives longest when the non-breeder pool has characteristics which enable the population to save as many non-breeders as possible. Nevertheless, the non-breeder pool is not able to preserve “enough viability” as variability is too strong. This is observable for low reproduction rates and high environmental fluctuations. However, in this case the non-breeder pool does not “help” to meet the viability criterion of $P_0(100) < 0.05$.

CASE III The non-breeder pool becomes a key factor for population viability. It can, depending on its characteristics, enable the population to survive with $P_0(100) < 0.05$. Depending on the fluctuation strength, different aspects of the non-breeder pool are relevant: For weak environmental fluctuations mainly the sink functionality is decisive to reduce over-compensatory effects. For strong environmental fluctuations the source functionality is additionally important to enable the population to survive sequences of highly negative effective reproduction rates.

These three CASES highlight the relevance of non-breeder characteristics for population viability: Preserving viability requires a certain accordance between non-breeder pool and environmental conditions. To a certain extent the size of

3.4. Discussion and Hypotheses for Management

the non-breeder pool can be seen as a link between non-breeder characteristics and population viability. This holds especially true for strong environmental fluctuations and low reproduction rates. In these cases non-breeder characteristics have to enable a large non-breeder pool to enhance population viability.

This role of the sink functionality is also pointed out by more theoretical studies which emphasize the effect of a source-sink structure on population dynamics. Howe et al. [1991] investigated the contribution of sinks in a stochastic meta-population model to the stability and size of the whole population. They found that sinks may delay extinction of the meta-population or even prevent it. This ability depends on the quality of sink patches and the possibility for individuals to disperse to a certain degree from the sink to the source. Furthermore, sinks allow a higher overall meta-population size. These results are analogous to those found here in the analysis of the role of non-breeders, which also feature a sink functionality. In contrast to the model assumptions in this study, sink populations are able to reproduce. But as shown above, the important feature is the “storage effect” and less the ability of sink populations to reproduce.

Gosselin [1996] designed a simple stochastic source-sink model to examine the influence of different dispersal strategies on the probability of extinction. He found that an increase of dispersal from source to sink increases the overall stability of the system. This corresponds to an increased parameter λ (strength of sink functionality) in the model analyzed in this study. In the model of Gosselin [1996], the stabilization of population dynamics is caused rather by reducing fluctuations in the size of the source than by recolonization of the source through the sink. This also corresponds to the findings of the preceding sections. The source functionality of the non-breeder pool reduces overshooting and overcompensation in the breeder stock. But, in the case of strong environmental fluctuations, the source functionality of the non-breeder pool gains importance for population viability.

The results also fit with the buffer effect (Brown [1969]) for birds mentioned in the introduction, which acts to smooth the dynamics of populations in better sites (Soutullo et al. [2006], Gunnarsson et al. [2005], Jackson et al. [2004], Howlett [2001] and Gill et al. [2001]). According to the results presented above, the buffer effect can be explained by the two functionalities of the non-breeder pool. Populations in better sites benefit in two ways from the emigration of individuals into poorer sites. First, emigration reduces intraspecific concurrence (sink functionality of the poorer sites) and second, in case of individual loss in better sites, immigration from poorer sites compensates for these losses (source functionality of poorer sites).

Penteriani et al. [2006] concluded that for a population of the Spanish imperial eagle (*Aquila adalberti*), the number of floaters is a function of breeders' fecundity, the impact of environmental fluctuations on breeders is lower if it only affects one part of the population, and that increasing floater mortality negatively affects breeders. The results presented here fit these conclusions well: The higher

the reproduction of breeders in the model is, the stronger the non-breeder pool is supplied. Furthermore, in case of breeders' losses (e.g. caused by environmental stochasticity) conversion of non-breeders into breeders can compensate and thus reduce variance in the breeding part. This mechanism only works as long as there are enough non-breeders, which might not be the case if non-breeder mortality is high.

Penteriani et al. [2006] analyzed an individual-based model of a population of the Spanish imperial eagle and found among other results that a very high floater mortality leads to a positive density-fecundity relationship for the breeders. They argue, that a lack of floaters results in not filling all vacancies in the breeding part of the population. In the model presented here, the breeder stock is assumed to follow logistic growth dynamics. This leads to the same behavior as in the individual based model by Penteriani et al. [2006]. If conversion from non-breeders into breeders is too weak to increase the size of the breeder stock above half of its capacity K , a positive relationship between density and offspring number can also be observed. Thus, the model presented here may also provide a tool to further analyze the relationship between non-breeder and breeder dynamics as observed in the population of the Spanish imperial eagle in a very fundamental way. The findings of this chapter also agree with the results for floater populations found in the literature. For example, for great skuas (Klomp and Furness [1992]) or farmland birds (Sarah et al. [2004]) a smoothing effect of non-breeders on population dynamics was found.

In this chapter a tool was developed for the estimation of the relevance of non-breeders for maintaining population viability. This enables a fast estimation to which of the three CASES a given situation belongs. This might be helpful in the context of management to determine whether the non-breeder pool has to be preserved or not.

From the results of the analyzes of the primary effects of the non-breeder pool on population dynamics some first hypotheses for management can be derived. It turns out that especially under strong environmental fluctuations, non-breeder mortality δ , which influences the size of the non-breeder pool, is of crucial importance. Therefore under strong environmental fluctuations, increasing non-breeder mortality in order to reduce population size may not be an appropriate measure, at least as long as population size is only to be reduced and not set to zero. For scenarios with weak fluctuations, increasing non-breeder mortality may be possible up to a certain degree without decreasing viability.

Another possible strategy is to reduce reproduction rate r . Under strong environmental fluctuations this may be "dangerous", because the population then loses its ability to recover quickly via high reproduction and can only resort to compensation by the non-breeders. Thus, a shift from a 25s-like to a 05s-like scenario may happen, which in turn can lead to an increase of $P_0(100)$.

Under low environmental fluctuations the same strategy (i.e. reducing r) may be appropriate, because over-compensations are reduced. The population may

3.4. Discussion and Hypotheses for Management

thus be carried over from a $25w$ -like to a $05w$ -like situation, which means that non-breeder characteristics become less important for population viability. However, the non-breeder pool affects the mean size of the breeder stock and the variance in it and thus, it can be expected that the ability of the population to resist regulation attempts is also affected. Thus, for the performance of regulation strategies in terms of effort, the non-breeder characteristics can still play an important role. But in any case, in the face of changing fluctuation regimes (and thus a certain uncertainty about environmental conditions) reducing reproduction can be dangerous and therefore, may not be the best option.

A reduction in the size of the breeder stock could also represent a possibility. This would reduce the supply of the non-breeder pool. And again for weak environmental fluctuations, where λ is not sensitive, this could be an applicable measure. However, for strong fluctuations it might be dangerous to reduce the non-breeder supply, because this reduces the non-breeder size itself and thus the source functionality of the non-breeder pool.

Non-Breeder Pool and Regulation

After dealing with basic population dynamics and interactions and processes in the preceding chapter, the aim of this chapter is to assess the performance of various regulation strategies in terms of reaching the regulation target while maintaining population viability and adhering to the budget (cf. Section 2.4). In order to meet this goal, the interplay between regulation strategy and population dynamics and its effect on the criteria of performance must be understood. Of particular interest in this context is the role of non-breeders. As such, the hypotheses derived above will lead the analysis.

The questions to be answered in this chapter aim towards a fundamental understanding of the role of the non-breeder pool and its characteristics for the performance of regulation strategies. Thereby, this chapter focuses on situations belonging to CASE III, where the non-breeder pool is a key factor for population viability (cf. Section 3.4). According to this, the starting hypotheses for this chapter are that

1. under conditions corresponding to CASE III, the performance of regulation strategies becomes sensitive to the preservation of the non-breeder pool.
2. the non-breeder pool plays a crucial role when strong catastrophic events are additionally likely to occur.

By including regulation strategies in the analysis, the system complexity increases, such that it is not possible to perform a comprehensive analysis over the whole parameter space. For this reason, the following analysis focuses on two particular reference scenarios, which are then used as a starting point to the exploration of limited parameter variation. The two reference scenarios and the variations are chosen in such a way that they qualitatively cover the range of population behavior completely.

4.1 Reference Scenarios

To cover the hypotheses, in Section 4.2 a reference scenario is chosen where the population has a low intrinsic reproduction rate r . Environmental fluctuations ξ_t are also low. To create a scenario corresponding to CASE III, additionally a single catastrophic event is introduced. This setting is chosen because by keeping the influence of two sources of fluctuations – intrinsic population dynamics (determined by r) and environmental fluctuations ξ_t – low it is possible to explicitly assess the effect of the catastrophe and the role of regulation. As regulation can also be a source of variation in population dynamics, this approach allows a clear analysis. For the same reason, first only regulation strategies are considered, which reduce both breeders and non-breeders directly. This would correspond to culling with no differentiation between breeders and non-breeders, which can be considered as the most ad hoc and straightforward approach to reduce population size.

In the second section (4.3) of this chapter, while keeping mainly the same reference population, the previously excluded sources of fluctuations in population size are reintroduced: reproduction rate r and environmental fluctuations ξ_t are set to higher values (Table 4.1). As the focus lies on the performance of regulation strategies in the face of strong fluctuations, catastrophes are not considered in this analysis. In this section a broad spectrum of possible regulation strategies is considered.

In the following, unless otherwise stated, the reference population will be characterized by the parameters shown in Table 4.1. Ecologically, the reference parameters characterize a population which features a potentially relatively large non-breeder pool ($\kappa = 2 = 2K$) with low mortality ($\delta = 0.1$). The sink functionality is considerably strong ($\lambda = 0.75$). The non-breeder response to loss of breeders is sluggish ($k = 0.9$) and strong ($\beta = 0.9$). The intrinsic reproduction rate r is varied ($r = 0.5$ in Section 4.2 and $r = 2.5$ in Section 4.3)) as well as the strength of environmental fluctuation ($\sigma_\xi^2 = 0.1$ in Section 4.2 and $\sigma_\xi^2 = 0.3$ in Section 4.3).

4.2 Non-Breeders and Catastrophic Events

This section focuses on the effect of regulation on the non-breeder pool and its consequences for population viability in the face of singular catastrophic events. In a first step, the pool of non-breeders is assessed in terms of its importance for the stability properties of the population persistence and resilience (Hansson and Helgesson [2003]), whereas the term *resilience* is used following the definition of the *Resilience Alliance* as “the capacity of the population to tolerate catastrophes without going extinct” (Carpenter et al. [2001]). The analysis involves comparing two scenarios: populations with and without non-breeders. Then, for

Table 4.1: Reference parameter values used unless otherwise stated.

parameter	default value	meaning
r	0.5 / 2.0	reproduction rate (sec. 4.2 / 4.3)
K	1	environmental capacity
λ	0.75	flux rate into non-breeder pool
β	0.9	strength of flux into non-breeder pool
k	0.9	sluggishness of flux into non-breeder pool
δ	0.1	death rate of non-breeders
κ	2.0	non-breeder capacity
σ_{ξ}^2	0.1 / 0.3	variance of env. fluctuations (sec. 4.2 / 4.3)

populations featuring non-breeders, the interplay between the two strategy parameters (rate ι , threshold θ) and two target parameters (target population size M , deviance from the target d^2) is investigated.

As a next step, an analysis is performed of how the setting of target population size M , maximum allowed deviance from the target ε_d , and available budget ε_b influences affordability of regulation targets. For this purpose, different settings are considered and assessed in terms of the existence of a certain strategy, which is effective and adheres to the budget. This analysis is performed for two types of non-breeder response to the loss of breeders. The varied parameter is k (sluggishness of non-breeder response to breeders' loss).

Stability properties

In Chapter 3 the two functional effects of the non-breeders, which affect the stability properties of the population under discussion (variance, persistence, and resilience) have already been discussed: Non-breeders can serve as a sink for surplus breeders. This reduces upward peaks in N_t , resulting in reduced overcompensation and, therefore, in milder downward peaks in N_{t+1} . Thus, the sink functionality reduces the extent of variation in both directions, hence the variance in the dynamics of N_t . On the other hand, non-breeders can serve as a source for breeders and reduce downward peaks in N_t , which is supposed to foster population persistence. Thus, non-breeders can support population viability, provided their pool is large enough.

Figure 4.1 illustrates this implication of the source functionality. It shows the dynamics of a population which is exposed to a strong pulse (N_t is set to $0.02N_t$) in the 80th time step. Figures 4.1a and 4.1b also indicate that, in the given example, the existence of non-breeders reduces the probability of extinction $P_0(100)$ of the population by two orders of magnitude. Without non-breeders ($\kappa = 0$ Figure 4.1b), the pulse is found to cause extinction of the entire population because losses may not be compensated sufficiently. With non-breeders present (Figure

4.2. Non-Breeders and Catastrophic Events

4.1a), however, the population survives with a high probability as non-breeders provide a supply for breeders. This is comparable to the rescue effect known from metapopulation dynamics (e.g. Brown and Kodricbrown [1977]) and gives rise to the hypothesis that source functionality of the non-breeder pool protects the breeders from extinction in the case of extreme catastrophic events. This has the implication that removing this non-breeder pool strongly reduces both the persistence and resilience of the population. In the following, this is examined.

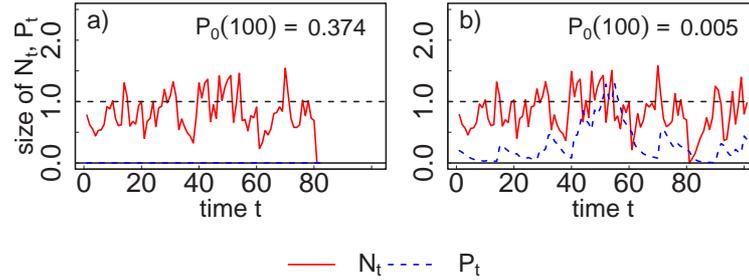


Figure 4.1: Number of breeders N_t and non-breeders P_t vs. time t . At $t^* = 80$ a pulse sets the breeder size N_{t^*+1} to $0.02N_{t^*}$. $P_0(100)$ is the probability of extinction within the shown 100 time steps. **a)** shows the population without non-breeders ($\kappa = 0$) and **b)** the population with non-breeders.

For now, only culling strategies are considered, which affect both breeder size N_t and non-breeder size P_t . Figure 4.2a shows the same population as in Figure 4.1a, but with the regulation strategy $S_1 = (0.3, 1.2)$ applied. In comparison with Figure 4.1 it can be seen that even though S_1 affects both parts of the population at the same time with the same rate, non-breeders are more strongly reduced than breeders. Nevertheless, the number of non-breeders remains large enough to provide a supply to the breeders that is sufficient to enable the population to survive the pulse with a high probability. But as can be seen in Figure 4.2b, even only a slightly stronger strategy $S_2 = (0.4, 1.0)$ leads to the removal of the non-breeder pool and to a high risk of extinction of the population after the pulse. This is also reflected by the corresponding probabilities of extinction $P_0(100)$ that differ by one order of magnitude.

These findings provide insight into the effects of regulation on the two functionalities of the non-breeder pool highlighted above. On the one hand, regulation decreases upward fluctuations in population dynamics, which is comparable to the effect of the sink functionality of the pool of non-breeders. On the other hand, however, regulation reduces (S_1 , Figure 4.2a) or even removes (S_2 , Figure 4.2b) the source functionality of the non-breeder pool. Both scenarios are caused by the reduction of N_t , which in turn reduces surplus breeders and thus the supply of non-breeders. Therefore, non-breeders are affected in two ways: they get less supply from breeders and are themselves subject to regulation.

All of these results show that regulation leads to a trade-off: It reduces mean

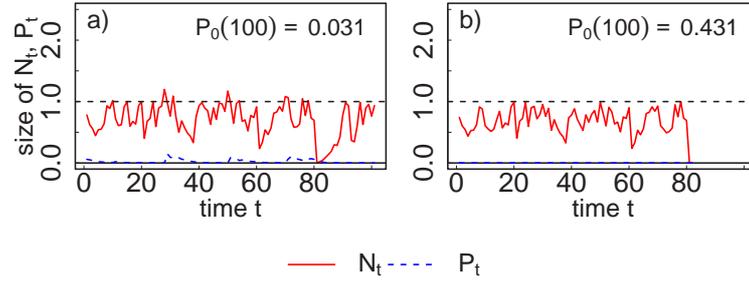


Figure 4.2: Number of breeders N_t and non-breeders P_t vs. time t . At $t^* = 80$ a pulse sets the breeder size N_{t^*+1} to $0.02N_{t^*}$. $P_0(100)$ is the probability of extinction within the shown 100 time steps. **a)** shows the population as in Figure 4.1b) with regulation strategy S_1 applied; **b)** shows the population under a stronger regulation strategy S_2 . S_1 and S_2 affect both breeders (N_t) and non-breeders (P_t) equally.

population size and upward fluctuations in population size, but at the same time it may degrade the non-breeder pool, which in case of extreme catastrophic events can affect stability properties. Eventually, this can affect the viability criterion $P_0(100)$ by which performance of regulation strategy is assessed.

Figures 4.1 and 4.2 demonstrate that non-breeders can influence the resilience and thus the viability of populations, which can be negatively affected by regulation. Because of this and the results from Section 3.3, where it was shown that non-breeder size and population viability are positively correlated, the question emerges if the same holds in the given scenario (Table 4.1). In other words: Do regulation strategies, under which the population is viable, allow for a minimum size of the non-breeder pool? Figure 4.3 provides an answer. It shows the relationship between probability of extinction $P_0(100)$ and the mean size of the non-breeder pool \bar{P}_t (Figure 4.3a), and the mean size of the breeder stock \bar{N}_t (Figure 4.3b) for a range of regulation strategies with threshold $\theta \in 0.1, 0.2, \dots, 1.2$ and rate $\iota \in 0.1, 0.2, \dots, 0.9$, respectively. The two figures show that $P_0(100)$ decreases with \bar{P}_t and \bar{N}_t , but they also indicate that probabilities of extinction $P_0(100)$ below 5% can only be assured if the mean sizes of both non-breeder pool (\bar{P}_t , Figure 4.3a) and breeder stock (\bar{N}_t , Figure 4.3b) exceed certain critical values. This means that population viability requires certain minimum sizes in both population parts. This condition reflects the fact that population viability requires a sufficiently strong source functionality in the non-breeder pool and hence a minimum size, which can only be achieved if non-breeders are sufficiently supplied by breeders.

Figure 4.3c shows the reference case of the same population without non-breeders. It can be seen that, without non-breeders, the viability criterion $P_0(100) < 0.05$ cannot be reached by any regulation strategy. Therefore, it can be concluded that in the given scenario (Table 4.1), population viability is crucially dependent on the existence of a non-breeder pool, which must have a certain

size. Thus, only strategies which maintain the non-breeder pool at a certain sufficiently large size allow for $P_0(100) < 0.05$.

In Section 3.3 it was shown that non-breeders can support population viability, provided their pool is large enough. Figures 4.1 to 4.3 confirm that this property is of particular importance in the face of strong catastrophic events. The existence of a sufficiently large non-breeder pool can reduce the risk of extinction by two orders of magnitude. The importance of the size of the non-breeder pool for resilience and viability directly leads to the question of the relation between the non-breeder pool and the performance of regulation strategies.

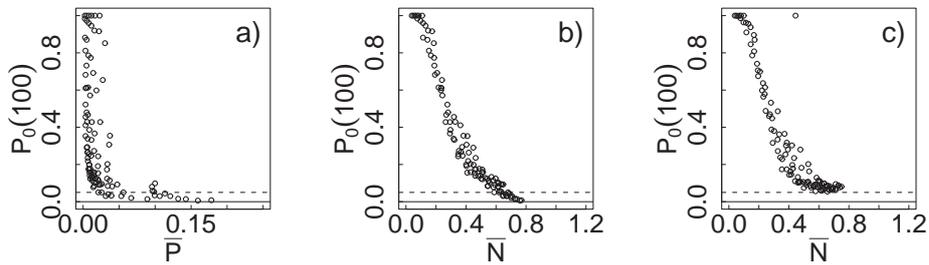


Figure 4.3: Probability of extinction $P_0(100)$ vs. mean non-breeder pool size resp. mean size of the breeder stock. **a) & b)** Non-breeders and breeders of the same population; **c)** reference population without non-breeders ($\kappa = 0$). Circles mark sizes under one of the regulation strategies $S = (\theta, \iota)$ with $\theta \in 0.1, 0.2, \dots, 1.2$ and $\iota \in 0.1, 0.2, \dots, 0.9$. Dashed lines: $P_0(100) = 0.05$.

Performance of regulation

Figures 4.3a to 4.3c already indicated that not all regulation strategies maintain population viability. Now it is investigated how strategies which keep the population viable are characterized and how strategies match with the target parameters *maximum deviance* ε_d from desired population size and *available budget* ε_b . For this purpose the measures of regulation strategy performance (deviance from desired population size d^2 , population viability $P_0(100) < \varepsilon_p$, and adherence to the budget $e < \varepsilon_b$) are calculated for all strategies $S = (\theta, \iota)$ with threshold $\theta \in 0.1, 0.2, \dots, 1.2$ and rate $\iota \in 0.1, 0.2, \dots, 0.9$. Figure 4.4 illustrates how these measures of performance are influenced by different targets. Here, scenarios with and without catastrophes for two different desired population sizes ($M = 1.2$ and $M = 0.4$) are shown.

In the cases without catastrophes (Figures 4.4a and 4.4c), every considered regulation strategy (θ, ι) keeps the population viable (each strategy is represented by \blacklozenge). Strategy performance in these cases is only dependent on deviance from desired population size $d^2 < \varepsilon_d$ and adherence to the budget $e < \varepsilon_b$.

This picture changes when a catastrophe is added to the scenario (Figure 4.4b) and 4.4d)) – then, only strategies with low rate ι and high threshold θ fulfill the viability condition $P_0(100) < \varepsilon_p$. These are strategies, which reduce the size of the breeder stock by only a small extent and, in doing so, maintain the non-breeder pool (cf. Figure 4.1c). All other regulation strategies destroy the non-breeder pool to the detriment of population viability.

The range of strategies with $e < \varepsilon_b$ (marked by \circ) is characterized by medium or high rates ι . These strategies reduce the number of breeders moderately or strongly and lead to lower fluctuations (cf. Figure 4.1d). In the latter case, this destroys the non-breeder pool and the catastrophe is not survived by the population. Because of these contrary effects of regulation strategies, only a small intersection is observable between strategies maintaining viability and strategies not exceeding the budget.

Figures 4.1a) and 4.1c) also show that neither the range of strategies with $P_0(100) < 0.05$ nor the range of strategies with $e \leq 0.02$ change with altered regulation target M . This invariance of $P_0(100)$ and e against regulation targets can be explained by the fact that $P_0(100)$ and e are only dependent on population dynamics influenced by the regulation strategy. Strategies are independent, however, of the criteria for the evaluation of performance, because these do not alter population dynamics.

Figure 4.4 also shows the relative deviance from the desired population size for $M = 1.2$ (Figure 4.4a) & b)) and $M = 0.4$ (Figure 4.4c) & d)) (the lighter the background the bigger the deviance). For the lower desired population size $M = 0.4$ (Figure 4.4c) & d)), only strategies with a high deviance allow for $P_0(100) < \varepsilon_p$, because only strategies reducing the total population size $N_t + P_t$ by a small amount conserve non-breeders and keep the population viable. Relaxing (i.e. increasing) the desired population size M allows for smaller deviances (Figure 4.4a) & b)).

Achievability of target settings

The results presented in Figure 4.4 indicate that some target settings regarding desired target population size M and maximum allowed deviation ε_d may not be achievable or affordable. This means that for some target settings no strategy may be found, which achieves the target without exceeding $\varepsilon_p = 0.05$. If a strategy can be found that meets the target settings, the effort required may still be higher than the budget allows. Such a target would be achievable, but not affordable.

Figure 4.5 displays various dimensions of this issue. Its left part (Figure 4.5a) shows results for the parameterization used throughout the previous analyzes (listed in Table 4.1). In Figure 4.5a all achievable targets with maximum extinction probability $\varepsilon_p = 0.05$ are colored lighter. The circles (\circ) mark targets which are additionally affordable given a budget of $\varepsilon_b = 0.02$. Not all achievable tar-

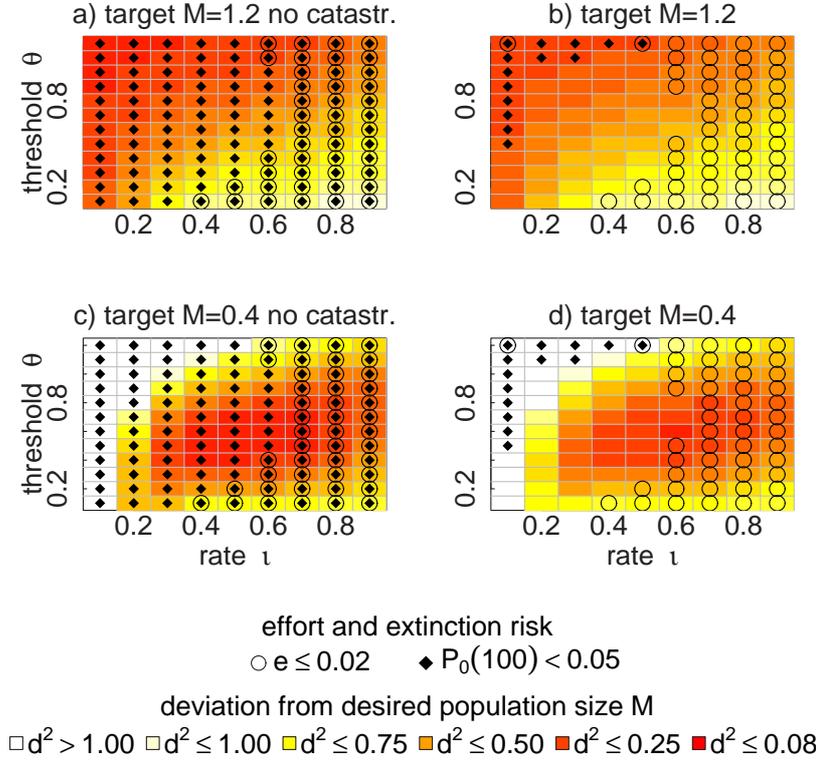


Figure 4.4: Performance of culling strategies (θ, τ) without (a and c) and with (b and d) catastrophe occurrence for target population sizes $M = 1.2$ (a and b) and $M = 0.4$ (c and d). Note: $e < \varepsilon_b = 0.02$, (marked by \circ) and $P_0(100) < \varepsilon_p = 0.05$ (marked by \blacklozenge) are independent of M .

gets are affordable, but they could be if ε_b is increased. The dark colored targets become additionally achievable when maximum extinction probability $P_0(100)$ is allowed to increase up to $\varepsilon_p = 0.1$. These new targets are also affordable. This shows that in this case, allowing a higher extinction risk only slightly increases the range of achievable or affordable targets.

This alters strongly when the characteristics of the non-breeder response to individual losses among breeders are changed. Figure 4.5b shows the population with non-breeders responding more rapidly ($k = 0.1$) to breeders' losses (in contrast to the sluggish response ($k = 0.9$) assumed in Figure 4.5a). Here the range of achievable targets is strongly reduced for $\varepsilon_p = 0.05$. If this constraint is relaxed to $\varepsilon_p = 0.1$ the range of achievable targets increases considerably. In this case not all achievable targets are affordable; this could however be changed by increasing the budget.

Thus, the ranges of achievable and affordable targets are both sensitive to the characteristics of non-breeder response to loss of breeders, which alter with non-breeder response sluggishness k , but also with response strength β (not shown

here). The range of achievable population size and deviance from this size may be increased by relaxing ε_p . But again, how far this range can be increased depends on the characteristics of the non-breeder response. By increasing the budget, the range of affordable targets (\circ in Figure 4.5) can be increased, but only as far as the achievability of targets (colored area in Figure 4.5) allows.

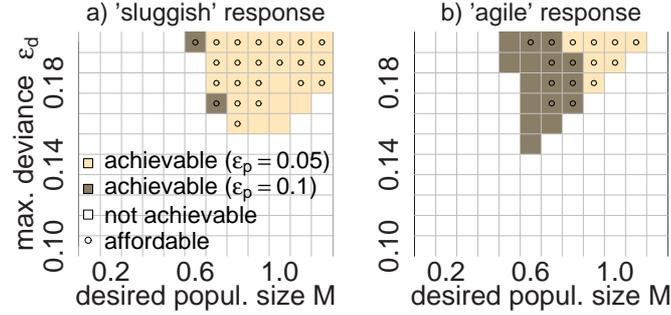


Figure 4.5: Non-breeder response sluggishness k to breeders' loss (a) $k = 0.9$ and b) $k = 0.1$) and achievability resp. affordability of regulation targets. Targets are defined by M , ε_d , ε_p and ε_b . Achievable targets: strategies exist, meeting conditions M , ε_d and ε_p . Affordable targets: strategies exist, meeting M , ε_d , ε_p and ε_b .

This section dealt with regulation strategies which reduce both population parts – breeders and non-breeders – directly, e.g. by culling. The aim was to assess the performance of such regulation strategies in terms of reaching regulation targets while maintaining population viability and adhering to the budget. Within this section environmental fluctuations and reproduction rate were chosen to be low. Disturbances were introduced by one singular but heavy catastrophe. This kept the complexity of population dynamics low and enabled the explicit assessment of the role of the non-breeder pool. The results gained here will be discussed at the end of this chapter.

4.3 Non-Breeders and Strong Variability

In this section, the complexity of the population dynamics is increased by increasing the strength of environmental fluctuations to $\sigma_\xi^2 = 0.3$ and the intrinsic reproduction rate to $r = 2.0$. For this new scenario, the performance of different types of regulation strategies will be assessed. The results of the preceding section will aid in understanding the current results.

In the last section, regulation strategies which directly reduce both the breeder stock and non-breeder's pool were investigated in detail. Now, a more aggregated approach is chosen to keep the analysis clearly delineated. In this section four different types of regulation strategies are investigated: strategies are assumed to

affect either the size of the breeder stock N_t , the size of the non-breeder P_t , the reproduction rate r or the environmental capacity for breeders K . These strategies are applied to scenarios with non-breeder pools with different characteristics in their response to losses among breeders.

The question of interest now is how the interplay between regulation strategies and the pool of non-breeders can best be characterized and what the best way might be to reduce the size of such a stock without endangering it while still adhering to the budget. Furthermore, this section addresses whether non-breeder response characteristics can influence the effectiveness of strategies and achievability of targets. Finally, it is briefly examined whether the strength of environmental variation qualitatively alters the results found.

The reference parameterization of the population is shown in Table 4.1. Again, the system is rescaled to $K = 1$, which means that everything is measured in units of K . This includes σ_ξ^2 , ι and θ , as well as d^2 and e . In contrast to the last section catastrophic events are not considered explicitly. But, as environmental fluctuations and reproduction rate are high, extreme fluctuations which lead to population extinction can still occur.

Performance of strategies

In the following, the criterion of performance used (see Section 2.4) are $P_0(100) < \varepsilon_p = 0.05$ and $d^2 < \varepsilon_d = 0.11$, which corresponds to a deviation from the target size of $1/3K$. Targets considered in this analysis range from $M = 0.1$ to $M = 1.2$. Figures 4.6 to 4.9 show image plots for the four different types of regulation strategies (reducing N_t , P_t , K or r). The images illustrate the minimum targets M for which the performance criteria of $P_0(100) < \varepsilon_p$ and $d^2 < \varepsilon_d$ are met by strategies. This approach to assessing the minimum possible target sizes M also allows to gain insights into their achievability.

First, it is started with regulation enforced by reducing the size of the breeder stock N_t . Figure 4.6 shows the assessment of strategy performance according to the minimum target M , which can be reached with a deviance of $d^2 < \varepsilon_d$ (marked by different colors), and according to population viability ($P_0(100) \leq \varepsilon_p$ marked by '*'). The strategies can achieve targets M , which reach from $N_t + P_t \approx 0.1$ to $N_t + P_t \approx 0.7$. For higher targets M (Figure 4.6a), the deviance d^2 exceeds the limit of $\varepsilon_d = 0.11$, because then N_t is also higher, which leads to stronger fluctuations due to over-compensation ($r = 2.0$). Furthermore, variance in the size of the breeder stock caused by environmental fluctuations ξN_t , depends on N_t itself (see Equation 2.4). Thus, strategies allow higher regulation targets M only if a higher deviance $d^2 > \varepsilon_d$ is accepted.

For lower thresholds θ , $P_0(100)$ shows a trade-off in ι : At medium regulation rates ι , $P_0(100) \leq \varepsilon_p$ can not be fulfilled (Figure 4.6). This is due to the fact that for intermediate regulation rates ι , the size of the breeder stock N_t does not exceed K and thus the non-breeder pool P_t is not supplied. On the other

hand, fluctuations ξN_t can still lead to breeders' extinction, which then means population extinction as the non-breeder pool is empty (Figure 4.6b).

Note that the trade-off of $P_0(100)$ and τ would not be observable, if, as in the preceding section, a strong catastrophic event would be additionally considered, or if the model would include demographic stochasticity. In such cases strategies which lead to population dynamics as shown in Figure 4.6c would threaten population viability as demonstrated above in Section 4.2.

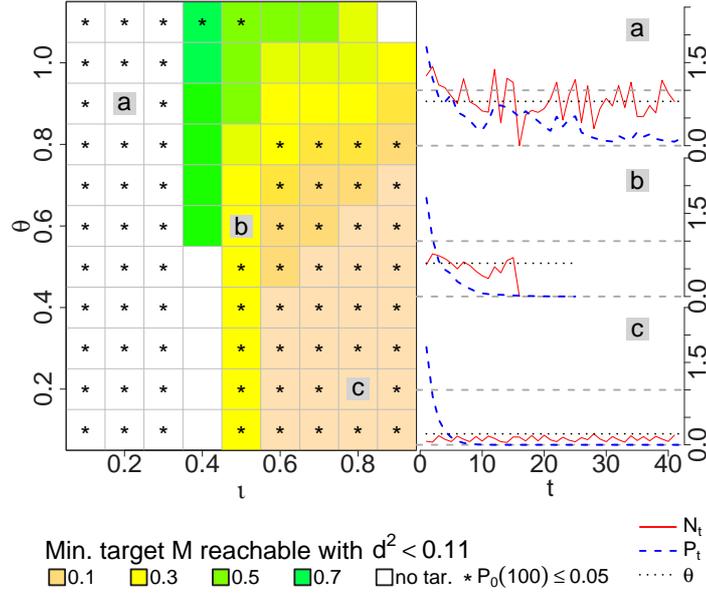


Figure 4.6: Regulation by means of reduction of N_t : The image plot on the left shows the minimum achievable target M for a maximum allowed deviance of $d^2 < \varepsilon_d = 0.11$. Strategies which lead to a probability of extinction at time $t = 100$ of $P_0(100) < 0.05$ are marked with '*'. For the τ - θ combinations a, b and c, exemplary dynamics are plotted on the right. White areas ('no tar.') in the image plot depict τ - θ combinations for which no target can be reached with the given maximum deviance $\varepsilon_d = 0.11$. There is a trade-off in $P_0(100)$ depending on τ and θ .

This is illustrated by the population dynamics plotted to the right of the image. The dynamics in Figure 4.6a show the regulation strategy with $\tau = 0.2$ and $\theta = 0.9$. In this case N_t fluctuates strongly and supplies the non-breeder pool by exceeding K from time to time. As a result the non-breeder pool is maintained and the extinction risk $P_0(100)$ is kept low. However, these strong fluctuations are too strong to match the requirement of deviance $d^2 < 0.11$ from the respective target size M .

The dynamics shown in Figure 4.6b is an example ($\tau = 0.5$ and $\theta = 0.6$) for strategies which keep fluctuations low enough to fulfill $d^2 < 0.11$. However, as a result, N_t exceeds K only rarely. The non-breeder pool is seldom supplied and runs to $P_t = 0$. As fluctuations ξN_t can still lead to $N_t = 0$, the population is prone to extinction.

4.3. Non-Breeders and Strong Variability

Figure 4.6c shows exemplary dynamics for a strict regulation strategy with $\iota = 0.8$ and $\theta = 0.2$. This brings N_t to a very low level at which the pool is not supplied anymore. Due to the slow increase of the logistic growth model at low population levels, fluctuations ξN_t are moderate and the dynamics are far from over-compensation. Therefore the extinction risk is low at $P_0(100) \leq 0.05$.

Regulating the stock by reducing the size of the non-breeder P_t results in completely different population dynamics (Figure 4.7). First, there is no way of matching any regulation target $M \leq 1.2$ with a deviance of $d^2 < \varepsilon_d = 0.11$ by any combination of ι and θ . But in turn, the majority of strategies yield a low extinction risk of $P_0(100) < \varepsilon_p = 0.05$ and only strategies with a high rate ι lead to a higher extinction risk of $P_0(100)$. Again this can be explained by looking at the dynamics a, b and c. In particular, a and b show, that the reduction of the non-breeder pool does not diminish the strength of fluctuations in N_t . But as long as non-breeders are present, fluctuations do not lead to extinction. When the non-breeder pool is removed, as in c, the population dies out because losses in N_t can not be compensated.

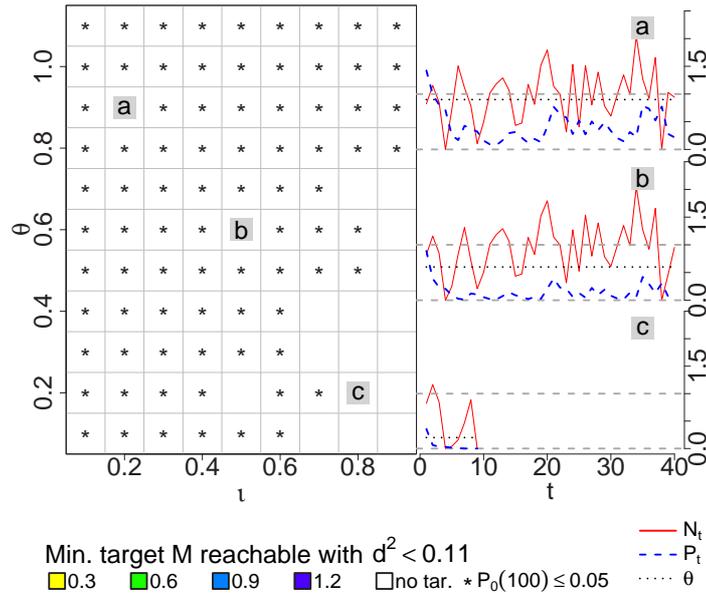


Figure 4.7: Regulation involving a reduction in P_t : The image plot on the left shows that there is no achievable target for a maximum allowed deviance of ε_d (only white areas are present ('no tar.')). Strategies which lead to a probability of extinction before 100 time steps of $P_0(100) < \varepsilon_p$ are marked with '*'. For the ι - θ combinations a, b and c, exemplary dynamics are plotted on the right.

When the population is regulated by reducing the environmental capacity K for breeders (Figure 4.8), a large variety of regulation targets can be reached (from $M = 0.2$ to $M = 1.1$) and all ι - θ combinations lead to a low extinction risk

of $P_0(100) < \varepsilon_p$. This can be explained by the fact that reducing K reduces the size of the non-breeder pool, by bounding it, but still allows for $N_t > K$ and thus a supply of the non-breeder pool.

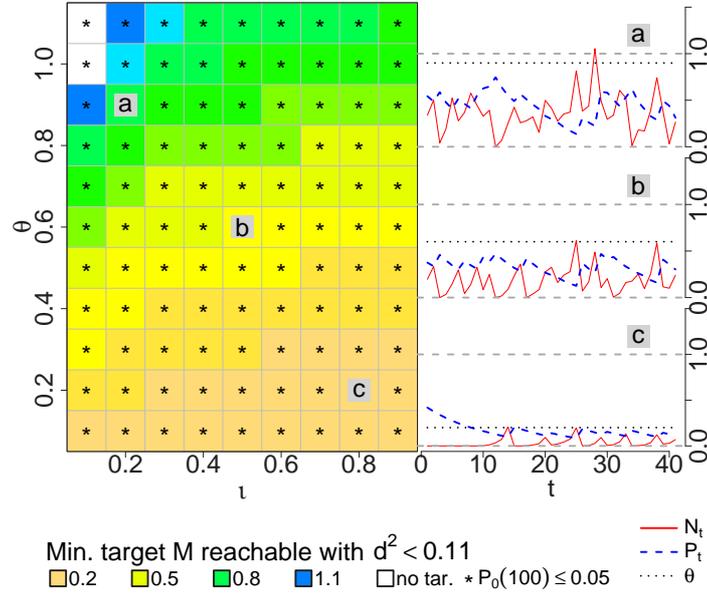


Figure 4.8: Regulation by reducing K : The image plot on the left shows the minimum achievable target for a maximum allowed deviance ε_d and marks strategies which lead to a probability of extinction before 100 time steps of $P_0(100) < \varepsilon_p$ with '*'. For the τ - θ combinations a, b and c, exemplary dynamics are plotted on the right. White areas ('no tar.') in the image plot mark τ - θ combinations for which no target can be achieved with the given maximum deviance ε_d . There are no τ - θ combinations which lead to $P_0(100) > \varepsilon_p$.

The strategy approach that reduces r is less successful (Figure 4.9). None of these strategies achieves targets $M \leq 1.2$ with $d^2 < \varepsilon_d$, however most of the strategies lead to $P_0(100) \leq \varepsilon_p$. Reducing r does not reduce the variance in N_t because as soon as $N_t + P_t < \theta$ holds, r returns to its initial value of $r = 2.0$. It is only by reducing r very strongly with $\tau \approx 0.9$ and $\theta \leq 0.2$ that N_t is reduced so strongly that the non-breeders are not supplied frequently enough to be maintained (c).

Note that in the scenarios investigated here the population experience relatively strong fluctuations. If these would be reduced by setting $\zeta_\xi^2 = 0.1$ and $r = 0.5$ as in Section 4.2, all strategies would perform well, i.e. no strategy would lead to population extinction and a broad range of targets could be achieved (not shown here). This corresponds to the hypothesis stated in Section 3.4. Concentrating on the strongly fluctuating scenarios enables the discovery of strategies which would perform best under extreme conditions.

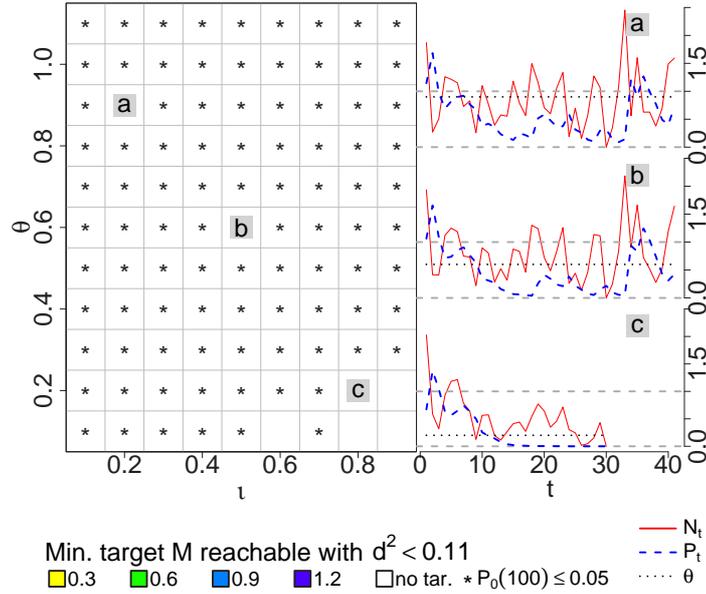


Figure 4.9: Regulation by reducing r : The image plot on the left shows that there is no achievable target for a maximum allowed deviance of $d^2 < \varepsilon_d$ (only white areas ('no tar.')). Nearly all strategies lead to a probability of extinction before 100 time steps of $P_0(100) < \varepsilon_p$ (marked with '*'). For the t - θ combinations a, b and c, exemplary dynamics are plotted on the right.

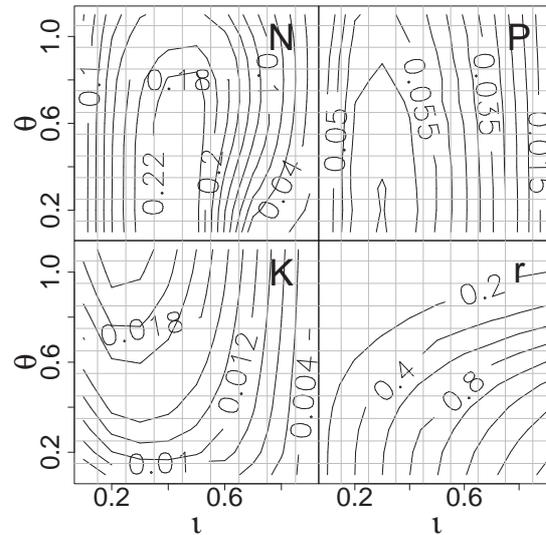
Adhering to the budget

To find strategies which adhere to the budget, the effort e of regulation is measured (see 2.4). Figure 4.10 shows the effort for the different types of strategies described above. In cases of reducing N_t as well as for reducing P_t , there is a trade-off in t . The first can be explained by the shape of the logistic growth function for which the first deviation is highest for $K/2$. Regulating with a medium rate t brings N_t to around $K/2$, where the population resists most against regulation because of its growth dynamics. Thus, the effort e for approximately medium t is highest.

For P_t -reducing strategies, a similar but weaker trade-off can be observed. The explanation for this is very similar to the one for the N_t -trade-off. The t - θ combinations leading to the highest effort, keep non-breeder pool size P_t , and thus the flux into the breeder stock at a level which enables N_t to be around $K/2$. This in turn causes the strongest intrinsic fluctuations and thus raises the effort.

The effort involved in reducing K decreases roughly with decreasing θ . At low increasing t the effort increases as well, but then decreases as t increases further. This can be explained by the plotted dynamics in Figure 4.8. The lower K is kept, the less N_t and P_t fluctuate, and thus the lower the effort needed to keep $N_t + P_t$ approximately around θ .

The effort to regulate $N_t + P_t$ by reducing r increases with decreasing θ and



4.3. Non-Breeders and Strong Variability

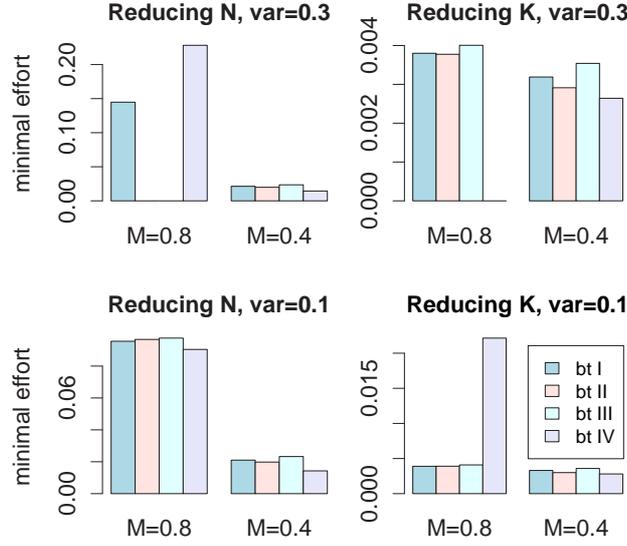


Figure 4.11: Minimal effort of reaching the targets $M = 0.8$ resp. $M = 0.4$ by reduction of N_t resp. K . The different bars represent non-breeder response types: bt I is the reference case of strongly and sluggishly responding non-breeders. bt II represents a weak and agile non-breeder response, bt III weak and sluggish, and bt IV strong and agile. **Upper row:** environmental variances are as in the rest of the study: $\sigma_{\xi}^2 = 0.3$. **Lower row:** shows the efforts for regulation under environmental fluctuations with $\sigma_{\xi}^2 = 0.1$. (Note: the y-axes scales in all plots are different as minimum effort can only be compared within one strategy type.)

($k = 0.1$) which is referred to as bt II in Figure 4.11, weak and sluggish ($\beta = 0.1$, $k = 0.9$, bt III), and strong and agile ($\beta = 0.9$, $k = 0.1$, bt IV).

The upper row of Figure 4.11 shows the minimum effort of effective strategies (fulfill the criteria $P_0(100) \leq 0.05$ and $d^2 < 0.11$) of two strategy types (N - and K -reducing), two regulation targets ($M = 0.8$ and $M = 0.4$) and the four different response types bt I - bt IV. Environmental fluctuations are considered to be characterized by ξ_t with $\sigma_{\xi}^2 = 0.3$.

For the two weak non-breeder response types and the regulation target $M = 0.8$ no N -reducing strategies can be found which match the criteria of effectiveness ($P_0(100) \leq \varepsilon_p$ and $d^2 < \varepsilon_d$). This can be explained by stronger fluctuations in $N_t + P_t$ induced by the weaker response: If the response of non-breeders is weak ($\beta = 0.1$), the non-breeder pool maintains a bigger average size. Thus, N_t has to be reduced more strongly than for the strong non-breeder response types ($\beta = 0.9$), to meet the regulation target M . Strategies which lead to a mean size of $N_t + P_t \approx 0.8$ reduce the size of the breeder stock to values around $N_t \approx 0.5$. At this point, effective reproduction $r(1 - N_t/K)$ is highest, as are fluctuations of N_t , and thus fluctuations of $N_t + P_t$ are also strong. Hence the criterion of $d^2 < \varepsilon_d$ can not be fulfilled for these two weak response types. For the two strong response types the strategy leads to differences between the efforts involved in reaching

$M = 0.8$ and $M = 0.4$ on the order of about one magnitude.

The K -reducing strategy type shows only small differences in efficiency between the four non-breeder response types. Only $M = 0.8$ for bt IV can not be reached. This is caused by the high fluctuations induced by the quick and agile responding non-breeders. Thus the criterion $d^2 < 0.11$ can not be met with this response type. The first row of Figure 4.11 shows that efficiency not only depends on the target but also on the characteristics of non-breeder response to breeders' loss.

This statement can be immediately extended to the dependency on the strength of environmental fluctuations. This is shown in the second row of Figure 4.11, where σ_ξ^2 is reduced to $\sigma_\xi^2 = 0.1$. There, for every response type, strategies can be found which match the two criteria of effectiveness ($P_0(100) \leq \varepsilon_p$ and $d^2 < \varepsilon_d$). Furthermore, the regulation effort of N -reducing strategies under lower environmental fluctuations is reduced. It should be noted, however, that the minimum effort of strategies in Figure 4.11 can only be compared within each strategy type, because of the above-mentioned missing weighting of the effort for different strategy types.

The other two types of strategies (P -reducing and r -reducing) are also tested under the lower environmental fluctuations with $\sigma_\xi^2 = 0.1$. An strategy, which fulfill the criteria $P_0(100) \leq 0.05$ and $d^2 < 0.11$ with minimum effort e , can be found in only two cases for the r -reducing type: For $M = 0.8$ for bt II and for $M = 0.4$ for bt III. In the first case the minimum effort is about 0.015, in the second 0.8.

4.4 Discussion of Regulation Strategies

The starting point of this thesis was the conflict emerging when populations of protected species grow to large sizes and cause considerable economic damage, as for example in the case of the Great Cormorant (Parrott et al. [2003]; Santoul et al. [2004]; Christensen et al. [2007]) or the Canada Goose (Hauser et al. [2007]). Strategies to reduce population size are one way to resolve the conflict in these cases. Nevertheless, it was unclear how regulation strategies would affect populations featuring pools of non-breeders.

Having analyzed the basic dynamics of such populations under differently fluctuating environmental conditions in the preceding chapter, this chapter aimed to asses the performance of regulation strategies in terms of reaching regulation targets while maintaining population viability and adhering to the budget. Within this chapter, potential pitfalls and limitations were explored by both defining appropriate regulation targets and designing feasible regulation strategies for populations featuring non-breeders. This was done using the example of strategies reducing breeder and non-breeder size proportionally at the same time (Section 4.2). After that, in Section 4.3 the performance of other strategy types was as-

sessed. In both sections, the focus was on situations in which environmental conditions and/or strength of intrinsic fluctuations were set to values at which the non-breeder pool is a key factor for population viability. Hence, all conclusions derived in this chapter hold for these particular situations belonging to CASE III.

The most important limitation here is the fact that the constraint of maintaining population viability narrows down the range of achievable regulation targets (desired population size and deviance from it). In the case studied in Section 4.2, keeping the population viable requires the conservation of its non-breeders. As soon as the non-breeder pool is destroyed by regulation, the population is prone to extinction by catastrophic events. Provided their pool is large enough, non-breeders can foster resilience. This certainly gains importance in the face of current climate change, where extreme events (e.g. droughts, floods, storms etc.) are becoming ever more likely, and environmental pressure on ecological systems is increasing.

A major pitfall may also be the trade-off caused by the fact that regulation reduces variance in dynamics of the breeders (which is in accordance with the findings of May (May et al. [1978]), which could be regarded as a kind of “stability increasing” effect on the population. However, as a side-effect, the non-breeder pool may be removed, which may increase population vulnerability to strong environmental fluctuations or catastrophes. It was shown in Section 4.3 that this also holds for regulation strategies that only affect breeders. Therefore, at least for the type of situations investigated in this study, a certain minimum size and variance of breeder size are needed to maintain the non-breeders and thus foster resilience. This fact leads to a threshold behavior of the system when the rate of regulation is increased: above a certain rate the risk of extinction increases strongly.

Uncertainty denotes another limitation in designing a regulation strategy. The range of achievable regulation targets depends on the characteristics of non-breeder response to losses of breeders. As in reality these parameters, as well as population size, are unlikely to be estimable (Balmford et al. [2003]), designers of regulation strategies are forced to be careful if their aims include the preservation of the population. Taking this uncertainty into consideration leads to more conservative regulation targets, which will then result in higher thresholds for regulation. This complements the results of Saether et al. [2005a], who concluded that proportional threshold harvesting should be carried out less intensively in case of low precision of estimated parameters determining population dynamics (i.e. the form of density regulation).

Section 4.2 also shows that having a stop loss-rule alone may not prevent the population from extinction. All of the regulation strategies investigated in this study are threshold strategies (see Section 2.3). Such strategies respect a threshold population size below which the stock is not reduced. Studies by Lande et al. [1997, 1995] suggest that this type of strategy minimizes the risk of extinction.

Although the stop loss-rule could be regarded as a kind of buffer mechanism, its functioning is different from that of an actual non-breeder pool, which can be seen as an insurance mechanism: Potentially reproductive individuals are stored in the non-breeders pool during “good times” and used for compensation in “bad times”. This is completely different from resting the population if a minimum size is passed, as the stop loss-rule does. There, the aspect of storage is missing. Thus, stop loss-rules can perform well under “normal” environmental conditions, but may fail in cases of strong variability and/or heavy catastrophic events. In these cases, the presence of the non-breeder pool is a key factor for viability.

In a broader sense, the non-breeders can also be seen as potential providers of a buffer mechanism (Grimm et al. [2005]): Non-breeders can compensate for losses among breeders and thus buffer a population’s reproductivity against adverse environmental influences. This mechanism, however, only works as long as “enough” non-breeders are present to fill vacancies among the breeders. This required minimum size of the non-breeder pool depends on the “demand”, i.e. the strength of the reduction of breeders. This finding is analogous to the *minimum viable population*, below which a population is prone to extinction due to demographic stochasticity (Thomas [1990]).

The result, that due to dynamical population properties not every arbitrarily set regulation target can be achieved, is very similar to the well known Maximum Sustainable Yield (e.g. Chapman et al. [1962]). It determines the maximum amount, which can be taken from a harvested population without driving the population towards an instable equilibrium point. Small disturbances from this point can drive the population to extinction. Even though the model, model dynamics, and assumptions are different in this study, the overall take-home message is the same: population size cannot be reduced to arbitrarily low levels without strongly endangering the population. The results of Section 4.2 are also relevant for the regulation of invasive species featuring non-breeders, like the American mink in Europe (Bonesi and Palazon [2007]). Such species may remain resilient to reduction attempts as long as their non-breeder pool stays intact.

If strong catastrophes are taken into account and only direct reductions of sizes $N_t + P_t$, N_t or P_t – e.g. by culling – are considered, then possibilities to reconcile a conflict such as that considered here are limited, and different sub-targets (conservation of population persistence, target population size and maximum deviance from this size, not exceeding the budget) interact. If a given set of targets can not be met and direct reductions are the only possible regulation measurements, the only option is to relax sub-targets. This means accepting higher population sizes and/or higher deviances on the one hand, or accepting a higher extinction risk for the population on the other hand. Increasing the budget would be another, albeit limited, possibility: no matter how much one is willing to pay, as soon as the non-breeder pool is destroyed by regulation, the population is prone to extinction by catastrophic events. Another possibility would be not to rely on direct regulation methods like culling, but to instead think of indirect

measures for population regulation, like reducing environmental capacity for the population. This is to some extent already being done in cormorant regulation, e.g. by limiting access to foraging sites (FRA [2004]).

This was assessed in Section 4.3. The class of K -reducing strategies is the only one which maintains population structure, in the sense of conserving the non-breeder pool, over the whole range of rates and thresholds. Furthermore it does not manipulate population dynamics directly, but does so by means of changing the environmental conditions for the population. In this way the functional relationship between the two population groups is conserved as well.

When the size of the breeder stock is reduced directly and strongly, the population may survive, as long as the strength of environmental fluctuations scales with breeder size and no catastrophes occur. However, this means that the non-breeder pool is removed and population structure is changed, which might be critical in case of unexpected catastrophes or changes of fluctuation regimes (Section 4.2), which become more likely in the face of climate change. Furthermore, small populations tend to face a higher extinction risk, in any case (Ludwig [1996]). An alternative solution to this problem is to accept higher regulation targets and/or allow for higher deviances from the target.

In the situation analyzed in Section 4.3, reducing only the non-breeder pool is simply ineffective, and is even dangerous if it is removed entirely. For strategies reducing the reproduction rate, the outlook is similar. Both strategy types do not effectively reduce neither population size or variation in size of the breeder stock, but when they are applied at a high rate, the effect is too strong and the population is highly threatened by extinction. Thus, both strategy types are not flexible and are hard to quantitatively apply under the given conditions representing CASE III (Section 3.4).

As the fluctuation regime applied in Section 4.3 represents CASE III, it is relatively strong. Without the non-breeders the population cannot survive, as shown by the P -reducing strategy with low threshold and high rate. This confirms again that the non-breeders can act as a mechanism which reduces the adverse effects of environmental stochasticity. For lower environmental fluctuations (corresponding to CASE I), non-breeders are less necessary for viability and most targets can be reached easier. Here, the extinction risk induced by the environment is lower and strategies that do not involve reducing environmental capacity can be found.

However, if strategies are to be conservative especially in the face of uncertainty about recent and future environmental conditions, the results suggest the choice of strategies reducing environmental capacity of the non-breeder pool. Besides the safety ($P_0(100) < 0.05$) and robustness (many targets can be achieved) of this K -reducing strategy type, the costs for different non-breeder response types and targets vary relatively little. This is an advantage with respect to the uncertainty about the actual non-breeder response characteristics or total stock size.

Finally, and according to the preceding results, in the case of stocks featuring a non-breeder pool, which is to be conserved, and which are found in environmental conditions corresponding to CASE III, rules of thumb for the design of regulation strategies can be formulated as follows.

Given situations corresponding to CASE III of Section 3.4:

- If the actual effective strength of environmental fluctuations and the risk of catastrophes is unknown, the pool of non-breeders must not be removed;
- If possible, environmental capacity should be reduced;
- If not, the size of the breeder stock should be reduced carefully;
- Medium reductions of the breeder stock are most risky;
- Strong reductions of the breeder stock are risky if the risk of catastrophes is high;
- Direct manipulations of the non-breeder pool or of the reproduction rate are ineffective.

These are rough rules, which only hold for populations structured and following dynamics as assumed here. Admittedly, these rules have yet to be checked against more realistic models and case studies, and have yet to be adapted for CASE I (cf. Part II). However, they provide important insight into the actions that could be dangerous and therefore should be avoided.

These rules of thumb account for the result that increased variability or strength of extreme events reduces the set of regulation strategies that conserve population viability. This result shows that a straightforward optimization approach to find regulation strategies based on current environmental conditions, might not be sufficient and may lead to “dangerous” strategies. Instead of such approaches, “robust” regulation strategies have to be found, which take mechanisms into account that foster population viability. The approach chosen in this thesis, which involves the comparison of very different environmental scenarios, supports this.

Future studies could involve more complex and realistic population models assuming different growth dynamics, sophisticated cost functions of regulation measurements or environmental fluctuations with different characteristics, such as for example auto-correlated fluctuations.

4.4. Discussion of Regulation Strategies

PART II
REGULATION OF THE GREAT
CORMORANT

The case of the Great Cormorant (*Phalacrocorax carbo sinensis*) is highly debated nearly all over Europe. According to the European Birds Directive, the cormorant is a protected species. However, due to the effective protection and good foraging conditions in fish ponds, cormorant numbers have increased strongly over the last decades (Bregnballe et al. [2003]). These increasing numbers of the fish-consuming birds have meant that fisheries sustain heavy losses. Thus, though the cormorant is a protected species, some EU member states permit measurements for cormorant regulation on a regional or local scale (FRA [2004], RED [2002]). Despite these measures, the total cormorant number in Europe is still increasing (e.g. SYKE – Finnish Environment Institute [2007], RED [2002]), although in some countries like Denmark cormorant numbers seem to be stabilizing Bregnballe et al. [2003].

The ongoing increase in cormorant numbers suggests that the regulation measures currently being applied are ineffective. According to the results of the conceptual model, this could be caused by the capacity of non-breeders (in the literature also often termed as *floaters*) to compensate for breeders' losses. On the other hand, a study by Frederiksen et al. [2001] suggests that overestimating this capacity may endanger the cormorant population.

The urgency and challenging nature of the cormorant case is reflected by a number of EU-funded projects (FRA [2004], RED [2002], INT [2009]) dealing with the reconciliation of the conflict between the protection of the cormorant and interests of fisheries. In November 2008, the European Parliament launched an initiative for pan-European cormorant management. Although there is great interest in cormorant regulation and thus in the ecology of cormorants, the issue of the relevance of non-breeding mature individuals for the performance of regulation strategies is rarely brought up explicitly.

In this part of the thesis, the case of the Great Cormorant serves as an example to test the overall hypothesis that the non-breeder pool and the characteristics of breeder-non-breeder interactions influence the performance of regulation strategies. If so, this could be useful information for the upcoming design of pan-European regulation strategies for the Great Cormorant.

In Part I, an understanding was gained of the primary role which non-breeders and breeder-non-breeder interactions can play in influencing population dynamics and the performance of regulation strategies. In this part, it will be assessed whether these results and hypothesis hold for the case of the cormorant.

In the following, an age-structured model of a cormorant population will be developed. Again, the breeder-non-breeder structure is explicitly modeled. The model is parametrized with data from a study of a Danish cormorant colony (Frederiksen et al. [2001]) and attempts, while still having a simple structure, to represent reality as well as possible. After the model is introduced some preliminary analyzes will be performed to link this part with the analysis of the conceptual model and to provide an understanding of parameter sensitivity. After this the performance of regulation strategies will be assessed. This will be done

from different economic perspectives. Finally the influence of the characteristics of breeder-non-breeder interchange will be demonstrated exemplarily.

Additionally, and to link the two parts of this thesis, the conceptual model will be applied. This will provide direct insights into the importance of the structure built up by non-breeders in contrast to the role of the structure introduced by age-classes.

The Adapted Model Framework

5.1 Age-Structured Cormorant Model

The following model is age-structured, discrete in time and stochastic. From the first age class on, it distinguishes between breeders (reproductively active) and non-breeders (reproductively *inactive*, including immature individuals in younger age classes). The general model structure is shown in Figure 5.1. Note, the model developed in the following is a adapted, age-class structured version of the conceptual model presented in 2.1.

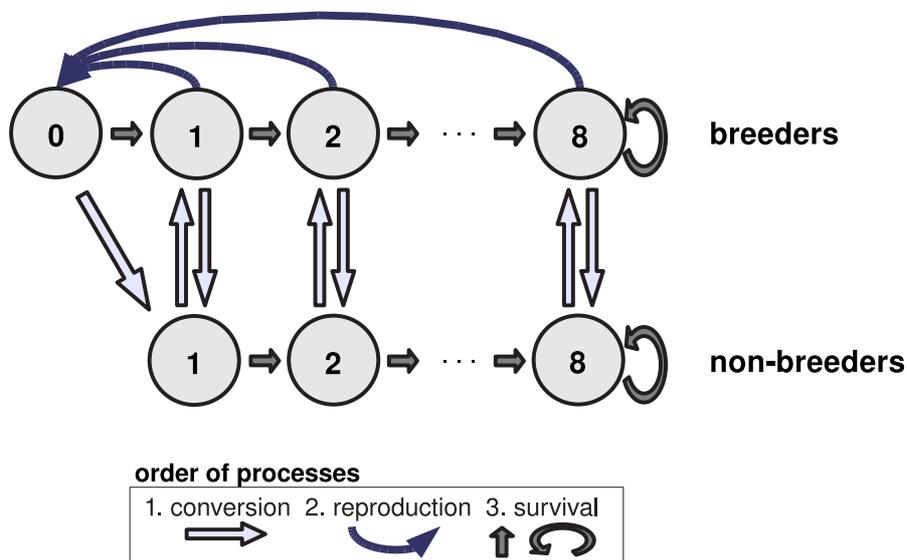


Figure 5.1: Scheme of the general model structure. Breeders reproduce into the 0th age class. Each age class represents one year of individuals' life-span. From the first age class on, individuals are considered to be either breeders or non-breeders.

Conversion

Apart from the age classes, this model consists, like the conceptual model, mainly of two parts: breeders and non-breeders. At time step t in age class i , the total amount $c_{i,t}^{bn}$ of individuals converting into non-breeders is assumed to be determined by the age-dependent sensitivity $s_i \in [0, 1]$ to overall breeder density and the age-dependent disposition $\lambda_i \in [0, 1]$ to leave the breeder stock and join the non-breeders. With N_i as size of age class i , conversion into non-breeders reads:

$$c_{i,t}^{bn} = \max\left(0, \lambda_i(N_{tot,t} - (1 - s_i)K_{eff,t}) \frac{N_{i,t}}{N_{tot,t}}\right) \quad (5.1)$$

Conversion takes place if the total size of the breeder stock $N_{tot,t} > (1 - s_i)K_{eff,t}$. $K_{eff,t}$ denotes the effective capacity for breeders, which would be the equilibrium breeder size, if no extrinsic fluctuations were present:

$$K_{eff,t} = \left(1 - \frac{\sum_i d_i N_{i,t}}{\sum_i b_i N_{i,t}}\right) K \quad (5.2)$$

d_i denotes mortality of breeders of age class i , and b_i their birth rate. K is the environmental capacity for breeders, which would be reached as equilibrium if no environmental fluctuations were present.

Conversion $c_{i,t}^{nb}$ in the other direction (from non-breeder to breeder) is determined by the age-class dependent ability $1 - h_i$ to detect ‘‘vacancies’’ among breeders and the disposition β_i to convert to non-breeders.

$$c_{i,t}^{nb} = \beta_i P_{i,t} \frac{\max[0, (K_{eff,t} - N_{tot,t})^2]}{(K_{eff,t} - N_{tot,t})^2 + (h_i K)^2} \quad (5.3)$$

$P_{i,t}$ represents the number of non-breeders in age class i at time step t . Equation 5.3 is similar to the functional response of Holling-type III (Holling [1959]). For the reasoning behind these conversion functions, see Section 2.1.

Before breeder and non-breeder dynamics are calculated, conversions in both directions take place. The breeder size *after* conversion then provides the basis for further calculations. It can be considered as the gross size of the breeder stock $N_{i,t}^g$. It reads

$$N_{i,t}^g = N_{i,t} - c_{i,t}^{bn} + c_{i,t}^{nb} \quad (5.4)$$

Dynamics of breeders and non-breeders

The dynamics of breeders is based on a derivate of the logistic growth model (Equation 5.5), which is extended to an age-class model.

$$N_{t+1} = N_t + b \left(1 - \frac{N_t}{K}\right) N_t - dN_t \quad (5.5)$$

N_t denotes the size of the non-breeder pool, b is its birth rate and d the rate of death. Note that density regulation is now assumed to affect only the birth process. Equation (5.5) can be rewritten as

$$N_{t+1} = (bN_t + (1-d)N_t) \left(1 - \frac{b}{b+(1-d)} \frac{N_t}{K}\right) \quad (5.6)$$

The first factor can be interpreted as the *potential* population size, which is the sum of new born offspring and surviving individuals from the previous time step. The second factor is the term for effective density regulation, which affects both new offspring and old survivors in the same way.

In Equation (5.6) it can be seen that extinction occurs when $\frac{b}{b+(1-d)} \frac{N_t}{K} \geq 1$ holds. This happens for

$$N_t \geq N_{crit} = \frac{b+(1-d)}{b} K \quad (5.7)$$

Equation (5.6) can be rearranged, and the effective birth and survival rates extracted:

$$b^{eff} = \max \left[0, b \left(1 - \frac{N_t}{N_{crit}}\right) \right] \quad (5.8)$$

$$= \max \left[0, b \left(1 - \frac{b}{b+(1-d)} \frac{N_t}{K}\right) \right] \quad (5.9)$$

$$s^{eff} = \max \left[0, (1-d) \left(1 - \frac{N_t}{N_{crit}}\right) \right] \quad (5.10)$$

$$= \max \left[0, (1-d) \left(1 - \frac{b}{b+(1-d)} \frac{N_t}{K}\right) \right] \quad (5.11)$$

Both rates are 0 for $N_t \geq N_{crit}$. N_{crit} determines the strength of density dependence of b^{eff} and s^{eff} and depends on the process parameters b and d .

Equations (5.6) and (5.7) provide the basis for determining the effective birth and survival rates for the age-structured model. Here, it is assumed that density regulation has a global effect. The rates for age class i are:

$$b_i^{eff} = \max \left[0, b_i \left(1 - \frac{N_{tot,t}}{N_{crit,t}}\right) \right] \quad (5.12)$$

$$s_i^{eff} = \max \left[0, (1-d_i) \left(1 - \frac{N_{tot,t}}{N_{crit,t}}\right) \right] \quad (5.13)$$

with $N^{tot} = \sum_i N_i$, where N_i denotes the size of age class i . These two effective rates describe the processes driving the dynamics of the breeder stock. In the age-structured model, $N_{crit,t}$ becomes time dependent and reads

$$N_{crit,t} = \frac{\sum_i [b_i N_i + (1-d_i) N_i]}{\sum_i b_i N_i} K = \left(1 + \frac{\sum_i (1-d_i) N_i}{\sum_i b_i N_i}\right) K \quad (5.14)$$

5.2. Environment

Eight age classes are considered. It is assumed that individuals are potentially able to reproduce after their first winter. According to these assumptions, the basic dynamics of the zeroth age class (the offspring) can be expressed as

$$N_{0,t+1} = \sum_{i=1}^7 \max \left[0, b_i \left(1 - \frac{N_{tot,t}^g}{N_{crit,t}} \right) N_{i,t}^g \right] \quad (5.15)$$

$N_{0,t}$ denotes the number of offspring, b_i are birth rates of the respective age class $i \in \{1, \dots, 7\}$ and $N_{i,t}^g$ its gross size at time t . $N_{tot,t}^g$ is the total gross size of breeders after conversion at time t . The term $b_i(1 - N_{tot,t}^g/N_{crit,t})$ can be considered as the effective birth rate $b_{i,t}^{eff}$, with $N_{crit,t}$ as the critical total population size. If this size is reached or exceeded no reproduction takes place.

The dynamics of the older age classes $0 < i < 7$ are determined by the survival rate $(1 - d_{i-1})$ of the next younger age class:

$$N_{i,t+1} = \max \left[0, (1 - d_{i-1}) \left(1 - \frac{N_{tot,t}^g}{N_{crit,t}} \right) \right] N_{i-1,t}^g \quad (5.16)$$

As well as effective reproduction, *effective* breeder survival $s_{i,t}^{eff} = \max[0, (1 - d_{i-1})(1 - N_{tot,t}^g/N_{crit,t})]$ is density dependent. If $N_{tot,t}^g = N_{crit,t}$ is reached the population becomes extinct.

The dynamics of the oldest age class $i = 7$ is additionally determined by its own survival rate $(1 - d_7)$:

$$N_{7,t+1} = \max \left[0, ((1 - d_6)N_{6,t}^g + (1 - d_7)N_{7,t}^g) \left(1 - \frac{N_{tot,t}^g}{N_{crit,t}} \right) \right] \quad (5.17)$$

Non-breeder dynamics of all age classes $1 \leq i < 7$ are also determined by survival $(1 - \delta_{i-1})$ of non-breeder individuals:

$$P_{i,t+1} = (1 - \delta_{i-1})(P_{i-1,t} - c_{i-1,t}^{nb} + c_{i-1,t}^{bn}) \quad (5.18)$$

$P_{0,t}$ is set to zero. The oldest non-breeder age class is again also influenced by its own survival:

$$P_{7,t+1} = (1 - \delta_6)(P_{6,t} - c_{6,t}^{nb} + c_{6,t}^{bn}) + (1 - \delta_7)(P_{7,t} - c_{7,t}^{nb} + c_{7,t}^{bn}) \quad (5.19)$$

Note, non-breeder dynamics are *not* density dependent.

5.2 Environment

Stochasticity

Stochasticity is assumed to affect both birth and death rates. For birth rates, noise is assumed to be induced multiplicatively to the effective birth rates $b_{i,t}^{eff}$ via a

log-normally distributed random variable η . This ensures that negative effective birth rates $b_{i,t}^{eff}$ are avoided.

$$b_{i,t}^{eff} = b_i \left(1 - \frac{N_{tot,t}^g}{N_{crit,t}} \right) \eta_t \quad (5.20)$$

Thus, Equation 5.15 must be changed to

$$N_{0,t+1} = \sum_{i=1}^8 \left(\max \left[0, b_i \left(1 - \frac{N_{tot,t}^g}{N_{crit,t}} \right) \right] \eta_t \right) N_{i,t}^g \quad (5.21)$$

In the following, the reasoning behind Equation 5.20 is explained. For simplicity no age classes are considered. Note, a log-normally distributed random variable η_t reads

$$\eta_t = e^{\mathcal{N}(\mu, \sigma)} \quad (5.22)$$

with $\mathcal{N}(\mu, \sigma)$ denoting a normal distribution with mean μ and standard deviation σ . The advantages of using a log-normal distribution are that no values of zero or less than zero occur, and that the distribution is determined by two parameters, as for the normal distribution. The statistical measures relevant in the given context are the expectation of η_t

$$E(\eta_t) = e^{\mu + \frac{\sigma^2}{2}} = e^\mu e^{\frac{\sigma^2}{2}} \quad (5.23)$$

and the variance of η_t

$$\text{Var}(\eta_t) = (e^{\sigma^2} - 1)e^{2\mu + \sigma^2} = (e^{\sigma^2} - 1)e^{2(\mu + \frac{\sigma^2}{2})} = (e^{\sigma^2} - 1)E^2(\eta_t) \quad (5.24)$$

As stochasticity is assumed to be found in the effective birth rate $b_{eff,t} = b(1 - N_{tot,t}/N_{crit,t})$, it has to be ensured that

$$E(b_{eff,t}) \stackrel{!}{=} b \left(1 - \frac{N_{tot,t}}{N_{crit,t}} \right) \quad (5.25)$$

This requires

$$b \left(1 - \frac{N_{tot,t}}{N_{crit,t}} \right) \stackrel{!}{=} b \left(1 - \frac{N_{tot,t}}{N_{crit,t}} \right) E(\eta) = b \left(1 - \frac{N_{tot,t}}{N_{crit,t}} \right) e^{\mu + \frac{\sigma^2}{2}} \quad (5.26)$$

$$\Rightarrow e^{\mu + \frac{\sigma^2}{2}} = 1 \quad (5.27)$$

$$\Rightarrow \mu = -\sigma^2/2 \quad (5.28)$$

Now, only σ determines environmental stochasticity. The term defining the stochastically fluctuating birth rate finally reads:

$$b_{eff,t} = b \left(1 - \frac{N_{tot,t}}{N_{crit,t}} \right) e^{\mathcal{N}(-\sigma^2/2, \sigma^2)} \quad (5.29)$$

Theoretically, $b_{eff,t} \in [0, \infty[$ holds. Although the probability of higher values decreases rapidly, it is appropriate to limit the effective birth rate $b_{eff,t}$. Independently of time, the effective birth rate is highest for $N_{tot} = 0$. Thus, one way to limit b_{eff} is to assign a small probability ε to a fixed maximum effective birth rate b_{eff}^{max} , for which holds $P(b_{eff} > b_{eff}^{max}) < \varepsilon$ if $N_{tot,t} = 0$. This determines the maximum variance σ^2 of environmental fluctuations. The probability is calculated by using the probability density function f of the log-normal distribution.

$$\int_{b_{eff}^{max}}^{\infty} f(b_{eff,t}) db_{eff} \stackrel{!}{<} \varepsilon \quad (5.30)$$

which is together with Equation 5.28

$$\frac{1}{\sigma\sqrt{2\pi}} \int_{b_{eff}^{max}}^{\infty} \frac{1}{b_{eff}} e^{-\frac{(\ln(b_{eff})+\sigma^2/2)^2}{2\sigma^2}} db_{eff} \stackrel{!}{<} \varepsilon \quad (5.31)$$

This inequality yields for the reference parameterization used later on (see Table 5.2) a maximum effective birth rate of $b_{eff}^{max} = 2.0$ and a probability for this rate of $\varepsilon = 0.001$ a variance of $\sigma^2 = 0.05$. The noise introduced by the random variable η_t affects all age classes of breeders the same way. Thus it can be considered as global environmental stochasticity.

Noise on effective survival rates of breeders $s_{eff} = (1-d)(1-N_{tot,t}^g/N_{crit,t})$ and non-breeders $s_p = (1-\delta_i)$ is modeled analogously. For breeders it is assumed to be

$$s_t^{eff} = \max \left[0, (1-d_1) \left(1 - \frac{N_{tot,t}^g}{N_{crit,t}} \right) \zeta_t \right] \quad (5.32)$$

with

$$\zeta_t = e^{\mathcal{N}(\sigma_\zeta^2/2, \sigma_\zeta)} \quad (5.33)$$

and correspondingly, non-breeder survival is modeled as $s_p = (1-\delta)\rho_t$ with $\rho_t = e^{\mathcal{N}(\sigma_\rho^2/2, \sigma_\rho)}$. For the two survival rates it must be ensured that $s^{eff} \in [0, 1]$ and $s_p \in [0, 1]$. To preserve the shape of the log-normal distribution in the interval $I = [0, 1]$, ζ_t and ρ_t are redrawn in cases where they exceed I . For the reference parameterization used later on (see Table 5.2), the variances are set to $\sigma_\zeta^2 = 0.05$ and $\sigma_\rho^2 = 0.05$ as these are values leading to realistic fluctuation patterns (T. Bregnballe, personal communication). Note that noise in survival rates is assumed to be the same for all age classes.

Catastrophe

In Part I, the potential importance of catastrophes for the assessment of the role of non-breeders for population viability was pointed out. Therefore, also in this model in addition to stochastic environmental fluctuations, it is assumed that the

population is exposed to an extreme event, e.g. an epidemic outbreak. Because of higher settling density and increased stress through breeding, breeders are considered to be more affected than non-breeders. The catastrophe is assumed to last five years and reduce breeders by 70% and non-breeders by 10% each year. This represents a very heavy catastrophe, which lies at the extreme end of imaginable impacts of any adverse event for the cormorant (T. Bregnballe personal communication). Applying such an extreme catastrophe ensures that a conservative assessment of the probability of extinction under a given regulation strategy can be achieved. The catastrophe starts at time t^* , and the size of every age class is reduced by the respective percentage at the end of each time step $t \in t^*, t^* + 1, \dots, t^* + 4$:

$$N_{i,t} = N_{i,t} - 0.7N_{i,t} \quad (5.34)$$

$$P_{i,t} = P_{i,t} - 0.1P_{i,t} \quad (5.35)$$

5.3 Regulation Strategies

In the age-structured cormorant model, the same regulation strategies are applied as in the conceptual model in Part I (cf. Section 2.3). In the case of the Great Cormorant the abstract regulation strategies introduced in Section 2.3 correspond to concrete measurements, which are already applied in practice (e.g FRA [2004]). Measurements, conditions and strength of measurements are summarized in Table 5.1.

Table 5.1: The five different types of regulation strategies (reducing N_t , P_t , N_t and P_t , r_t or K_t) affect different system components. Regulation is executed if $N_t + P_t > \theta$, in which case the term in the second column is subtracted from the respective component. Otherwise, if $N_t + P_t \leq \theta$ the reduced component recovers.

measurement	affected component	reduced by (if $N_t + P_t \leq \theta$)	recovery (if $N_t + P_t > \theta$)
culling of breeders	$N_{i,t}$	$\iota N_{i,t}$	cf. Eq. 5.15 – 5.17
culling of non-breeders	$P_{i,t}$	$\iota P_{i,t}$	cf. Eq. 5.18 – 5.19
egg-oiling	$r_{i,t}$	$\iota r_{i,t}$	$r_{i,t} = r_i$
e.g. closing colonies and preventing new ones	K_t	ιK_t	if $K_t < K$, $K_t = K_t + 0.5(K - K_t)$

If the regulation strategy aims to reduce the total size of breeders N_t and non-breeders P_t , both parts are affected equally. Age classes are also assumed to be affected equally. Note, by regulation $r_{i,t}$ and K_t become time-dependent. The initial values towards which $r_{i,t}$ and K_t recover are referred to as r_i and K .

5.4 Modification of Criteria for Strategy Performance

In principle, the assessment of the performance of regulation strategies follows the same scheme as for the generic model (cf. Section 2.4), but now the criteria for reaching the target and adhering to the budget are merged into a single criterion of optimality.

Maintaining population viability. As for the conceptual model, here the population is said to be *viable* if the probability of extinction $P_0(100)$ after 100 years meets the following condition: $P_0(100) < \varepsilon_p$, with ε_p being the Maximum Accepted Extinction Risk. In the following it will be set to $\varepsilon_p = 0.05$.

Being optimal. A strategy is said to be optimal if $P_0(100) < \varepsilon_p$ and total costs $c(e_t, N_t, P_t)$, consisting of costs for cormorant regulation and damage caused by cormorants, are minimal. Total costs $c(e_t, N_t, P_t)$ are calculated as follows

$$c(e_t, N_t, P_t) = u(\bar{e}_t^2 + q(\bar{N}_t + \bar{P}_t)) \quad (5.36)$$

The parameter u defines one cost unit needed to reduce the population by one cormorant. As it will not qualitatively alter the results, it will be set to $u = 1$. Parameter q quantifies the costs (i.e. the damage) caused by one cormorant in units of u , in relation to the costs of reducing the population by one cormorant. e is the effort for regulation (note, the effort is calculated according to the rule given in Equation 2.7). In the cost function, it is assumed that costs for regulation effort increase progressively in a quadratic way with \bar{e}_t , while costs of cormorant damage increase linearly with $\bar{N}_t + \bar{P}_t$.

For several reasons, this measure is particularly appropriate in the case of cormorant regulation. In contrast to the Canada goose (Hauser et al. [2007]) for example, the aim here is not to maintain a *certain* size of the cormorant population but rather to keep the population viable while minimizing the costs caused by regulation and damage by cormorants. Thus, the separation of a target size and a deviation from it is no longer appropriate. The chosen cost function has the advantage that it allows the economic aspect of the problem to be directly addressed and also allows for the application of an optimization procedure.

5.5 Parameterization of the Cormorant Models

To parametrize the age-structured model, cormorant data published by Frederiksen *et al.* (Frederiksen et al. [2001]) regarding birth and death rates are used. The interchange between breeders and non-breeders is parameterized according to expert guesses by Thomas Bregnballe (personal communication). To further improve the guesses about the interchange parameters, the distribution of the proportion of breeding individuals per age class generated by the model is fitted

Table 5.2: Reference parameter set. (b.: breeders, n.: non-breeders)

parameter	age class i							
	0	1	2	3	4	5	6	7
b. birth rate $b_i^{ref} \in [0, \infty[$.0	.1	.75	.9	1.	1.	1.	1.
b. death rate $d_i^{ref} \in [0, 1]$.4	.13	.12	.11	.1	.1	.1	.1
b. to n. convers. dispos. $\lambda_i \in [0, 1]$	1.	.95	.3	.2	.1	.05	.05	.05
b. density sensitiv. $s_i^{ref} \in [0, 1]$.96	.7	.5	.25	.15	.1	.05	.05
n. to b. convers. dispos. $\beta_i^{ref} \in [0, 1]$.0	.5	.6	.8	.95	.99	.99	.99
n. vacancy detection $1 - h_i^{ref} \in [0, 1]$.0	.09	.85	.85	.8	.8	.8	.7
n. mortality $\delta_i^{ref} \in [0, 1]$.4	.13	.12	.11	.1	.1	.1	.1
min. ind. number per age class	1							
breeders' environmental capacity K	100,000							
fluctuation variance σ_ξ^2	.05							
max. effective birth rate b_{eff}^{max}	2.							
probability $P(b_{eff}^{max})$	< .05							
fluctuation variance $\sigma_{\zeta_d}^2$ and $\sigma_{\zeta_\delta}^2$.05							

to the observed distribution (also published in Frederiksen et al. [2001]). This technique of fitting model-generated patterns to observed ones is known as indirect parameterization or pattern-oriented modeling (Kramer-Schadt et al. [2007], Grimm et al. [1996]). In ecology it is mainly used to parameterize complex and highly structured models. The fit of the pattern in the proportion of breeding individuals is shown in Figure 5.2. The parameters gained are shown in Table 5.2.

According to these parameters, birth rates b_i increase and death rates d_i and δ_i decrease with age. The latter also holds for the breeder disposition to convert to non-breeders λ_i , and breeder sensitivity to their own density s_i . This reflects

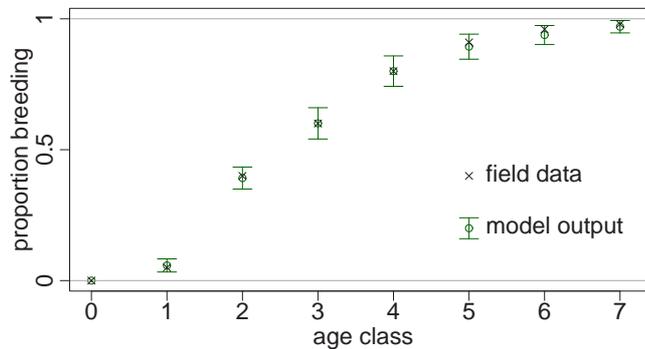


Figure 5.2: The observed and modeled pattern of the age-class dependent proportion of breeding individuals, estimated using the reference parameterization (see 5.2).

5.5. Parameterization of the Cormorant Models

the fact that younger cormorants tend to leave the breeding colony more than older individuals. The non-breeder disposition to convert back to breeders β_i , which increases with age, points in the same direction. The ability to detect vacant breeding opportunities first increases strongly with age but then levels off. This might be explained by the early increases in experience and later decreases in mobility of individuals. Unless stated differently, the model is parameterized according to these reference parameters. They are the starting point for further analyzes and determine a reference population to test regulation strategy performance.

Table 5.3: Parameter values derived from cormorant data (shown in Table 5.2) using the mean field approach

parameter	default value	meaning
r	1.0	reproduction rate
K	1	environmental capacity
λ	0.5	flux rate into non-breeder pool
β	0.9	strength of flux into non-breeder pool
k	0.1	sluggishness of flux into breeder stock
δ	0.1	death rate of non-breeders
κ	5.0	non-breeder capacity
σ_{ξ}^2	0.05	variance of env. fluctuations

To link this more closely to the earlier discussion of the conceptual model, the conceptual cormorant model is parameterized according to the data shown in 5.2. Thereby the mean field approach is applied, which means that the mean parameter values of all individuals are taken (Table 5.3). (Note that in general these means are different from the means of the parameter values shown in Table 5.2.)

Chapter 6

Population Dynamics

Following the sequence used in part I, population dynamics are first analyzed without considering regulation before the performance of regulation strategies is assessed. To link the two major parts of this thesis, both the conceptual cormorant model and the age-structured cormorant model are applied to assess population viability. This allows the generation of hypotheses regarding the regulation of the cormorant, which then are tested in the next chapter. In the first section of this chapter a sensitivity analysis of the population parameters will be performed. This also provides a link to the preceding part and allows a comparison the two models according to the influence of different parameters on population viability. Finally, the algorithm for the estimation of the importance of non-breeders (cf. Section 3.3) is applied to gain further insight into the dynamical properties of the population.

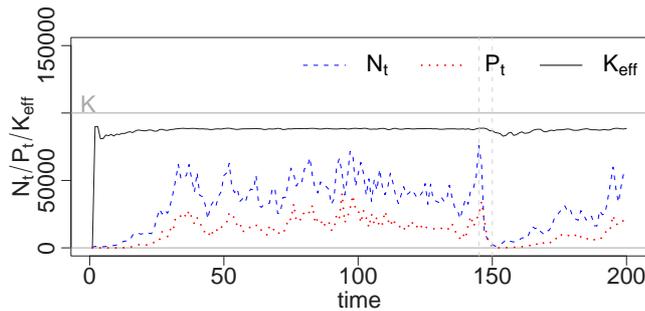


Figure 6.1: Exemplary dynamics of total breeder and non-breeder size, and age classes of breeders and non-breeders, carried out using the reference parameterization (see 5.2). Dashed lines mark the five-year duration of the catastrophe.

6.1 Sensitivity to Population Parameters

As a starting point, the dynamics and viability of the population with the reference parameterization is considered before the sensitivities of the parameters are assessed. Figure 6.1 shows the exemplary dynamics of the population, starting with $N_i = 10$, $i \in \{0, 2, \dots, 7\}$. The catastrophe starts at time $t = 145$. It takes five time steps and strongly reduces the population (see Section 5.2) for more details). After that the population recovers. Calculating the probability of extinction within the hundred time steps from $t = 100$ to $t = 200$ yields $P_0(100) \approx 0$. This indicates that the population as set up in Chapter 5 is fairly robust, which means that the pool of non-breeders may not play a crucial role for population survival.

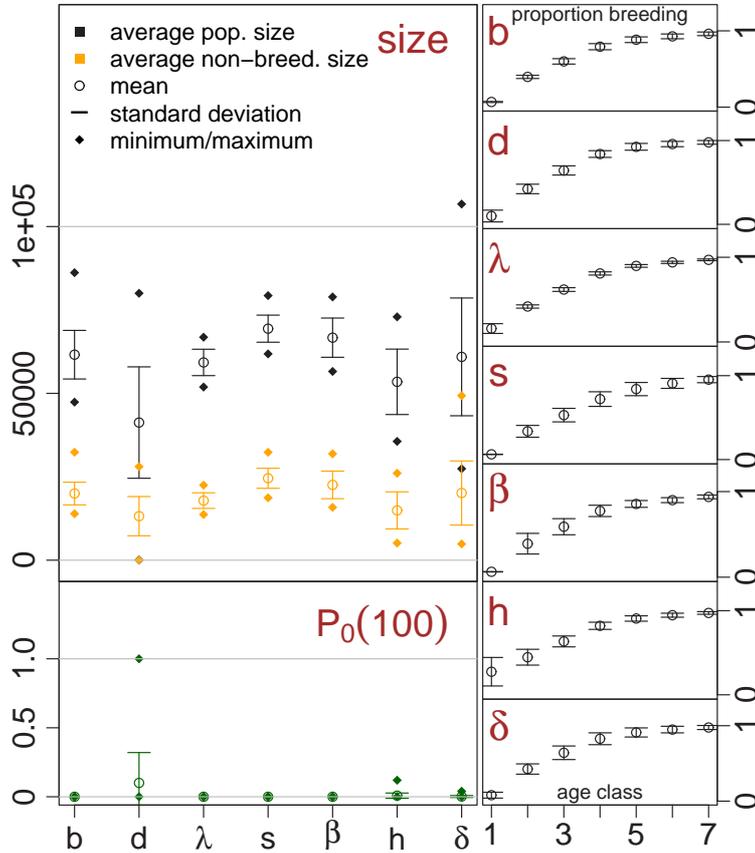


Figure 6.2: Result of local sensitivity analysis of single parameters. Parameters are varied around the reference parameterization (Table 5.2).

The following sensitivity analysis will show how far this will hold if population parameters are varied. The mean total population size $\bar{N}_t + \bar{P}_t$ and mean size of non-breeders \bar{P}_t , the probability of extinction $P_0(100)$, as well as the proportion of breeding individuals, are the measures used in the following sensitivity

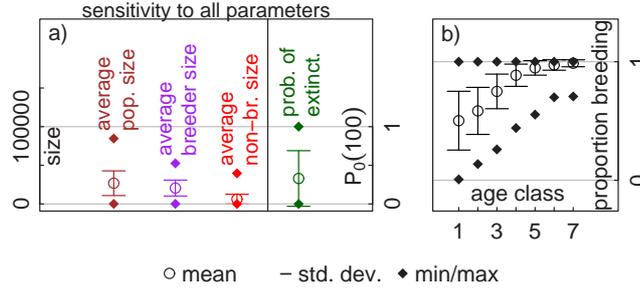


Figure 6.3: Result of sensitivity analysis, varying all parameters at the same time around reference parameter values (Table 5.2). **a)**: measures of size and viability; **b)**: proportions of breeding individuals in each age-class.

analysis. Parameter vectors $\underline{v} = (v_0, \dots, v_7)$, representing parameters for the eight age-classes, are varied according to the following scheme: Beginning with the reference parameterization (Table 5.2), a range $z \in [0, 1]$ of variation is defined for every vector element v_i . In the following this range will be set to $z = 0.5$. Then, an equally distributed random number $x_i \in [-z/2, z/2]$ is drawn and added to v_i . In case the varied parameter value $v_i^* = v_i + x_i$ exceeds the domain of definition of v_i , a new x_i is drawn. In the following, for every parameter variation, 1,000 vectors $\underline{v}^* = (v_0^*, \dots, v_7^*)$ are calculated. Every \underline{v}^* is applied in 100 simulations over 200 time steps. For the calculation of measures the transient phase of the first 100 time steps is skipped.

First, only single parameter vectors are varied while the others are held at their reference values (Table 5.2). The plot of size in Figure 6.2 shows the effect of the variation of each parameter on the average population size $\bar{N}_t + \bar{P}_t$ and the average non-breeder size \bar{P}_t . Breeder and non-breeder mortalities d and δ are the most sensitive parameters. Figure 6.2 also shows the probability of extinction $P_0(100)$, which here is most affected by breeder mortality d . Rapidness of vacancy detection h and non-breeder mortality δ also affect but less. The low impact of parameter variations on $P_0(100)$ corresponds to the findings of the sensitivity analysis of the conceptual model (Section 3.2), where for low fluctuation scenarios almost no extinction occurs. The right side of Figure 6.2 shows the effects of the parameter variation on the proportion of breeding individuals N_t in every age class. Here, β (strength of non-breeder response) and s (breeder sensitivity to density) appear to be the most sensitive. More important is, nevertheless, the qualitative pattern in the proportion of breeding individuals remains unchanged and thus is robust against the applied changes in parameters.

Second, parameters are all varied together around their reference values, again with $z = 0.5$. Figure 6.3a) shows that the ranges of $\bar{N}_t + \bar{P}_t$ and \bar{P}_t as well as probability of extinction $P_0(100)$ are fairly different from any single variation of parameters (Figure 6.2). Thus, there are interactions of parameters in the inves-

6.1. Sensitivity to Population Parameters

tigated range of parameter space. The pattern in the age-dependent proportion of breeding individuals (Figure 6.3b)) behaves on the average, qualitatively as before, but varies strongly. This also points to interactions between parameters. This corresponds to the findings of the sensitivity analysis in Part I (Section 3.2), where strong interactions were observed.

To detect the interactions in the age-structured model, parameters are grouped according to their biological meaning. In the first instance, mortalities d and δ are varied at the same time while the remaining parameters are kept at their respective reference values (Figure 6.3c) & d)). The variation of d and δ at the same time already explains most of the variation in sizes of total population $\bar{N}_t + \bar{P}_t$ and non-breeders \bar{P}_t and in risk of extinction $P_0(100)$ as observed in Figure 6.3a) & b). Thus, the mortalities of breeders and non-breeders govern sizes of the total population $\bar{N}_t + \bar{P}_t$ and its part \bar{P}_t , as well as the risk of extinction $P_0(100)$. Nevertheless, variation of mortalities cannot fully explain variation in the age-dependent proportion of breeding individuals, as observed in Figure 6.3b).

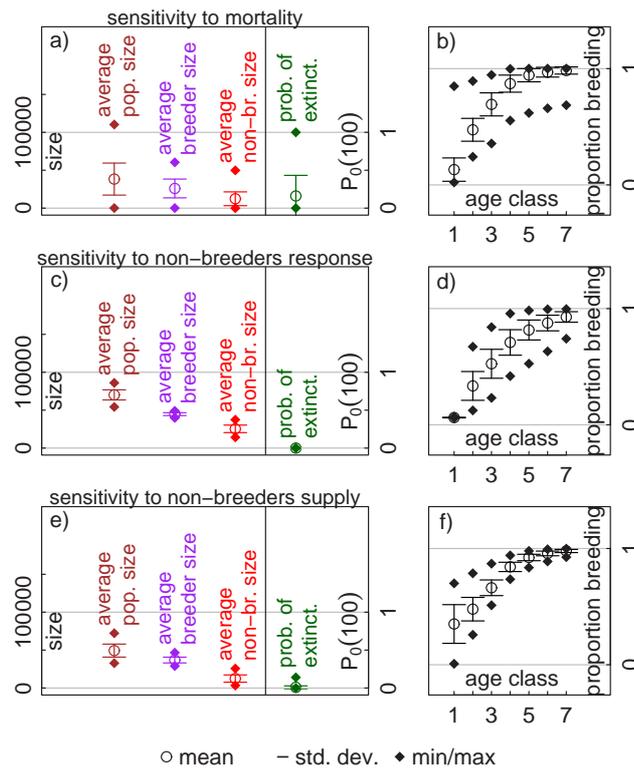


Figure 6.4: Result of sensitivity analysis. **a) & b):** mortalities d and δ varied at the same time around their reference parameter values (Table 5.2). **c) & d):** non-breeder supply λ and s varied at the same time around their reference parameter values. **e) & f):** non-breeder response β and h varied at the same time around their reference parameter values. The remaining parameters are held constant at their reference value.

Variation of non-breeder supply (λ and s) accounts only little for variation in sizes and not at all for variation in survival time (Figure 6.4a)). The same holds for varying non-breeder response to breeders' loss (β and h), shown in Figure 6.4c). However, both parameter groups contribute considerably to variations in the age-dependent proportion of breeding individuals (Figure 6.4b) & d)).

Finally, all parameters together are varied over their whole domain of definition (Figure 6.5) beyond their reference values. This decreases mean sizes $\overline{N}_t + \overline{P}_t$ and \overline{P}_t as well as increasing risk of extinction $P_0(100)$ and variation in all these measures. The pattern in the proportions of breeding individuals in each age-class is completely destroyed. Hence around reference parameterization – apart from changes in mortality d – sensitivity of the used measures ($\overline{N}_t + \overline{P}_t$, \overline{P}_t and $P_0(100)$) against parameter variation is relatively low, as seen in Figure 6.3. However, as is evident here, this does not hold for the whole range of parameter definitions. Thus, the observed pattern in the age-class dependent proportions of breeding individuals is not implied by the model structure but depends on the parameterization of the model. Therefore, it can be used to calibrate the model, as done in Section 5.5.

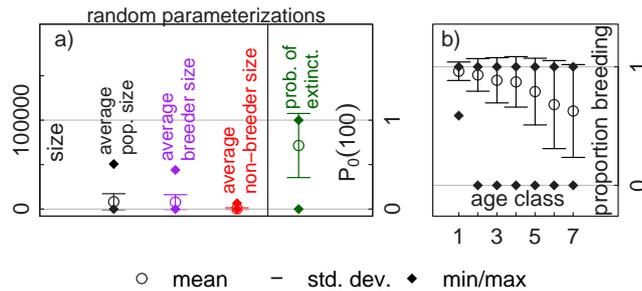


Figure 6.5: Result of sensitivity analysis varying all parameters randomly at the same time. (All parameter values chosen from the interval $[0, 1]$, except $b \in [0, 2]$)

6.2 Importance of the Non-Breeder Pool

Section 6.1 showed that population viability in the age-structured model is high and does not depend greatly on non-breeder characteristics. This leads to the hypothesis that the non-breeder pool is not crucial for population survival and that the situation found for the cormorant belongs to CASE I (cf. Section 3.4). That hypothesis can be tested mechanistically by applying the conceptual model: In Section 3.3 a method was developed to estimate the importance of the source functionality of the non-breeder pool for population viability. This method uses trajectories of the conceptual model in the N_t - N_{t+1} phase space, given the non-breeder size $P_t = 0$. Thereby, two trajectories are considered, which represent

6.2. Importance of the Non-Breeder Pool

two extreme fluctuations ξ^{high} and ξ^{low} towards high and low values of stochastic environmental fluctuations ξ_t . These two extreme fluctuations mark the 0.001-quantiles of the distribution of ξ_t . Given this setting, a measure is calculated, to quantify how likely fluctuations are that lead to the extinction of the breeder stock $N_t = 0$. In these cases of $N_t = 0$ the source functionality of the non-breeder pool could protect the whole population from extinction. If the occurrence of fluctuations leading to breeders' extinction $N_t = 0$ is unlikely, the non-breeder pool plays a minor role for population viability. (Note that in contrast to the previous section, catastrophes can not be considered with this method.)

Following this procedure, which is explained more in detail in Section 3.3, two values L and H are found. L is the intersection point of the trajectory for ξ^{low} with the N_t -axis. H represents the N_{t+1} -value of the maximum of the trajectory for ξ^{high} . Applying the conceptual cormorant model (parameterized according to Table 5.3), the points for $L = 1.62$ and $H = 1.81$ are found. Figure 6.6 shows that they are fairly close together.

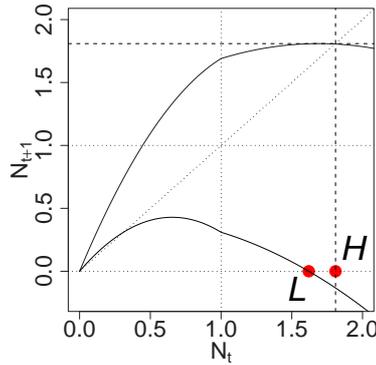


Figure 6.6: Curves in the N_t - N_{t+1} -phase space defined by 0.001-quantiles of environmental fluctuations. Point L marks the null of the curve defined by the 0.001-quantile and thus the N_t -value for ξ_t , above which the population becomes extinct. H denotes the maximum N_t -value which can be reached for ξ_t within the 0.001-quantiles. The source functionality of the non-breeder pool is set to zero ($\beta = 0$).

L and H can be thought of as indicating trajectories of two extreme *subsequent* environmental fluctuations, first to a very high then to a very low ξ_t -value and each occurs with a probability of $p_{occ} = 0.001$. If the actual breeder size N_t is close to the point H , then breeder size would drop to zero and non-breeders would be needed to compensate breeders' losses and to help the population recover. Thus, the close positions of L and H indicate that fluctuations leading to $N_t = 0$ seldom occur and thus the need for the non-breeders to compensate breeders' losses is low. This corresponds to the finding from Section 6.1 that population viability is insensitive to the non-breeder characteristics.

Taking into account the close positions of L and H , it could be hypothesized that the cormorant population is rather "robust" even in the face of regulation.

This would correspond with the findings of the analysis of the conceptual model. There (Section 3.2), it was shown that for low reproduction rates, where no over-compensatory dynamics occur, and under low environmental fluctuations, the non-breeder pool is not crucial for population viability.

In this chapter, the role of the non-breeder pool for population dynamics without regulation has been investigated. This allows the formulation of hypotheses regarding the influence of the non-breeder pool on regulation performance. According to the presented results, it can be hypothesized that the characteristics of the non-breeder pool may not affect the performance of regulation strategies regarding population viability (the situation belongs to CASE I, as stated in Section 3.4). However, it may be the case that these characteristics affect the costs of regulation measurements. To verify if this holds true, regulation strategies are applied to the two cormorant models in the next chapter.

6.2. Importance of the Non-Breeder Pool

Performance of Regulation Strategies

The overall question in this chapter is whether the non-breeder pool and its characteristics influence the performance of regulation strategies. In Part I of this thesis it was shown that for the generic conceptual model, the non-breeder pool can indeed affect the performance of regulation strategies (Sections 4.2 & 4.3). This especially holds in cases of strong intrinsic or environmental fluctuations or heavy catastrophic events. Here, this question is addressed in the context of the more specific cormorant models. In the first step, the conceptual cormorant model is analyzed, and in the second step the age-structured model is subject of analysis. This approach links the two parts of this study and shows the extent to which the results are comparable and to which they differ. This comparison will also aid in the understanding of the role of the non-breeders: If the results of the conceptual and the age-structured cormorant models differ strongly, then they indicate strong combined effects and a high importance of age-structure on the performance of regulation strategies.

7.1 Applying the Conceptual Cormorant Model

In this section the conceptual cormorant model (cf. Table 5.3) is applied. In contrast to Part I, the performance of regulation strategies is now judged according to the target function given in Section 5.4. For this first short analysis, relative cormorant-caused damage is assumed to be $q = 100$. This means that the damage caused by a single cormorant during its life time is a hundred times higher than the costs for measures which would kill it or prevent it from being born. Later, in Section 7.3 this ad hoc assumption will be subject to further analyzes.

Figure 7.1 shows the performance of the different considered types of regulation strategies (culling breeders N_t , non-breeders P_t or both, reducing breeder capacity K and egg-oiling (reduction of b); cf. Section 5.3). The darker areas indicate strategies (defined by rate ι and threshold θ) which lead to an extinction risk of $P_0(100) \geq 0.05$. The contours show lines of equal total costs $c(e_t, N_t, P_t)$.

7.1. Applying the Conceptual Cormorant Model

The lighter-colored point marks the minimum and the darker point the optimal strategy of the given type in the considered range of ι and θ . (Note that in this context *Optimality* of a strategy denotes causing minimum total costs while keeping the extinction risk $P_0(100) < 0.05$ low.)

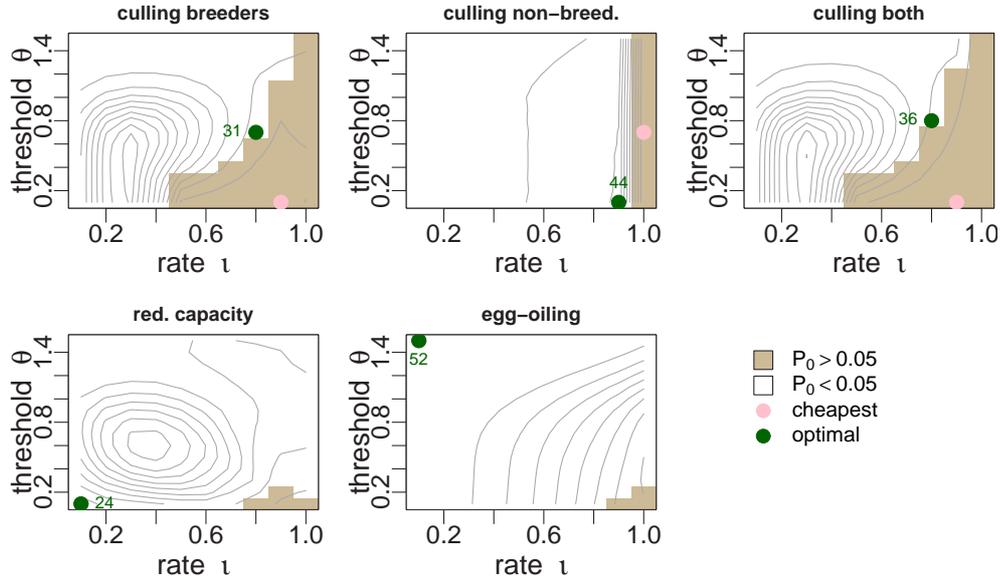


Figure 7.1: Performance of regulation strategies applied to the conceptual model parameterized with cormorant data (Table 5.3). For strategies involving a reduction in the environmental capacity K for breeders or egg-oiling, the optimal and cheapest strategy fall together. The numbers give the total costs of the optimal strategy in units of 10^5 .

The results shown in Figure 7.1 are in accordance with the previous findings: Culling breeders N_t or breeders *and* non-breeders P_t above a certain rate ι and below a certain threshold θ increases the probability of extinction to $P_0(100) > 0.5$. Culling only non-breeders P_t endangers population viability for $\iota = 1.0$, which corresponds to complete removal of the non-breeder pool. Strong reductions of breeders removes the pool of non-breeders and thus can degrade population viability.

In Section 6.2 it was concluded that non-breeders play a minor role for population viability in the face of the assumed strength of environmental fluctuations. However, if catastrophes are additionally considered, non-breeders are not completely irrelevant for population survival, otherwise culling non-breeders on a high rate of $\iota = 1.0$ would not degrade population viability (cf. Figure 7.1).

Figure 7.1 shows that when culling is applied to breeders N_t or to both breeders N_t *and* non-breeders P_t , the costs are highest for rates of $\iota \approx 0.3$ and medium or low thresholds θ . This shape of the contour plots of the cost-function $c(e_t, N_t, P_t)$ can be explained by the following effects. Starting with $\iota = 0$, increasing it and keeping $\theta = 0.5$ constant first leads to an increase of total costs, because

the amount of culling is increased. At the same time, the population is only slightly reduced, which in turn leads to little reduced cormorant damage (this non-linearity in the population response to culling is explained later when Figure 7.2 is discussed). Increasing regulation rates beyond $\iota > 0.3$, the population size is reduced to lower and lower sizes, which means that damage caused by the population is reduced, which in turn reduces total costs. Increasing regulation rate ι further leads to even lower population sizes, at which point population viability is degraded. For a constant, low regulation rate ι of e.g. $\iota = 0.2$ and increasing thresholds up to $\theta \approx 0.6$, the costs $c(e_t, N_t, P_t)$ remain constant because due to the low rate ι , regulation is executed permanently. Further increases beyond $\theta > 0.6$ yield decreasing total costs $c(e_t, N_t, P_t)$, because the higher θ is, the less frequently regulation measurements are carried out. In this case the decrease of the regulation effort is stronger than the increase of the damage caused by the cormorants, which shows that culling at low rates does not lead to a strong reduction of the population size in this model. For higher constant regulation rates ($\iota > 0.5$), total costs $c(e_t, N_t, P_t)$ increase with θ , because for $\iota > 0.5$ population size and thus damage caused by cormorants can be reduced strongly. Increasing θ means allowing higher population sizes $N_t + P_t$ and higher cormorant damage, which then leads to higher total costs $c(e_t, N_t, P_t)$.

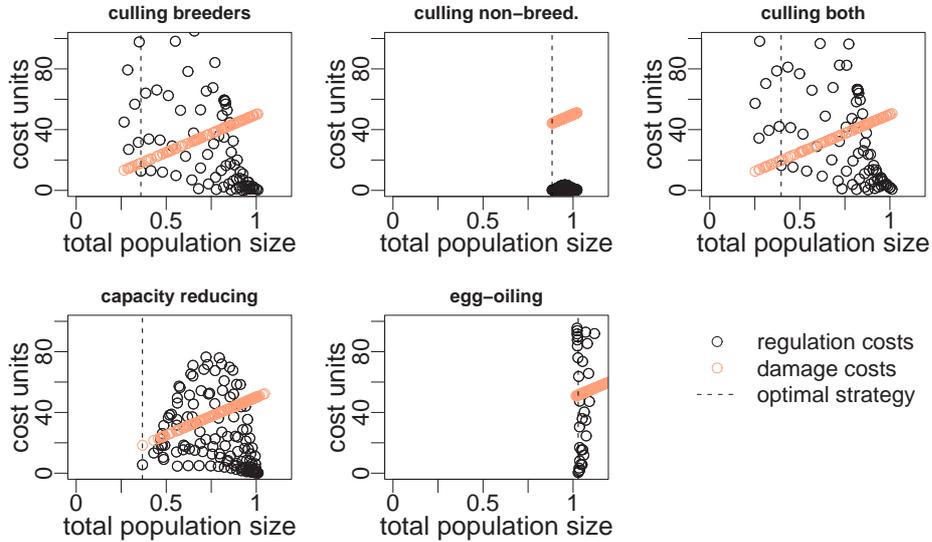


Figure 7.2: Mean regulation costs resp. damage costs vs. mean total population size $N_t + P_t$ in the conceptual model for the entire range of (θ, ι) . The dashed lines indicate the population size of the optimal strategy, as marked in Figure 7.1.

Culling only non-breeders P_t with constant threshold θ and increasing regulation rate ι leads to a monotonic decrease in total costs $c(e_t, N_t, P_t)$. This indicates that there are no complex dynamic interactions between non-breeder size P_t and regulation rate ι or threshold θ .

Among culling strategies, the total costs $c(e_t, N_t, P_t)$ of strategies can be compared, as the type of regulation measurements is the same for these strategies. Culling only breeders N_t in an optimal way causes the least total costs among all culling strategies. For all types of culling strategies it is optimal to choose a regulation strategy close to those which do not maintain population viability. Optimal and cheapest strategies are different, which means it would be cheapest to accept an high extinction risk.

Reducing the environmental capacity K for breeders does not endanger population survival over a wide range of regulation strategies. The shape of the contour plot of total costs $c(e_t, N_t, P_t)$ has a maximum at $\iota \approx 0.3$ and $\theta \approx 0.8$. The contour is caused by the same interplay between regulation effort and cormorant-caused damage, as in the case of culling breeders, but looks different because the dynamic response of the population is different when its capacity is reduced (cf. Section 4.3). Therefore, it is optimal to reduce environmental capacity with a low threshold θ and low rate ι . The optimal and cheapest strategy are the same for this type of regulation, which corresponds to the results of Section 4.3.

In case of egg-oiling, Figure 7.1 shows that it would be optimal not to regulate if egg-oiling were the only possible type of regulation strategy. Increasing regulation intensity ι or lowering threshold θ only increases effort but does not reduce population size, and thus damage, considerably. Even degrading population viability is more expensive. Thus, the cheapest and optimal strategy coincide at the strategy of regulating as little as possible ($\iota = 0.1$ and $\theta = 1.5$). This corresponds to Section 4.3, where it was shown that reducing the reproduction rate (i.e. egg-oiling) does not lead to a significant reduction of the population size.

The relation between population size $N_t + P_t$ is also shown in Figure 7.2. The plots show regulation costs and damage costs of those strategies that keep the population viable ($P_0(100) < \varepsilon_p = 0.05$). In all plots the damage costs increase linearly, as was assumed for the definition for of the costs function $c(e_t, N_t, P_t)$ (cf. 5.36).

In Figure 7.2, in strategies involving culling breeders N_t , culling both breeders N_t and non-breeders P_t , as well as for reducing breeder capacity K , the points seem to be ordered along families of lines. These lines indicate trade-offs caused by the fact that the effective reproduction rate $r_{eff} = r(1 - N_t/K)$ is highest for population sizes at $N_t = K/2$. This means that the resistance of the population against regulation attempts and thus the effort and costs of regulation are highest in this region of $N_t = K/2$. This mechanism is mainly responsible for the observed shapes of the contour plots of total costs $c(e_t, N_t, P_t)$ in Figure 7.1.

Figure 7.2 shows that neither culling of non-breeders P_t nor egg-oiling reduces total population size $N_t + P_t$ considerably. Furthermore, no trade-off is observable for these two types of regulation strategies. For culling non-breeders P_t the total costs are mainly caused by damage costs, whereas egg-oiling itself can be very costly, too. This plot makes clear that *in this conceptual model* egg-oiling can be a waste of resources.

7.2 Applying the Age-Structured Cormorant Model

The sensitivity analysis of the age-structured cormorant model, which provided insights into the role of the single parameters for population dynamics, and the application of regulation strategies to the conceptual cormorant model suggest that a wide range of regulation strategies might be applicable without an associated risk of degrading population viability. This hypothesis is now tested by applying regulation strategies to the age-structured cormorant model and assessing their performance.

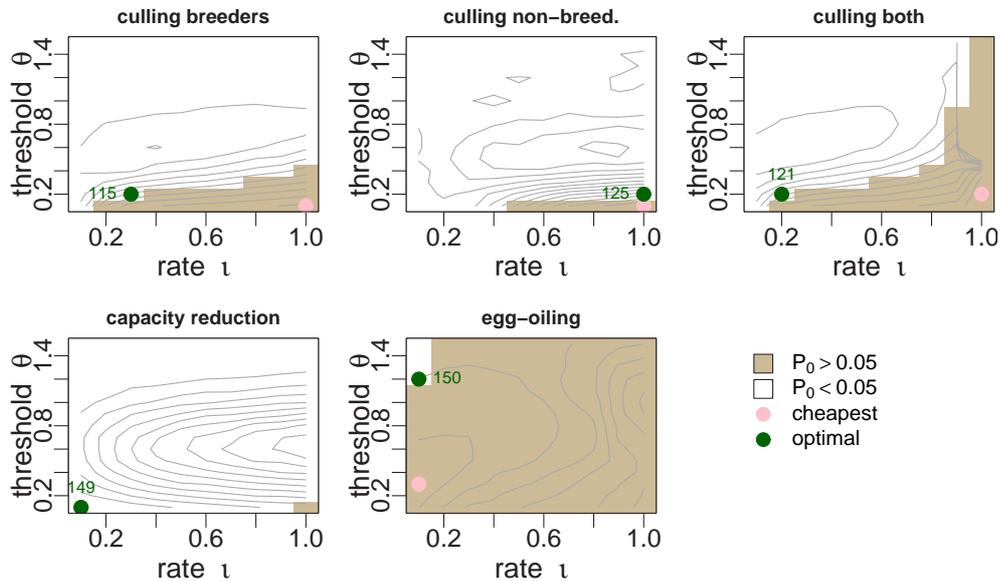


Figure 7.3: Total costs and population viability for the different types of regulation strategies. The cormorant model is parameterized with the reference parameterization. Total costs are given in units of 10^5 .

Figure 7.3 is organized as Figure 7.1 before: darker areas indicate strategies leading to $P_0(100) > \varepsilon_p = 0.05$. Aside from the lines of equal total costs, the strategy causing the lowest total costs (lighter point) and the optimal strategy (darker point) are marked. Figure 7.3 shows that culling breeders N_t or breeders *and* non-breeders P_t with a low threshold θ degrades the population viability. If both population parts N_t and P_t are culled at the same time with a high rate τ , population viability is also degraded. Culling only non-breeders P_t or reducing the environmental capacity K for breeders is only dangerous for very low thresholds or not at all. Apart from egg-oiling all other strategy types conserve population viability over a broader range of strategies than in the conceptual case (cf. Figure 7.1). Nevertheless, the fact that only extreme regulation strategies degrade population viability is similar to the results seen using the conceptual model (cf. 7.1).

The lines of equal total costs in the contour plots of culling strategies are different from the conceptual model. The smallest differences occur for strategies involving culling breeders $N_{i,t}$ only, because in this case the dynamical response of the age-structured model is similar to the one in the conceptual case. For culling non-breeders P_t only, Figure 7.3 shows distinct differences in the contour plot of total costs $c(e, N_t, P_t)$. This is a consequence of the fact that individuals from the youngest age-class nearly always convert to non-breeders (cf. Table 5.2) before they later convert back into breeders. Hence, breeders are much more strongly affected by culling non-breeders than in the conceptual model. Therefore, the contour plots of culling breeders and culling non-breeders are similar to a certain extent – both culling breeders N_t and culling non-breeders P_t affect breeder dynamics. Therefore, combined effects occur in the case of culling breeders and non-breeders at the same time. However, despite these differences, optimal strategies for all culling strategies are located close to the strategies which degrade population viability ($P_0(100) > 0.05$) and which cause lower total costs than the optimal strategy.

Figure 7.3 shows that in strategies reducing the capacity K , total costs increase monotonically with increasing regulation rate ι . It also shows a trade-off in the regulation threshold θ , which again is caused by the interplay between regulation effort and cormorant-caused damage: Regulation is worth its effort when population size $N_t + P_t$ declines below a certain value. Then the reduction of cormorant-caused damage is stronger than the effort of regulation. As in the conceptual model (Section 7.1) the optimal strategy is characterized by low regulation rate ι and a low threshold θ . Again, it coincides with the strategy causing least total costs.

The results for egg-oiling strategies shown in Figure 7.3 are completely different than in the conceptual case. They degrade population viability over a wide range of ι and θ and the strategy causing least total costs and the optimal strategy are different. The reason for the differences lies in the model structure. Egg-oiling is not directly comparable to the reproductivity r reducing strategies in the conceptual model. The reduction of reproduction rate r in the conceptual model is $(1 - \iota)r > 0$. Egg-oiling in the age-structured model reduces birth rates b_i and can lead to $(1 - \iota)b_i - d_i < 0$. In this latter case the population is prone to extinction. Stochasticity in birth b_i and death rates d_i amplifies this effect. Therefore, egg-oiling can easily lead to population extinction. Furthermore, egg-oiling affects the effective capacity $K_{eff,t}$ (cf. Equation 5.2) of the population, which is dependent on b_i . Therefore, by reducing b_i , $K_{eff,t}$ and population size $N_t + P_t$ can be decreased. For stronger reductions of b_i very low values of $K_{eff,t}$ can be reached, to which breeder size N_t , and total population size $N_t + P_t$ follow. If population size is low, environmental stochasticity can lead to population extinction.

Analogously to Figure 7.2 in Section 7.1, Figure 7.4 shows the relationship between population size $N_t + P_t$ and the components of the cost function $c(e, N_t, P_t)$,

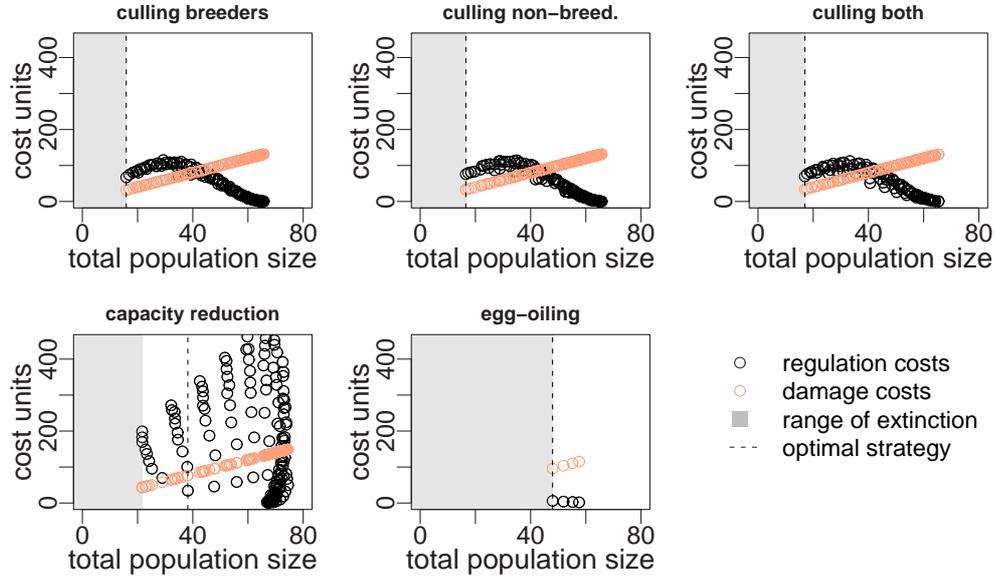


Figure 7.4: Regulation costs resp. damage costs vs. population size $N_t + P_t$ in the age-structured model for the entire range of (θ, ι) . The dashed lines indicate the population size of the optimal strategy as marked in Figure 7.3.

i.e. regulation costs and damage costs (cf. Equation 5.36). Additionally, Figure 7.4 shows the range of population sizes $N_t + P_t$ where population viability is degraded (gray areas in Figure 7.4).

For all culling strategies there is a noticeable functional relationship between population size $N_t + P_t$ and regulation costs. This functional relationship shows a clear trade-off in regulation costs depending on the population size, which again is caused by the fact that for intermediate breeder sizes N_t , the effective growth rate is highest and thus the population is most resistant against regulation attempts. As in the conceptual model, this trade-off explains the shape of the contour plots for culling shown in Figure 7.3. Figure 7.4 indicates that for all types of culling there are various strategies which lead to population sizes $N_t + P_t$ and total costs, which are close to the ones of the optimal strategy. This means that the performance of culling is less dependent on the actually chosen regulation threshold θ or rate ι , but on the population size achieved by the strategy.

Furthermore, the plots of the three types of culling in Figure 7.4 show that there is only a small difference between the functional relationships for total population size $N_t + P_t$ and regulation costs. This means that with different culling strategies the same total population sizes $N_t + P_t$ can be achieved with equal *regulation costs* (which does not necessarily mean that strategy parameters ι and θ have to be equal, as Figure 7.3 shows). That the three culling strategies perform equally, contrary to the results found in the conceptual model (Figure 7.2), can be explained by the fact, that in the age-structured model younger individu-

7.3. Sensitivity of Optimum to the Cost Function

als strongly tend to convert into non-breeders and thus, regardless of the breeder size N_t , the exchange between the two population groups is high. This means that even though only non-breeders are culled, nearly every individual is exposed to culling during its life time. Hence, culling non-breeders can achieve reductions comparable to the two other culling strategies.

The performance of strategies, which reduce the environmental capacity K for breeders, depend strongly on regulation threshold θ and rate ι , and a particular population size $N_t + P_t$ can be achieved with strongly differing regulation costs. Again there is a trade-off in regulation costs depending on population size, but in contrast to culling, and similarly to the conceptual case, the trade-off in regulation costs is strongly influenced by the regulation intensity ι .

For the few egg-oiling strategies which do not degrade population viability, the achieved reduction of population size is less than for the other strategy types. Regulation costs increase only marginally with decreasing population size $N_t + P_t$ and total costs are mainly caused by damage costs.

7.3 Sensitivity of Optimum to the Cost Function

Up to now it was assumed that the damage costs q caused by one cormorant is 100 times higher than the costs u of killing one cormorant or preventing it from being born. This is a rather arbitrary setting. But, as data on realistic cormorant damage differ strongly (RED [2002]) and the costs of regulation measurements are also hard to estimate (van Dam and Asbirk [1997]), it remains unclear how to parameterize q . Furthermore, the position of the optimal strategy in the ι - θ -plain is the result of the interplay between ecological and economic factors,

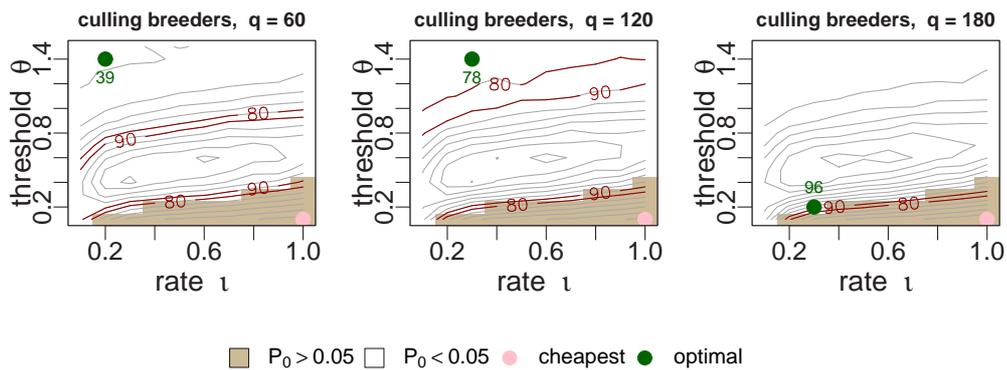


Figure 7.5: Variation of damage costs q for culling breeders N_t . Two lines of total costs are marked ($c(e_t, N_t, P_t) = 80$ and $c(e_t, N_t, P_t) = 90$) to show that increasing q affects the total costs of strategies with high threshold θ and low intensity ι more than total costs of strategies with low threshold θ and high rate ι . Total costs are given in units of 10^5 .

which is also reflected by the cost function $c(e, N, P)$. Getting an idea about the importance of the different cost elements for the optimum regulation strategy is an important issue. Therefore, in this section the role of the costs caused by cormorants in relation to the costs of regulation is assessed. For this purpose q will be varied. Despite these rather technical issues, the results of the cost-function can be viewed and interpreted in different ways. This will also be discussed in this section.

It is started with an example illustrating the role of damage costs q . Figure 7.5 shows how increasing the damage costs q changes the contour plot of the cost function and the position of the optimal strategy, using the culling of breeders N_t as an example. In Figure 7.5 two lines of equal total costs are marked. They mark $c(e_t, N_t, P_t) = 80$ and $c(e_t, N_t, P_t) = 90$. They indicate that increasing q raises total costs and that this increase is stronger for high thresholds θ and low rates ι of regulation. In Figure 7.5 for $q = 60$ and $q = 120$, it is optimal to regulate only with high thresholds θ . Between $q = 120$ and $q = 180$, the situation changes and it becomes optimal to regulate with low thresholds θ . For the strategy which causes least total costs, this change already occurs between $q = 60$ and $q = 120$, because this strategy does not take population viability into account.

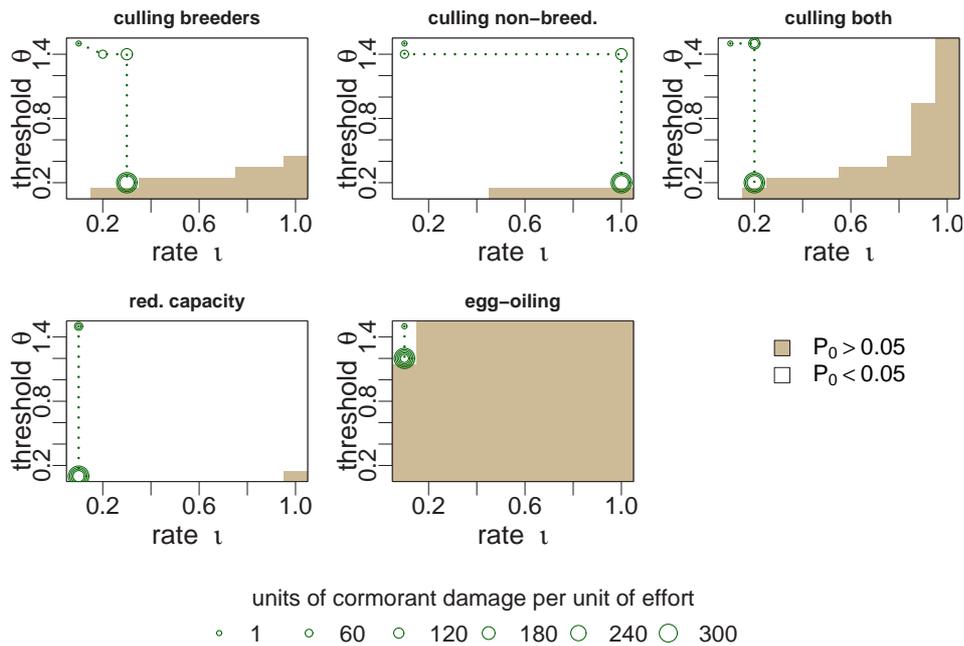


Figure 7.6: Variation of damage costs q for the five regulation types (reducing breeders (N), non-breeders (P) or both (B), reducing breeder capacity (K) or birth rates (B)). Circles mark the position of the optimal regulation strategy for the respective weighting of cormorant damage.

This shows that gradually increasing damage costs q causes a threshold behavior in the position of the optimal strategy. This threshold is caused by the

7.3. Sensitivity of Optimum to the Cost Function

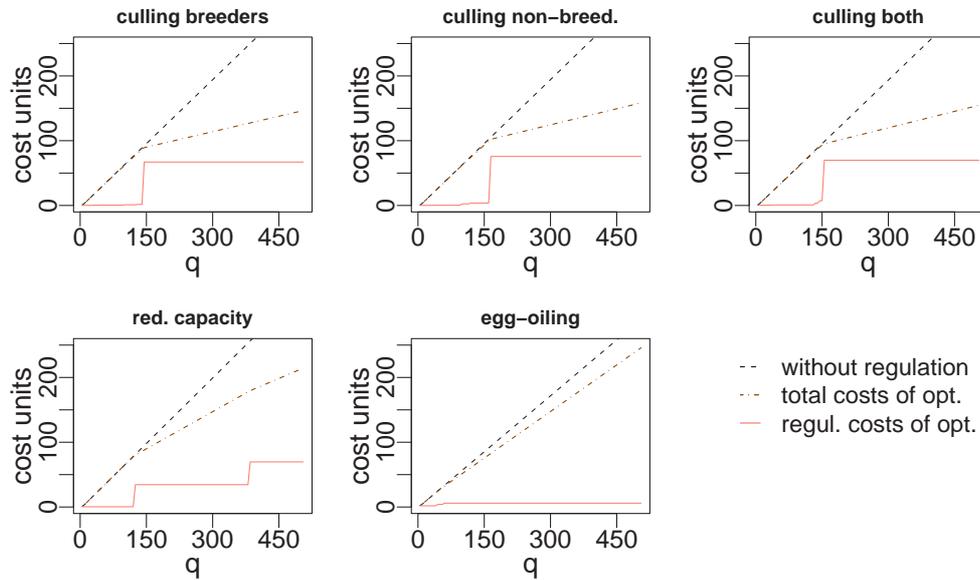


Figure 7.7: Mean total costs $c(e_t, N_t, P_t)$ (see Equation 5.36) of the optimal regulation strategies for increasing relative cormorant-caused damage q for the five considered types of cormorant regulation strategies. All costs are measured in units of 10^5 .

shape of the contour plot of total costs, which has its maximum for medium regulation thresholds θ and medium regulation rates ι . (The reason for this shape was discussed in Section 7.2.) Whether the optimum lies on a certain side of the maximum of the contour plot of the cost function depends on the damage costs q .

Figure 7.6 illustrates that the threshold behavior, which was exemplarily shown for the culling of breeders in Figure 7.5, is also observable for the other two culling strategies and for reducing breeder capacity K : Increasing the damage costs q leads to increased total costs. Above a certain threshold, which lies between $q = 120$ and $q = 180$ for all culling strategies, and between $q = 60$ and $q = 120$ for reducing K , it becomes optimal to reduce the population with a low regulation threshold θ . After this “jump“, i.e. when damage costs q are high, in the considered range of q the position of the optimal strategy becomes insensitive to further increases of q . For egg-oiling this distinct threshold behavior of the optimal strategy is not observable. Nevertheless, for relative cormorant damage of $q \leq 60$ it is optimal not to regulate. For $q \geq 120$ the optimal egg-oiling strategy is close to strategies which lead to an increased extinction risk of $P_0(100) > 0.05$.

Figure 7.7 shows how, depending on damage costs q , total costs are affected by regulation. It reflects the existence of critical q -values for the culling and capacity K reducing strategies. The figure also shows that the reduction of total costs is strongest for culling strategies, whereas reducing capacity K and egg-oiling yield only a low reduction of total costs. This corresponds to the results of

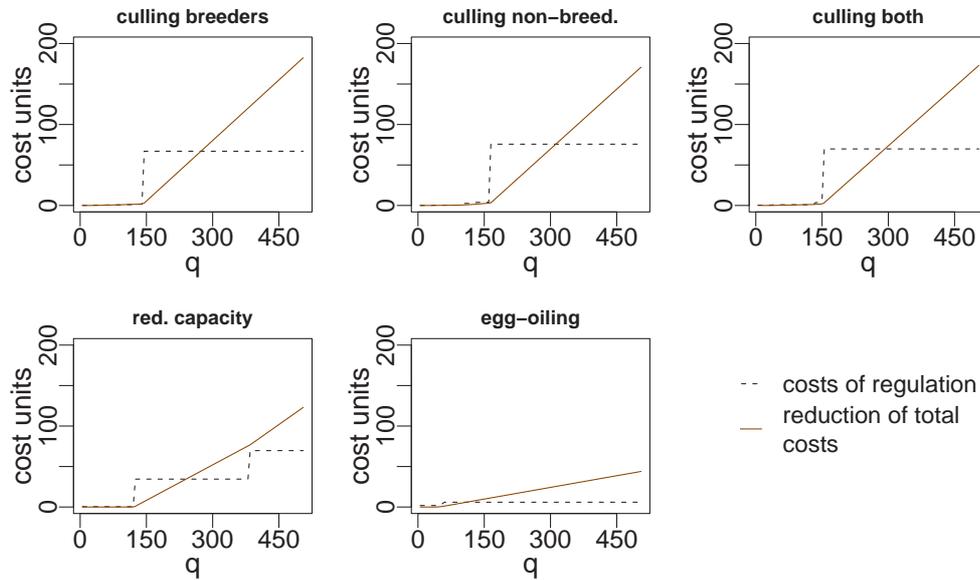


Figure 7.8: Benefit (reduction of total costs $c(e_t, N_t, P_t)$, see Equation 5.36) and regulation costs of the optimal regulation strategies for increasing cormorant-caused damage costs q . Costs are plotted without (upper row) and with (lower row) a limiting budget for regulation of 50 cost units. All costs are given in units of 10^5 .

the sensitivity analysis, which showed that total population size is most sensitive to mortality of breeders d and non-breeders δ . However, it should be noted that as no data regarding the real damage costs is included here, only culling strategies can be compared directly. Figure 7.7 also shows that, for culling, the majority of total costs are caused by regulation, if regulation takes place, whereas for reducing capacity and egg-oiling the main part of the total costs is caused by the cormorant population (damage).

Figure 7.8 shows another perspective. There, regulation costs and the achieved reduction of total costs are compared directly, which provides a cost-benefit perspective into the performance of regulation strategies. Even though regulation reduces total costs $c(e, N_t, P_t)$ (regulation costs plus damage costs), for all types of strategies a certain range of q exists, where regulation costs exceed the reduction of total costs. This means that for optimal strategies (which minimize total costs $c(e, N_t, P_t)$) the invested *regulation costs* can exceed the benefit.

Figure 7.8 also shows that even though optimal strategies for culling differ in θ and ι , they perform equally. This corresponds to the finding shown in Figure 7.4. From the perspective of cost-benefit and in the considered range of q , egg-oiling can yield a higher benefit per invested unit of regulation cost than the other strategies.

In practice it is most likely that the budget for regulation measurements is limited. In Figure 7.9 the budget for regulation is arbitrarily set, such that only

7.3. Sensitivity of Optimum to the Cost Function

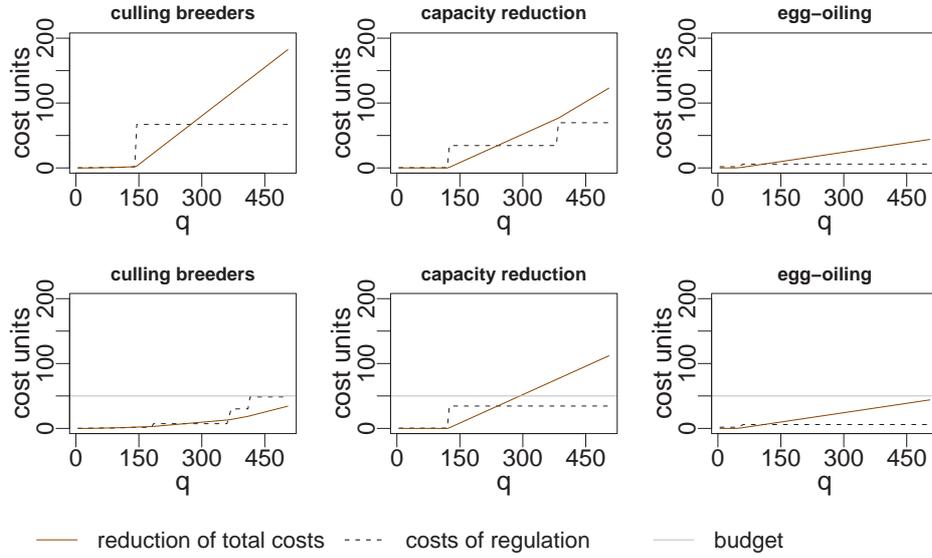


Figure 7.9: Benefit (reduction of total costs $c(e_t, N_t, P_t)$, see Equation 5.36) and regulation costs of the optimal regulation strategies for increasing cormorant-caused damage costs q for the five considered types of cormorant regulation strategies. For costs of regulation a limited budget is assumed. All costs are given in units of 10^5 .

those regulation strategies are considered for which $\bar{e}_t^2 \leq 5 * 10^6$ hold (note, as the scaling factor is $u = 1$, cf. 5.36, the line marking the budget is drawn at $costs = 50$ in Figure 7.9). In the case of the considered budget, the benefit of culling strategies is strongly decreased and falls below the regulation costs. This can be explained by the fact that the limited budget does not allow the choice of culling strategies with a low threshold θ , because this would mean regulating frequently, which in turn causes higher costs. Hence, in the case of this limited budget the optimal culling strategies have higher regulation thresholds θ (not shown here). Reducing breeder capacity K is only a little, and egg-oiling not at all, affected by the given exemplary budget. This shows that, depending on the real costs and budget, these two strategies might be considerable options.

Figure 7.9 also shows that for all three types of culling strategies it might not be optimal to scoop the entire budget. Furthermore, limiting the budget for culling can lead to a strongly decreased reduction of damage costs q . For the given budget this is different for capacity K reducing strategies and egg-oiling, as long as the regulation costs do not exceed the budget (cf. Figure 7.9), i.e. the budget does not limit regulation measurements in this case. Thus, both are not affected by the limited budget.

This section showed that the optimal regulation strategy depends on the damage costs q and by the budget at hand. Up to now, a dependence of the results to the characteristics of the non-breeder pool was not considered. In the following the influence of breeder-non-breeder interchange is assessed.

7.4 Sensitivity to Breeder-Non-Breeder Interchange

In this section, the age-structured cormorant model is used to examine the sensitivity of the performance of regulation strategies to the parameters of breeder-non-breeder interchange (λ , s , β , and h). The results of the conceptual analysis (Part I, Chapter 4) suggest that these parameters can also influence regulation effort and thus costs of regulation (see sections 4.2 and 4.3). To see if this holds for the more complex cormorant model, the parameters defining non-breeder response to breeders' loss (β and k) are varied first, then parameters defining non-breeder supply (λ and s). This is done in the same way as in the sensitivity analysis in Section 6.1. The range z (cf. Section 6.1) within which the age-dependent parameters are varied is $z = 0.4$.

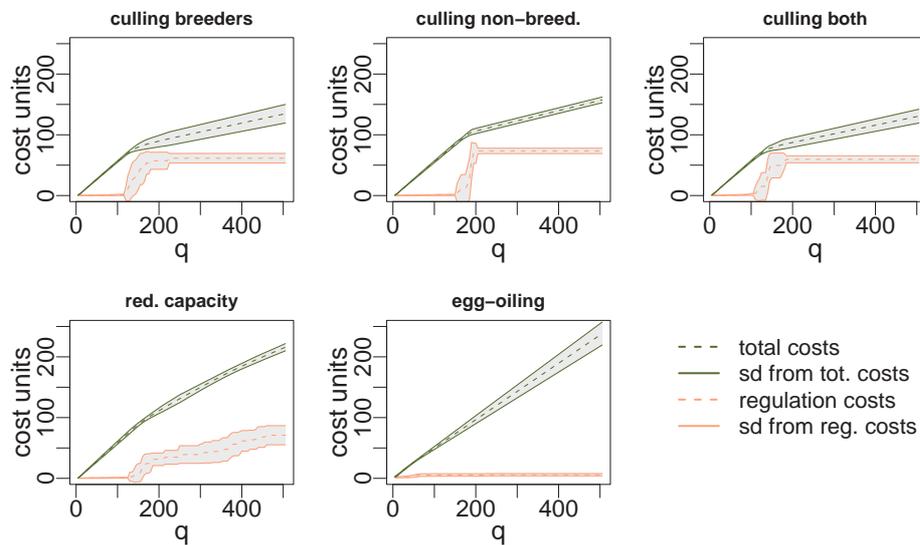


Figure 7.10: Mean and standard deviation of costs for regulation, and total costs. The characteristics of non-breeder response to breeders' loss (β and k) in the age-structured model are varied around the reference parameterization (Table 5.2). Costs are given in units of 10^5 .

Figure 7.10 shows the total costs and the costs of regulation measurements, depending on relative cormorant-caused damage q , and the standard deviation induced by varying the parameters β and k . (Note, it is only parameter variation that induces the deviations in costs, not statistical effects caused by environmental stochasticity.) For all strategies, the standard deviation is low. It increases slightly for total costs with increasing damage costs q . This means that costs are not strongly influenced by the characteristics of the non-breeder response to breeders' loss. What is influenced by these characteristics is the value of q for which another strategy becomes optimal. This is indicated by the higher standard deviation around the “jump” in regulation costs from low to high mean values.

Figure 7.11 shows the results for the variation of the parameters determining

7.4. Sensitivity to Breeder-Non-Breeder Interchange

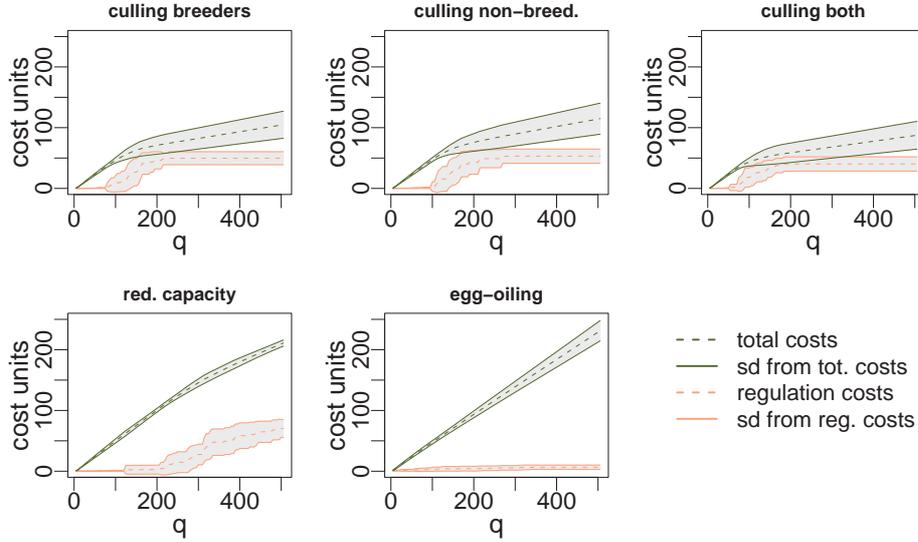


Figure 7.11: Mean and standard deviation of costs for regulation, and total costs. The characteristics of non-breeder supply by breeders (λ and s) in the age-structured model are varied around the reference parameterization (Table 5.2).

non-breeder supply λ and s . For this variation, standard deviations of costs of culling are higher than in Figure 7.10, because λ and s influence the density dependence of breeders N_t : The lower s and λ , the more breeders stay in the breeder stock when the breeder density increases. This leads to a lower supply of the non-breeder pool and to higher losses of breeders due to density regulation. These two effects reduce total non-breeder size and, thus, total population size, which in turn influences regulation costs and total costs.

The link between population characteristics and the costs of optimal strategies is provided by the contour plots of the total cost function $c(e_t, N_t, P_t)$. This function is also affected by non-breeder supply by breeders, determined by s and λ . This is exemplarily illustrated in Figure 7.12 for the variation of breeder sensitivity to density s_i and culling of breeders. It shows the optimal strategies and the strategies causing least costs for varying relative cormorant-caused damage q . Two values of s_i are considered: s_i^{ref} in the top row and $s_i = \max[s_i^{ref} - 0.1, 0]$ in the second row. It can be seen that for reduced s_i , the range of strategies which degrade population viability increases. Furthermore, depending on s and q , the position of the optimal strategy in the ι - θ -plane can vary considerably, as well as the total costs of the optimal strategy. In this example total costs $c(e_t, N_t, P_t)$ are lower in the case of a reduced parameter s than in the reference case.

The explanation of both effects caused by reduced breeder sensitivity s_i is as follows: If s_i is reduced, breeders are less sensitive to their own density and breeders tend more to stay in the breeder stock. Thus, density regulation affects breeder size N_t more strongly. At the same time, the non-breeder pool is less

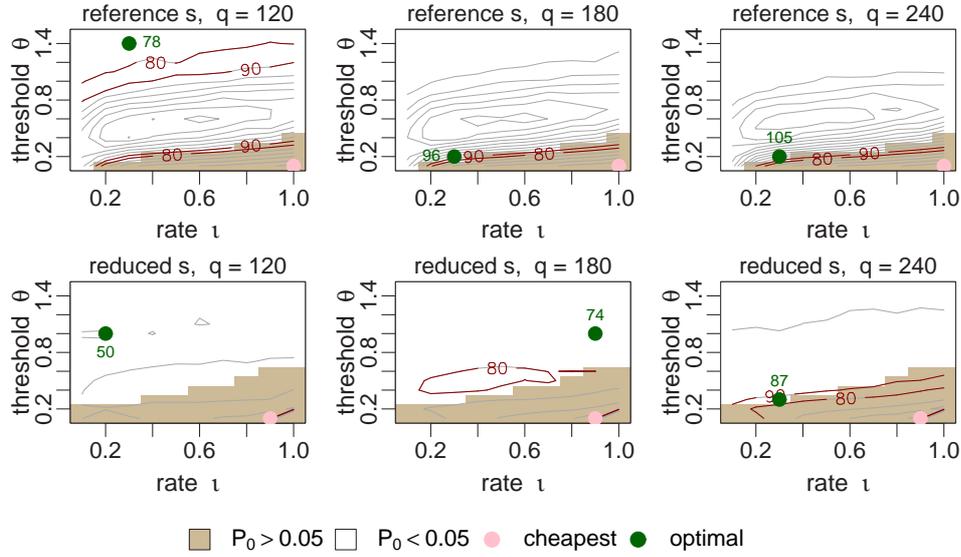


Figure 7.12: Influence of breeder sensitivity s_i on their own density can influence the structure of the cost landscape in the example strategy of culling breeders. Upper row: reduced sensitivity $s_i = \max[s_i^{ref} - 0.1, 0]$. Lower row: sensitivity on reference value s_i^{ref} . All other parameters are held on their reference values (Table 5.2). Costs are given in units of 10^5 .

supplied and hence its size is reduced. Thus, lower sensitivity of breeders to their own density decreases population size, which in turn leads to lower regulation costs but also to lower population viability in the case of strong regulation.

The example in Figure 7.12 also shows that changed population parameters may also change the contour plot of total costs, which again explains the standard deviations in the costs of optimal culling strategies shown in Figure 7.11. Finally, Figure 7.13 provides an additional perspective on the influence of the variation of parameter s_i on the performance of regulation strategies. There it is shown that the relation between regulation costs and total population size $N_t + P_t$ changes for decreased s_i values (cf. Figure 7.4). The trade-off in regulation costs, which was observed for culling strategies in the reference scenario (Figure 7.4), is not observable for decreased s_i (Figure 7.13). Furthermore, Figure 7.13 confirms the earlier statement that the range of population sizes is smaller for decreased s_i .

Figures 7.10 to 7.13 show that the characteristics of the breeder-non-breeder interactions, and especially breeder sensitivity s_i to density, can influence the performance of regulation strategies. This not only holds in a quantitative way but also qualitatively, as can be seen in Figure 7.13. The effects are mainly caused on the level of regulation costs and damage cost and less on the level of population viability (cf. Figure 6.2).

7.5. Summary of Results for Cormorant Regulation

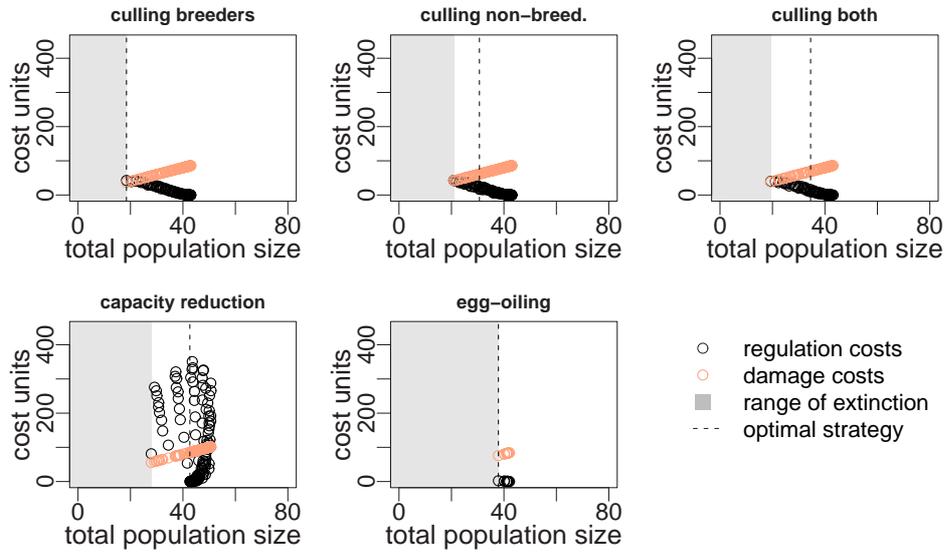


Figure 7.13: Population size $N_t + P_t$ vs. regulation costs and damage costs in the age-structured model for reduced sensitivity $s_i = \max[s_i^{ref} - 0.1, 0]$. The dashed lines indicate the population size of the optimal strategy.

7.5 Summary of Results for Cormorant Regulation

Before the part of this thesis is discussed as a whole, the last chapter on regulation of the cormorant population is briefly summarized. Both models, conceptual and age-structured, suggest that the cormorant population can be considered as rather viable. This holds even in the face of strong environmental catastrophes. Therefore, regulation (with the exception of the egg-oiling strategy) only degrades population viability when carried out with very low regulation thresholds θ and/or high regulation rates ι .

On the economic side, the response of the population to regulation attempts can cause a trade-off in regulation costs depending on the achieved population size. This trade-off means that above certain damage costs, regulation (except egg-oiling) is optimal when carried out such that population size is as low as possible. This is achieved by low regulation thresholds θ and, for culling breeders N_t or both N_t and P_t or for reducing capacity K , by low regulation rates ι . For culling only non-breeders P_t , the regulation rate has to be high in order to achieve the lowest viable population size. All optimal culling strategies reduce population size $N_t + P_t$ to values near non-viable population sizes. Egg-oiling plays a special role because it can easily degrade population viability by influencing K_{eff} and/or by decreasing birth rates b_i below death rates d_i .

As data about costs of regulation are not included in this study it can not be stated which *type* of regulation strategy is optimal. What would be optimal in practice depends on the actual regulation costs, the budget at hand and the aim

of regulation, i.e. if the cost-benefit ratio is to be optimized or if total costs are to be minimized.

The performance of regulation strategies is not only influenced by these externally set conditions but also by characteristics of the breeders-non-breeder interchange. These characteristics affect population size, population response to regulation and thus population viability, regulation costs, and total costs.

7.5. Summary of Results for Cormorant Regulation

Discussion

Part II of this thesis focused on two major aims: first, to test the rules of thumb developed in the first part using the conceptual model, and second, to contribute to the development of appropriate regulation strategies for the Great Cormorant. Of special interest was the role of the pool of non-breeders featured in the cormorant population. In the following, Part II will be discussed from different perspectives, namely the viability of the cormorant population, the performance of regulation strategies, and general methodological aspects.

8.1 Viability of the Cormorant Population

Both the conceptual and the age-structured cormorant models reveal a strong viability of the cormorant population. Hence, the situation belongs to CASE I, where the non-breeder pool is not decisive for population viability. This is caused by several factors: First, birth rates b_i , and thus the corresponding mean reproduction rate r , are relatively small ($r \approx 1$). Second, the strength of environmental stochasticity $var(\eta)$ was assumed to be relatively low ($var(\eta) = 0.05$) and the considered catastrophic event was moderate. Both assumptions lead to a situation where over-compensation or environmental stochasticity do not cause strong declines in population size, which also corresponds to the results of Part I. Third, the consideration of age classes leads to less over-compensation, but also to the continuous supply of the non-breeder pool by young individuals, which is independent of the emergence of a surplus among breeders. All this results in a high viability of the population, which in turn leads to a reduced importance of the non-breeder pool. This is in agreement with the findings of Part I, where it was pointed out that the non-breeder pool plays a minor role in cases with low environmental and intrinsic fluctuations.

In the age-structured model, the sensitivity s_i of breeders to their own density ensures a permanent supply and thus preservation of the non-breeder pool, which stabilizes dynamics and increases the robustness of the population against distur-

bances and also causes resistance against regulation attempts. As a consequence, the majority of the regulation strategies (with the single exception of egg-oiling) were found to be non-risky for population viability for a broad range of regulation thresholds θ and regulation intensities ι . Nevertheless, population viability can be degraded if the population size is reduced too strongly. Then, the situation might become similar to that of the Spanish imperial eagle, for which Penteriani et al. [2005] showed that non-breeder survival affects population viability.

In the case of the cormorant, in many situations strategies with $\theta < 1$ are optimal. This indicates that it is *not* necessary to ensure the supply of the non-breeder pool by only allowing high thresholds θ , but the assumed stop-loss-rule is already sufficient to protect regulated cormorant populations from extinction. This is consistent with findings of studies on threshold harvesting (e.g. Lande et al. [1997], Lande et al. [1995]). Without the stop-loss-rule, regulation would endanger population viability much more, as the study of Frederiksen et al. [2001] reveals. Applying a model of the Danish cormorant population, they found that the population becomes extinct if the culling quota exceeds a certain threshold.

The sufficiency of the stop-loss-rule, for a broad range of ι and θ , identified in this study, however, is a direct consequence of the conditions found for the cormorant population and its resulting high viability and robustness (see above). As Part I showed, populations with strong over-compensation which are exposed to moderate environmental stochasticity and catastrophes, for instance, can show different behavior. They are found to be dependent on a powerful non-breeder pool. In such cases a stop-loss-rule alone is insufficient to prevent the population from extinction. Then, regulation strategies additionally have to meet the condition of refilling the non-breeder pool sufficiently.

8.2 Performance of Regulation Strategies

In this section, the results of the analysis of the performance of regulation strategies are discussed. For this purpose the issue will be viewed from different (normative) perspectives, which will concern reduction of total costs, reduction of damage, cost-benefit, and the decomposition of total costs. These different perspectives correspond to different situations of “who has to pay for what”, i.e. which costs are considered to be relevant for decisions about regulation. Finally the role of uncertainty in the performance of regulation strategies will be discussed.

Reduction of total costs The analysis showed that for every type of regulation strategy, total costs and population viability respond differently to changes in the strategy parameters. This was shown by the contour plots of the total cost function (e.g. Figure 7.3), which subsumed all relevant effects of the interplay of ecological dynamics, management, and economic evaluation. These plots al-

lowed the identification, for each type of strategy, of the characteristics of the optimal regulation strategy, i.e. of the strategy which causes least costs while still conserving population viability.

The analysis showed that, regardless of the strategy type, optimal strategies are characterized by either high or low regulation thresholds θ . Regulation with intermediate thresholds θ leads to high total costs for all strategy types or in the case of egg-oiling, to a degradation of population viability. The high costs for medium thresholds θ reflect that the effective growth rate of the population is highest for $N_t \approx K/2$ as therefore is the resistance of the population against regulation attempts. This finding appears to be robust for a broad range of ecological and economic parameters.

Whether it is optimal to regulate weakly or strongly, depends for all strategies except for egg-oiling on parameter q , which is the damage caused by a single cormorant in relation to the cost of reducing the population size by one cormorant. Increasing q does *not* cause gradual changes of the optimal strategy, but rather an abrupt switching from low to high regulation thresholds θ .

The different types of regulation strategies can be directly compared if their real costs u and the real damage costs q are known. Currently, this data is not available or only vaguely summarized (RED [2002]). Therefore, in the following it is assumed, that all strategy types share the same u (an assumption which certainly can be questioned). If this is so, then below certain damage costs q^* , regulation does not pay off for any strategy except egg-oiling. Egg-oiling can already achieve reductions of total costs for smaller values of $q < q^*$. Above q^* and under the given assumptions, a ranking of strategy types according to the reduction of total costs can be given:

culling \triangleright capacity reduction \triangleright egg-oiling

Reduction of damage If the reduction of damage is the aim, for all types of strategies it holds that below certain per capita damage costs q^* , costs cannot be further reduced by regulation measurements. Hence, inactivity is found to be optimal. For egg-oiling, q^* is considerably smaller than for the other strategy types. Under the same assumptions as before (u is equal for all strategy types), for small values of q a ranking of strategy types according to damage reduction would be:

egg-oiling \triangleright inactivity

For higher values of damage costs q , optimal culling (regardless of the type) yields the highest reductions of damage costs followed by optimal reducing capacity K and then optimal egg-oiling. Hence, the resulting ranking reads:

culling \triangleright capacity reduction \triangleright egg-oiling

This ranking is not only influenced by the per capita damage costs q but may also be altered by the size of the budget at hand. Such a budget limits the resources that can be used for regulation and can, if set “too low”, lead to a strong decrease in the achieved reduction of damage. This can alter the ranking of strategy types.

Cost-benefit Another perspective emerges if the minimization of cost-benefit ratio is the aim. In the midsection of the considered range of q , for culling as well as for capacity reduction, regulation costs exceed the reduction of total costs. The target function $c(e, N_t, P_t)$ for the optimization does not incorporate the cost-benefit perspective. If it would, then in the midsection of q either different strategies or no regulation would be optimal.

If per capita damage costs q are high and under the assumption that u is equal for all types of strategies, egg-oiling leads to the lowest cost-benefit ratio. It is followed by culling and capacity reduction:

egg-oiling \triangleright culling \triangleright capacity reduction

Again, assuming a budget that limits regulation costs, can alter the ranking. For the presented exemplary budget, culling leads to the worst cost-benefit ratio:

egg-oiling \triangleright capacity reduction \triangleright culling

The rankings from different perspectives show that, depending on the economic perspective, statements about regulation options can strongly differ qualitatively. The considered types of costs, as well as the parameters of the cost function, influence which strategy of which type will be judged to be optimal. The different perspectives reflect that all costs (damage and regulation) can be internalized when total costs are considered, but can also be viewed as partly external in cases where only the reduction of damage is considered. This differentiated result is important in the face of the fact that, first, different parts of total costs (damage and regulation) may affect different groups of stakeholders, which might then prefer different target functions. Second, both the different perspectives and partly the damage costs q (i.e. what is considered as damage, e.g. loss of fishing industry profits or loss of fish species) are societal settings which have to be subject to negotiations (Behrens et al. [2008]).

Decomposition of total costs Both viability and cost function have proven of value in this study and provided insight into the functioning and performance of regulation strategies. However, both criteria are highly aggregated and do not reveal the consequences of the regulation strategies for population dynamics. This is different from Part I, where regulation targets were stated explicitly in terms of desired population size, which allowed the analysis of population dynamics in more detail. To link the aggregated measures of viability and costs of

Part II with Part I, the different components of total costs were examined explicitly (cf. Figure 7.4 or 7.13).

In particular, the decomposition of total costs revealed that, except for capacity reduction, in the age-structured model a unique relation exists between mean population size and mean costs. This relationship allows for the calculation of optimum population sizes (according to the target sizes M in part I) and the assessment of the performance of a given regulation strategy by monitoring population size. For capacity reduction this does not hold. There, it is possible to reach many population sizes on arbitrarily high costs.

Role of uncertainty The model analyzes allowed the assessment of the role of uncertainties on different levels, namely in ecological-economic targets, in relative per capita damage and in ecological parameters. Uncertainty about the first can lead to incorrect rankings of regulation opportunities. The same holds for the damage costs q . Furthermore, uncertainty in q can lead to the choice of strategies which are far from the real optimum. In the extreme case, regulation is executed strongly, where no regulation would be optimal. This in turn may cause strongly increased total costs. In any case, uncertainty in q entails uncertainty about the real total costs.

Uncertainty in the parameters defining breeder-non-breeder interactions, i.e. non-breeder supply (λ_i and s_i) by breeders and non-breeder response to breeders' loss (β_i and h_i), have different effects. Being out of the estimation of non-breeder response matters only marginally, whereas population viability under regulation regimes and the population response to regulation and thus regulation costs are sensitive to the non-breeder supply. In the worst case, an overestimation of breeder sensitivity s_i to their own density would not only lead to misjudgment of total costs but also to a decrease in population viability. Therefore, good estimations of non-breeder supply are crucial for the design of adequate regulation strategies. This renders the findings of Part I – that the parameters defining the interchange between the two population parts influence the performance of strategies more precisely – for the case of the cormorant. The importance of the non-breeder supply in the case of the cormorant complements with the finding of Part I that regulation has to conserve the non-breeder pool: In Part I the non-breeder pool has to be maintained by specific requirements for regulation; in Part II non-breeders are maintained by the characteristics of their supply by breeders.

This is closely related to the uncertainty about strength and even the presence of density dependence in cormorant populations (Smith et al. [2008], Green [2008], Frederiksen et al. [2001]). This study shows that if the model assumption of a derivate of logistic growth of the breeder stock holds (but see Saether et al. [2005b]), distinguishing between breeders and non-breeders differentiates between the response of only the breeder stock and the response of the entire population to density. Accordingly, the contradictory findings in the time series of the dynamics of cormorant populations which give evidence to both density

dependence and independence (Smith et al. [2008]) can now be better understood.

8.3 General Methodological Remarks

The following remarks focus on and discuss three methodological aspects, which are characteristic for Part II of this study: working with a sequence of complementary ecological-economic analyzes, working with a comprehensive cost function and optimization, and working with two cormorant models incorporating different levels of structural information.

Working with a sequence of complementary ecological-economic analyzes The performance of regulation strategies depends on a variety of ecological, technical and economic factors: the species-dependent characteristics of population dynamics, the characteristics of the regulation strategy (threshold θ , rate ι), and the species- and strategy-dependent characteristics of the cost function (per capita damage q , per capita regulation costs u). In this study, systematic complementary analyzes were performed that allowed for the analysis of the same system from different ecological-economic perspectives. For instance, the contour plots (e.g. Figure 7.3) of the cost function over the ι - θ -plane allow an assessment of different strategy types according to the performance criteria “viability” and “total costs”. On this basis, the optimal strategy can be identified and characterized.

However, that perspective does not allow for the implications of the optimal strategies for population dynamics or how total costs are composed. This is dealt with in the plots of mean costs vs. mean population size (e.g. Figure 7.4). These plots provide an understanding of the impacts of regulation on mean population dynamics and composition costs without being explicit in the strategy parameters. The optimum strategy marked in the latter plots provides “two pieces of information in one”: population size $N_t + P_t$ reached and total costs $c(e, N_t, P_t)$ induced by the optimum strategy.

This also bridges Part II and I, where the regulation strategies were assessed regarding the ability to reach a certain population size $N_t + P_t$. This demonstrates that this point of view, as chosen e.g. in Figure 7.4, also allows for the analysis of the functional relationship between the economic factors of interest and mean population size resulting from regulation, which were used in Part I.

Working with a comprehensive cost function and optimization The cormorant conflict is based on fishery losses caused by cormorants, which means that incorporating damage costs and, depending on the perspective, also the regulation costs, is crucial in order to find strategies to reconcile the conflict. The applied total cost function reflects this. It summarizes all relevant effects of the

interplay between intrinsic population dynamics, the response to the regulation, and the economic evaluation in terms of damage caused by the cormorant population and effort expended to regulate it.

The distinction made between “damage costs” and “regulation costs” also allows the assessment of the costs which would arise if no regulation takes place. This, admittedly on a different level, follows the approaches of the report of the IPCC (Intergovernmental Panel on Climate Change), which focused on the costs of inactivity in the context of climate change (IPC [2007]), or the TEEB report (The Economics of the Preservation of Ecosystems and Biodiversity), which focused on the costs of not preventing further damage to ecosystems (TEE [2008]). Thus, the cost function applied here enables the identification of inevitable costs, which are either caused by damage or regulation.

It is common to use Population Viability Analysis (PVA) in the context of endangered species (Coulson et al. [2001], Brook et al. [2000], Shaffer [1981]), but it is rather unusual – but nevertheless important – to explicitly include structures that can act as a *buffer* mechanism (Grimm et al. [2005]) into PVA. The developed optimization approach respects this and unifies PVA with the management of a pest, which is also rarely done (Smith et al. [2008]). To incorporate regulation and damage costs into such a framework appears to be even more uncommon.

Working with two cormorant models with different levels of structural information Two models were applied in this study. An age-structured model and a conceptual model. Both models explicitly incorporate the structure induced by breeders and non-breeders. In Part II, both models were parameterized on the basis of the same cormorant data (Frederiksen et al. [2002] and Bregnballe, personal communication). As model results can be sensitive to structural assumptions (Wood and Thomas [1999]), the outcomes of both models were compared. This provided insight into the additional effects of the inclusion of more biological details: age-structure and breeder sensitivity to their own density as well as the specific density regulation which only affects effective birth rates. The results indicate that both details alter dynamical properties of the population towards higher viability. Furthermore, the population response to different regulation strategies and consequently the shape of the contour plots of the cost function change. The altered population response to regulation becomes clearest when the dependency of regulation costs on total population size $N_t + P_t$ (Figure 7.4) is viewed. There it is shown that the biologically more realistic model exhibits a clear relationship between total costs of culling and population size.

During the analysis of the more detailed age-structured model, it turned out that breeder sensitivity s_i to their own density influences population viability under culling. This parameter determines the dependency of non-breeder supply on breeder size: the lower this sensitivity s_i , the more the non-breeder supply depends on high breeder numbers. Contrasting the two models shows that decreas-

ing s_i moves the response of the age-structured model to culling qualitatively towards that of the conceptual model.

As already mentioned, there are some aspects for which the conceptual and the age-structured models agree, as for example roughly in the range of culling strategies, which lead to high extinction risks. This corresponds with other studies, which show that under certain circumstances mean field models can capture the main dynamical aspects (Frank and Wissel [2002], Fahse et al. [1998]).

8.4 Concluding Remarks

This study developed a framework for the design of regulation strategies, which allows the explicit assessment of the performance of regulation strategies. It includes and integrates ecological as well as economic aspects and, thus, can guide the development of regulation strategies. Because of this it can be hoped that this study may help to bring more objectivity to the cormorant conflict.

However, the study is a *model* study, which naturally implies some limitations due to the necessary abstraction and restriction to a few aspects of a broader and more complex problem. Thus, it could be extended in several directions. For example, structurally different cost-functions might be considered, which could change the outcomes. Furthermore, space could be considered explicitly. Doing so would allow the inclusion of the fact that not all cormorant colonies are affected in the same way by adverse environmental conditions. Given the relatively high mobility of these birds (Frederiksen et al. [2002]), the population might then be considered to be even more robust in the face of catastrophes (Sole and Bascompte [2006], Huffaker [1958]). Another important point is the density regulation (Henle et al. [2004]), which was assumed to have the effect implied by the logistic equation. The comparison of the two models, which implement this density regulation in slightly different ways, shows evidence for this. As it is unclear, which is an appropriate assumption for density regulation (Green [2008], Saether et al. [2005b], Frederiksen et al. [2001]), different methods of density dependence could be included. By expanding the logistic equation in both models a decision about the order of processes taking place in every time step has been taken. Changing the order of these processes can change internal dynamics which might alter the model results. Other crucial decisions were taken about the characteristics of the environmental fluctuations. Assuming auto-correlated fluctuations or fluctuations distributed differently to those considered here, might also change model results (Heino and Sabadell [2003]; Morales [1999]). Thus, other than the modeling framework, neither the results from the conceptual model nor from the more detailed cormorant model can automatically be transferred to other species.

These are rather technical issues. Apart from this, the cormorant conflict has other dimensions, which are far beyond the scope of modeling applied in this

thesis. For example, there are political and institutional (Behrens et al. [2008]) as well as ethical aspects, to name only few of these other highly relevant dimensions.

Further studies on this issue could try to overcome the technical shortcomings and include space or even go down to the individual level. On the economic side, cost functions could allow for more realism, but would require more data which is currently lacking (van Dam and Asbirk [1997]). Cost functions should also include the effective losses of fisheries and effective impact of the cormorant on aquatic ecosystems (impact on fish species composition or lake eutrophication), which is also hard to assess (Rutschke [1998]). This could then be a further step towards a sound basis of considerations about cormorant regulation strategies.

8.4. Concluding Remarks

The Thesis in a Nutshell

This last chapter summarizes and concludes the thesis and states the lessons learnt.

Background. The starting point for this study was the conflict between nature conservation and economic interests, which emerges when populations of protected species grow to sizes that cause remarkable economic damage, as in the case of the Great Cormorant (e.g. Parrott et al. [2003]; Santoul et al. [2004]; Christensen et al. [2007]) or the Canada Goose (Hauser et al. [2007]). One approach for conflict reconciliation is to regulate the size of the respective population (e.g. Smith et al. [2008]; Rutschke [1998]). Regulation strategies have to meet multiple targets: first, population size, and thus the damage caused by the population must be reduced; second, the viability of the population has to be maintained; and third, strategies have to adhere to the budget at hand. This study focused on populations featuring pools of mature non-breeding individuals (e.g. Sarah et al. [2004]; Gunnarsson et al. [2005]; Penteriani et al. [2005]; Soutullo et al. [2006]). The dynamics of such populations and the effects of regulation have yet to be clarified and understood.

A prime example for such a species featuring a non-breeder pool is the Great Cormorant (*Phalacrocorax carbo sinensis*) (Rutschke [1998]). The increasing cormorant population has caused a Europe-wide conflict between fisheries and conservationists by feeding on fish (Behrens et al. [2008]). This study also aimed to contribute to the reconciliation of this conflict.

Questions. Given this background, the three major aims of the thesis were 1) to develop a modeling framework and a conceptual model to provide an understanding of the functioning and effect of the population structure induced by non-breeders on population dynamics in a fluctuating environment, 2) to uncover the relation between non-breeder characteristics and the performance of regulation strategies, and 3) to apply the modeling approach to the regulation of the

Great Cormorant in order to evaluate the results from the conceptual model and find statements to support decisions on concrete management strategies for the Great Cormorant in Europe.

Hypothesis. The starting hypothesis was that the pool of non-breeders increases population viability. However, it was a priori unclear under which conditions this may hold and how regulation may affect the non-breeder pool and population viability. Furthermore, it was hypothesized that the non-breeder pool influences the performance (effectiveness and effort) of regulation strategies. The exact interplay between the non-breeder pool and regulation effort was however unclear.

Methods. To answer the questions and test the hypotheses, a conceptual model was first developed. This model was time-discrete, based on the logistic map with overlapping generations, and explicitly included the pool of non-breeders. Model behavior was systematically analyzed under deterministic and stochastic environmental fluctuations without the application of regulation strategies. The analyzes focused on the influence of the characteristics of the non-breeder pool on the size of the breeder stock, variance within it, and population viability.

The results of this analysis enabled the construction of hypotheses regarding the regulation of such populations. These hypotheses were tested by applying different types of threshold regulation strategies on the model. These strategies differed in which part of the model was affected by regulation: *a*) regulation applied only to breeders, *b*) regulation applied only to non-breeders, *c*) regulation applied to both breeders and non-breeders, *d*) regulation applied to the environmental capacity for breeders, and *e*) regulation applied to the reproduction rate of breeders. The analyzes were performed for a reference population, for which the characteristics of the non-breeder pool were varied, as well as environmental conditions and reproduction rate. First, fluctuations were kept low, but strong singular catastrophic events were applied to explicitly assess the role of the non-breeder pool and the performance of regulation under these conditions. There, the focus lay on the primary limitations and pitfalls for regulation. Thereafter, the performance of regulation strategies under strong environmental conditions were assessed.

The results of the analyzes of the conceptual model allowed the drafting of rules of thumb for the regulation of populations featuring pools of non-breeders. These rules of thumb were tested by applying them to a biologically more realistic model of a population of the Great Cormorant. This model was also based on the logistic equation, included the non-breeder pool explicitly and was, in addition, age-structured. It was parametrized with data gained from a study on a cormorant colony in Denmark. Analyzes of this model focused again on the ecological-economic performance of regulation strategies and resulted in rankings of regulation options. Regulation performance was judged from different

economic perspectives to further assess the influence of normative settings in the definition of the regulation target on the rankings.

Lessons on population dynamics. The analyzes of the conceptual model showed, that the effect of the non-breeder pool has two basic aspects: a source and sink functionality. The first reduces over-shooting of breeders over their capacity and thus effects of over-compensation, which can reduce variance in breeder size. The second can reduce downward fluctuations by compensating losses in breeders with non-breeders.

The analyzes partly confirmed the hypothesis that the pool of non-breeders increases population viability. Here, three situations must be distinguished: First (CASE I), in the case of low fluctuations (note: fluctuations in the time-discrete model can be environmental or intrinsic, caused by high reproduction rates), the presence or absence of the non-breeder pool does not change high population viability. Second (CASE II), in the case of very strong fluctuations, population viability is low, regardless of the characteristics of the non-breeder pool. Third (CASE III), there is an intermediate range of fluctuation strength for which the non-breeder pool and its characteristics are crucial for high population viability.

It turned out that in CASE III, depending on the main source of fluctuations, intrinsic or environmental, strength of sink functionality or non-breeder mortality is most crucial for population viability. If in CASE III environmental fluctuations are the main source of variability, the linking element between non-breeder characteristics and population viability is the mean size of the non-breeder pool – population viability can only be preserved if the non-breeder pool exceeds a certain minimum size.

Lessons on regulation. According to the three above-mentioned cases, regulation can affect population viability differently. In CASE I, where fluctuations (environmental and intrinsic) are low, regulation strategies only degrade population viability if carried out with very high rates and low thresholds. In CASE II of strong fluctuations, where population viability is low in any case, any regulation further decreases viability. In CASE III of intermediate fluctuations, the performance of regulation strategies depends on the extent to which the size of the non-breeder pool is reduced.

CASE III is covered by the following rules of thumb for regulation of populations featuring non-breeders that are to be kept viable:

1. If the actual effective strength of environmental fluctuations and the risk of catastrophes is unknown, the pool of non-breeders should be conserved, because it can act as a resilience mechanism which increases population viability and ensures robustness against catastrophic events;
2. If possible, environmental capacity should be reduced, because this main-

tains the population structure built up by the pools of breeders and non-breeders;

3. If environmental capacity can not be reduced, the size of the breeder stock could be reduced with low rate and high threshold, because this maintains the non-breeder pool;
4. Medium and strong reductions of the breeder stock are risky, because this removes the non-breeder pool;
5. Reducing the non-breeder pool directly is less effective and, in case of strong reductions, decreases population viability because of the first point above;
6. Reducing the reproduction rate is ineffective, because it does not affect population size.

It should be noted that these six rules of thumb apply only in CASE III mentioned above. In CASE I and CASE II, where the non-breeder pool is either not needed for viability or is unable to increase it, these rules of thumb do not apply, as in the example of the cormorant.

Lessons on cormorant regulation. The cormorant population exhibits high viability, thus it is close to the above-mentioned CASE I, where the non-breeder pool is less crucial for population survival. This is due to several factors. First, reproduction rate is sufficiently low so as not to induce fluctuations caused by over-compensation. Second, compared to the strength of environmental fluctuations, reproduction rate is high enough to allow breeder number to be well above zero. Third, the assumed population size is large enough that even very strong but still realistic catastrophes threaten population survival only to a small extent. Because of these factors and the additional non-breeder pool, regulation would have to be carried out very heavily to drive the population to extinction. Concerning population viability, this has the following consequences for the different regulation types:

1. Culling. Extinction occurs for very low regulation thresholds (less than $\theta \approx 0.2K$, with K the capacity of breeders) or very high regulation rates ($t > 0.8$). If regulation is carried out above this threshold and below that rate, it does not matter for population survival which part of the population is affected by culling.
2. Reducing capacity. There is nearly no risk of extinction if the capacity of breeders is reduced. This is partly caused by the model assumption that the strength of environmental fluctuations scales with the size of the population.

3. Egg-oiling. If egg-oiling decreases birth rates below death rates, it drives the population to extinction.

The situation found in the cormorant example belongs to the above-mentioned CASE I, where the non-breeder pool is not needed for population viability. This leads to a relaxation of the listed rules of thumb: For the regulation of the cormorant population it is not crucial to pay special attention to the non-breeder pool. Therefore, culling can perform well in contrast to the results for CASE III examined in Part I.

For each type of regulation (culling, capacity reduction, egg-oiling), an optimal strategy can be found, whose characteristics depend on the economic parameters (regulation costs, damage costs caused by cormorants, targets). According to the performance of the optimal strategy, types of regulation can be ranked. This ranking is also sensitive to the economic parameters.

Hence, to determine optimal regulation strategies for the Great Cormorant, data about the following would be very helpful: costs of and budget for regulation measurements, relative cormorant-caused damage and size of the European cormorant population. If culling turns out to be the economically best option, then characteristics of the non-breeder supply by breeder surplus are important.

Lessons on the methodological approach. Including catastrophic events to cover potential worst case scenarios in the face of climate change helps to uncover potential pitfalls or shortcomings of regulation strategies. If catastrophes had not been considered, the crucial role which non-breeders can play for population survival would have remained undiscovered.

The generic model provided good insight into the basic interactions between breeder stock and non-breeder pool. But as it does not cover many structural aspects, it is not sufficient for finding optimal regulation strategies. By including more ecological realism the predicted performance of all types of regulation strategies is changed.

The study includes both economic and ecological aspects. These aspects are closely interlinked and need to be considered together in order to find optimal regulation strategies, which allow for minimum total costs as well as for population survival.

Future research. Building on this study future research could focus on various theoretical aspects of population dynamics as well as environmental conditions or data. In this study, time-discrete population dynamics are assumed. This leads to over-compensatory density regulation in case of high reproduction rates. As this strongly influences population dynamics and viability, it would be interesting to consider different kinds of density regulation. For the non-breeder pool no density dependence is assumed. Introducing density dependence or the

possibility of over-compensation might change overall population dynamics and viability, as well as performance of regulation strategies.

Environmental fluctuations are assumed to be uncorrelated. Assuming auto-correlated environmental fluctuations may enlarge the time periods which the non-breeder pool is needed to compensate breeders' loss. This may lead to different requirements for the optimality of regulation strategies.

To further support and improve the rules of thumb gained here, more detailed models are needed of other species featuring pools of non-breeders. Such models should also include the possibility to evaluate the extent to which spatial structure and properties might reduce the effects of non-breeder pools.

In the particular case of the cormorant, it would be useful to acquire more detailed information and data on costs and cost functions, as well as on non-breeder supply by breeders. The additional consideration and investigation of other conflict reconciliation strategies, like renaturation of lakes and rivers to release pressure on fish populations may also prove to be useful.

Acknowledgments

This PhD-thesis was funded by the *Deutsche Bundesstiftung Umwelt* (DBU), which I thank for the confidence in and the support of my work. I especially thank Dr. Volker Wachendörfer, who supervised my grant on the part of the DBU.

My scientific supervisor PD Dr. Karin Frank strongly supported my work over the last years. She helped me to further develop a sound way of scientific thinking and of structuring scientific work, and she provided lots of (meta-)knowledge crucial for scientific survival but beyond a university education. She also gave me several opportunities to develop my teaching affinity. Despite all her other obligations she always tried to help me as much as possible to overcome any kind of obstacle. I truly thank her for all of this.

On the part of the University of Osnabrück, Prof. Dr. Horst Malchow supervised this thesis. It was always an atmosphere of trust and compliance which made me enjoy the meetings in Osnabrück. It was his lectures during my studies which initiated my deeper interest in theoretical ecology.

I am indebted to Dr. Thomas Bregnballe for the great support in questions of the ecology of cormorants. I enjoyed the easy but sound way of communication and collaboration, which I know can not be taken for granted in interdisciplinary collaborations.

I thank the members of the common research group *eco-eco* from the Helmholtz Centre for Environmental Research (PD Dr. Karin Frank, Prof. Dr. Martin Quaas and Dr. Birgit Müller) and the University of Heidelberg (Prof. Dr. Stefan Baumgärtner, Dr. Christian Becker and Eva Kiesele) for the introduction into ecological-economics and the support in these questions.

I am grateful to the FRAP-project (Framework for biodiversity Reconciliation Action Plans), which provided an important basis for my thesis, and especially to Dr. Reinhard Klenke, who was the coordinator of this project.

There are many members of the Department of Ecological Modeling who helped and supported me scientifically and personally. I thank PD Dr. Volker Grimm who helped me through times of doubts about my work and science itself. I also owe thanks to Dr. Hans Hermann Thulke who introduced me to

the deeper secrets of presenting scientific work. His support was crucial for the success of my contribution to the contest *Wissenschaft verstehen*. I truly thank Dr. Birgit Müller not only for being a supportive colleague or for starting her maternity leave right in time to allow me to cover her position after my DBU fellowship, but also for being a friend. I learnt a lot about teaching and organizing workshops from Michael Müller, above this he helped and supported me with much valuable and amicable advice. Thanks also to Florian Hartig for the fruitful discussions we had about various details of this study.

The Department of Ecological Modeling would not be the same without our secretary Gabriele Nagel. I appreciated her authentic and reliable no-problem attitude and thank her for all the patient help in many situations. Thanks also to Andreas Thiele, who (as well as Michael Müller) kept my computer running and may have suffered from sometimes exotic requirements. Many thanks also to all the other not mentioned members (like my room mates Dr. Nadja Rüger, Dr. Maja Schlüter and Alvaro Gutierrez) of the Department of Ecological Modeling and all the other people who contributed to the vivid and livable working environment over the last years. Many of these people contributed with extensive discussions to the success I had for example with the application talk at the DBU or the talk at the contest *Wissenschaft verstehen*.

Many thanks also to Cliodhna Quigley who kindly revised this thesis and turned my English into an English which a native speaker could understand.

Finally, I would like to thank all the cormorants for structuring their populations so nicely and eating their daily fish and causing the conflict on which I could write a thesis, and last but not least from which I could make a living for three years.

List of Figures

2.1	General model structure. If N_t (Equations 2.3 & 2.4) exceeds its capacity K , flux $m_N(N_t)$ (Equation 2.2) occurs. If N_t falls below K , flux $m_P(N_t, P_t)$ (Equation 2.1) takes place. In the non-breeder pool P_t no reproduction occurs (Equation 2.5).	12
2.2	Modeling framework. Regulation strategies define regulation, which influences population dynamics and effort. Mean effort e , probability of extinction $P_0(100)$, and deviance d^2 from the desired population size M are calculated in multiple simulation runs. These are compared to the target values ε_b , ε_p and ε_d	16
3.1	Variation of λ . All other parameters are set to their reference values ($\lambda = 0.5, \beta = 0.5, k = 0.5, \delta = 0.1$ and $\kappa = 0.7$). Environmental fluctuations are modeled deterministically $\xi_t = a_\xi \sin(2\pi f_\xi t)$, with $a_\xi = 0.2$ and $f_\xi = 1/20$	21
3.2	The term for conversion from non-breeders to breeders $\frac{(K-N)^2}{(k^2+(K-N)^2)}$ with $K = 1$ for different values of k . The value of k determines the “rapidity” respectively “sluggishness” of the non-breeder response to breeder loss.	23
3.3	Interplay between k and β . Values of the other parameters are $\lambda = 0.9, \delta = 0.1$ and $\kappa = 0.7$	24
3.4	The role of δ . Values of the other parameters not shown are $\lambda = 0.9$ and $\kappa = 0.7$	26
3.5	The role of non-breeder capacity κ . Values of parameters not shown are $\lambda = 0.9$ and $\delta = 0.1$	27
3.6	Effects of sink functionality and combination of source and sink functionality compared with dynamics of the population without non-breeder pool. Parameters are chosen as for the sluggish but strong non-breeder response to breeders’ loss (see Table 3.1). . .	28

3.7	Effects of increasing reproduction rate r on a population with a sluggish but strong non-breeder response to breeders' loss. (see Table 3.1).	29
3.8	$P_0(100)$ vs. λ , β and δ for different values of δ , k and κ in scenarios with strong fluctuations (05s and 25s). All parameters, which are not varied are set to their respective reference values.	35
3.9	Mean size of breeder stock \bar{N} vs. λ for different values of δ in all scenarios. All parameters, which are not varied are set to their respective reference values.	36
3.10	Mean size of breeder stock \bar{N} vs. β and δ for different values of k and κ in scenarios with strong fluctuations (05s and 25s). All parameters, which are not varied are set to their respective reference values.	37
3.11	Variance of size of breeder stock var_N vs. λ for different values of δ in all scenarios. All parameters, which are not varied are set to their respective reference values.	38
3.12	Variance of size of breeder stock var_N vs. β and δ for different values of k and κ in scenarios with strong fluctuations (05s and 25s). All parameters, which are not varied are set to their respective reference values.	39
3.13	Curves in the N_t - N_{t+1} -phase space defined by 0.001-quantiles. Also depicted are points in the N_t - N_{t+1} -phase space. For the two strong-fluctuation scenarios, points are generated in several runs, because under these conditions the population becomes extinct very quickly. This explains the fact that there is more than one point on the N_t -axis. Strength of sink functionality is set to $\lambda = 0.75$. The dashed lines mark the environmental capacity K for breeders.	43
3.14	Curves in the N_t - N_{t+1} -phase space defined by 0.001-quantiles. Point L marks the null of the curve defined by the 0.001-quantile and thus the N_t -value for $\xi_t = q_{0.05/0.4}^-$ above which the population becomes extinct. H denotes the maximum N_{t+1} -value (dashed lines) which can be reached for $\xi_t = q_{0.05/0.4}^+$. Strength of sink functionality is set to $\lambda = 0.75$	44
3.15	Relationship between risk of extinction $P_0(100)$ and the mean size of breeders \bar{N} resp. non-breeders \bar{P} . Plotted are all parameterizations as given in Equations 3.9 to 3.11.	45
4.1	Number of breeders N_t and non-breeders P_t vs. time t . At $t^* = 80$ a pulse sets the breeder size N_{t^*+1} to $0.02N_{t^*}$. $P_0(100)$ is the probability of extinction within the shown 100 time steps. a) shows the population without non-breeders ($\kappa = 0$) and b) the population with non-breeders.	54

4.2	Number of breeders N_t and non-breeders P_t vs. time t . At $t^* = 80$ a pulse sets the breeder size N_{t^*+1} to $0.02N_{t^*}$. $P_0(100)$ is the probability of extinction within the shown 100 time steps. a) shows the population as in Figure 4.1b) with regulation strategy S_1 applied; b) shows the population under a stronger regulation strategy S_2 . S_1 and S_2 affect both breeders (N_t) and non-breeders (P_t) equally.	55
4.3	Probability of extinction $P_0(100)$ vs. mean non-breeder pool size resp. mean size of the breeder stock. a) & b) Non-breeders and breeders of the same population; c) reference population without non-breeders ($\kappa = 0$). Circles mark sizes under one of the regulation strategies $S = (\theta, \iota)$ with $\theta \in 0.1, 0.2, \dots, 1.2$ and $\iota \in 0.1, 0.2, \dots, 0.9$. Dashed lines: $P_0(100) = 0.05$	56
4.4	Performance of culling strategies (θ, ι) without (a and c) and with (b and d) catastrophe occurrence for target population sizes $M = 1.2$ (a and b) and $M = 0.4$ (c and d). Note: $e < \epsilon_b = 0.02$, (marked by \circ) and $P_0(100) < \epsilon_p = 0.05$ (marked by \blacklozenge) are independent of M	58
4.5	Non-breeder response sluggishness k to breeders' loss (a) $k = 0.9$ and b) $k = 0.1$) and achievability resp. affordability of regulation targets. Targets are defined by M , ϵ_d , ϵ_p and ϵ_b . Achievable targets: strategies exist, meeting conditions M , ϵ_d and ϵ_p . Affordable targets: strategies exist, meeting M , ϵ_d , ϵ_p and ϵ_b	59
4.6	Regulation by means of reduction of \mathbf{N}_t : The image plot on the left shows the minimum achievable target M for a maximum allowed deviance of $d^2 < \epsilon_d = 0.11$. Strategies which lead to a probability of extinction at time $t = 100$ of $P_0(100) < 0.05$ are marked with '*'. For the ι - θ combinations a, b and c, exemplary dynamics are plotted on the right. White areas ('no tar.') in the image plot depict ι - θ combinations for which no target can be reached with the given maximum deviance $\epsilon_d = 0.11$. There is a trade-off in $P_0(100)$ depending on ι and θ	61
4.7	Regulation involving a reduction in \mathbf{P}_t : The image plot on the left shows that there is no achievable target for a maximum allowed deviance of ϵ_d (only white areas are present ('no tar.')). Strategies which lead to a probability of extinction before 100 time steps of $P_0(100) < \epsilon_p$ are marked with '*'. For the ι - θ combinations a, b and c, exemplary dynamics are plotted on the right.	62

4.8	Regulation by reducing \mathbf{K} : The image plot on the left shows the minimum achievable target for a maximum allowed deviance ε_d and marks strategies which lead to a probability of extinction before 100 time steps of $P_0(100) < \varepsilon_p$ with '*'. For the ι - θ combinations a, b and c, exemplary dynamics are plotted on the right. White areas ('no tar.') in the image plot mark ι - θ combinations for which no target can be achieved with the given maximum deviance ε_d . There are no ι - θ combinations which lead to $P_0(100) > \varepsilon_p$	63
4.9	Regulation by reducing \mathbf{r} : The image plot on the left shows that there is no achievable target for a maximum allowed deviance of $d^2 < \varepsilon_d$ (only white areas ('no tar.')). Nearly all strategies lead to a probability of extinction before 100 time steps of $P_0(100) < \varepsilon_p$ (marked with '*'). For the ι - θ combinations a, b and c, exemplary dynamics are plotted on the right.	64
4.10	Mean effort per time step of regulation strategies in units of K . The characters in the upper right corner mark which part of the population is affected by regulation. (Note: the effort is independent of the regulation target and is only determined by regulation rate ι and threshold θ .)	65
4.11	Minimal effort of reaching the targets $M = 0.8$ resp. $M = 0.4$ by reduction of N_t resp. K . The different bars represent non-breeder response types: bt I is the reference case of strongly and sluggishly responding non-breeders. bt II represents a weak and agile non-breeder response, bt III weak and sluggish, and bt IV strong and agile. Upper row: environmental variances are as in the rest of the study: $\sigma_\xi^2 = 0.3$. Lower row: shows the efforts for regulation under environmental fluctuations with $\sigma_\xi^2 = 0.1$. (Note: the y-axis scales in all plots are different as minimum effort can only be compared within one strategy type.)	66
5.1	Scheme of the general model structure. Breeders reproduce into the 0th age class. Each age class represents one year of individuals' life-span. From the first age class on, individuals are considered to be either breeders or non-breeders.	77
5.2	The observed and modeled pattern of the age-class dependent proportion of breeding individuals, estimated using the reference parameterization (see 5.2).	85
6.1	Exemplary dynamics of total breeder and non-breeder size, and age classes of breeders and non-breeders, carried out using the reference parameterization (see 5.2). Dashed lines mark the five-year duration of the catastrophe.	87

6.2	Result of local sensitivity analysis of single parameters. Parameters are varied around the reference parameterization (Table 5.2).	88
6.3	Result of sensitivity analysis, varying all parameters at the same time around reference parameter values (Table 5.2). a) : measures of size and viability; b) : proportions of breeding individuals in each age-class.	89
6.4	Result of sensitivity analysis. a) & b) : mortalities d and δ varied at the same time around their reference parameter values (Table 5.2). c) & d) : non-breeder supply λ and s varied at the same time around their reference parameter values. e) & f) : non-breeder response β and h varied at the same time around their reference parameter values. The remaining parameters are held constant at their reference value.	90
6.5	Result of sensitivity analysis varying all parameters randomly at the same time. (All parameter values chosen from the interval $[0, 1]$, except $b \in [0, 2]$)	91
6.6	Curves in the N_t - N_{t+1} -phase space defined by 0.001-quantiles of environmental fluctuations. Point L marks the null of the curve defined by the 0.001-quantile and thus the N_t -value for ξ_t , above which the population becomes extinct. H denotes the maximum N_t -value which can be reached for ξ_t within the 0.001-quantiles. The source functionality of the non-breeder pool is set to zero ($\beta = 0$).	92
7.1	Performance of regulation strategies applied to the conceptual model parameterized with cormorant data (Table 5.3). For strategies involving a reduction in the environmental capacity K for breeders or egg-oiling, the optimal and cheapest strategy fall together. The numbers give the total costs of the optimal strategy in units of 10^5	96
7.2	Mean regulation costs resp. damage costs vs. mean total population size $N_t + P_t$ in the conceptual model for the entire range of (θ, ι) . The dashed lines indicate the population size of the optimal strategy, as marked in Figure 7.1.	97
7.3	Total costs and population viability for the different types of regulation strategies. The cormorant model is parameterized with the reference parameterization. Total costs are given in units of 10^5	99
7.4	Regulation costs resp. damage costs vs. population size $N_t + P_t$ in the age-structured model for the entire range of (θ, ι) . The dashed lines indicate the population size of the optimal strategy as marked in Figure 7.3.	101

7.5	Variation of damage costs q for culling breeders N_t . Two lines of total costs are marked ($c(e_t, N_t, P_t) = 80$ and $c(e_t, N_t, P_t) = 90$) to show that increasing q affects the total costs of strategies with high threshold θ and low intensity ι more than total costs of strategies with low threshold θ and high rate ι . Total costs are given in units of 10^5	102
7.6	Variation of damage costs q for the five regulation types (reducing breeders (N), non-breeders (P) or both (B), reducing breeder capacity (K) or birth rates (B)). Circles mark the position of the optimal regulation strategy for the respective weighting of cormorant damage.	103
7.7	Mean total costs $c(e_t, N_t, P_t)$ (see Equation 5.36) of the optimal regulation strategies for increasing relative cormorant-caused damage q for the five considered types of cormorant regulation strategies. All costs are measured in units of 10^5	104
7.8	Benefit (reduction of total costs $c(e_t, N_t, P_t)$, see Equation 5.36) and regulation costs of the optimal regulation strategies for increasing cormorant-caused damage costs q . Costs are plotted without (upper row) and with (lower row) a limiting budget for regulation of 50 cost units. All costs are given in units of 10^5	105
7.9	Benefit (reduction of total costs $c(e_t, N_t, P_t)$, see Equation 5.36) and regulation costs of the optimal regulation strategies for increasing cormorant-caused damage costs q for the five considered types of cormorant regulation strategies. For costs of regulation a limited budget is assumed. All costs are given in units of 10^5	106
7.10	Mean and standard deviation of costs for regulation, and total costs. The characteristics of non-breeder response to breeders' loss (β and k) in the age-structured model are varied around the reference parameterization (Table 5.2). Costs are given in units of 10^5	107
7.11	Mean and standard deviation of costs for regulation, and total costs. The characteristics of non-breeder supply by breeders (λ and s) in the age-structured model are varied around the reference parameterization (Table 5.2).	108
7.12	Influence of breeder sensitivity s_i on their own density can influence the structure of the cost landscape in the example strategy of culling breeders. Upper row: reduced sensitivity $s_i = \max[s_i^{ref} - 0.1, 0]$. Lower row: sensitivity on reference value s_i^{ref} . All other parameters are held on their reference values (Table 5.2). Costs are given in units of 10^5	109

-
- 7.13 Population size $N_t + P_t$ vs. regulation costs and damage costs in the age-structured model for reduced sensitivity $s_i = \max[s_i^{ref} - 0.1, 0]$. The dashed lines indicate the population size of the optimal strategy. 110

List of Figures

List of Tables

2.1	The four different types of regulation strategies (reducing N_t , P_t , N_t and P_t , r_t or K) affect different system components. Reduction takes place if $N_t + P_t > \theta$, which in case the term in the second column is subtracted from the respective component. Otherwise, if $N_t + P_t \leq \theta$ the reduced component recovers.	15
3.1	Parameter sets for which the non-breeder pool has the greatest smoothing effect.	28
3.2	Settings of reproduction rate and environmental fluctuations in the investigated scenarios. (w stands for “weak” and s for “strong” fluctuations)	30
3.3	Comparison of parameter values which define a populations with minimum variance in breeder dynamics (min. var_N), maximum mean size of breeders (max. \bar{N}) and probability of extinction within 100 time steps ($P_0(100)$). Gray shaded lines indicate reference parameters.	33
3.4	Sensitivities $P_0(100)$	33
3.5	Sensitivities \bar{N}	34
3.6	Sensitivities var_N	34
3.7	Correlations between mean time to extinction T_m and the mean size of breeders \bar{N} , and non-breeders \bar{P} over all parameterizations of the model as given in Equations 3.9 to 3.11.	46
4.1	Reference parameter values used unless otherwise stated.	53
5.1	The five different types of regulation strategies (reducing N_t , P_t , N_t and P_t , r_t or K_t) affect different system components. Regulation is executed if $N_t + P_t > \theta$, in which case the term in the second column is subtracted from the respective component. Otherwise, if $N_t + P_t \leq \theta$ the reduced component recovers.	83
5.2	Reference parameter set. (b.: breeders, n.: non-breeders)	85

List of Tables

5.3	Parameter values derived from cormorant data (shown in Table 5.2) using the mean field approach	86
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