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Optimal management of invasive species with different reproduction and survival strategies

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Abstract

In this paper, a numerical model is developed where the role of species life history and age structure for the optimal management of a harvested resident species which is exposed to an invasive species. It is shown that reproduction and mortality characteristics of both species as well as age structure of the invader at the time of invasion are important for the costs of invasions when the invader and resident species compete for scarce resources. Species with low juvenile survival and high reproduction is found to be most robust against invasions and more damaging as an invader. Properties of the harvesting cost function as well as the discount rate are shown to be of importance for the development of the invader population. Hence, it is possible to identify specific combinations of biological and economic conditions under which invasions cause particularly large economic and ecologic damage.

Key words: invasive species, resident species, control, harvest, age-structured model, optimization.

1. Introduction

Ever since people began travelling they have, sometimes intentionally but mostly accidentally, carried new species with them which have affected the ecosystems where they are introduced (Bax et al., 2003). The currently large and increasing scale of trade and tourism contributes to an escalating dispersal of species. There is a growing awareness of the potential economic damages that may result from the introduction of non-native species. A number of studies estimate the environmental damage and/or control costs for species invasions (Gren, 2008, 2009; Pimentel et al., 2005).

The economic damage caused by invasive species depends on the possibilities for the non-native species to grow and disperse in the new habitat and the associated impact on resident species. The probability of a successful invasion where the non-indigenous species is established in the host region depends on characteristics of the non-indigenous species and the native species and on habitat conditions with respect to availability of food and other survival opportunities. This interaction is, in turn, determined by the life history, i.e. reproduction and survival strategies of the two types of species. However, the literature on ecology and economics has mostly focused on finding and establishing characteristics of a successful invading species and the associated management without explicit consideration of the interaction with the native species (e.g. Williamson, 1996; Perrings et al., 2000; Lockwood et al., 2005; Colautti et al., 2005; Gren, 2008).

The purpose of this study is to identify optimal management strategies for different combinations of reproduction and survival strategies of the non-indigenous species and native species. Our study thereby differs from much of the literature where the focus is on the optimal timing and allocation of control of the invader (Saphore and Shogren, 2002; Perrings et al., 2000; Olson and Roy, 2005; Perrings, 2005; Finnoff et al., 2005; Finnoff et al. 2007; Keller et al. 2007). Instead, we model a situation where technologies for controlling the non-indigenous species are not available, such as is often the case in a marine environment, e.g. for the round goby (*Neogobius melanostomus*) in the Baltic Sea (Ojaveer, 2006). Our study is most similar to Settle and Shogren (2002) who analyze and carry out numerical simulations of optimal management of two species, an invasive predator (lake trout) and a resident prey (cutthroat), in the Yellowstone Lake region. We follow their approach as well as Knowler et al. (2002) and Knowler (2005) through

estimating costs of biological invasions as impacts on a commercial resident species. In contrast to those, age cohorts are here modeled explicitly in order to identify the role of age structure and life history for the invasion process and consequently for optimal management.

Age structured models similar to the biological model used in this paper are used to an increasing extent in the fishery economics literature, see e.g. Grafton, Kompas and Hilborn (2007), Bjørndal et al. (2004), Bjørndal and Brasao (2006), and Duarte, Brasão and Pintassilgo (2000). Their use is motivated by the more realistic approach to the underlying biology compared to the traditional models, where the total biomass is used as a single descriptor of the state of the population. Age-structured models are also relevant to the analysis of the introduction of non-native species because of the importance of the age at the time of introduction and of the life history for invasion success. One drawback is the difficulty of deriving analytical solutions (see e.g. Tahvonen, 2009). Therefore, like in most earlier work, the results in this paper are derived from numerical simulations.

The article is organized as follows: first, the role of species life history for the likelihood of a successful invasion is discussed. Next a presentation of the bio-economic model and a description of data used are given. Then, results are presented and finally, the article ends with a discussion.

2. Bio-economic model

The invasiveness, i.e. the ability of an organism to spread and become established in new locations where it may harm resident organisms, is determined by the introduction pattern and invasion success depends on the number of individuals of a species arriving into a new ecosystem as well as the frequency of the arrivals (Williamson, 1996; Lockwood et al., 2005, Colautti et al., 2005). The literature predicts the age of the invader to be an important determinant of invasiveness. There is a great variation in observed age of invading species. The round goby (*Neogobius melanostomus*), native to e.g. the Black and Caspian Seas but successfully invading the Great Lakes in the US, and the European Green Crab (*Carcinus maenas*), native to the North and Baltic Seas but successfully invading both the east and west coast of the US, are introduced as larvae or eggs from ship ballast water (Jude et al. 1992, Grosholz and Ruiz 1995). Pregnant individuals of different benthic organisms have been found in ballast water which is suggested to imply an increased likelihood of the establishment of these organisms in new environments (Smith et al., 1999). Big snakes, kept as pets, are often introduced as old adults since they are released by their owners when they become too large (Reed, 2005). Bird migration can involve most age classes (Greenwood and Harvey, 1982). Plants have been introduced to new ecosystems both intentionally as seeds or adult plants for food production, research, gardening and conservation and unintentionally as seeds contributing e.g. to weed dispersal (Pegtel, 1998). However, the age at which individuals are introduced need not coincide with the optimal age for dispersal and establishment. MacArthur and Wilson (1967) argued early that the ideal age of a colonizer should overlap with age of maximum reproductive value. Their results have been questioned in later work where juveniles are suggested to have an advantage with regard to dispersal (Johst and Brandl 1999; Loison et al. 1999) and that the optimal age for dispersal is

determined by density (Johst and Brandl 1999) or genetic pool (Johnson 1986) regulation of the invader population in its original habitat. Moreover, differences in age-specific survival and reproduction probabilities for migrating and non-migrating individuals (Williamson and Charlesworth, 1976) may determine dispersal success. There is limited empirical evidence on the correlations between life-history and invasiveness (Williamson and Fitter, 1996). The habitat invaded is likely to be of importance for the optimal age of a colonizer (Cox, 1999; Rejmánek and Richardson, 1996; Martin et al., 2008) but there seems to be no consensus among ecologists as to what type of organism is most invasive in an undisturbed ecosystem, given the presence of a resident species. Given the increase over time in human-assisted dispersal of organisms, the ability of species to compete and survive in the new habitat is likely to become increasingly more important compared to dispersal ability (MacArthur and Wilson, 1967). The focus in this paper is therefore on survival and reproduction and the role that they play for economic damage of invasions, while we abstract from the role of drivers of dispersal.

We develop a discrete dynamic optimization model, which reflects life-history characteristics of the invasive and resident species. We analyze a two-population system, with one resident species and one invading species introduced in small numbers. It is assumed that a single decision-maker chooses optimal harvest of an economically valuable resident species, given the introduction of an invasive species. The choice of species' life histories is motivated by the aim of illustrating the role of major differences in life-history. We aim at analyzing from an economic perspective what type of organism is the most invasive in an ecosystem, given the presence of not only a resident species but also human interference. In the following, the biological and economic parts of this model are described.

2.1 Species classification and population dynamics

To focus on the role of the interaction between invading and the resident species with different characteristics, it is assumed that both of those can be classified into one of two different types. The classification is based on the observation that there is a biological trade-off between survival and fecundity; without this trade-off organisms could live forever. We therefore consider two fundamentally different life history characteristics for allocating resources between reproduction and survival. The types considered are iteroparous species of Type I and III. Iteroparous species produce offspring in annual or seasonal cycles and survive over multiple seasons. They are divided into Type I and III organisms, depending on the age specific survival rates (Deevey, 1947). One survival strategy is found among e.g. mammals, who give a great deal of adult protection to their relatively few young, thereby increasing the survival probability in early years. Those are classified as iteroparous type I (Deevey, 1947; Polis and Farley, 1980; Pointier et al., 1993). Another strategy is to produce high numbers of young given that the high reproduction comes at a cost of low year-to-year survival of juveniles. Such species, common among fish, insects, marine invertebrates, and plants can be classified as Type III organisms. The characteristics of the two different life histories included in this paper are as follows: A species of type *A*, corresponding to an iteroparous species type I, survives several years. It has initially a high survival rate, which falls as age increases. Reproduction is relatively low once the individuals have reached maturity and are more

or less constant over time. For type B , survival of juveniles is low for young individuals but increases over time. The number of offspring produced by different age classes is assumed to increase with age, such as is typical for organisms that continue to grow after reaching sexual maturity (Pianka and Parker, 1975). Reproduction is high once the individual becomes mature and increases with age (cf. e.g. Williams, 1966). Given that we have two different species types this generates four different possible combinations of resident and invading species.

We use a stock transition relationship which describes the development of the populations over time. Each of the two populations is assumed to be of an origin k , with $k=I,R$, where I =invasive and R =resident and associated with a life history j , with $j=A,B$. The proportion of individuals of cohort i at time t surviving until the following year $t+1$ is denoted $\alpha^{i+1,jk}$. The number of individuals of the resident and invasive species in a habitat is assumed to affect survival and offspring production for both species due to competition for limiting resources. Survival and offspring production of the species from one year to another is therefore assumed to be determined by a factor

$e^{-\left(\sum_{i,k} \beta^{ijk} N_t^{ijk}\right)}$, implying that survival and reproduction is decreasing in the number of residents and invaders. The coefficients β^{ijk} are indicators of the carrying capacity of the environment, or equivalently, the density dependence of the species. The initial number of individuals in different cohorts of the resident species, N_0^{jR} , is exogenously given by:

$$N_0^{jR} = \bar{N}_0^{jR} . \quad (1)$$

The number of a particular cohort of the resident species of type A or B , counted just before the reproductive season, $N_{t+1}^{i+1,jR}$, is determined by the stock size in prior period, survival rate, density dependent competition, and harvesting according to:

$$N_{t+1}^{i+1,jR} = N_t^{ijR} \alpha^{i+1,jk} e^{-\left(\sum_{i,k} \beta^{ijk} N_t^{ijk}\right)} - H_t^{ijR} \quad \forall j = A, B$$

where

$$H_t^{ijR} = 0 \quad \forall i < \underline{h}$$

where N_t^{ijR} denotes the number of individuals of cohort i of species j at time t . The term \bar{i} denotes the life length of the species and H_t^{ijR} is the harvest of cohort i of species j at time t .

The formulation in (2) differs from earlier formulations in age-structured models in the fishery management literature by assuming that natural mortality is endogenously determined by population density/ies (cf. Tahvonen, 2009). Moreover, mortality in fishery management models is typically assumed to be decreasing over time (cf. Tahvonen, 2009), which is fully adequate for most fish species given that those are

usually of type B . This assumption is however not applicable for type A species wherefore we need to allow for both increasing and decreasing natural mortality. Harvest in this model, like in most age-structured models in fishery economics, is assumed to exhibit knife-edge selectivity in that no fish below age \underline{h} is captured (cf. Tahvonen, 2009).

Individuals of a resident species of type $j=A,B$ are assumed to be juvenile until the age of \underline{i} , when they reproduce for the first time and then continue to reproduce, until they die at an age of \bar{i} . Recruitment of the resident species is determined by a modified version of the Ricker (1954) recruitment function, allowing recruitment to be affected by competition between species:

$$N_t^{0,jR} = \sum_{i \geq \underline{i}}^{\bar{i}} \left[N_t^{ijR} \alpha^{0,jR} e^{-\left(\sum_{i,k} \beta^{0,jk} N_t^{ijk}\right)} m^{0j} e^{-\left(\sum_{i,k} \beta^{0,jk} N_t^{ijk}\right)} \right] \quad \forall j = A, B, \quad (3)$$

where $m^{ij} e^{-\left(\sum_{i,k} \beta^{0,jk} N_t^{ijk}\right)}$ is the gross number of offspring produced and $\alpha^{0,jR} e^{-\left(\sum_{i,k} \beta^{0,jk} N_t^{ijk}\right)}$ expresses the (instant) survival rate in the same year. Both the gross number of offspring and the survival are thus affected by inter- and intra-species competition through the latter term in these expressions.

The stock dynamics for the invading species are similar to those of the resident species, and are written as:

$$N_{t+1}^{i+1,jI} = N_t^{ijI} \alpha^{ijI} e^{-\left(\sum_{i,k} \beta^{ijI} N_t^{ijk}\right)} + \bar{V}_t^{ijI} \quad \forall i \geq 1, j = A, B, \quad (4)$$

where the last term, \bar{V}_t^{ijI} is the exogenously introduced number of the species, with $\bar{V}_t^{ijI} \geq 0$. The natural recruitment of the invading species is similar to that of the resident, although the number of exogenously introduced invasive species of age 0, $\bar{V}_t^{0,jI}$ is added:

$$N_t^{0,jI} = \sum_{i \geq m} \left[N_t^{ijI} \alpha^{0,jI} e^{-\left(\sum_{i,k} \beta^{0,jk} N_t^{ijk}\right)} m^{0j} e^{-\left(\sum_{i,k} \beta^{0,jk} N_t^{ijk}\right)} \right] + \bar{V}_t^{0,jI} \quad \forall j = A, B \quad (5)$$

This approach to population dynamics is based on the widely used matrix models, originally introduced by Leslie (1945, 1948), which have been found proven to be convenient tools to analyze populations when data on demographic parameters for different age cohorts are available (see e.g. Crouse et al., 1987; Caswell et al., 1998).

2.2 Economic model

The objective function of the decision maker, which is assumed to be the sole manager of the two-population system, includes the costs and revenues from joint management of the resident and invasive species. The revenue from harvests of the resident species, TR_t^{jR} , is defined by

$$TR_t^{jR} = p^{jR} \sum_i w^{ijR} H_t^{ijR}, \quad (6)$$

where p^{jR} is the constant price per kilo of the harvest, w^{ijR} is the age-specific weight per individual of the resident species and H_t^{ijR} is the catch of a particular cohort. The use of a constant price, independent of the harvest, is motivated if there is an elastic demand for the harvested species¹. The total cost is the cost of harvesting the resident species:

$$TC_t^{jR} = \eta^{jR} \left(w^{ijR} N_t^{jR} \right)^{\gamma^{jR}} \left(w^{ijR} H_t^{jR} \right)^{\delta^{jR}}, \quad (7)$$

where γ^{jR} denotes the stock elasticity, δ^{jR} is the output elasticity and η^{jR} is a calibration parameter (cf. Sandberg, 2006; Danielsson et al., 1997). Thus, the harvesting cost is assumed to depend on the size of both stock and harvest. Assuming a single decision maker, profits (π_t) in a given time period are defined by:

$$\pi_t = TR_t^{jR} - TC_t^{jR} \quad (8)$$

and the total net present value, $TNPV$, is defined by

$$TNPV = \sum_{t=1}^T \left(\frac{1}{1+r} \right)^t \pi_t, \quad (9)$$

where r is the discount rate. The manager of the two-population system is assumed to choose harvests of the resident species in order to maximize (9) given (1)-(8).

3. Data

Data used for the biological model are chosen with an aim to illustrate the typical life histories A and B , see Table 1. Both species are assumed to survive six years, implying six different age cohorts $i=0, \dots, 5$. Survival data are chosen to illustrate the characteristics of the different species types, while the number of offspring is calculated such that the finite rate of increase in the biological equilibrium implying that differences in population growth between the types are attributed to age or competition effects only. As a consequence, the type B organism produces more offspring than the type A , but has a lower juvenile survival (see e.g. Lack, 1954), which is also characteristic for the life

¹ This is shown to sometimes be the case in the fishery sector, e.g. for cod supplied by Danish, Icelandic and Norwegian fishery (Arnason et al., 2004). However, it is not likely to apply for harvested species in general, and this simplification is thus motivated by convenience of modeling.

histories of type B species as described above. In the absence of competition between species, the age of highest reproductive value² is 3 for type A organism and 5 for type B . For the economic model, reproduction is calibrated to give identical steady state stocks for all species types under harvesting in the absence of competition with other species, implying that stocks are normalized such that meaningful comparisons can be made. We arbitrarily set the age specific inter-species competition effect, β^{jk} for $l \neq k$, and the age-specific density dependence, β^{jk} for a species k , to 0.00001 for all age classes and species. Data on weight at age³, w^{jR} in eqn. (8) and (9), have been obtained from data for cod in Kuikka et al. (1999), and fitted in order to have a linear increase in weight over time. This is a simplification compared to age-structured fisheries models, where individual weight is assumed to follow a sigmoid curve⁴, motivated by the lack of studies that compare the weight development for type A and B species. All parameter values that characterize the life histories of the different species types are given in Table 1.

[Table 1 about here]

Economic data for the revenue and harvesting cost functions were obtained from data on cod fishery. This choice is motivated by cod being an economically important harvested species, and shown to be sensitive to competition from introduced species (Koehn, 2005; Haslob et al., 2007; Janas and Zgrundo, 2007). Also important for this choice is the availability of revenue and cost data in the literature, which were applied to both species types. The price of harvest, p^{jR} in eq. (8) is assumed equal to the mean price of cod in July 2008, which is 2.08 EUR/kg (Swedish Board of Fisheries, 2008). It is assumed that only individuals age 2 or older can be harvested. For schooling fish species, a stock elasticity (γ^{BR} in eqn. (9)) significantly less than one can generally be expected (Bjørndal, 1987, 1988). Thus for a given effort level, harvesting costs are less sensitive to changes in stock size, because it is more easy to detect fish schools even with a low stock size, compared to fish stocks not gathered in schools. Also non-schooling, demersal species, such as the Northeast Arctic cod, may have a stock elasticity smaller than one (Sandberg, 2006). Scale economies, implying that the output elasticity is less than one, are common in fishery (see e.g. Bjørndal, 1987; Bjørndal and Gordon, 2001; Eide et al., 2003; Eggert and Tveterås, 2007). Based on Sandbergs (2006) estimates for Norwegian pelagic cod fishery we assume a stock elasticity of -0.4 and an output elasticity of -0.2 is assumed. The parameter η^{BR} in eqn. (9) is arbitrarily set to 4000, implying that the average harvesting cost is 0.07 EUR/kg when 30 percent of the initial stock is harvested. The initial vector \bar{N}_0^{jR} in eqn. (9) is set as the steady-state stock in the economic profit-maximizing equilibrium with harvest in the absence of introduced species. The discount rate in eqn. (11) is set to 5 percent.

² The age with the highest expected reproduction of an individual from their current age onward, given that they have survived to their current age.

³ The weight at age without fishing is used and is calculated as the mean under slow and fast growth, respectively (Kuikka et al., 1999, table 2).

⁴ E.g. the so called von Bertalanffy function.

In the following, optimal harvests are calculated over 50 years⁵. With the resident species initially at the economic equilibrium, there is constant harvesting for approximately 30 years in the absence of the introduction of a non-native species. Given that there is a final time period T , the resident species is completely harvested when time approaches T .

4. Results

The explicit modeling of different age classes and species types allows for a large number of different invasion scenarios with results in terms of optimal $TNPV$ and associated harvest and populations of the two species. In the following the importance of (i) invader life history and age, (ii) resident species life history, (iii) economic variables and the time of detection of the invader for these results are explored. Results are computed with GAMS (Brooke, Kendrick and Meeraus, 1988) using a CONOPT solver.

The role of invader life history and age

To see whether invader type and age matter for the economic damage from an invasion, the optimal $TNPV$ have been calculated for different combinations of species types assuming there is an invasion at time $t=1$ of 10 individuals of different age, see figure 1. As the figure reveals, economic damages are small when there is an invasion of 0 or 1-year old individuals and higher when the invaders are of age 2 or older. Invasions of A cause less economic damage compared invasions of B for a given age of the invader except when there is an invasion of 0-year olds. This is explained by the fact that a very large fraction of 0-year olds of type B will not survive until they reach reproductive ages and thus, they will cause very limited harm. For each invader type the largest economic damage is done when the invader age is such that the invader population expands the fastest, which is for an invasion of 2-year olds of type A , and 4-year olds of type B .

[Fig. 1. about here]

These findings can be compared to those in the population ecology literature, where invasiveness of different species types in undisturbed habitats is analyzed. MacArthur and Wilson (1967) suggest that a good colonizer should have a high birth rate to mortality rate ratio, but emphasize that a low mortality rate is most important. Here, the per capita number of births of the type B organism is much higher than that for the type A , and the survival probability for the type B organism is low at young age classes. Since the number of individuals is highest in young age classes, the birth to mortality ratio for type B is lower than for A . One would then expect the type A organism to be a superior colonizer and a better invader than the type B organism. This is not confirmed by this economic model, but type B seems to cause larger damage, explained by a more successful invasion.

When entering a new to the ecosystem, an invader could potentially be more vulnerable compared to its already established equivalent. We have therefore investigated the

⁵ The choice of time frame is made considering that it is the management in the short and medium term that seems of the largest interest here from a policy perspective rather than the identification of a possible steady state solution. In addition, longer time frames tend to generate more pulse harvesting (see e.g. Tahvonen, 2009).

sensitivity of results when invader survival and reproduction are assumed to be 10 percent lower and density dependence 10 percent higher compared to the baseline scenario. Results show that the optimal *TNPV* is more sensitive to assumptions about survival than about reproduction. The slightly higher impact of survival is explained by the number of invaders being low – decreasing the number of reproductive individuals then results in a higher net effect on reproduction of the invader than decreasing the per capita reproduction. Results are insensitive to assumptions about density dependence of the invader. There is a larger variation in the sensitivity of *TNPV* to an assumed decrease in survival of the invader when the invader is of type *B*, explained by a larger variation in the speed of increase in the population between invasions of different age classes.

The role of the resident species life history

With a type *B* resident species, the economic damage is smaller than with a type *A*, given the invader type, see figure 1. The explanation for *B* being an economically more robust species is the following. First, knife-edge selectivity of harvest implies that with a resident *A* and in the absence of invasions, all 4-year old individuals are harvested each year as well as a share of the 3-year olds, implying that there are no 5-year olds in the population. With a resident *B*, only 5-year olds are harvested. Thus, with a resident *B*, the marginal cost today of abstaining from harvesting one 5-year old individual is modest, given the assumed linear weight increase and hence linear increase in the economic value of an individual with age. The marginal benefit of abstaining from harvesting is, on the other hand, comparatively high in the presence of an invader: It consist of the discounted value of the high reproduction of the 5-year old individual *B*, where the offspring can be harvested at a later date and until then, the offspring will compete with the invader, thereby limiting its growth. With a resident *A*, the cost of abstaining from harvesting a 3-year old individual, which is the individual harvested on the margin, is lower given its lower body weight but the marginal benefit of abstaining from harvesting is even lower, given the much lower reproduction.

Results show that the *TNPV* is more sensitive to a lower survival or reproduction of the invader when the resident species is of type *A*. The explanation is just a reversal of the argument in the foregoing paragraph: a lower survival of the invader implies that the relative disadvantage with a resident *A*, because of the smaller marginal impact of the invader from a harvest reduction, will be reduced. In order to investigate the importance of the relationship between the resident species and its habitat, the sensitivity of results with regard to an increase in density dependence of the resident. Results show that with lower carrying capacity of the habitat w.r.t. the resident species, a larger share of the harvest must be abstained from today in order to “crowd-out” the invader by a given number, implying that the economic damage is larger.

The effect of the economy on the jointly managed species

The properties of the jointly managed species are determined not only by species characteristics but also by economic variables. The optimal *TNPV* is more sensitive to assumptions about discount rate and stock elasticity compared to assumptions about harvesting cost and output elasticity. However, the effects on the *TNPV* are mainly those

that one would have in a harvested single-species system. Our interest here is therefore mainly the consequences for resident and invader populations.

With baseline parameters, introduction of an invader leads to an initially much lower harvest, see figure 2a where we have a resident B and an invasion of ten 2-year olds of type A , in order to increase the resident population such that the invader is “crowded out”, see figure 2b. Over the medium time frame, harvests are lower than without an invasion. With a 10 percent higher discount rate, it is too costly to abstain from early harvests implying that the initial harvest reduction is no longer optimal. As a consequence, harvesting and resident population is lower in the medium time frame and hence the invader population increases more rapidly.

[Fig. 2a-b. about here]

Looking at the same invasion scenario, a 10 percent higher harvesting cost, i.e. higher η^{jR} , leads to slightly lower harvests over the first 8 years, followed by slightly higher harvests in most of the following time periods due to the resulting increase in the stock of the resident and the small stock elasticity. The net effect is a slower growth of the invader population. A 10 percent higher output elasticity will slightly increase harvest over the first 5 years compared to the invasion with baseline parameters, but in the medium time frame harvests will be slightly decreased. This is explained by the higher economies of scale, which imply that radical reductions in initial harvests become more costly. The consequence is a more rapid expansion of the invader population, illustrating the importance of harvest choices in the first time periods. The effects of an assumed 10 percent higher stock elasticity are qualitatively similar to those of higher output elasticity but somewhat larger in magnitude.

So far, we have assumed that harvests are chosen optimally in all time periods. However, in reality invaders might not be detected for several years implying that optimal feedbacks are delayed. We therefore investigate the implications of harvests remaining for several years at the levels that would be optimal with no invasion. The costs of delayed detection or, equivalently, delayed policy action, can then be calculated by comparing the economic outcome for different delays. For these calculations we choose the “best” and “worst” invasion scenarios from figure 1 with a resident B , i.e. invasions of 0- and 4-year olds of type B . The impact on the optimal $TNPV$ is below 1 percent in both scenarios for up to a 30-year delay with 0-year olds and a 20-year delay with 4-year olds⁶. The $TNPV$ is more sensitive with an invasion of 4-year olds. A later detection implies that the immediate harvest reduction in the reference scenario is delayed until the detection year and increased in magnitude, and thereafter harvests follow the path in the scenario with immediate reductions. The delay will lead to a more rapid growth of the invader population.

⁶ Longer delays are not feasible with fixed harvests.

5. Discussion

Compared to the earlier literature, the novelty is the use of an age-structured model to analyze introduction of alien species. Earlier age-structured models, used in fishery economics for their more realistic population dynamics, are used to compare optimal and open-access harvesting in a single-species context and to analyze the associated choice of policy instruments. This paper differs by analyzing the role of life histories for species interaction and hence for harvesting strategies. Compared to the earlier literature on invasive species, this paper contributes through the analysis of the implications of age-structure and life history, earlier emphasized in the population ecology literature as important determinants of invasibility and invasiveness.

The analysis in the paper is based on hypothetical cases, in which invading and resident organisms with different life histories, and hence different evolutionary history, interact. However, also species belonging to the same group of organisms can have different survival curves, such as shown to be the case for e.g. herbaceous perennials (Harper and White, 1974) and cycads (Octavio-Aguilar et al., 2008). Thus, although our results are stylized, they may be relevant in many different ecological settings.

One result from the analysis is that a resident species of type B is economically robust against invasions. Many fish species have a type B life history and the result thus contrasts with the empirical observation that many fish species are threatened by invaders. However, the degree of threat depends strongly also on invader life history, as shown above. Other factors may also explain economic vulnerability of harvested fish species, such as high exposure of freshwater and marine species to invasions as well as vulnerability of habitats and entire ecosystems. Moreover, the economic consequences of invasions depend on the value of the species as a food resource. Investigation of these issues would require analysis of differences and uncertainties in vectors of alien species, characteristics of the affected ecosystems and the role of demand for the harvested species.

Another noteworthy result is the observation that for an economically managed resident species not only propagule pressure, i.e. the number of individuals of a non-indigenous species released, but also the age of introducees is a key factor for the need for management of biological invasions. One example that may be relevant is the round goby (*Neogobius melanostomus*), which has become established in the Gulf of Gdansk. It may be introduced to other parts of the Baltic Sea as a juvenile by ballast water and also by active dispersal by large adults, i.e. satellite individuals (Ojaveer, 2006). If active dispersal by large adults is associated with a much higher probability of establishment, actions to reduce ballast water infestation may well be a suboptimal strategy.

The results in the paper further show that not only the relative characteristics of the resident and invading species matter for the economic and ecologic consequences of invasions but also the economic conditions. This suggests that it is possible to identify combinations of life histories and economic conditions that are associated with particularly high or low economic and ecologic risks in the case of an invasion, e.g. a schooling species of type A , harvested by an industry with strong scale economies in a

context when discount rate is high, which invaded by a type *B* species could be particularly vulnerable to invasions in both economic and ecologic terms.

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Table 1. Weight at age, kg/individual and initial number of the resident species.

Age	0	1	2	3	4	5
Age specific survival (α^{ijk}), sp. A	0.80	0.70	0.50	0.32	0.22	0.14
Age specific survival (α^{ijk}), sp. B	0.10	0.29	0.48	0.58	0.68	0.77
Fecundity (m^{ijk}), sp. A	0	0	4	4	4	5
Fecundity (m^{ijk}), sp. B	0	0	20	40	80	150
Intra- and interspecies Competition (β^{ijk})	0.00001					
Weight at age, sp. A and B	0	0.44	0.88	1.32	1.76	2.2
Number of individuals, sp. A	2061	1385	663	60	0	0
Number of individuals, sp. B	2667	768	368	212	142	12

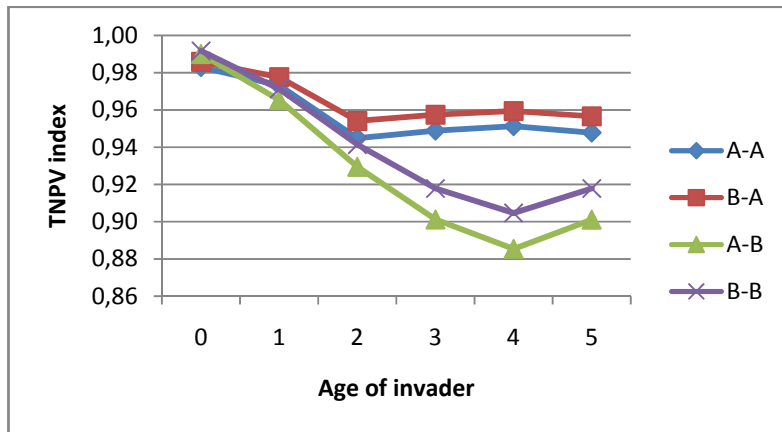


Fig. 1. $TNPV^1$ of harvest under different invasions² of 10 individuals at $t=1$.

1. The vertical axis shows the NPV in the invasion scenario divided by NPV in the case with no invasion.
2. The different curves refer to different combinations of resident and invasive species types, denoted by “resident species type - invasive species type”.

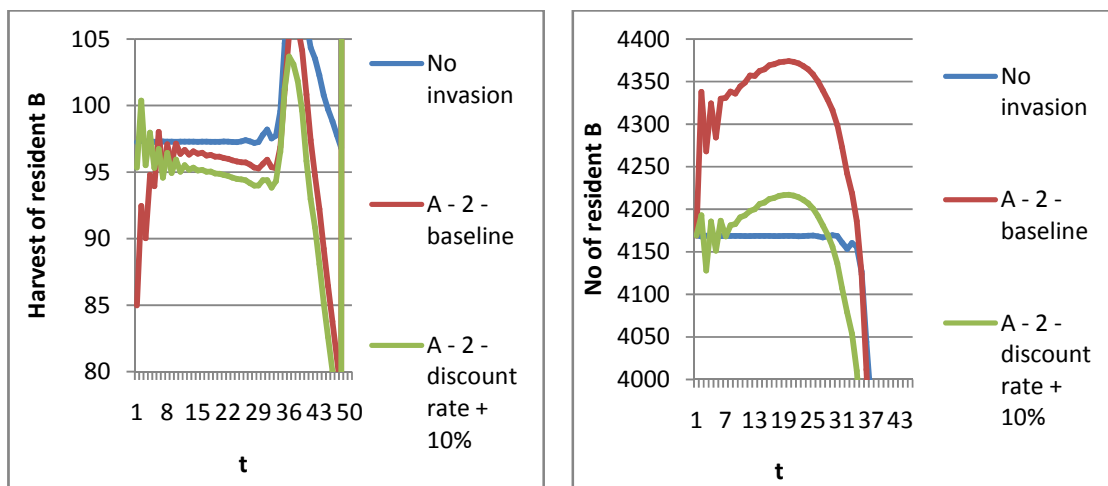


Fig. 2a-b. Effects of a higher discount rate for a resident B with an invasion of ten 2-year-olds of type A.