Ecosystems Conservation and Management Exercises

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Chapter 1

Extinction risk analysis

1. In an insect pest population with sexual reproduction the percentage of recessive homozygotes (genotype aa) is 36%. Calculate:

   - The frequency of recessive and dominant alleles in the population
   - The frequency of dominant homozygotes and of heterozygotes
   - The frequency of the two possible phenotypes under the assumption that A is completely dominant with respect to a.

2. Assume that 96% of the Algerian human population has dark eyes (dominant allele A). What would the heterozygote frequency be in the population? What is the probability that a child born of a pair with dark eyes has fair eyes?

3. The common eider (*Somateria mollissima*, Fig. 1.1) is a large sea-duck that is distributed over the northern coasts of Europe, North America and eastern Siberia. Here below we report the genetic data (Milne e Robertson, 1965) of a small Scottish population; they pertain to two alleles (F and S) at an egg-white protein locus.

Genotypes	FF	FS	SS	total
Numbers	37	24	6	67

Figure 1.1: A pair of common eiders.

   - calculate the frequencies of genes F and S and the genotypic frequency H of heterozygotes;
   - calculate the theoretical frequency H_{EQ} of heterozygotes that would establish if the population were actually at Hardy-Weinberg equilibrium; verify that $H_{EQ} > H$;
   - assume that the smaller frequency of heterozygotes is due to a bottleneck: at the very beginning the duck population was large, thus the heterozygote frequency was H_{EQ}; then the population has been drastically reduced so that the effective population size was 30 ducks for

a certain time T, during which genetic drift has been operating; calculate the time T (years, because reproduction occurs once a year) that is necessary for letting heterozygosity go down to H.

4. The Laysan finch (*Telespiza cantans*) is a Hawaii species classified as vulnerable by the IUCN (see Fig. 1.2). A genetic analysis conducted on 44 individuals evidenced a microsatelite locus (https://en.wikipedia.org/wiki/Microsatellite) with three alleles called 91, 95, 97. Below are the absolute frequencies of the genotypes in the 44 individuals sample

Genotypes	91/91	91/95	91/97	95/95	95/97	97/97	total
Numbers	7	10	8	5	11	3	44

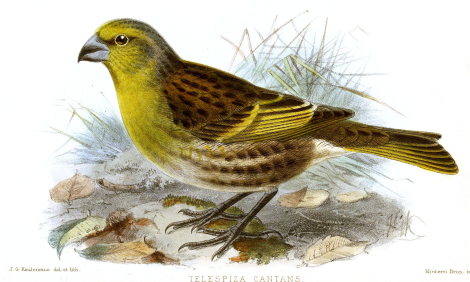
Figure 1.2: The Laysan finch.

a) Derive the frequencies of the three alleles (91, 95, 97); b) calculate the theoretical frequencies at Hardy-Weinberg equilibrium for the 6 genotypes and compare with the data from 44 finches .

5. Wright's formula describes the decrease of heterozygosity due to genetic drift from one generation to the next. For simplicity, the interval between one generation and the other was set equal to one year in the illustration presented to your class, but the formula applies more generally, provided we replace one year with one generation. Ryder et al. (*Oikos*, 1981) have studied three moose populations in Sweden (henceforth indicated with the letters B, C, F) which have different generation times depending on the different hunting regulations that hold for each population. More precisely:

Population B: 4.2 years from one generation to the next

Population C: 9.9 years

Population F: 7.5 years.

The graph (see Fig. 1.3) shows the time trend over a century of the estimated heterozygosity (natural logarithm of the proportion of heterozygous moose against time in years) for each of the three populations.

Calculate the effective population size for each of the three moose populations.

6. The Grünwald Park hosts a relict population of woolly bears (*Ursus laniger*). A team of German ecologists has been studying the demography of this rare species and finally has proposed the following discrete-time model:

$$N_{t+1} = L\left(N_t\right) N_t$$

where N is the bear number and $L(N)$ is the finite rate of increase which depends on N via the following relationship

$$L(N) = \frac{6N}{480 + 0.8N + 0.01N^2}.$$
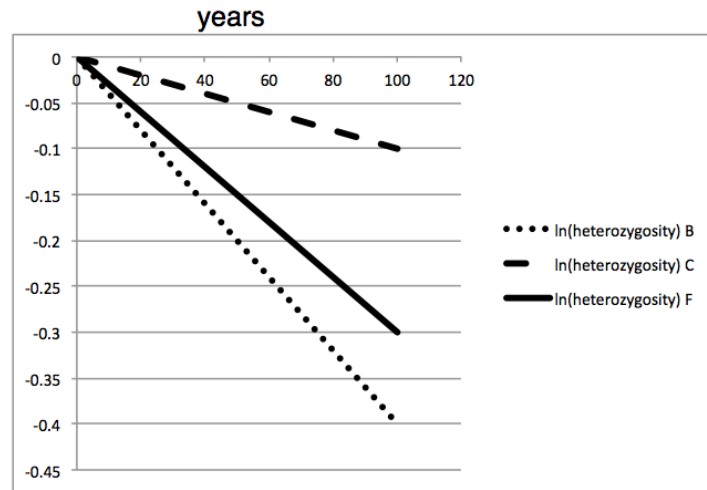
You are required to

Figure 1.3: Variation of moose heterozygosity in three Swedish populations.

- qualitatively draw the Moran diagram for the population of *U. laniger* Grünwald Park ;
- calculate the bear densities at equilibrium and assess their stability;
- assess the long-term fate of the population, given that the last count evaluated the bear population size to be 80 individuals.

7. The small lake of Darkwaters has been repopulated with a rare fish species: the dwarf catfish *Silurus minusculus*. To this end, 30 individuals have been released (sex ratio 1:1). A previous demographic analysis determined that the instantaneous mortality rate is 0.16 year^{-1} while the birthrate is 0.2 year^{-1}. Calculate the long-term probability of success for the reintroduction at Darkwaters.

8. In 2003 a population of pink finches in the natural reserve of Greybeeches consists of only three adult reproductive females (from now on called A, B, C). They breed in mid spring. You know that:

   (a) Female A produces 7 eggs, of which only 5 hatch; 3 nestlings are female and of them 2 will survive till adulthood and will reproduce in 2004; female A dies in December 2003;

   (b) Female B produces 4 eggs, all of which hatch; 1 nestling is female but will not survive till adulthood; female B is still alive in mid spring 2004;

   (c) Female C produces 9 eggs, of which only 6 hatch; 4 nestlings are female and of them 3 will survive till adulthood and will reproduce in 2004; female C is still alive in mid spring 2004;

   Calculate the individual fitness of A, B e C and the finite rate of increase of the population between 2003 and 2004.

9. It has been estimated that the brown bear population in southern Sweden is characterized by an environmental variance of 0.003 while the demographic variance is 0.16. Calculate the critical number of bears below which the population is captured by the vortex of demographic stochasticity.

10. The average lifetime of the golden civet (*Civettictis aurata*) is 2 years and its instantaneous rate of demographic increase is zero. In 2010, 40 civets (sex ratio 1:1) are used to repopulate the Kwakingame reserve, which is the only available habitat for the civet in the Kingland region. Calculate the extinction probability in 2030 for this new population. What is the long-term extinction probability for the civet population at Kwakingame?

11. A population of spotted deer (*Dama variegatus*) is driven by environmental stochasticity only. Its median finite rate of increase is $\lambda = 1.03$ while the demographic variance σ_ε^2 (namely the variance of the logarithm of the multiplicative noise that influences the population abundance) is 0.025. In

2015, 210 deer have been counted. How will the population abundance be distributed in 2025 if the growth is Malthusian?

12. The following table reports the percent changes between one year and the next for the chamois population of Valparadiso (measured whenever the provincial administration has got the funds to conduct the relevant censuses)

Year	1985	1986	1988	1991	1992	1994	1997	1998	2001
Annual increase	105%	98%	92%	112%	107%	88%	93%	101%	97%

Assume that the population has a Malthusian dynamics and estimate both the instantaneous and the finite rate of demographic increase of the chamois.

The nearby Department of Animal Ecology has independently estimated that the population dynamics is driven by a multiplicative noise. The logarithm of such a noise is approximately white, Gaussian, with null mean value and variance σ_ε^2 equal to $6 \cdot 10^{-4}$. In 2014, the provincial administration has counted 350 chamois in Valparadiso. Calculate the probability that the chamois numbers drop below 200 individuals in 2040. To this end use the attached table (Fig. 1.4) that reports the areas of a standard normal distribution.

13. The following table reports the numbers of a lynx (*Lynx lynx*) population in Sweden (see Fig. 1.5) as censused during a decade

Year	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966
Numbers	11	8	3	10	10	18	11	21	19	55	45

Estimate the instantaneous rate of demographic increase for the Swedish lynx population. Suppose that you want to repopulate an Alpine region in which *Lynx lynx* is no longer present because it was exterminated in the past centuries. You decide to release 10 lynxes (sex ratio 1:1) which have been captured in Sweden. Calculate the long-term extinction risk for the new population. To this end assume that the average lifetime of a lynx is about 10 years and that the rate of demographic increase is the same as the one you estimated for the Swedish population.

14. The bearded vulture (*Gypaetus barbatus*, Fig. 1.6) is a bird of prey that eats mainly carrion and lives and breeds on crags in high mountains. Recently, it has been introduced again in the Alps (in particular in the Stelvio National Park, Italy). Shaub et al. (2009) report data on the numbers of vultures in the Alps between 1996 and 2006 (see table here below) and estimate that the birth rate (number of juveniles produced by a pair of vultures that will survive up to the reproductive age) is 0.6 year^{-1}.

Year	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Number of pairs	1	1	2	4	4	5	6	6	8	9	9

The reintroduction has been luckily successful because, given an initial population of two birds only in 1996, the vultures have now established in the Alps and the most recent estimate evaluates their population to have reached about one hundred individuals.

However, owing to demographic stochasticity, the reintroduction might have been less successful. Estimate how many vultures (males + females) should have been introduced into the Alps in order to have a long-term probability of success equal to 95%.

15. The golden-beak parrots (*Parrotus chrysaetos*) were captured in the past for ornamental purpose; in recent times they have been protected in the Montes Rojos reserve. Here below you can find the population numbers as recorded by the Guanavaca Ornithological Institute

Year	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003
Numbers	21	98	285	379	273	313	290	345	330	288	301	314

TABLE II. Areas of a Standard Normal Distribution

An entry in the table is the proportion under the entire curve which is between $z = 0$ and a positive value of z. Areas for negative values of z are obtained by symmetry.
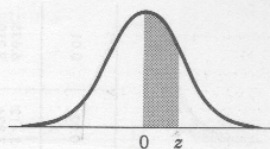
z	.00	.01	.02	.03	.04	.05	.06	.07	.08	.09
0.0	.0000	.0040	.0080	.0120	.0160	.0199	.0239	.0279	.0319	.0359
0.1	.0398	.0438	.0478	.0517	.0557	.0596	.0636	.0675	.0714	.0753
0.2	.0793	.0832	.0871	.0910	.0948	.0987	.1026	.1064	.1103	.1141
0.3	.1179	.1217	.1255	.1293	.1331	.1368	.1406	.1443	.1480	.1517
0.4	.1554	.1591	.1628	.1664	.1700	.1736	.1772	.1808	.1844	.1879
0.5	.1915	.1950	.1985	.2019	.2054	.2088	.2123	.2157	.2190	.2224
0.6	.2257	.2291	.2324	.2357	.2389	.2422	.2454	.2486	.2517	.2549
0.7	.2580	.2611	.2642	.2673	.2703	.2734	.2764	.2794	.2823	.2852
0.8	.2881	.2910	.2939	.2967	.2995	.3023	.3051	.3078	.3106	.3133
0.9	.3159	.3186	.3212	.3238	.3264	.3289	.3315	.3340	.3365	.3389
1.0	.3413	.3438	.3461	.3485	.3508	.3531	.3554	.3577	.3599	.3621
1.1	.3643	.3665	.3686	.3708	.3729	.3749	.3770	.3790	.3810	.3830
1.2	.3849	.3869	.3888	.3907	.3925	.3944	.3962	.3980	.3997	.4015
1.3	.4032	.4049	.4066	.4082	.4099	.4115	.4131	.4147	.4162	.4177
1.4	.4192	.4207	.4222	.4236	.4251	.4265	.4279	.4292	.4306	.4319
1.5	.4332	.4345	.4357	.4370	.4382	.4394	.4406	.4418	.4429	.4441
1.6	.4452	.4463	.4474	.4484	.4495	.4505	.4515	.4525	.4535	.4545
1.7	.4554	.4564	.4573	.4582	.4591	.4599	.4608	.4616	.4625	.4633
1.8	.4641	.4649	.4656	.4664	.4671	.4678	.4686	.4693	.4699	.4706
1.9	.4713	.4719	.4726	.4732	.4738	.4744	.4750	.4756	.4761	.4767
2.0	.4772	.4778	.4783	.4788	.4793	.4798	.4803	.4808	.4812	.4817
2.1	.4821	.4826	.4830	.4834	.4838	.4842	.4846	.4850	.4854	.4857
2.2	.4861	.4864	.4868	.4871	.4875	.4878	.4881	.4884	.4887	.4890
2.3	.4893	.4896	.4898	.4901	.4904	.4906	.4909	.4911	.4913	.4916
2.4	.4918	.4920	.4922	.4925	.4927	.4929	.4931	.4932	.4934	.4936
2.5	.4938	.4940	.4941	.4943	.4945	.4946	.4948	.4949	.4951	.4952
2.6	.4953	.4955	.4956	.4957	.4959	.4960	.4961	.4962	.4963	.4964
2.7	.4965	.4966	.4967	.4968	.4969	.4970	.4971	.4972	.4973	.4974
2.8	.4974	.4975	.4976	.4977	.4977	.4978	.4979	.4979	.4980	.4981
2.9	.4981	.4982	.4982	.4983	.4984	.4984	.4985	.4985	.4986	.4986
3.0	.4987	.4987	.4987	.4988	.4988	.4989	.4989.	.4989	.4990	.4990

Figure 1.4: Table of the standard normal distribution.

Figure 1.5: Swedish lynx in the snow.

Figure 1.6: The bearded vulture.

Fit a Ricker model to the population data (**Hint**: calculate the finite growth rates, then take logarithms and find the appropriate regression line). Find the nontrivial equilibrium of the deterministic model and assess its stability. Which is the long-term average of the parrot population at Montes Rojos?

16. Dennis and Taper (1994, *Ecological Monographs*) report the population numbers of the red deer (*Cervus elaphus*) population in the Yellowstone Park.

Year	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
Numbers	3172	4305	5543	7281	8215	9981	10529	12607	10807	10741	11855	10768

First, establish whether a Malthusian model can correctly describe the red deer dynamics. If the answer is negative, see whether a Ricker model can aptly describe the time evolution of the deer population. In any case find the variance of the environmental stochasticity σ_ε^2 (namely the variance of the logarithm of the multiplicative noise that influences the population abundance).

Chapter 2

Spatial ecology

1. Scientists want to measure the diffusion ability into the surrounding environment of the genetically modified predator insect *Typhlodromus vorax*. It attacks the larvae of *Eotetranychus octomaculatus*, a defoliator that likes apple trees very much. For environmental safety, the GMO has been made sterile. 1,000 individuals of the species *T. vorax* are released in an experimental garden . In the following two months the expansion radii of the GMO in the garden are monitored and recorded:

Day	1	4	8	13	20	35	45	60
Radius (metres)	5	12	16	21	26	34	39	45

   Estimate the diffusion coefficient of *T. vorax* assuming that mortality during the two months is negligible and that scientist cannot find 5% of the population outside the expansion radius.

2. Consider again the GMO of the previous exercise and assume that, owing to a fault in genetically engineering the insect, a few individuals are not sterile; so they can not only disperse but also grow in numbers with a Malthusian instantaneous growth rate $r = 0.5$ year^{-1}. Estimate the expansion speed (m year^{-1}) of the GMO into the surrounding environment.

3. The ragweed (genus *Ambrosia*) is an alien species that has been unfortunately introduced to both Europe and Asia from North America. Ragweed pollen is notorious for causing allergic reactions in humans, specifically allergic rhinitis. Therefore, many countries have decided to employ biological control against ragweed, specifically by a leaf-eating beetle, *Ophraella communa* Le Sage (Fig. 2.1), which is quite effective (Fig. 2.2).

Figure 2.1: The defoliator *Ophraella communa*

Yamamura et al. (2007) studied the mobility of *Ophraella communa* in Japan. On August 8, 2000, they released a number of beetles which they have recaptured after 20 hours by means of traps located at various distances. Here below you can find a table with the results in terms of fractions of caught beetles (for instance, 7.6% is the percentage of beetles recaptured between 20 and 30 m).

Figure 2.2: The ragweeds before biological control (left panel) and after biological control (right).

Distance (m)	0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90
Fraction (%)	50	14.5	7.6	10	5.2	4.8	3.2	2.4	2

Assume that beetles dispersed into the environment according to an isotropic two-dimensional model of diffusion. Estimate the diffusion coefficient D.

4. A new reserve is being set up to protect the species *Perdix polyvarians*, a bird threatened with extinction. Scientists estimated that the yearly finite rate of Malthusian increase for *P. polyvarians* is 1.05, while the diffusion coefficient is 9 km^2/year. Calculate the critical reserve size for the circular and the square shape.

5. Lab experiments have been undertaken to study the dispersal ability of the alien insect *Lymantria australis*. To this purpose, several *L. australis* individuals are released from the same location and monitored for a few days. During this period there is no mortality or reproduction. Scientists observations confirm that the insects disperse randomly in all directions within the lab habitat (which can be assumed to be two-dimensional). By indicating with R the radius inside which 95% of the organisms are spotted, the following results have been obtained

Day	1	4	8	13	20
R (metres)	3	6	8.5	10.5	13

Estimate the diffusion coefficient D of *L. australis*. Unfortunately, in 1985 the insect was inadvertently released in the natural habitat too, where it has fared quite well, expanding its spatial range and growing in numbers. The expansion radii of *L. australis* in the wild have been recorded. They are reported in the following table

Year	1990	1992	1997	2000	2004
Radius (metres)	100	145	237	304	383

From this information estimate the instantaneous rate of demographic increase r of the alien species.

6. The zebra mussel (*Dreissena polymorpha*, Fig. 2.3) is a freshwater invasive species which in the past 25 years has been responsible for enormous damages, both environmental and economic, specially in the United States (and marginally in Italy too). The average lifetime of *D. polymorpha* is about 4 years, and each female produces in the average 2×10^5 eggs per year, with sex ratio 1:1. The fraction of eggs surviving up to adulthood is very low, approximately equal to 0.005%. Adult individuals are basically sessile, while larvae can be transported by the river stream for a few days, after which they settle in the river or lake bed and become mature adults that can reproduce.

Recently, the species has been accidentally introduced into the Yellowish River, downstream of the dam of Deep Lake. The downstream expansion speed of the species has been estimated to be 640 km/year. You know that the river current implies a drift of the larvae of about 600 km/year. Estimate the diffusion coefficient of *D. polymorpha*, assuming that the spatiotemporal dynamics of the population is well described by a model including advection, diffusion and Malthusian growth.

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Figure 2.3: Zebra mussels.

7. Since the beginning of 1900 the Eurasian collared dove (*Streptopelia decaocto*, Fig. 2.4) has expanded its spatial range from Turkey to the whole Europe so that in 1970 Scandinavia, British Isles and Russia have been reached by the bird. Fig. 2.5 displays the exponential increase of the total number $P(t)$ of doves in a sequence of successive years. Estimate the instantaneous rate of Malthusian increase r of *S. decaocto*.

It has been further estimated that the range expansion speed for this dove has been 43.7 km year^{-1}. From this information estimate the diffusion coefficient D of this alien species.

Figure 2.4: The collared dove *Streptopelia decaocto*.
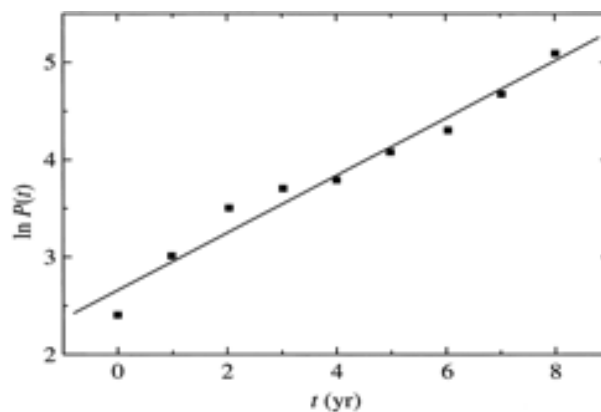
Figure 2.5: Data on the diffusion of collared doves in Europe.

8. The sea otter (*Enhydra lutris*, Fig. 2.6) was on the verge of extinction in California, because of overharvesting, but fortunately in 1911 an international treaty was signed in order to protect the species. Its numbers have been exponentially increasing, as shown in the table below

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Year	1938	1947	1950	1955	1957	1959	1963	1966	1969	1972
No. of otters	310	530	660	800	880	1050	1190	1260	1390	1530

The sea otter has not only increased its abundance but has also expanded its range along the Californian coastline with a speed of about 2.2 km year^{-1}. From this information estimate the diffusion coefficient D of the otter, assuming that the habitat (coastline) is one-dimensional.

Figure 2.6: The sea otter.

Suppose then that you want to introduce a new population of *E. lutris* into the country of Whatsoever, where only a piece of shoreline, 80 km long, is the right habitat for hosting *E. lutris*. Outside that piece of shoreline the sea otter cannot survive at all. Assuming that the new population shares the same demographic and dispersal parameters with the Californian population, assess whether the new population can be successful or not.

9. The metapopulation dynamics of the fork-tailed viper *Vipera forceps* at Mont Ventoux can be approximately described by a Levins-like model in which the extinction probability rate e of each local population is 0.05 year^{-1} while the colonization coefficient c from occupied to empty patches is 0.075 year^{-1}. Calculate the fraction of extinct local populations at equilibrium.

10. The European tree frog (*Hyla arborea*, Fig. 2.7) although it is arboreal does anyway need water bodies for reproduction. Carlson and Edenhamn (2000) studied a metapopulation of this frog in Sweden (378 ponds over an area of about 1200 km^2) and estimated in subsequent years the fraction of occupied ponds and the rate of colonization, namely the fraction of empty ponds being colonized in the course of each year (see Fig. 2.8)

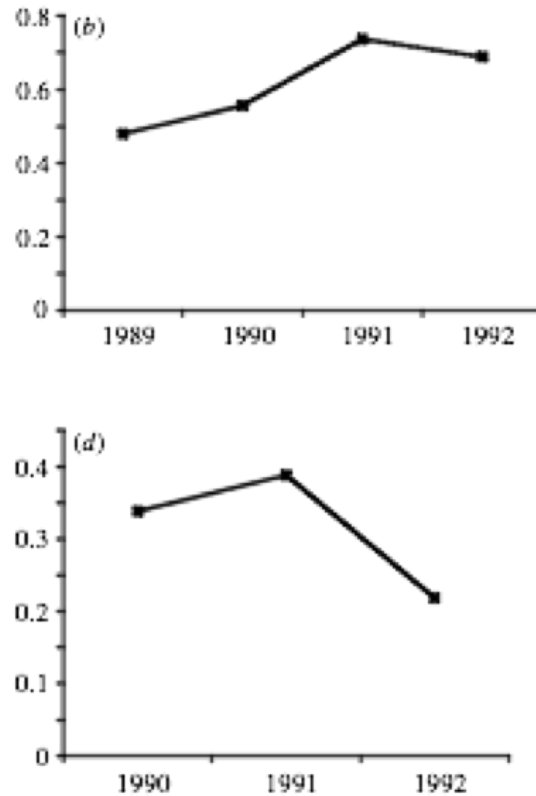Figure 2.7: The European tree frog swimming in a pond.

Figure 2.8: Data of a Swedish metapopulation of *H. arborea* between 1989-1992. Top panel: fraction of occupied ponds in subsequent years. Bottom panel: fraction of ponds that were empty in the previous year and turn out to be occupied in the current year.

Assume that the values recorded in 1992 can be considered as values at equilibrium. Use the Levins model in order to estimate the extinction parameter e and the colonization parameter c. If 40% of the ponds were dried up, what effect would this disturbance have on the frog metapopulation?

11. You are required to study the metapopulation of the butterfly *Euphydryas casagrandi* in the Tuahutu archipelago, which consists of very many small islands. The local extinction probability per unit time in each island is 0.05 year^{-1}. Extinction is counterbalanced by immigration, which can take place because of migration from the mainland or from surrounding islands where *E. casagrandi* is still present. The colonization rate of an empty island from mainland is 0.01 yr^{-1}, while the colonization rate from other islands follows the Levins model and is 0.045 yr^{-1}. Write down the metapopulation model that governs the dynamics of the fraction of occupied islands. Calculate the fraction of occupied islands at equilibrium.

Suppose then that tourism development plans are devised that aim at urbanizing both the Tuahutu archipelago and the nearby coastline on the mainland. According to plan A the archipelago is heavily urbanized, thus leading to the destruction of one fourth of the insular habitat of *E. casagrandi*; according to plan B it is the coast of the mainland that is heavily urbanized, thus leading the whole butterfly mainland population to the complete destruction. Evaluate the impacts of both plan A and plan B on the fate of the butterfly metapopulation.

12. Colonization rate c in metapopulations is generally a decreasing function of the average distance between patches that constitute the metapopulation habitat. Therefore, a further impact of habitat destruction is the increase of the average distance between patches, which implies the decrease of the colonization rate. Include this further effect into the Levins model with habitat destruction that has been illustrated in class. Assume that the metapopulation you are studying is characterized by an extinction rate $e = 0.2$ year^{-1}, that 1/4 of the original habitat is being destroyed and that this

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destruction implies an increase of the average distance d from 1 km to 1.3 km. You have estimated that c [year^{-1}] $= 0.4/d^2$. Explain whether the metapopulation can persist in the long term after the habitat has been destroyed. If it can persist, estimate the fraction of occupied patches at equilibrium.

13. Consider a simple metapopulation consisting of 2 patches linked by migration. The area of patch 1 is 1 km^2, that of patch 2 is 4 km^2. The probability that a propagule released by patch i reaches patch j is $l_{ij} = 0.37 \exp(-\alpha d_{ij})$ where $\alpha = 0.3$ km^{-1} and $d_{12} = d_{21} = 5$ km. The colonization rate is $c = 0.15$ km^{-2} year^{-1}, while the extinction rate is $e = 0.1$ km^2 year^{-1}.

    Write down the two Levins-like equations describing the dynamics of p_1 and p_2, namely the probabilities that patch 1 and patch 2 are occupied. Analyze the equations via the isocline method and find out the fate of the metapopulation. If it can persist, calculate p_1 and p_2 at equilibrium. Calculate the metapopulation capacity and verify the condition for metapopulation persistence.

14. Consider a 3-patch metapopulation in which patch 2 and patch 3 are linked to patch 1, but patch 2 and 3 are not connected by migration (Fig. 2.9).
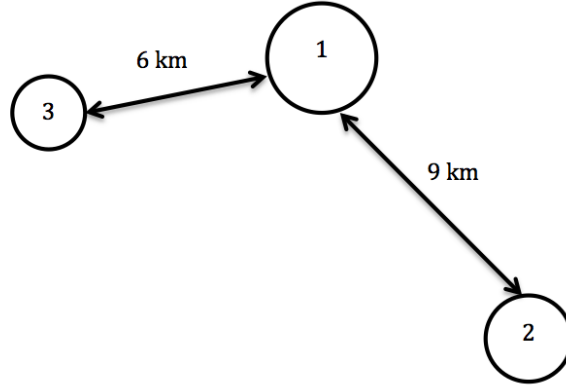

Figure 2.9: Scheme of the 3-patch metapopulation.

More precisely, the probability l_{ij} that a propagule released by patch i reaches patch j is detailed as follows: $l_{23} = l_{32} = 0$, $l_{12} = l_{21} = 0.027 \exp(-\alpha d_{12})$, $l_{13} = l_{31} = 0.09 \exp(-\alpha d_{13})$ with $\alpha = 0.4$ km^{-1}. The areas of the patches are $A_1 = 10$ km^2, $A_2 = 7$ km^2, $A_3 = 4$ km^2. The colonization rate is $c = 0.1$ km^{-2} year^{-1}, while the extinction rate is $e = 0.08$ km^2 year^{-1}. Calculate the metapopulation capacity and check whether the condition for metapopulation persistence is verified. Assume that ecological corridors are built to improve the migration between 1 and 2 and between 1 and 3. This implies a decrease of α from 0.4 km^{-1} to 0.25 km^{-1}. Check the condition for persistence again.

Chapter 3

Management of renewable resource harvesting

1. The northern right whale dolphin (*Lissodelphis borealis*, Fig. 3.1) is often caught in the northern Pacific Ocean by the big high seas driftnets used for fishing commercial species. Mangel (1993) provides information on the demographics and the capture of these dolphins. The dynamics, when there is no fish harvesting, can be described by a generalized logistic model of this kind

$$\frac{dN}{dt} = rN\left(1 - \left(\frac{N}{K}\right)^z\right)$$

   with $K = 900{,}000$ dolphins and $z = 2.39$. Calculate the abundance N_0 at which the maximum sustainable yield of dolphins would be obtained by an appropriate harvesting policy. The exercise is purely theoretical because hunting marine mammals should be avoided.

Figure 3.1: The northern right whale dolphin.

2. The common pheasant (*Phasianus colchicus*) was introduced into Protection Island in 1937. By following the demographic growth of this bird along time it has been possible to obtain the relationship linking the population rate of increase to the population size (see Fig. 3.2)

   Assume that pheasant hunting is permitted and the regulation policy is based on granting licenses. You know that

   - effort is measured as No. of operating hunters
   - the catchability coefficient is 0.01 No. hunters^{-1} year^{-1}
   - only half of licensed hunters is actually hunting in the average.

   Calculate the number L of licenses to be granted that guarantees the maximum sustainable yield and the corresponding pheasant population size at equilibrium. Finally calculate the effort E_{ext} that would lead population to extinction.
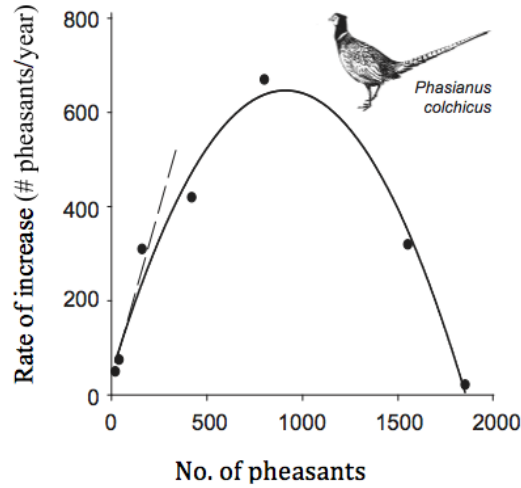
Figure 3.2: The rate of increase of the common pheasant in Protection Island.

3. The graph shown in Fig. 3.3 reports the stock-recruitment relationship for the sockeye salmon (*Onchorhynchus nerka*) of river Skeena (British Columbia, Canada). Approximately determine the maximum sustainable yield (as million fish).
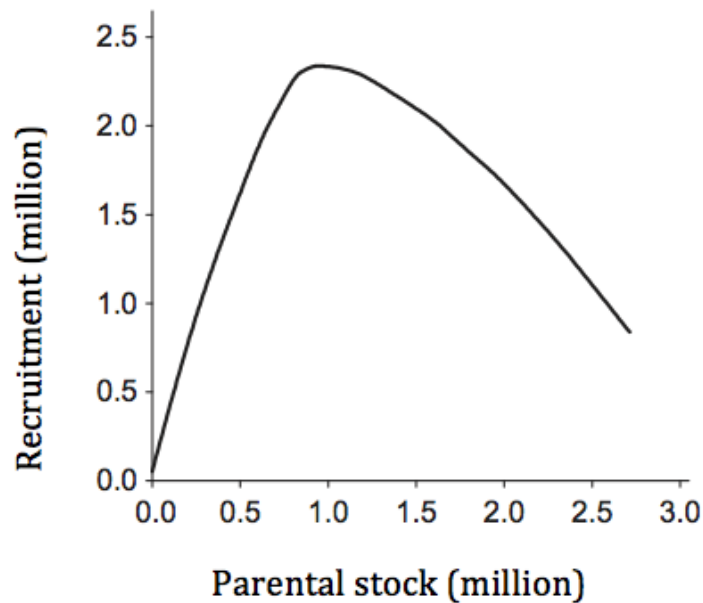

Figure 3.3: The stock-recruitment relationship for sockeye salmon in river Skeena.

4. McCullough (1981) studied the dynamics of grizzly bears (*Ursus arctos*)in the Yellowstone Park. He reports the stock-recruitment curve shown in Fig. 3.4, which links the number P_k of adult bears in year k (namely, the individuals that are 4-years-old or older in year k) to the recruitment (R_k), namely the number of adult bears four years later.

Assume that the Park management allows hunting of adult grizzlies according to the following policy

$$H_k = \begin{cases} 0 & \text{if } R_k \le 35 \\ 0.5(R_k - 35) & \text{if } R_k > 35 \end{cases}$$
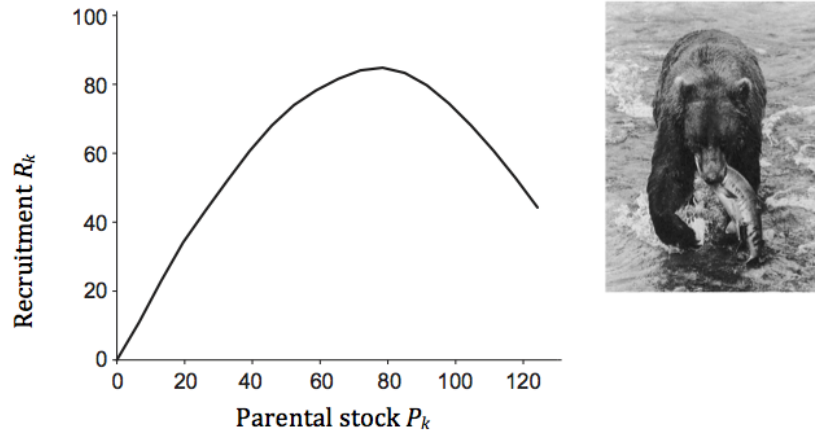
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Figure 3.4: The stock-recruitment relationship for grizzly bears in the Yellowstone Park.

so that a minimal recruitment of 35 adult bears is guaranteed. Evaluate the implications of implementing this policy on the population dynamics.

5. There has been an international debate in the past regarding the opportunity of catching Antarctic krill (*Euphausia superba*, Fig. 3.5), a small crustacean that forms huge swarms in the waters surrounding Antarctica and is a fundamental food for many baleen whales. As the whale stocks have collapsed (and their recovery following the international moratorium on whale hunting will take decades), some researchers proposed that krill might be fished without impairing the functioning of the Antarctic ecosystem.
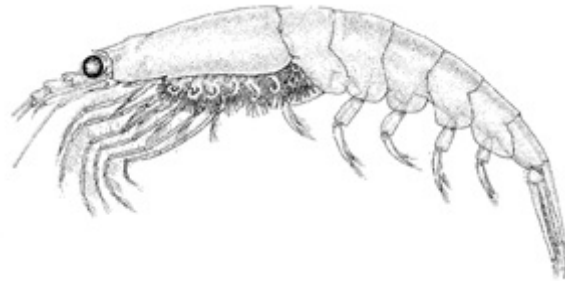

Figure 3.5: The Antarctic krill *Euphausia superba*.

Discuss the problem by writing a simple prey-predator (krill biomass-whale biomass) of the Lotka-Volterra kind, in which the prey grows in a logistic way. Assume that krill is fished with a constant effort E, while hunting of whales does not take place. Determine the stable equilibria of the prey-predator system while the parameter E varies. Find out how the biomass of the sustainable krill catch varies for increasing E.

6. Assume you want to rationally regulate deer hunting in a grassland where the animals can extensively graze. To that end, describe the resource (grass) - consumer (deer) system dynamics by the equations

$$\frac{dG}{dt} = w - d_G G - pGD$$

$$\frac{dD}{dt} = -d_D D + epGD - uD$$

where G and D, respectively, indicate the biomass of grass and of deer (tonnes) and u is the mortality rate due to deer hunting. You know that

- w = net primary production = 100 tonnes year^{-1}
- d_G = grass death rate = 10 year^{-1}
- p = grazing rate coefficient = 0.2 tonnes^{-1} year^{-1}
- e = conversion coefficient = 0.1
- d_D = deer death rate = 0.1 year^{-1} .

Calculate the sustainable yield of deer biomass as a function of hunting mortality u. Then find the maximum sustainable yield.

7. Fig. 3.6 shows the relationship between the number of pups given birth every year (P) and the reproductive adult stock (S) for a population of harp seals (*Pagophilus groenlandicus*) of the Northwestern Atlantic (Carl Walters, personal communication). The pups were harvested for their priced fur (the slaughter is still going on even if the European Union and more recently Russia have banned the import of seal products). About 50% of the pups would survive up to age 4 years if none were killed; animals 4-years-old or older (S) have an annual mortality that is approximately 12%, if both natural mortality and hunting is accounted for.
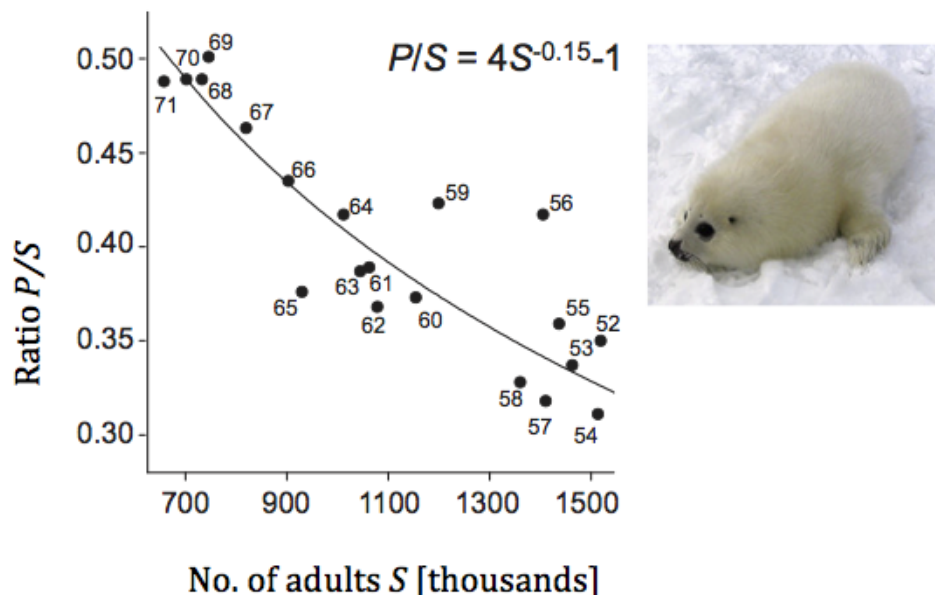

Figure 3.6: The stock recruitment relationship of a harp seal population in the Northwestern Atlantic.

Find out the equilibrium population size if the pups are not harvested. Estimate the number of pups produced every year given such an equilibrium population. Calculate, in case pups were harvested using an annual quota, the maximum sustainable yield and the corresponding adult population that would be necessary to produce such a yield.

Assume then that for several years the adult population equals 600,000 individuals; if 100,000 pups were harvested every year, what would the population dynamics be in the subsequent 4 years? What if the quota were increased to 200,000 pups every year?

8. The whales of the genus *Balaenoptera* have been severely depleted by the extensive hunting carried out during the twentieth century. A very rough way of measuring their total biomass is the Blue Whale Unit (BWU), adopted by the International Whaling Commission which equated two fin whales and six sei whales to one blue whale. For the complex of these whales one can use a Schaefer model (logistic growth of whales and harvesting rate proportional to the product of effort

and whale stock). The effort was measured as the total number of hunting days per year. Assume the following parameters

(a) K = carrying capacity = 400,000 BWU

(b) r = intrinsic instantaneous rate of increase = 0.05 year^{-1}

(c) q = catchability coefficient = 1.3×10^{-5} (hunting days)$^{-1}$

and calculate the bionomic equilibrium under the hypothesis that the opportunity cost of one hunting day is € 5,000 and the selling price of one BWU is € 75,000.

9. The dynamics of the stock of the European hake (*Merluccius merluccius*, Fig. 3.7) of the Adriatic sea can be described by the Schaefer model (see problem 8). Levi and Giannetti (1973) estimated the following demographic parameters:

K = carrying capacity = 5,000 tonnes

r = intrinsic instantaneous rate of increase = 1.7 year^{-1} .

Figure 3.7: The European hake *Merluccius merluccius*.

They also used the tonnes of consumed fuel per year as a measure of effort and estimated the catchability coefficient as $q = 2 \times 10^{-5}$ (fuel tonne)$^{-1}$.

Assume that the selling price of hake is € 6,000 per hake tonne, while the opportunity cost is c = € 140 per fuel tonne. Find the values of the hake stock and the effort at bionomic equilibrium. Then calculate the effort that would guarantee the maximum sustainable profit and the corresponding stock, catch and profit.

10. The dynamics of the fin whale (*Balaenoptera physalus*, Fig. 3.8) is reasonably well described by the following generalized logistic model (N is the whale numbers)

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)^a$$

with $r = 0.06$ year^{-1} , $K = 400,000$ and $a = 0.143$. This stock is now protected, because it has been overexploited. Assume that, once the stock recovers (which will take several decades), hunting is permitted again, but is regulated. Implement a rational management scheme based on the information that the catchability coefficient is $q = 1.3 \times 10^{-5}$ (hunting days)$^{-1}$, the price of one whale is € 40,000, the opportunity cost of one hunting day is € 4,000.

Figure 3.8: The fin whale *Balaenoptera physalus*.

Find the effort E_0 that maximizes the sustainable profit, and the corresponding profit. Suppose you want to utilize a tax τ (which is levied on each caught whale) as a regulation tool. Calibrate τ so that effort stabilizes to the same E_0 you have already calculated.

11. Consider an open-access renewable resource, which is simply regulated by imposing a tax on the net profit obtained by each economic operator exploiting the resource. Comment on the efficacy of such a regulation method by using H. S. Gordon's theory on open-access resources.

12. One of the main tenets of social welfare is progressive taxation. Assume that decision makers want to levy a progressive tax on the amount of biomass removed. The tax is structured as follows

$$\tau = \begin{cases} 0 & \text{if } Y \leq Y_0 \\ \tau_{\max} \dfrac{Y - Y_0}{Y} & \text{if } Y > Y_0 \end{cases}$$

where τ is the amount that is levied on each unit of biomass being harvested and Y_0 is the biomass yield below which the exploiters are exempted from paying taxes. Discuss the efficacy of this regulation method by using a Gordon-Schaefer model (logistic demography, harvest proportional to effort times biomass, and bionomic equilibrium).

13. In the forested areas of North America the beaver (*Castor canadensis*), which is no longer hunted for its fur, is becoming an important factor of nuisance to timber production. In fact, this herbivore can fell mature trees up to a diameter of 40 cm (Fig 3.9). A cost-benefit analysis estimated the annual damage of one beaver to be \$ 45. Assume that the local authority wants to implement a culling policy in an area where the beaver carrying capacity is 1 individual km^{-2} and the intrinsic instantaneous rate of demographic increase is 0.3 year^{-1}. Culling is expensive and the cost C can be evaluated as dollars per year per km^2. C can be assumed to be proportional to the inflicted mortality rate m [year^{-1}] and inversely proportional to the beaver density N [No. of beavers km^{-2}], because capturing beavers is harder when their density is lower. Specifically, assume $C = 2.5m/N$.

Figure 3.9: A beaver felling a tree.

Find the best mortality rate, namely the one that minimizes the sum of the damages to timber plus the cost of culling. Estimate the beaver density at equilibrium corresponding to the optimal culling rate.

14. A tree species can be harvested for producing either pulpwood or sawlogs. Fig 3.10 reports the net profit that can be obtained from clear-cutting a forest lot at different ages. Assume that the discount rate is zero and find out the optimal rotation periods for the two alternatives. Evaluate whether it is more convenient to produce pulpwood or saw-logs.

Figure 3.10: Net profit per hectare as a function of age for a tree species that can be harvested for producing pulpwood or saw-logs.

15. Many seal populations are protected by law and international treaties. Fishermen, however, have often complained that the increase of seal numbers damages their catches, because these marine mammals subtract fish biomass that, without increased protection, would actually end up in their nets. Investigate the problem with reference to a constant-recruitment fish population in which the weight w of each individual fish varies with age τ [years] according to the following law

$$w(\tau) = w_{\max} \left(1 - exp(-k\tau)\right)$$

where

$w_{\max}$ $= 10$ kg
k $= 0.1$ year^{-1}

while survival from age 0 (recruitment age) up to age τ follows the following law

$$p(x) = exp(-\mu\tau)$$

with μ being a constant. Assume that cost of fishing effort is negligible and that the mortality rate without seals is $\mu_0 = 0.1$ year^{-1}, while the mortality rate with seals is $\mu_S = 0.2$ year^{-1}. Calculate the optimal age to be selected by the fishing gear in the two cases by assuming that the fishermen optimize the sustained biomass yield. Calculate the variation of yield between the two cases.

16. You have been requested to manage aquaculture in the lagoon of *Stillwater*. Every year, juveniles of the species *Argenteus bonissimus*, which is very much appreciated by gourmets, are recruited from the open sea to the lagoon. The weight w [kg] of the fish increases with age τ [years] according to

$$w(\tau) = w_{\max} \left(1 - exp(-k\tau)\right)$$

where $w_{\max} = 2$ kg and k is a growth coefficient which depends on the food provided to *A. bonissimus*. It equals 0.25 year^{-1} if a highly caloric fish-meal C_1 is fed to the fish or 0.15 year^{-1} if a poorer food C_2 is employed. The mortality rate of the fish is constant with age and equal to 0.1 year^{-1}. Also, there is no reproduction in the lagoon and the recruitment is constant and equal to 100,000 juveniles per year. The following economic data are available:

(a) the selling price of 1 kg of *A. bonissimus* is 10 euros;
(b) the harvesting cost is negligible whatever the harvested biomass and the mesh of the gear;

(c) the annual cost of using C_1 is 400,000 euros while that of C_2 is 150,000 euros.

Determine the best harvesting policy (selected age) and the optimal fish-meal.

Chapter 4

Ecology of parasites and disease

1. Rabies is a serious microparasitic disease due to the transmission of a virus between hosts. One of the most important animal hosts is the red fox. Write down an *SI* model for this mammal assuming that demography is logistic, transmission is density-dependent and no infected animal can recover from the disease. Use the following parameters:

   - birth rate $\nu = 0.6$ year^{-1}
   - natural death rate $\mu = 0.2$ year^{-1}
   - carrying capacity $K = 5$ foxes km^{-2}
   - disease-related death rate $\alpha = 5$ year^{-1}
   - basic reproduction number of rabies $R_0 = 3$.

   Compute (a) the transmission coefficient β of rabies in foxes; (b) the endemic equilibrium densities of susceptible and infected foxes; (c) the equilibrium prevalence of the disease.

2. The polytechnical rhinitis is a viral disease that strikes humans with usually benign consequences. However, some individuals with a weakened immune system may die from secondary complications. The disease does not confer immunity. Describe the rhinitis dynamics within the Engineeropolis community by means of an *SI* model with density-dependent transmission and characterized by

   - birth rate $= 0.05$ year^{-1}
   - natural death rate $= 0.01$ year^{-1}
   - carrying capacity $= 15,000$ individuals
   - disease-related death rate $= 0.04$ year^{-1}
   - rhinitis transmission coefficient from infected to susceptible $= 0.001$ year^{-1} No. of infected^{-1}
   - recovery rate $= 5$ year^{-1}

   Based on these data (a) write down the model for the disease dynamics, (b) compute the basic reproduction rate of rhinitis, (c) determine whether rhinitis can permanently establish within the community, and (d) compute the numbers of infected and susceptibles at the endemic equilibrium.

3. The gonorrhoea of striped kangaroos is a bacterial disease that strikes kangaroos as a consequence of sexual contacts. The contact rate increases with the number of kangaroos and then saturates, because the maximum number of sexual contacts per unit time is obviously finite. The disease does not confer immunity. Describe the gonorrhoea dynamics in Marsupiumland by an *SI* model with saturating transmission and characterized by

   - birth rate $= 0.2$ year^{-1}
   - natural death rate $= 0.05$ year^{-1}
   - carrying capacity $= 50$ kangaroos km^{-2}
   - disease-related death rate $= 0.01$ year^{-1}

- infection rate $= \beta I/(\delta + N)$, with $\beta = 3$ year^{-1} and $\delta = 10$ kangaroos km^{-2} (with $N = S + I$)
- recovery rate $= 2$ year^{-1}

Based on these data (a) write down the model for the gonorrhoea dynamics, (b) compute the basic reproduction number of the disease, (c) determine whether gonorrhoea can permanently establish within Marsupiumland kangaroos, and (d) compute the prevalence at the endemic equilibrium.

4. In many microparasitic diseases a fraction of infected and infectious individuals is not symptomatic and thus can reproduce. For instance, cholera and amoebiasis are diseases with this peculiarity. Analyse the effect of asymptomatic individuals in an SI system without immunity, with density-dependent transmission and Malthusian demographics. Assume that:

   - the birth rate of susceptibles and asymptomatics is $\nu = 0.7$ year^{-1}
   - the natural death rate is $\mu = 0.2$ year^{-1}
   - the disease-related death rate is $\alpha = 0.01$ year^{-1}
   - S and I are measured as No. of individuals km^{-2}
   - the transmission coefficient from infected to susceptible is $\beta = 2$ year^{-1} (No. of individuals km^{-2})$^{-1}$
   - the average recovery time from the disease is 15 days
   - a fraction σ of infected is symptomatic and cannot reproduce.

   Write down the SI model equations and determine how the model equilibria vary for increasing σ. Find out the values of σ for which the disease can demographically regulate the Malthusian population.

5. Selective culling is a method that can be employed to try to control wildlife diseases (e.g. rabies). Perform a simple analysis of the efficacy of this control method by using an SI model without immune response and with density-dependent transmission. Assume the following values for the parameters

   - birth rate of susceptibles $\nu = 1.5$ year^{-1}
   - natural death rate $\mu = 0.5$ year^{-1}
   - disease-related death rate $\alpha = 1$ year^{-1}
   - S and I are measured as No. of individuals km^{-2}
   - carrying capacity $K = 13$ individuals km^{-2}
   - transmission coefficient from infected to susceptible $\beta = 1$ year^{-1} (No. of individuals km^{-2})$^{-1}$
   - average recovery time from the disease $= 2$ months

   Find out whether the disease can establish in the population. If it can, analyse whether culling can eradicate the disease. Assume that hunters can distinguish and kill the infected animals only, inflicting a death rate h (year^{-1}). How big should h be to permanently eliminate the disease from the wildlife population?

6. Fish populations can harbour several species of macroparasites. For instance the yellow perch (*Perca fluviatilis*) can be infected by the cestode worm *Triaenophorus nodulosus*. The characteristics of the parasite load distribution in the perch is shown in figure 4.1 which reports the mean parasite load and the clumping parameter k. The yellow perch lives 5 years in the average. The mortality inflicted to the fish by the macroparasite is not easy to quantify, but one can approximately assume that a parasite load of 5 worms per fish inflicts a mortality which is about half the natural mortality of the perch. The estimated carrying capacity of the perch (e.g. in Lake Varese, northern Italy) is about 6,000 individuals km^{-2}. Its intrinsic instantaneous rate of increase is approximately 0.05 year^{-1}. The average life time of the adult *T. nodulosus* is not exactly known but can be assumed to be about 2 years.

   Assume that the basic reproduction number of the disease is 1.2 and that the average parasite load reported in figure 4.1 is the one that would establish at the equilibrium between hosts and parasites.
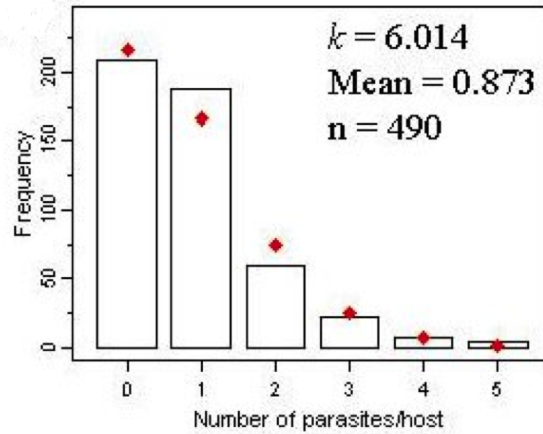
Figure 4.1: Distribution of *Triaenophorus nodulosus* loads inside the yellow perch *Perca fluviatilis*.

By using the model by Anderson and May, evaluate the abundance of hosts at equilibrium. Also, estimate the values of the two parameters λ and H_0 in the relationship $\lambda H/(H_0 + H)$ that links the fertility of one adult worm to the host density.

7. The blue partridge of the Po valley (*Lagopus padanus*) is often infested by nematode worms of the genus *Trichonicus*, which are not lethal, but have noxious effects on the bird fertility. When the partridge population is disease-free, the carrying capacity is $K = 40$ individuals km^{-2}, while the death rate is $\mu = 0.2$ year^{-1} and the intrinsic rate of demographic increase is $r = 0.1$ year^{-1}. Let L be the parasite load (i.e. the average number of adult worms inside the guts of each partridge); then the decrease of the per capita natality rate is εL with $\varepsilon = 0.05$ (No. of parasites/No. of partridges)$^{-1}$ year^{-1}. The death rate m of the parasite is 0.6 year^{-1}, while its reproduction rate (year^{-1}) is a function of the density H of partridges: $2H/(10 + H)$.

Find the coexistence equilibrium between parasites and hosts. Then graph the isoclines and determine the epidemiological dynamics.