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The invasion success and invasiveness of the introduced *Rana lessonae* and its hybrid associate *R.* kl. *esculenta* (Amphibia) in Southwest Norway

Louise-Marie J. B. Holst

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Supervisor: Ole Kristian Berg, IBI
Co-supervisor: Dag Dolmen, NTNU Vitenskapsmuseet

Norwegian University of Science and Technology
Department of Biology

Abstract

In 2003, congeners of the green frog complex, *R. lessonae* and *R.* kl. *esculenta*, were intentionally and illegally introduced to Finnøy, an island in Southwest Norway. All freshwater localities on the island were investigated for three consecutive years from 2009 to 2011 to study the aliens' establishment, dispersal and habitat requirements.

In 2009, the frogs were confined to the northern half of the island and present in approximately 30% of all the freshwater localities. The population as a whole expanded its geographical range every year. *R.* kl. *esculenta* dispersed further and faster than *R. lessonae*. In 2011, *R. lessonae* and *R.* kl. *esculenta* were present throughout the study area, in 51% and 62% of the localities, respectively. Successful reproduction occurred in half of the occupied localities.

The frogs displayed low habitat selectivity on Finnøy. Sun exposure was the strongest limiting factor on the probability of presence of both forms of frogs and reproduction. Other possible habitat requirements included distance to nearest forest edge, water colour, pH and aluminium concentration.

Freshwater localities on the mainland near Finnøy were investigated for habitat suitability in the likely, but unwanted event of secondary introductions. Two scenarios, based on different interpretations of the habitat requirements on Finnøy, predicted suitable breeding localities on the mainland.

The results show that the green frogs on Finnøy have had a formidable invasion success and high level of invasiveness and should be considered as a valid conservation problem in Norway.

Sammendrag

I 2003 ble artsfrender i grønnfroskkomplekset, *R. lessonae* og *R.* kl. *esculenta*, ulovlig og bevisst introdusert til Finnøy i Sørvest-Norge. Alle ferskvannslokalitetene på øya ble undersøkt tre påfølgende år, fra 2009 til 2011, for å kartlegge den introduserte populasjonens etablering, spredning og habitatkrav.

I 2009 var froskene tilstede i omtrent 30% av alle ferskvannslokalitetene, begrenset til den nordlige halvdelen av øya. Populasjonen utvidet sin geografiske rekkevidde hvert år. *R.* kl. *esculenta* spredde seg lengre og raskere enn *R. lessonae*. I 2011 var *R. lessonae* og *R.* kl. *esculenta* tilstede i respektive 51% og 62% av lokalitetene, spredd utover hele øya. Suksessfull reproduksjon forekom i halvparten av de okkuperte lokalitetene.

Froskene viser lav habitatselektivitet på Finnøy. Soleksponering var den viktigste begrensende faktoren på sannsynligheten av tilstedeværelse og reproduksjon. Andre mulige habitatkrav var avstand til nærmeste skog, vannfarge, pH og aluminium konsentrasjon.

Ferskvannslokaliteter på fastlandet nær Finnøy, ble undersøkt med hensyn til habitategnethet i det sannsynlige, men uønskede tilfelle av sekundære introduksjoner. To prediksjonsscenarier, basert på ulike tolkninger av habitatkravene på Finnøy, forutsier at det finnes egnede reproduksjonslokaliteter på fastlandet nær Finnøy.

Resultatene viser at froskene på Finnøy har hatt en formidabel invasjonssuksess og invasive evner og ansees dermed som et gyldig bevaringsproblem i Norge.

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Louise-Marie J. B. Holst

Contents

1 Introduction

The movement of species to areas outside of their native ranges and the subsequent establishment of alien species are increasing and recognized as one of the major threats to global biodiversity. Invasive species alter ecosystem properties and processes as well as native community structure (Elton 1958, Schoener and Spiller 1996, Lockwood et al. 2007, Kraus 2009). Despite a delay in concern for alien amphibians and reptiles globally, the awareness and interest in invasive herpetology are expanding (Kraus 2009). This is due to the acquisition of evidence linking introductions to damage native species, for example the brown tree snake *Boiga irregularis* (Merrem, 1802) in Guam, the cane toad *Bufo marinus* (Linnaeus, 1758) in Australia and the bullfrog *Rana castabeina* (Shaw, 1802) in Western United States, and the fact that also herpetological introductions are growing exponentially (Lockwood et al. 2007, Kraus 2009). Norway is no longer a virgin to alien amphibians, which has given rise to this master thesis in applied freshwater ecology.

Until quite recently, it was generally accepted that only three species of anuran amphibians occur naturally in Norway; including the common toad *Bufo bufo* (Linnaeus, 1758), the common frog *Rana temporaria* Linnaeus, 1758 and the moor frog *Rana arvalis* Nilsson, 1842 (Hågvar 1998). In recent years, the number of species of anurans found to be living in the country has augmented; the new additions are all members of the green frog complex (also known as the water frog complex).

In 1986, a small isolated population of the pool frog *Rana (Pelophylax) lessonae* Camerano, 1882 was discovered in Southern Norway (Dolmen 1996). Its provenance was long misunderstood. It was at first assumed to be descendants of earlier introductions from mainland Europe. Eventually, it was found to be a relict: a native population belonging to the distinct northern clade of pool frogs together with Swedish and British populations (Dolmen 1996, Zeisset and Beebee 2003). Consequently, it was listed as critically endangered in the Norwegian red list (Artsdatabanken 2011a).

In 2009, the inhabitants of the island of Finnøy in Southwest Norway were intrigued by a new sound resonating in the landscape. Investigation revealed a large population of the southern clade of pool frogs and its hybrid associate *Rana* klepton *esculenta* Linnaeus, 1758 (Dolmen 2009a, b). The introduction had been intentional and illegal six years earlier, performed privately by a father and son presumably motivated by the perceived amenity of the frogs. The propagule constituted 20-30 metamorphosed green frogs originating from Poland. In 2009, the population was roughly estimated to be 1500-3000 adult individuals (Dolmen 2009b).

The negative ecological impact of the green frogs on Finnøy was assumed to be inconsequential because they live alongside the common toad and smooth newts *Triturus (Lissotriton) vulgaris* (Linnaeus, 1758) and do not appear to carry any diseases (Dolmen 2009a). Additionally, international herpetologists have not articulated concern when inquired on the subject owing to the fact that *R. lessonae* and *R.* kl. *esculenta* are not known to displace other species where they are native in Europe (Dolmen 2009b). Notwithstanding, the impact caused by alien herpetofauna have often proven to be insidious and "disbelief [that alien amphibians constitute problems] remains common among scientists as well, including many specializing in invasive species research" (Kraus 2009).

A corollary of a thriving population of day-active, pond-dwelling, sun-basking, boisterous and media-popularized green frogs on a populated island close to a relatively large city on the mainland (Stavanger) may be secondary anthropogenic introductions of the aliens to the mainland. Thus, increasing the potential of negative impact on the Norwegian biodiversity. If the green frogs thrive on the mainland in the same manner as they do on Finnøy they could, in the worst case scenario, become yet another stressor on the already declining native amphibian populations (Dolmen et al. 2004, Dolmen 2005) and possibly extirpate the endangered native northern clade of pool frogs in Aust-Agder by introgression or competition (Dolmen 2009b). Similar concerns have been stated in other parts of Europe where members of the green frog complex have been introduced (Arano et al. 1995). Secondary anthropogenic introductions of the green frogs to the mainland should be considered a realistic event within the next decades (Personal communication, Dolmen 2010).

As there is a wicked and sometimes equivocal terminological web of terms in the field of invasion ecology (Colautti and MacIsaac 2004, Lockwood et al. 2007) the terms used in this thesis needs clarification. The term invasion success describes to which stages in the invasion process an introduced species has reached: is it establishing, remaining local or spreading, and is it becoming widespread and dominant (Colautti and MacIsaac 2004). The term invasiveness also relates to the introduced species and is described as the believed ability a species has to colonize a non-native area (Alpert et al. 2000). On the other hand, invasibility relates to the environment and its susceptibility to future invasions (Alpert et al. 2000).

The objective of the present study was to determine the invasion success and invasiveness of the green frog population Finnøy and to assess whether the green frogs are a valid conservation problem in Norway. Are the green frogs expanding their geographical range on Finnøy? What are their habitat requirements? What characterizes a suitable breeding locality? These questions have been investigated relating to properties of the 53 freshwater localities on Finnøy. Conductivity, pH, total hardness, total nitrogen, water colour, aluminium-, calcium-, phosphorus-, and chloride content, sun exposure, distance to nearest forest edge and bottom vegetation cover were the investigated variables believed to have biological significance on the probability of presence of the frogs and reproduction.

Several lentic bodies of water on the mainland were evaluated in terms of habitat suitability. As known history of past invasions may be the best predictor of future invasions (Reichard and Hamilton 1997) the invasion success of the introduced frogs on Finnøy was used to predict whether future introductions of the green frogs to the mainland may be successful.

In order to understand why the newly introduced southern clade of pool frogs on Finnøy are thriving while the native populations of northern clade of pool frogs in Aust-Agder are on the brink of extinction, comparisons of climate, water chemistry and size of yearlings were made.

The null-hypotheses for this study were the following:

- *R. lessonae*, *R.* kl. *esculenta* and their reproduction are randomly distributed among the freshwater localities on Finnøy.
- Freshwater localities on the mainland close to Finnøy are homologous to breeding localities on Finnøy.
- Yearlings of the introduced Finnøy population and the native Aust-Agder population are of equal body size.

2 Studied species

The Central European green frog complex consists of the two species *R. lessonae* and *R. ridibunda* (Pallas, 1771), and the hybrid *R.* kl. *esculenta* (Figure 1). In contrast to the quiet and more terrestrial brown frogs native to Norway, the green frogs are often noisy, frequently aquatic and usually gregarious (Arnold and Ovenden 2002). *R. lessonae* occurs naturally from France eastward through Central Europe to West Russia, north to Estonia and south to the Po valley in Northern Italy. Small populations of *R. lessonae* have been found native in East-central Sweden (Sjögren et al. 1988), South of Norway (Dolmen 1996) and in England (Beebee et al. 2005). *R.* kl. *esculenta* is found approximately in the same range as *R. lessonae*, but occurs alone in Denmark and Sweden (Arnold and Ovenden 2002). Congeners of the green frog complex have on several occasions been introduced outside their native range, for instance in Belgium, Britain and Southern France due to escapes from the food industry or intentionally for ornamental purposes (Pagano et al. 2003, Holsbeek et al. 2008).

Figure 1. Individuals of *R. ridibunda*, *R. lessonae* and *R.* kl. *esculenta* which together constitute the Central European green frog complex (modified from Fog et al. 1997).

The lineage of *R.* kl. *esculenta* is maintained through the rare process of hybridogenesis. Initially, a hybrid (genome RL) originates from primary hybridization between *R. ridibunda* (genome RR) and *R. lessonae* (genome LL). Secondary hybridization between one of the parental species and a hybrid is then possible as one of the parental genome in the hybrid is destroyed prior to meiosis, followed by backcrossing to the other parental species (Figure 2). The hybrid usually coexists only with one of the parental host species. Most commonly, the hybrids coexist as diploid and/or triploid (genome LLR and LRR) with *R. lessonae* populations and less commonly with *R. ridibunda* populations (Uzzel and Berger 1975, Uzzel et al. 1975, Uzzel et al. 1977, Alford and Richards 1999, Christiansen et al. 2010). Rarely, it can form all hybrid population that are neither sympatric with parental species (Arioli 2007, Jakob 2007), nor clonal (Christiansen and Reyer 2009) and the hybrid has therefore been proposed reinstated as a species and renamed to *Rana (Pelophylax) esculenta* (Frost et al. 2006).

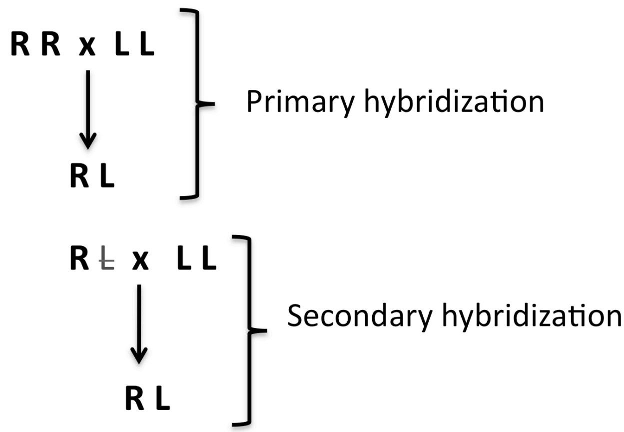

Figure 2. Sketch of the process of hybridogenesis. This process enables hybrids to maintain persisting populations. Primary hybridization results from reproduction between *R. ridibunda* and *R. lessonae*. Secondary hybridization results from reproduction between *R.* kl. *esculenta* and *R. lessonae* (modified from Plenet et al. 2000).

Hitherto, only individuals of *R. lessonae* and *R*. kl. *esculenta* have been observed on Finnøy (Dolmen 2009b). It is believed that *R.* kl. *esculenta* only exist as a diploid hydrid on Finnøy (Dolmen 2009b).

As explained by the process of hybridization, the green frogs on Finnøy belong to different categories of specions. *R. lessonae* is a mayron while *R.* kl. *esculenta* is, as the nomina indicates, a klepton. Without going further into the eidonomy, the field of taxonomy that addresses the species problem, *R. lessonae* and *R*. kl. *esculenta* will further on in this report be denominated as "forms" when mentioned together.

The forms are very similar to each other and at the same time highly variable, which makes them difficult to identify (Arnold and Ovenden 2002). The most useful features for field identification are the ratio between the metatarsal tubercle and the calf length, the shape of the metatarsal tubercle, the colour of the vocal sacs and the colour and texture of the skin (Engelmann et al. 1993, Fog et al. 1997, Arnold and Ovenden 2002, Dolmen 2009a) (Table 1 and Figure 3). Field identification of eggs and tadpoles is associated with error and has not been attempted in this study.

Table 1: Features for identifying *R. lessonae* and *R.* kl. *esculenta*, listed in order of reliability, bold numbers are averages.

	R. lessonae	*R.* kl. *esculenta*
Metatarsal tubercle : calf length	4.5-**5.5**-**7.0**-8.5	6.0-**7.0**-**9.0**-10.0
Shape of metatarsal tubercle	High and semicircular	Low and semiellipsoid skewed towards toes
Leg turned forward against the body	Heel does not reach eyes	Heel reaches between eyes and snout
Vocal sac colour	White	Light grey
Skin colour	Green - yellow	Green - brown
Skin texture	Smooth	Warty
Song	"Auwack...auwack...auwack..." immediately followed by ”Reh...reh...reh..." each croak lasting up to 1.5 seconds.	"Reh...reh...reh..." each growling croak lasting up to 1.5 seconds.

Figure 3. Identification of *R. lessonae* (left) and *R.* kl. *esculenta* (right) based on the heel's position when the leg is brought forward and the shape of the metatarsal tubercle. Photo: Louise-Marie Holst.

3 Area description

The study area is delimited to the island of Finnøy (position: 3°1'E and 65°6'N), located in Southwest Norway, in the county of Rogaland and the municipality of Finnøy (Figure 4). The island lies in Boknafjorden and has an area of approximately 25 km^2. The city Stavanger is situated approximately 20 km south of Finnøy and the two are indirectly connected by a set of subsea tunnels.

The study area has an elevation up to 153 meters above sea level. According to cartographic data from Skog og Landskap, a total of 75% of the island is agricultural land fairly divided between pastures and crops. Approximately 18% of the land is covered by forest, divided into coniferous (8%), deciduous (49%), and mixed forests (44%). Marsh and bog constitute one percent of the land area and fresh water, mostly ponds and lakelets, constitute another percent of the total land area. The extent of alteration of water bodies in benefit of agricultural land is unknown. Judaberg in the east is the island's most densely populated area and the municipality's administrative centre.

In the southern part of the island, the largest lakes are Bleievann, Lasteinvann and Sævheimsvann. In the northern part of the island, the largest lakes are Lauvsnesvann, Spannevann and Hauskjevann. All the abovementioned have a north-south orientation.

Although few areas are pristine due to agriculture, there remain important areas for nesting wetland birds. A nature reserve of 0.223 km^2 was created in 1996 around the mesotrophic/eutrophic lakes of Hauskjevann and Lauvsnesvann in the northeastern part of the island. The southern oligotrophic lakes Bleievann and Lasteinsvann are used as drinking water supplies for the island.

Metamorphosed Cambro-Silurian bedrock is found on the islands in the Boknafjord, including on Finnøy (Thorsnes 2009). For the most part, Finnøy consists of amphibolites and mica schist, which gives nutrient rich soils. An ore of gneiss bisects the island in an east-west axis (NGU 2010). The unconsolidated deposits are sparse, from very thin to non-existing (NGU 2010). The postglacial marine limit is situated at approximately 50 meters above sea level (Moen 1990).

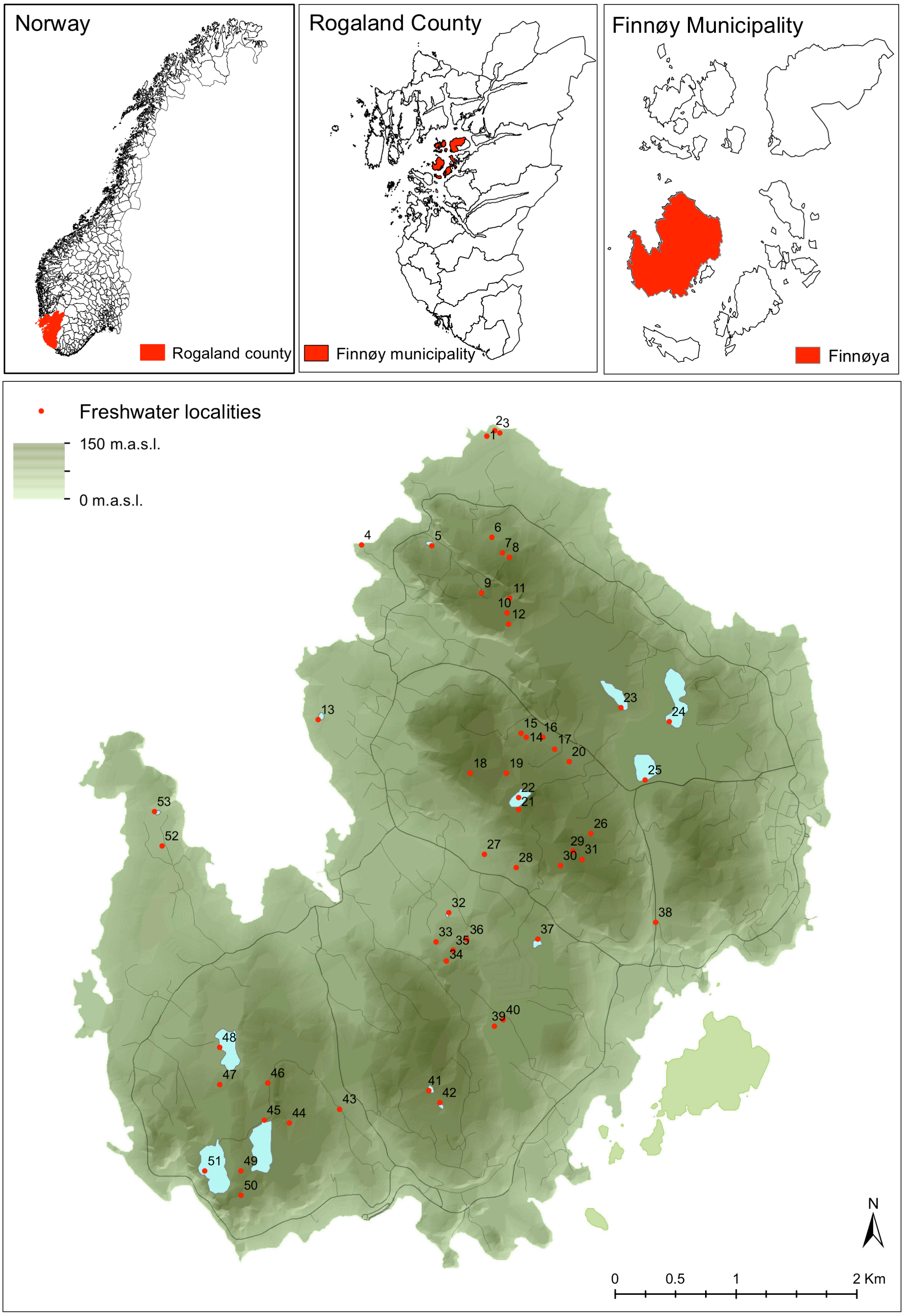

Figure 4. The study area and the investigated localities labelled with locality number. Inset maps show the study area's position in the country, county and municipality.

The climate on Finnøy is of typical maritime character with small temperature fluctuations, mild winters and summers. Climatic information (Figure 5) is based on standard normals for 1961-1990 at the meteorological station Judaberg (Norwegian Meteorological Institute 2010).

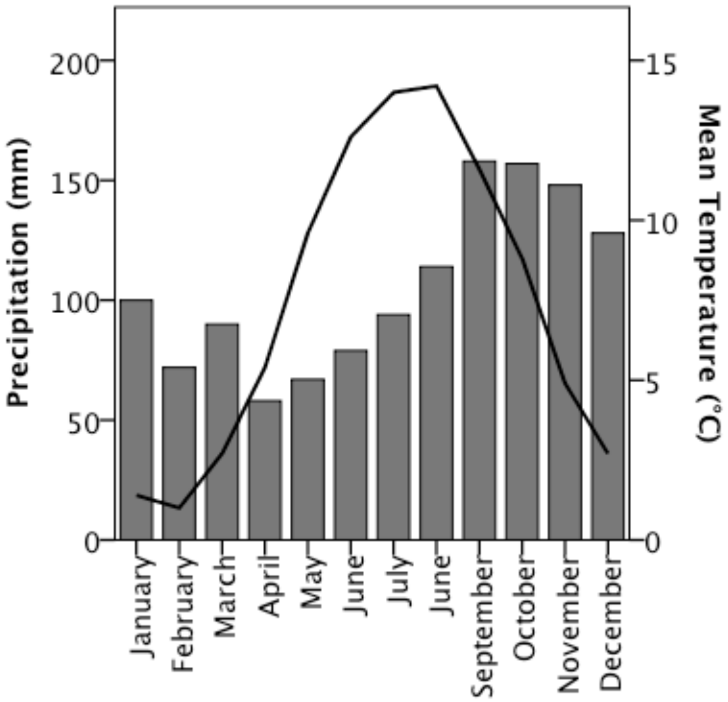

Figure 5: Mean temperature (line) and precipitation (vertical bars) on Finnøy calculated from normal 1961-1990 recorded at Judaberg weather station (modified from Norwegian Meteorological Institute).

The mean annual temperature on Finnøy is 7.4°C. February is the coldest month, with a mean temperature of 1°C. July and August are the warmest months with mean temperatures of 14°C. The mean annual precipitation amounts to 1265 mm. The precipitation is lowest in April with 58 mm and highest in September and October with 158 and 157mm, respectively. On average, Finnøy has more than 1 mm precipitation during 213 days of the year (StatisticsNorway 2010). The mean daily temperature is above 0°C every day of the year, and the annual vegetative period (days with temperatures above 6°C) is 118 days. Atmospheric data from Vikedal (approximately 40 km north of the study area) state that the liquid precipitation has an arithmetic mean of pH 5.33 (Aas et al. 2010).

Finnøy provides a habitat lacking closely related competitors to the introduced frogs as neither the common frog, nor the moor frogs exist on the island.

4 Methods

4.1. Fieldwork and water analyses

Data for this thesis have been collected during several periods of fieldwork timed for the peek breeding season and metamorphosing period for three consecutive years from 2009 to 2011. The sample units were all the permanent lentic freshwater bodies on Finnøy (n=53), dubbed as localities from hereon. In 2009, Dolmen studied the green frogs on Finnøy for the first time and has made his data available for this study. The emphasis was on mapping the distribution and taxonomic composition and reproduction on the island (Dolmen 2009a). In 2010, the dispersal of both forms and reproduction was registered, environmental variables at each locality were quantified and water samples from all localities were collected and later analysed. In 2011, the further dispersal was monitored by visiting localities on the limits of last year's distribution range. It was assumed that no locality with recorded frog presence the previous year were abandoned. In May 2011, yearlings from Finnøy and Aust-Agder were measured to allow for size comparisons. Also in 2011, water samples from lentic water bodies on the mainland close to Finnøy were taken and analysed in order to map mainland habitat suitability.

All field periods were timed for weather conditions optimal for green frog sighting (i.e. sunny and warm) and the fieldwork was performed during daytime. The 2010 field periods were the most comprehensive and form the core for the results in this report.

The presence of frogs at a locality was verified auditory and/or visually while slowly walking around a locality near the water's edge. Auditory cues of frog presence were male frog vocalisation and distinctive splashes from frogs jumping into hiding under the water surface. In order to distinguish the taxonomic composition at each locality, a high number of frogs were caught with the help of a fishing pole baited with chewing gum (no hook) and a landing net. Individuals were taxonomically identified by morphmetric measurements, using a slide caliper with an accuracy of 0.1 mm, comparing the tibia length to metatarsal tubercle size and the leg size compared to the total body length (snout-vent, with straight back). Additionally the shape of the metatarsal tubercle (round or semicircular) was used for identification (see Table 1). When catching was impossible, the form of individual frogs was sought identified visually (using binoculars) by skin colour and texture, and if it was a vocalizing male, by vocal sac colour. Individuals were caught until both forms were found present or until the majority of individuals at a locality were caught and identified. After identification, the frogs were immediately released at the site of capture.

The forms were recorded as absent or present, where absent means that our method did not record individuals, although they may be present in very low density. The catchability of the two forms was assumed to be identical.

The abundance of individuals at one locality was estimated by a mark-recapture scheme. The first sample was done midday on 31.06.2010 and the sampling effort was 4 surveyors for one hour. Individuals were tagged by toe clipping and released at the site of capture within approximately one hour. The second sample was conducted the following day.

The reproductive status was verified in August/September of each year by revisiting the localities that had frogs present in the previous field period. Occurrences of tadpoles and/or newly metamorphosed froglets were taken as evidence of reproduction at a locality. The taxonomic composition of the tadpoles and froglets was not investigated.

The body length and tibia length of yearlings from both Finnøy and Aust-Agder were measured using a slide caliper in May 2011.

Captured individuals were assessed for abnormalities and symptoms of the diseases chytridiomycosis and ranavirus. The symptoms being lethargy, subcutaneous oedema, ulcerations, reddening or shedding of the skin, disturbed swimming, loss of righting reflex or the absence of the flight response in adults and depigmentation of the mouthparts in larvae (Duffus and Cunningham 2010).

The bottom vegetation cover (in percent) was estimated by sight in relation to the locality's surface area without discriminating the types of vegetation. The sun exposure (in percent) was estimated by determining how much of the lake's surface got direct sunlight during the day. Indicators for the lack of sun exposure were the presence and amount of vertical objects like trees and buildings as well as the natural topography. The distance to the nearest forest edge (in meters) was estimated by sight.

Water samples from each locality on Finnøy were collected approximately 1 meter from the shore, 10 cm below the surface in clean polyethylene bottles (500 ml). Conductivity, pH and water colour were measured in the field or within 48 hours. The samples were kept in the dark at approximately 4°C until they were analysed for total hardness, calcium and chloride. Two subsamples, of which one was fixed with concentrated HNO_3, were sent to the laboratory of NTNU, Institute of Chemistry for analyses of total nitrogen, aluminium and phosphorus.

pH was measured both electrically and colorimetrically. For the electrical measurements a Radiometer PMH80 with pHC 2005-7 Red Rod electrode was used. The pH-meter was calibrated against buffer solutions with pH 7.00 and 4.01 before each series of measurement. For the colorimetric measurement, a PPG Hellige was used with standard indicator solutions (methyl red and bromthymol blue) and colour disks (#230 004 01 and #230 007 01).

The conductivity (K_{25}) was measured with a standard conductivity cell: WTW model Cond 330i. The meter was set to the water's temperature before the conductivity measurements and then corrected to 25 °C by the instrument before it was read off.

Water colour was measured as Pt-value with a “Hellige Colour comparator”, Nessler tubes and standard colour disks "Farbe des Wassers 1&2", #230 052 01.

Total hardness was measured in Deutsche Härte (°dH) by EDTA titration (ethylendiamintetra-acedic acid- sodium salt) and indicator buffer tablets after the method explained by Skei et al. (1991). One Deutsche Härte is defined as 10 mg CaO and/or MgO /l. Calcium content (μg/l) and chloride content (μg/l) were measured following the methods described in Skei et al. (1991).

A total of 17 freshwater localities on the mainland were investigated in 2011 for habitat suitability. The localities were chosen randomly with the restrictions that they should be within two hours drive from Finnøy, not larger than a lakelet and in proximity of a road. Water samples were taken and analysed for pH, water colour and conductivity following the same procedures as described above.

4.2. Statistical analyses

All statistical analyses were performed on the statistical software PASW Statistics 18.3 (SPSS Statistics).

Locality #4 (in close proximity to the beach) had extreme values of various chemical substances. The locality was excluded from statistical analyses on the basis of it probably not even being a fresh water locality due to its high seawater content.

In order to ensure representative results, only localities within the dispersal range of each form of frogs were included for the statistical analyses. Consequently, the sample size was reduced to 37 for *R. lessonae* and 47 for *R.* kl. *esculenta*. For analyses on reproduction, only localities within the *R. lessonae* dispersal range and with *R. lessonae* present were included ($n_{reproduction}$=25).

All environmental variables, with the exception of pH, had a non-normal distribution. The distributions did not improve with transformations and so did not meet the assumptions for parametric tests.

The variables within subsamples (dividing frog presence and absence) were summarized by the arithmetic mean, standard deviation (SD), minimum and maximum values (min-max) and subsample size (n). Mann-Whitney U-tests were conducted to evaluate whether environmental variables in one subsample were larger than in the other subsample. The results were given as U-statistics (U), statistical significance (P) and effect size (r).

The collected data for amphibian distribution were considered to be a binomial process as they were in the form of presence and absence at each locality. The forms and reproduction at each locality were either present with the probability p or absent with the probability 1-p, where var(p)=p(1-p).

The relationships between each single variable and the probability of presence of both form and reproduction on Finnøy were explored using univariate generalized linear models (family binomial). When biologically sound, both the first and the second order term of each variable were included in the analysis. If statistically insignificant the quadratic terms were removed. The results were given as the regression coefficient (β), standard error (SE), Wald chi-square (χ^2), degrees of freedom (DF), statistical significance (P) and exponential regression coefficient (Exp(β)).

The relative importance of each variable was investigated using multivariate generalized models (family binomial). To avoid overfitting the data, the number of explanatory variables included in any model was restricted to the sample size divided by 10 (Burnham and Anderson 2002). A high number of candidate models (<40) were investigated and ranked using Akaike's Information Criterion with a correction for finite sample sizes (AIC_C):

$$AIC_C = -\left[2\log\left(L\left(\hat{\theta}\right)\right)\right] + 2K + \frac{2K(K+1)}{n-K-1}$$

K denotes the number of parameters estimated in the model, and *n* the sample size. According to Akaike’s Information Criterion, the models with the lowest AIC_C value has the most support from the data. ΔAIC_C represents the difference in AIC_C value relative to the best model. Models with $\Delta AIC_C \leq 2$ are approved as equally fit as the best model. The principle of parsimony dictates that among models with $\Delta AIC_C \leq 2$ the model with the smallest number of parameters is the most appropriate for the data (Burnham and Anderson 2002). Due to space limitations only a fraction of the investigated models were reproduced in the results.

The various parameters within the best candidate models were given as the regression coefficient (β), standard error (SE), Wald chi-square (χ^2), degrees of freedom (DF), statistical significance (P) and exponential regression coefficient (Exp(β)). The relationship between the most important limiting factors and the probability of presence was illustrated separately using the predicted probability and 95% confidence intervals from the univariate analyses.

Requirements for habitat suitability for both forms and reproduction were summarized from 50% probability of presence on the significant variables in the best models.

Two scenarios were given for the predicted mainland suitability of the green frogs and their reproduction. One was based on the simplest models for habitat requirements (conforming to the principle of parcimony). The other was based on more complex candidate models (models within $AIC_C \leq 2$)

Due to the problem of multicolinearity in multiple regression analysis, pair wise correlations between variables were evaluated. In particular, there was strong intercorrelation among the various chemical substances measured. Total hardness was strongly correlated to Ca (r_p=.959) and Mg (r_p=.906). Conductivity was strongly correlated to NaCl (r_p=.723), Mg (r_p=.765) and Ca (r_p=.461) (Appendix 6). Strongly correlated variables were excluded from the analyses.

A population estimate at one locality was calculated from the mark-recapture scheme and Lincoln-Petersen estimator for closed populations:

$$\hat{N} = \frac{n_1 n_2}{m_2}$$

$\hat{N}$ is the estimated population, n_1 is the number of individuals caught and tagged in the first sample, n_2 is the number of individuals caught in the second sample and m_2 is the number of tagged individuals in the second sample.

4.3. Cartography

All maps in this report were generated using ESRI ArcGIS, Desktop 10. Cartography data originate from Digitale Kartdata and made available on NTNU's database. All maps are projected as Transverse Mercator using UTM zone 32N.

5 Results

5.1. Establishment and dispersal

In 2003, the green frogs were introduced to a single locality on Finnøy. In the following years the green frogs expanded their geographical range and number of occupied localities (Figure 6 and Figure 7). In 2009, *R. lessonae* occupied 32% of all localities on the study area (17 localities). The following year, the distribution increased with 15% and further 4% in 2011, resulting in *R. lessonae* being present in 51% of all localities in the study area (27 localities). *R.* kl. *esculenta* occupied 34% of all localities in the study area (18 localities) in 2009. The next year its distribution increased with 25% and another 4% in 2011, amounting to 62% of all localities in the study area (33 localities). Reproduction increased from 19% of all localities in 2009 (10 localities) to 25% in 2010 and to 26 % in 2011 (14 localities).

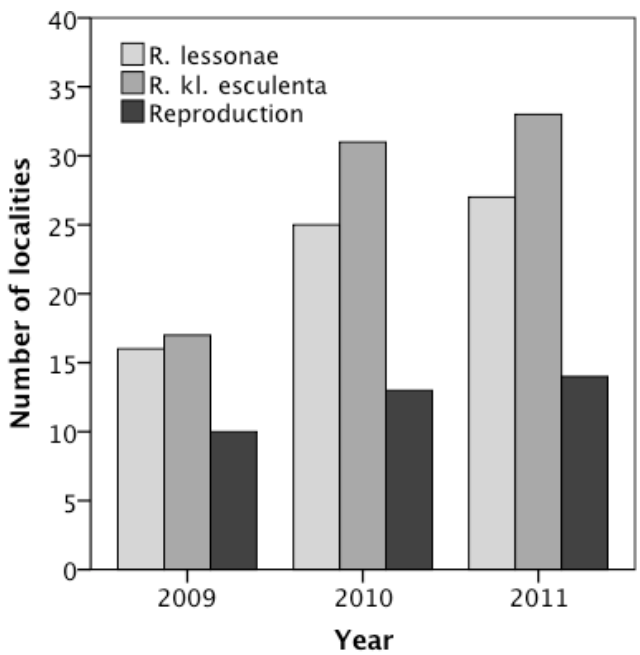

Figure 6. The number of localities with *R. lessonae*, *R.* kl. *esculenta* and reproduction present in 2009, 2010 and 2011.

In 2009, *R. lessonae* dispersed to localities up to 2600 meters away from the original release site. The next year, *R. lessonae* was found in localities up to 900 meters further south compared to the previous year. In 2011, *R. lessonae* was found in localities another 500 meters further south compared to 2010. *R.* kl. *esculenta* was found in localities up to 4000 meters away from the original release site in 2009. The following year it was found 1200 meters further south, while in

2011, the range had not expanded any further. Adult individuals, rather than juveniles, inhabited the newly occupied localities.

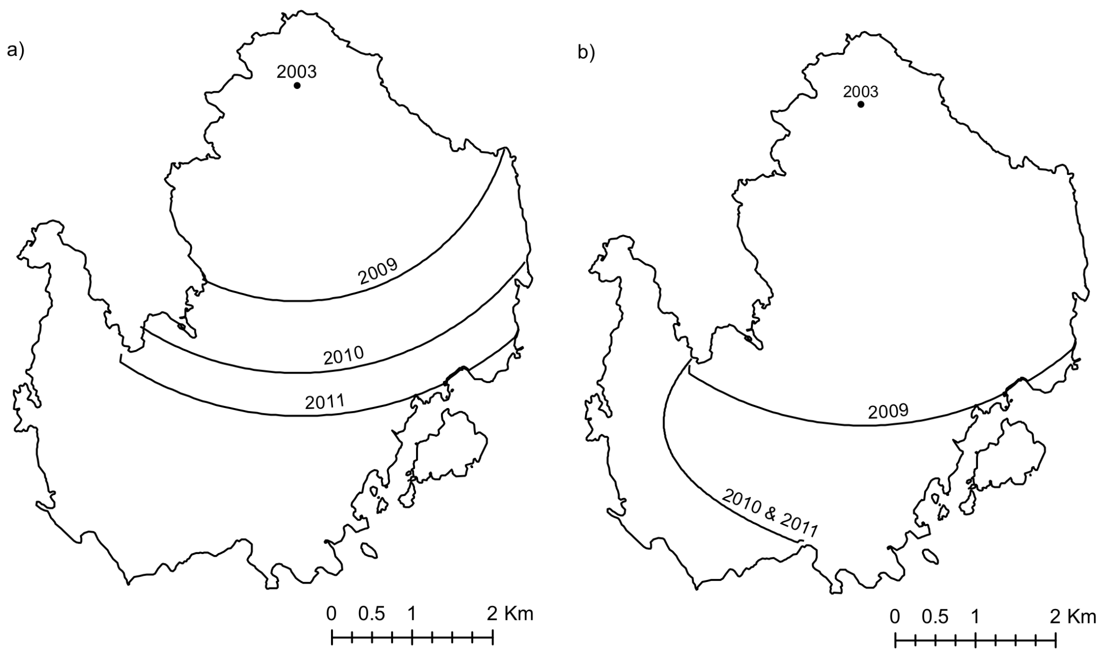

Figure 7. The geographical range of a) *R. lessonae* and b) *R.* kl. *esculenta* in 2003, 2009, 2010 and 2011.

Mark-recapture at one of the most densely populated localities on Finnøy (# 18) yielded a population estimate of approximately 280 individuals (SE=44) (Table 2). The captured frogs were of both forms and gender, but with a majority of *R. lessonae* (89%) and males (85%). In general, the observed densities of individuals at each locality were highest in the northern half of the island. A total of 5 localities are believed to have approximately the same density of frogs as the locality investigated by mark-recapture.

Table 2. The number of individuals caught on the mark-recapture scheme, and the population estimate calculated from the Petersen-Lincoln equation.

	# of individuals (Marked/Unmarked)
Capture	91
Recapture	55 (18/37)
Population estimate	278

There was no evidence of chytridiomycosis, ranavirus or other diseases among the adult individuals observed during fieldwork. Captured metamorphosed and adult individuals were vigorous and no frogs were found dead.

Of all the individuals caught during fieldwork on Finnøy (n>500), two were noticed to have abnormalities. There was one case of polymelia (a duplicate right hind limb) on a yearling and one case of anophthalmia (missing right eye) on a newly metamorphosed individual (Appendix 8).

5.2. Habitat requirements

The analyses on habitat requirements were based on the distribution of the frogs in 2010 (Figure 8). In 2010, the two forms coexisted in 20 localities. In addition, *R. lessonae* and *R.* kl. *esculenta* were present allopatrically in 5 and 10 localities, respectively. The taxonomic composition was unknown in one locality. Reproduction was successful in 11 localities, all of which with both forms of frogs present. 15 localities were not occupied by any of the green frogs.

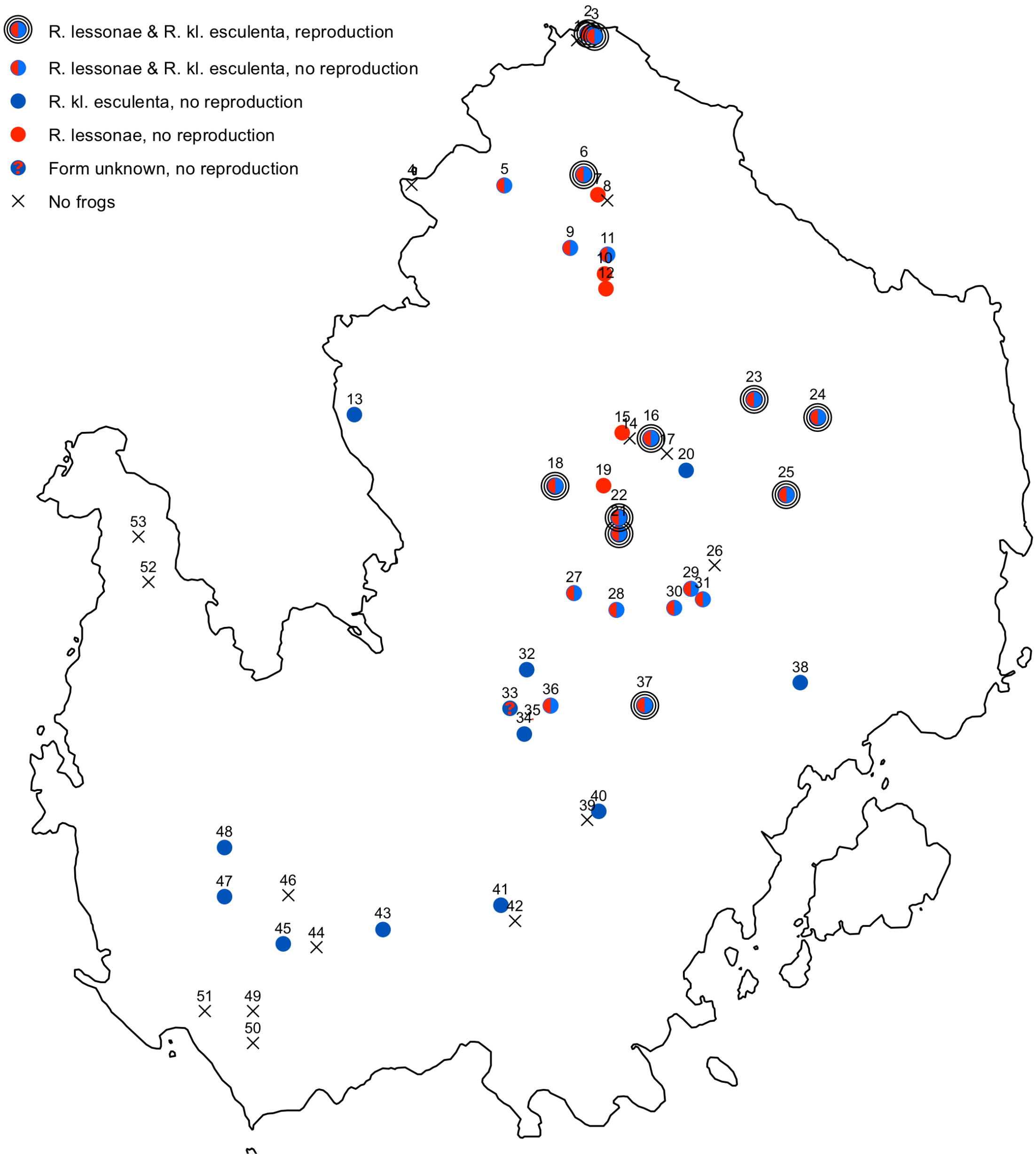

Figure 8. Taxonomic composition and reproductive status at each locality in the study area in 2010.

5.2.1 *R. lessonae*

Comparing localities with and without the presence of *R. lessonae,* the investigated variables were not significantly different from each other (Table 3). Univariate logistic regressions suggest that only sun exposure had a predictive power on the occurrence of *R. lessonae* (Table 4). None of the second order terms were close to statistical significance.

Table 3. Summary and comparisons between localities with *R. lessonae* present and absent.

R. lessonae	Present			Absent					
	Mean(±SD)	Min-Max	N	Mean(±SD)	Min-Max	N	U	P	r
Sun	79(±20)	30-99	25	55(±39)	5-99	12	105	0.142	-0.25
Forest	27(±36)	1-150	25	48(±91)	1-300	12	138	0.689	-0.07
Vegetation	27(±22)	1-70	25	23(±33)	1-85	12	106	0.151	-0.24
Ca	6.8(±4.4)	0.7-16.4	25	7.7(±4.1)	1.4-13.6	12	127	0.471	-0.12
Mg	3.6(±1.5)	1.3-6.9	25	3.9(±2.1)	0.9-9.1	12	141	0.786	-0.05
NaCl	2.7(±1.5)	1.4-8.2	25	2.6(±1.9)	1.4-8.6	12	125	0.432	-0.13
Al	186(±184)	27-724	25	138(±97)	41-354	12	140	0.761	-0.05
P	44(±38)	10-155	25	79(±101)	15-368	12	111	0.215	-0.21
Tot. N.	1.2(±1.4)	0.4-7.5	25	1.3(±0.8)	0.3-2.7	12	132	0.575	-0.10
Tot. Hard.	1.8(±0.9)	0.6-3.8	25	2(±0.9)	0.5-3	12	126	0.432	-0.13
Conductivity	111(±45)	51-248	25	118(±51)	65-251	12	134	0.620	-0.09
pH	6.8(±0.5)	5.1-7.8	25	6.7(±0.4)	5.9-7.2	12	142	0.786	-0.05
Water Color	73(±35)	35-180	25	86(±40)	40-160	12	118	0.296	-0.17

Table 4. The effect of each explanatory variable on the probability of presence of *R. lessonae*. Significant values are denoted in bold.

Explanatory variable	β	SE	χ^2	DF	P	Exp(β)
Sun	0.029	0.013	4.736	1	**0.030**	1.029
Forest	-0.006	0.006	0.938	1	0.333	0.994
Vegetation	0.006	0.014	0.208	1	0.648	1.007
Ca	-0.054	0.083	0.424	1	0.515	0.947
Mg	-0.112	0.204	0.302	1	0.583	0.894
NaCl	0.034	0.223	0.022	1	0.882	1.035
Al	0.002	0.003	0.701	1	0.402	1.002
P	-0.008	0.006	1.734	1	0.188	0.992
Tot. nitrogen	-0.023	0.292	0.006	1	0.937	0.977
Tot. hardness	-0.258	0.389	0.44	1	0.507	0.772
Conductivity	-0.003	0.007	0.134	1	0.715	0.997
pH	0.314	0.712	0.195	1	0.659	1.369
Water color	-0.009	0.009	0.984	1	0.321	0.991

The models that were best supported by the data included the explanatory variables sun exposure and distance to nearest forest edge (Table 5).

Table 5. Candidate models explaining the probability *R. lessonae* presence in localities on Finnøy. Models with $\Delta AIC_C \leq 2$ are denoted in bold.

Candidate model	AIC_C	ΔAIC_C	Rank
Sun, forest	**44.7**	**0**	**1**
Sun	**45.6**	**0.9**	**2**
Sun, Al	47.1	2.4	3
Sun, tot. hardness	47.1	2.4	4
Sun, tot.N.	47.6	2.9	5
Sun, pH	47.7	3	6
Sun, pH, Al	49.5	4.8	7
pH	50.8	6.1	8
pH, Al	52.2	7.5	9

Sun exposure was a significant predictive variable in the two best models. The relationship was positive: as the value in sun exposure increased so did the probability of *R. lessonae* being present in a locality on Finnøy. The variable distance to the nearest forest edge was not significant in the model. However, the trend was negative: as the distance to the nearest forest edge increased, the probability of finding *R. lessonae* decreased (Table 6 and Figure 9).

Table 6. Factors affecting the probability of finding *R. lessonae* present in localities on Finnøy.

	Explanatory variable	β	SE	χ^2	df	P	Exp(β)
Model 1	Constant	-1.353	0.984	1.889	1	0.169	0.259
	Sun	0.037	0.015	6.391	1	0.011	1.038
	Forest	-0.012	0.007	2.711	1	0.100	0.988
Model 2	Constant	-1.219	0.956	1.627	1	0.202	0.295
	Sun	0.029	0.013	4.736	1	0.030	1.029

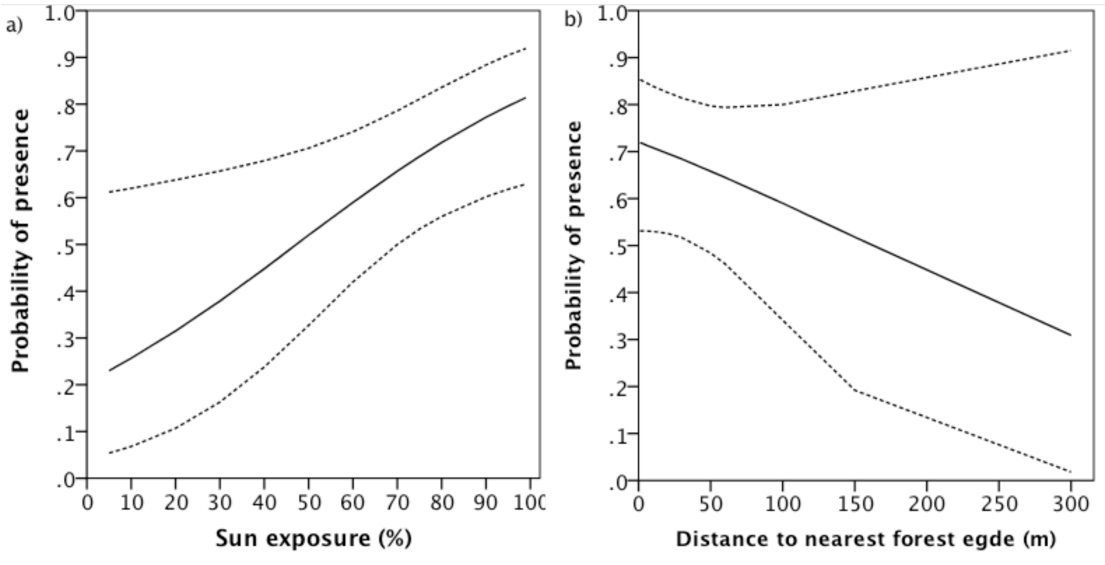

Figure 9. The relationship between a) sun exposure and b) distance to nearest forest edge and the *R. lessonae* probability of presence on Finnøy (generalized linear models given in Table 4). Full lines represent the predicted probability, while dashed lines represent 95% confidence intervals.

To sum up, the habitat requirements for *R. lessonae* on Finnøy in 2010 were:

- sun exposure above 50%
- possibly distance to the nearest forest edge less than 160 meters.

5.2.2 *R.* kl. *esculenta*

Localities with *R.* kl. *esculenta* present had significantly lower aluminium content and water colour compared to localities where *R.* kl. *esculenta* was absent (Table 7). Sun exposure, aluminium content and water colour were predictive explanatory variables for the probability of *R.* kl. *esculenta* being present (Table 11).

Table 7. Summary and comparison of localities with *R.* kl. *esculenta* present and absent in 2010. Statistically significant ($p<0.05$) and strong effects ($|r|>0.3$) denoted in bold.

	Present			Absent			Mann-Whitney U		
	Mean(±SD)	Min-Max	N	Mean(±SD)	Min-Max	N	U	P	r
Sun	80(±18)	40-99	31	58(±38)	5-99	16	186	0.159	-0.21
Forest	30(±40)	1-150	31	57(±99)	1-300	16	248	1	0
Vegetation	27(±27)	1-85	31	21(±25)	0-70	16	211	0.395	-0.12
Ca	6.5(±4.3)	1.4-16.4	31	6.3(±3.9)	0.7-13.6	16	246	0.955	-0.01
Mg	3.2(±1.6)	0.9-6.9	31	3.7(±1.9)	1.3-9.1	16	221	0.535	-0.09
NaCl	2.5(±1.3)	1.4-8.2	31	2.8(±1.7)	1.4-8.6	16	212	0.418	-0.12
Al	131(±134)	8-558	31	217(±173)	37-724	16	149	**0.026**	**-0.32**
P	50.1(±72.9)	3.5-367.5	31	39.5(±27)	5.9-112.1	16	225	0.606	-0.08
Tot. N.	1.0(±0.6)	0.1-2.7	31	1.4(±1.8)	0.3-7.5	16	237	0.805	-0.04
Tot. Hardness	1.7(±1)	0.5-3.8	31	1.7(±0.8)	0.6-2.8	16	232	0.710	-0.05
Conductivity	107(±42)	51-248	31	115(±46)	65-251	16	213	0.425	-0.12
pH	6.8(±0.5)*	5.6-7.8	31	6.6(±1.1)	5.1-9.7	16	183	0.141	-0.21
Water colour	65(±28)	15-125	31	89(±42)	40-180	16	155	**0.035**	**-0.31**

Table 8. The effect of each explanatory variable on the probability of presence of *R.* kl. *esculenta* (n=48). Bold values refer to statistically significant values ($p<0.05$).

Explanatory variable	β	SE	Wald	df	p	Exp(β)
Sun	0.029	0.0121	5.584	1	**0.018**	1.029
Forest	-0.006	0.0048	1.529	1	0.216	0.994
Vegetation	0.009	0.0126	0.491	1	0.484	1.009
Ca	0.012	0.0758	0.026	1	0.871	1.012
Mg	-0.144	0.1818	0.627	1	0.428	0.866
NaCl	-0.122	0.2091	0.339	1	0.561	0.885
Al	-0.004	0.0022	2.933	1	0.087	0.996
P	0.003	0.0061	0.31	1	0.578	1.003
Tot. N.	-0.316	0.2997	1.114	1	0.291	0.729
Tot. Hardness	-0.083	0.3421	0.058	1	0.809	0.921
Conductivity	-0.005	0.0071	0.441	1	0.507	0.995
pH	0.372	0.4732	0.617	1	0.432	1.450
Water colour	-0.02	0.0098	4.306	1	**0.038**	0.980

Two models gained substantial support from the data (Table 9). Both models included sun exposure and distance to forest as explanatory variables.

Additionally, water colour and aluminium content were present separately in each of the two best models.

Table 9. Candidate models explaining the probability *R.* kl. *esculenta* presence on Finnøy. * denotes the interaction effect between two variables. Models with $\Delta AIC_C \leq 2$ are denoted in bold.

Explanatory variable included in model	AIC_C	ΔAIC_C	Rank
Sun, Forest, Water colour	**53.0**	**0**	**1**
Sun, Forest, Al	**54.9**	**2.0**	**2**
Sun, Forest, Al * pH	55.3	2.4	3
Sun, Forest	55.7	2.8	4
Sun, Forest, Water colour, Al * pH	56.1	3.2	5
Sun, Al	56.2	3.2	6
Sun, Al * pH	56.5	3.5	7
Sun, Water colour	56.8	3.8	8
Sun, Forest, pH	57.7	4.8	9
Sun	57.9	4.9	10
Sun, pH	60.4	7.4	11
Al	61.3	8.3	12
Forest, Al * pH	63.2	10.2	13
Forest, Al, pH	63.6	10.7	14

In relation to the probability of presence of *R.* kl. *esculenta,* sun exposure had a significant positive relationship while distance to nearest forest edge, aluminium content and water colour had negative relationships (Table 10 and Figure 10).

Table 10. Factors affecting the probability finding *R.* kl. *esculenta* present on Finnøy.

	Parameter	β	SE	χ^2	DF	P	Exp(β)
Model 1	Constant	-1.012	0.993	1.040	1	0.308	0.363
	Sun exposure	0.040	0.014	8.059	1	0.005	1.041
	Distance to forest	-0.010	0.006	3.316	1	0.069	0.99
	Aluminium content	-0.004	0.002	2.906	1	0.088	0.996
Model 2	Constant	0.220	1.325	0.028	1	0.868	1.246
	Sun exposure	0.038	1.325	6.385	1	0.012	1.039
	Distance to forest	-0.012	0.005	4.819	1	0.028	0.988
	Water colour	-0.024	0.013	3.330	1	0.068	0.977

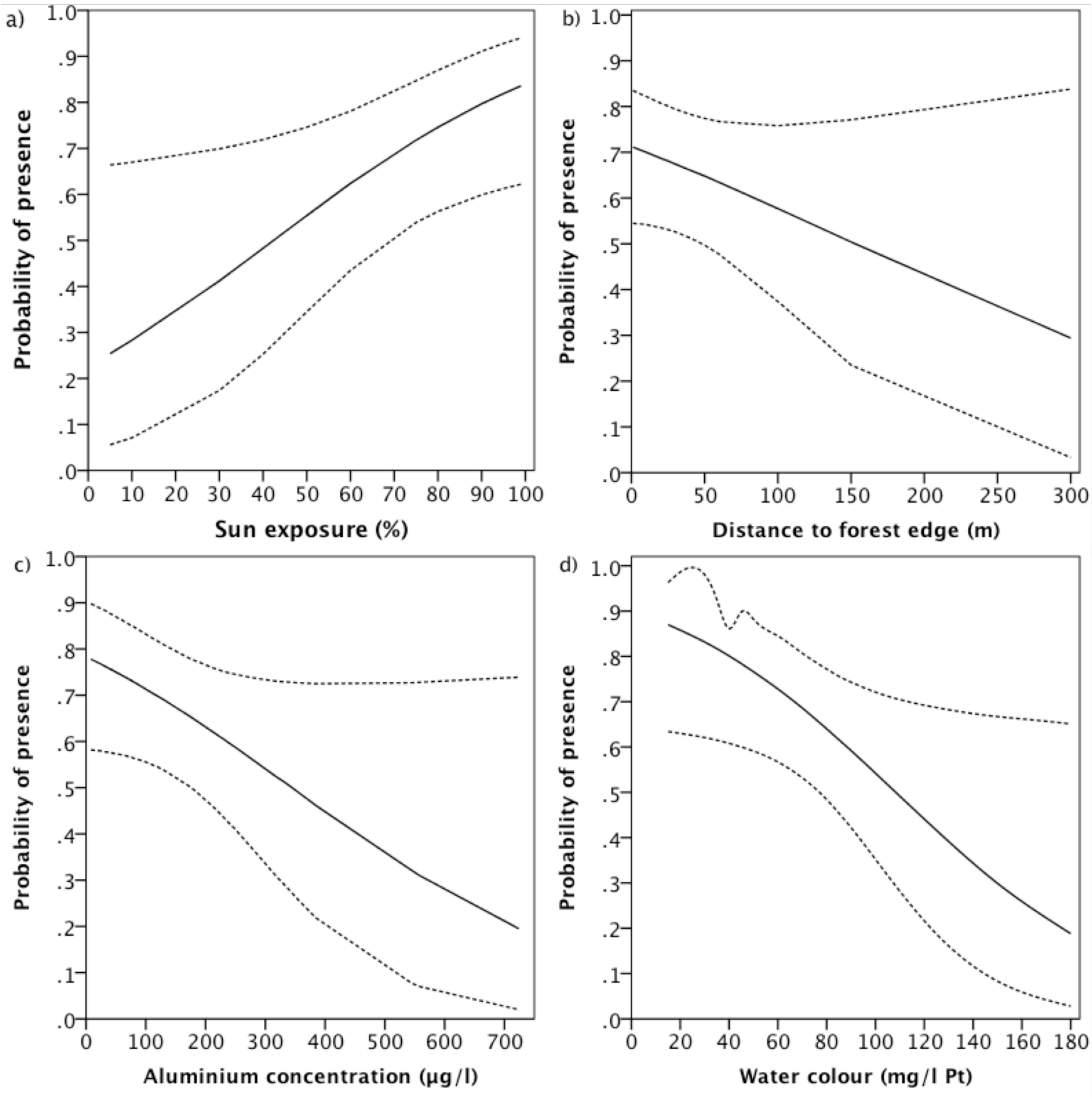

Figure 10. The relationship between a) Sun exposure, b) distance to forest edge, c) aluminium content and d) water colour and the probability of finding *R.* kl. *esculenta* present on Finnøy (generated from models in Table 8). Full lines represent the predicted probability while dashed lines represent 95% confidence intervals.

To sum up, the habitat requirements for *R.* kl. *esculenta* on Finnøy in 2010 were the following:

- sun exposure above 50%
- distance to the nearest forest edge less than 160 meters
- either aluminium concentration below 350 µg/l or water colour below 120 mg/l Pt

5.2.3 Reproduction

Sun exposure and pH had significantly different values when comparing localities with reproduction to localities without reproduction (Table 11). In addition, aluminium content was close to statistical significance.

Table 11. Comparisons of localities with reproduction present and absent in 2010. Statistically significant ($p<0.05$) and strong effects ($|r|>0.3$) are denoted in bold.

	Present			Absent			Mann-Whitney		
	Mean(±SD)	Min-Max	N	Mean(±SD)	Min-Max	N	U	P	r
Sun	91(±7)	80-99	13	65(±22)	30-99	12	24	**0.002**	**-0.60**
Forest	35(±41)	1-150	13	19(±29)	1-100	12	60	0.320	-0.21
Vegetation	23(±19)	1-70	13	31(±25)	2-70	12	64	0.470	-0.15
Ca	6.8(±4.3)	2.1-15.7	13	6.7(±4.6)	0.7-16.4	12	78	0.979	-0.01
Mg	3.6(±1.5)	1.7-6.9	13	3.5(±1.6)	1.3-5.6	12	75	0.894	-0.03
NaCl	2.9(±1.9)	1.4-8.2	13	2.5(±0.8)	1.4-3.7	12	76	0.936	-0.02
Al	136(±148)	27-558	13	239(±209)	37-724	12	45	0.077	**-0.36**
P	37(±40)	10-155	13	52(±35)	10-112	12	53	0.186	-0.27
Tot. N.	0.9(±0.3)	0.5-1.5	13	1.6(±1.9)	0.4-7.5	12	52	0.168	-0.28
Tot. Hardness	1.8(±0.9)	0.8-3.8	13	1.8(±1)	0.6-3.6	12	78	0.979	-0.01
Conductivity	109(±53)	51-248	13	114(±36)	61-172	12	66	0.503	-0.14
pH	7.0(±0.4)	6.6-7.8	13	6.5(±0.6)	5.1-7.5	12	32	**0.011**	**-0.50**
Water colour	69(±32)	35-125	13	78(±39)	45-180	12	64	0.437	-0.16

Univariate analyses state that the explanatory variables sun and pH had significant predictive power and a strong effect on the occurrence of reproduction (Table 12).

Table 12. The effect of each explanatory variable on the probability of presence of reproduction (n=25). Bold values refer to statistically significant values.

Explanatory variable	β	SE	χ^2	DF	P	Exp(β)
Sun	0.12	0.05	5.63	1	**0.018**	**1.13**
Forest	0.01	0.01	1.09	1	0.296	1.01
Vegetation	-0.02	0.02	0.96	1	0.327	0.98
Ca	0.01	0.09	0.00	1	0.960	1.01
Mg	0.06	0.27	0.05	1	0.827	1.06
NaCl	0.23	0.32	0.51	1	0.476	1.26
Al	0.00	0.00	1.78	1	0.183	1.00
P	-0.01	0.01	1.01	1	0.315	0.99
Tot. N.	-1.17	1.14	1.05	1	0.305	0.31
Tot. Hardness	0.05	0.44	0.01	1	0.908	1.05
Conductivity	0.00	0.01	0.06	1	0.805	1.00
pH	2.46	1.23	4.03	1	**0.045**	**11.70**
Water colour	-0.01	0.01	0.39	1	0.533	0.99

Four models were well supported by the data (Table 13). One model included sun as the only variable with predictive power; the relationship was positive and statistically significant (Table 14 and Figure 11). The remaining three best models included sun exposure together with either pH or aluminium content or the interaction between the two. None of the additional parameters were statistically significant. The trend was positive for pH and negative for aluminium and the interaction effect between pH and aluminium was low ($r^2_{no\ reproduction}$= 0.035 and $r^2_{reproduction}$= 0.13).

Table 13. Candidate models on the probability of finding *R.* kl. *esculenta* present in a locality on Finnøy. Models with $\Delta AIC_C \leq 2$ are denoted in bold..

Explanatory variables	AIC_C	ΔAIC_C	Rank
Sun	**25.9**	**0**	**1**
Sun, Al	**26.4**	**0.5**	**2**
Sun, pH*Al	**26.7**	**0.8**	**3**
Sun, pH	**27.2**	**1.3**	**4**
pH	32.9	7.1	5

Table 14. Factors affecting the probability reproduction.

	Parameter	B	SE	X2	DF	P	Exp(B)
Model 1	Constant	-9.528	4.247	5.032	1	0.025	0
	Sun	0.118	0.050	5.629	1	0.018	1.125
Model 2	Constant	-8.300	4.044	4.212	1	0.040	0.000
	Sun	0.113	0.047	5.709	1	0.017	1.119
	Al	-0.004	0.003	1.768	1	0.184	0.996
Model 3	Constant	-8.603	4.067	4.474	1	0.034	0
	Sun	0.115	0.047	5.861	1	0.015	1.122
	pH* Al	-0.001	0	1.545	1	0.214	0.999
Model 4	Constant	-19.360	11.195	2.991	1	0.084	0
	Sun	0.100	0.048	4.300	1	0.038	1.105
	pH	1.666	1.576	1.118	1	0.290	5.293

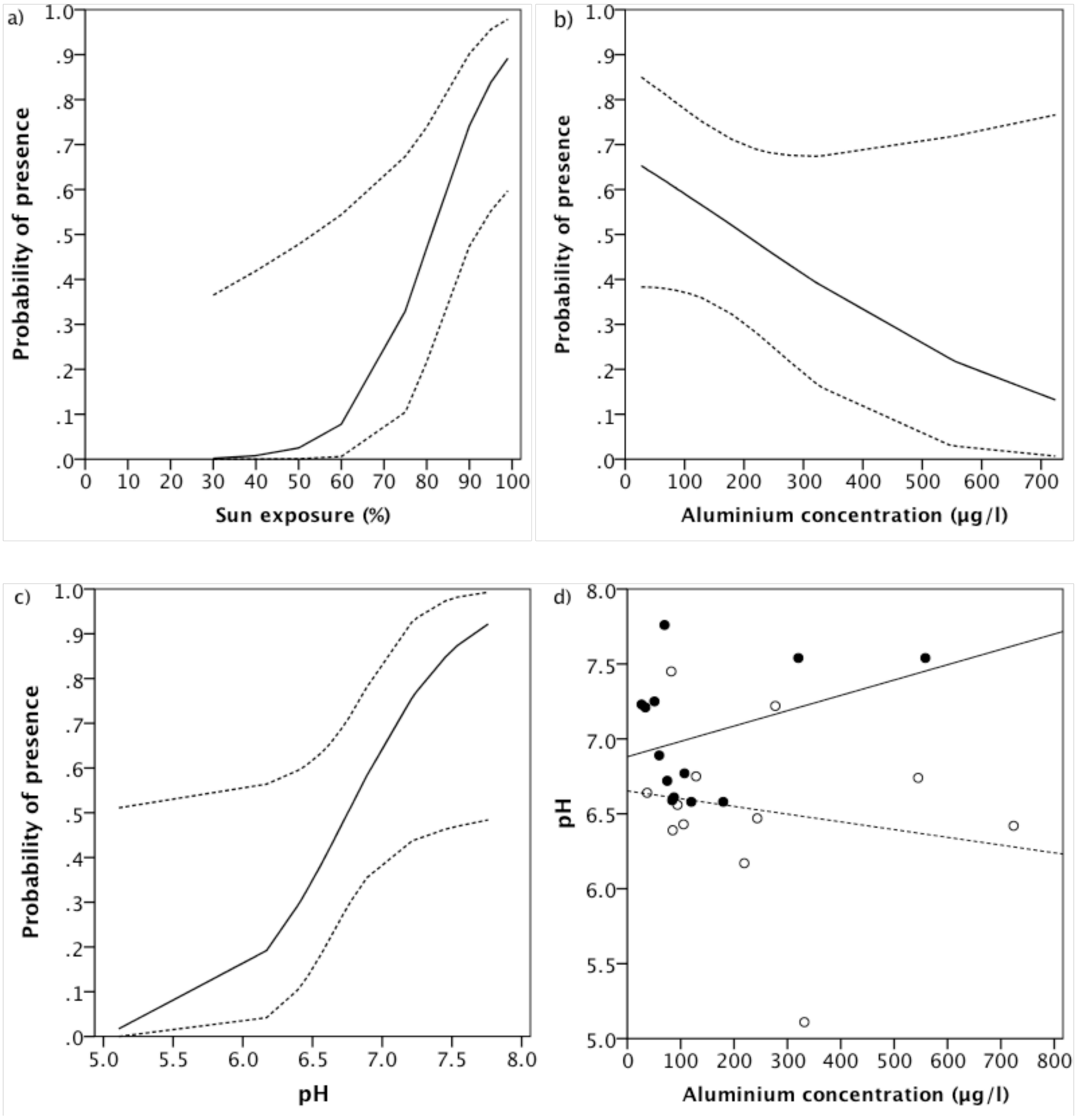

Figure 11. The relationship between a) sun exposure, b) aluminium concentration, c) pH and the probability of finding reproduction present in localities on Finnøy (generated from models in Table 12). Full lines represent the predicted probability while dashed lines represent 95% confidence intervals. d) Represents the interaction between pH and aluminium concentration.

To sum up, the habitat requirements for reproduction, given that *R. lessonae* is present, are the following:

- sun exposure above 80%
- either aluminium concentration below 200 µg/l or pH above 6.6 or interaction effect between pH and aluminium concentration; where high aluminium concentration and low pH is negative for reproduction, while high aluminium concentration and high pH is positive for the reproduction.

5.3. Mainland habitat suitability

The investigated localities on the mainland had values within the same range as localities on Finnøy (Table 15) and can therefore be used to predict the mainland suitability of the green frogs' presence and reproduction without extrapolations.

Table 15. Summary of the freshwater localities (n=17) on the mainland close to Finnøy.

	Mean (±SE)	Min – Max
Water Colour	74 (±16)	15 - 300
pH	6.0 (±0.1)	5.3 - 6.7
Conductivity	121 (±18)	55 - 286
Sun exposure (%)	90 (±1)	80 - 99
Distance to forest (m)	1.7 (±0.6)	0.2 - 10
Vegetation cover (%)	37 (±8)	2 - 95

In one scenario, all the investigated mainland localities were suitable for both forms of frogs and reproduction. In the other scenario, all investigated localities on the mainland were suitable for *R. lessonae,* 10 were suitable for *R.* kl. *esculenta*, but only one was suitable for reproduction (Figure 12).

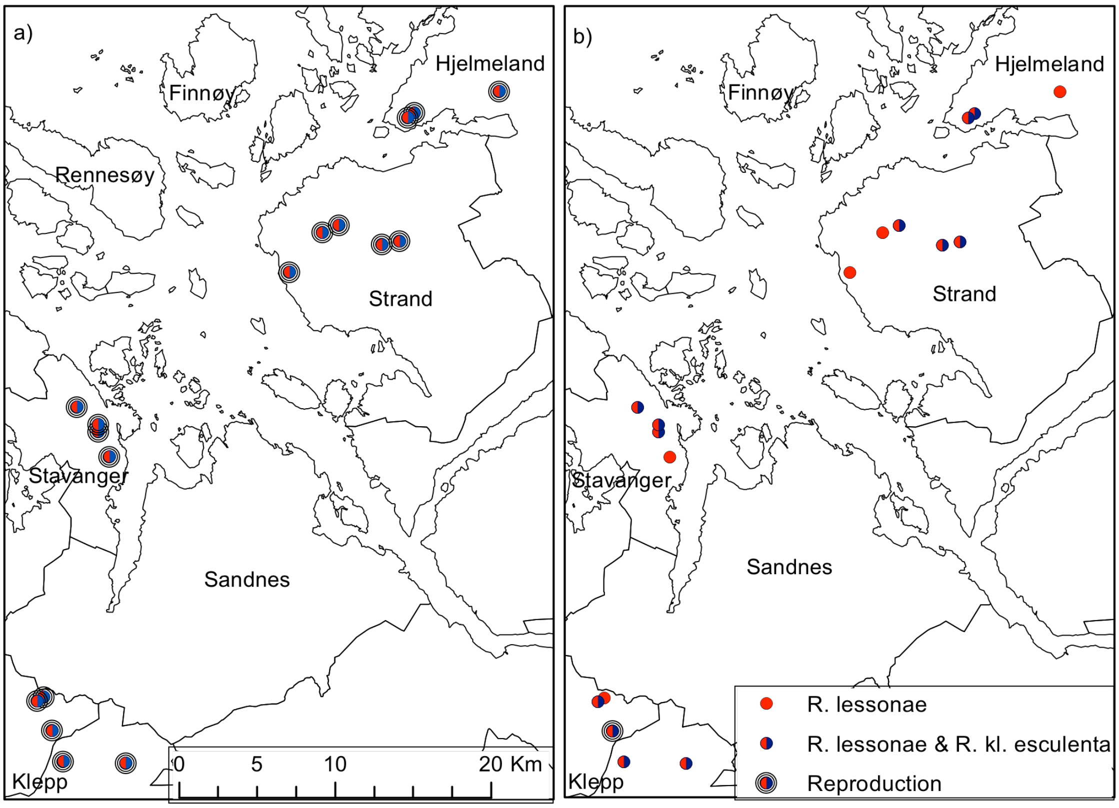

Figure 12. Predicted habitat suitability for *R. lessonae*, *R.* kl. *esculenta* and reproduction on 17 mainland localities based on habitat requirements calculated from Finnøy a) based only on sun exposure and b) based on sun exposure, distance from nearest forest edge, pH and conductivity.

5.4. Yearlings

Yearlings of *R. lessonae* on Finnøy ($median_{body}$=28.8mm and $median_{tibia}$=12.2mm) were approximately 7% smaller than yearlings of *R. lessonae* in Aust-Agder ($median_{body}$=31.1mm and $median_{tibia}$ =13.0mm) (Figure 13). The relationship was statistically significant for the comparison of the total body length (W_S=31.5, p=.001, r=-0.58), but not for the comparison of tibia length (W_S=65, p=.107, r=-0.30).

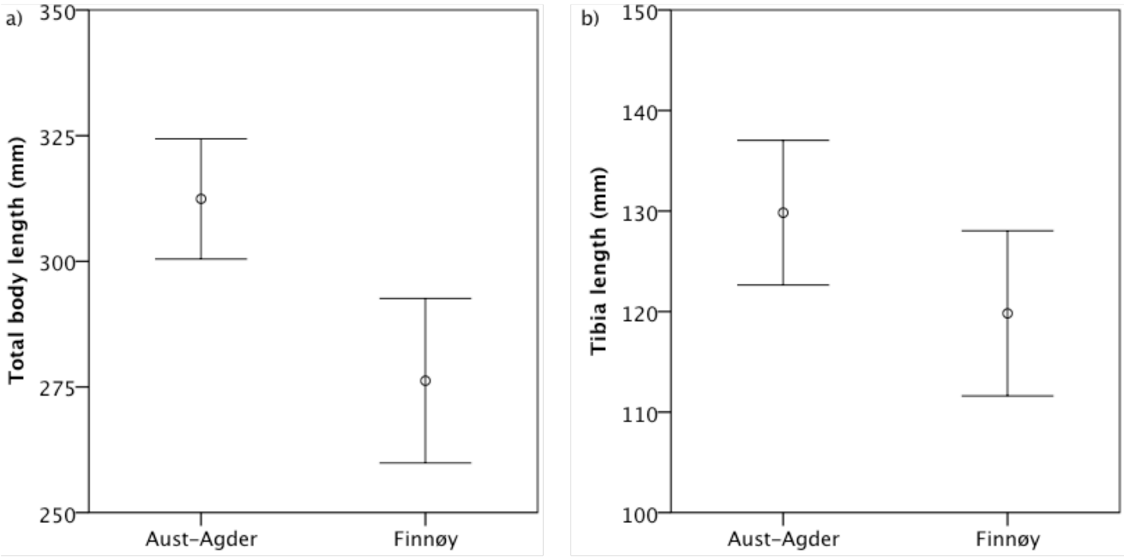

Figure 13. Comparisons of a) total body length and b) tibia length between yearlings of *R. lessonae* in Aust Agder (n= 12) and Finnøy (n= 17). Mean and 95% confidence intervals are represented.

6 Discussion

6.1. Error and uncertainty

One underlying assumption for any statistical analyses, including generalized linear models, is that the observations are independent and unbiased. However, all data collected in geographical space will always be spatially dependent explained by Tobbler's first law of geography (Legendre 1993, Longley et al. 2005). As the study units were scattered freshwater localities, the data were not independent. Although still in its infancy, there are ways to include spatial structure in statistical models (Legendre 1993, Peterson 2001), but generalized linear models remain the most popular technique in habitat suitability studies (Hirzel and Guisan 2002). The assumption of independence of data was relaxed as the data represent *all* localities in the study area, rather than being merely a sample.

Sample size is a major determinant of statistical power and sensibility of the models (Hirzel and Guisan 2002). A low sample size may lead to biased model estimations and a lessening of the predictive ability of the models (Hirzel and Guisan 2002, Taborsky 2010). In this study, the sample size could not have been made larger. As a remedy of the relatively small sample size, caution has been exerted when interpreting the results both in statistical and biological sense. The results deducted from the frog population on Finnøy cannot be blindly extrapolated to other areas and future experimental studies on the introduced frogs would better untangle their ecological niche and invasiveness.

As in all presence-absence data, the presence of a target species can often be confirmed, while the absence of the species is generally impossible to confirm: "an observed absence may simply be the result of the survey method failing to detect the presence of the species that is actually resident at the location" (MacKenzie 2005). Considerable field effort was put into locations where the presence of frogs was difficult to discern. The type of data collection implies that if errors exist in the dataset it is biased towards underestimating the presence of the frogs.

6.2. Invasion success

Since their introduction in 2003, the green frogs have rapidly dispersed to the majority of the freshwater localities on Finnøy. *R. lessonae* was present in slightly fewer localities compared to *R*. kl. *esculenta*, but also had a slower range expansion than *R*. kl. *esculenta*. This is consistent with findings on differences in dispersal rates in members of the water frog complex in Switzerland (Holenweg Peter 2001). *R. lessonae* will probably continue to expand its geographical range over the next years until it overlaps with the range of its hybrid associate.

The range expansion of *R.* kl. *esculenta* was halting in 2011, suggesting that the five unoccupied localities (##49-53 in Figure 8) may be either unsuitable or too isolated for the frogs. Indeed, the three unoccupied southernmost localities were in proximity of occupied ponds, but contrasted them as they were more oligotrofic and had low sun exposure. The two unoccupied westernmost localities are believed to provide suitable habitat for the frogs, but had a high degree of isolation.

Adult individuals, rather than juveniles, inhabited the newly occupied localities. Despite the fact that migrations among amphibians are generally associated with reproductive aggregation and dispersion of recently metamorphosed young (Duellman and Trueb 1994), these results are support by Holenberg Peter (2001) who found that dispersal is "not a phenomenon restricted to a specific life stage in water frog populations (mainly the juvenile stage, as often postulated); it seems to occur throughout the whole life".

At an optimal breeding locality on Finnøy, the local population was estimated at approximately 280 individuals and a density of 1.4 individuals/m^2. Because there was a majority of male frogs being caught during the mark-recapture, the estimate is considered to be conservative as the literature propose differences in catchability between genders linked to the asynchronous arrival of breeders; with males generally arriving earlier and being more active at a breeding site than females (Holenweg and Reyer 2000). Additionally, both the sex ratio and "*R. lessonae* to *R*. kl. *esculenta* ratio" can be either close to 1:1 (Berger et al. 1988) or with the excess of one gender or form in natural populations (Neveu 1991, Rybacki and Berger 2001). These relationships were not investigated in this study and the population estimate may have been unaffected by the fact or once again underestimated.

The abundance of frogs at the investigated locality is high and suggests that the frogs are dominant and have the ability to exert distinct impact on the dynamics of the invaded ecosystem.

At least five localities on the northern half of the island are believed to have approximately the same abundances of frogs as the locality investigated by mark-recapture. These observations confirm that the rough population estimate made by Dolmen in 2009 numbering the population at 1500-3000 adult individuals (Dolmen 2009b) is plausible and that the lower estimation is possibly too conservative. As the population expanded its geographical range every year, it was probably growing in numbers of individuals every year as well. The carrying capacity at each locality in the south of the island, has probably not yet been met, so that the population as a whole may still grow during the next few years.

It is evident that the frog population on Finnøy seemed healthy as no obvious symptoms of diseases were observed, the captured frogs were vigorous and the two observed cases of abnormalities are well within the 5% limit expected in any amphibian populations (Blaustein and Johnson 2003).

Despite the presumed healthiness of the green frogs on Finnøy, a more scientifically correct diagnose is seminal for the risk assessment of the alien population (Artsdatabanken 2011b). After all, the disease chytridiomycosis have been linked to major amphibian declines worldwide (Stuart et al. 2004, Duffus and Cunningham 2010, Kilpatrick et al. 2010) and have been found in European populations of the green frog complex (Garner et al. 2005, Simoncelli et al. 2005, Duffus and Cunningham 2010). It is not improbable that the population is burdened by disease even though it seemed healthy as a whole; usually the proportion of infected individuals is less than 10% (personal communication, Dirk Schmeller). Additionally, there is the possibility that individuals in the population are asymptomatic carriers (Simoncelli et al. 2005, Kraus 2009, Duffus and Cunningham 2010). Diagnostic detection of infections in amphibians is relatively simple (Brem et al. 2007, Kilpatrick et al. 2010) and hereby advised for future studies.

6.3. Invasiveness

In 2010 and 2011, the majority of the freshwater localities on Finnøy were occupied with either one or both forms of frogs and reproduction occurred in about half of these localities. Thus, the green frogs use the fresh water localities in relation to habitat quality. Some localities are not used at all; others are suboptimal as they are occupied only by metamorphosed individuals and without evidence of successful reproduction; whereas a subset of the localities is optimal as there is evidence of successful reproduction. As environmental variables were found to be limiting factors on the probability of presence of the frogs and their reproduction, the null-hypothesis regarding the random distribution of the frogs is rejected.

One should expect there to be more limiting parameters for reproduction than for the presence of adult individuals, as the tolerance of various chemical substances increases with time after hatching (Freda 1991). The same expectation is relevant for difference in the two forms since *R.* kl. *esculenta* is believed to be more tolerant than *R. lessonae* hypothesised by the alternative niche hypothesis (Moore 1977, Fioramonti et al. 1997, Plenet et al. 2000, Pagano et al. 2001). These patterns were not considered in this study, as the different sample sizes constricted the possible number of parameters to be included in each model.

Sun exposure was the most important environmental feature conditioning the frogs' presence and reproduction. The relationship is linked to shaded wetlands having lower light, lower dissolved oxygen, lower temperature and lower food resources (Werner and Glennemeier 1999). Low temperature and food scarcity mean lower tadpoles growth rate and survivorship (Bachmann 1969, Skelly et al. 2002). Additionally, the literature states that green frogs in the north of their native range are confined to really sunny ponds (Sjögren et al. 1988, Arnold and Ovenden 2002). Conforming to the principle of parsimony, sun exposure was the *only* predictor for *R. lessonae* and reproduction. This reflects the importance of sun exposure and a high degree of eurytopy to the other investigated variables in the study area. If is correct to conform to the principle of parcimony the green frogs can be characterized as habitat generalists.

Distance to the nearest forest edge was possibly a predictive parameter for the presence of *R. lessonae* and *R.* kl. *esculenta* and the relationship was negative. This relationship is supported by other studies when the distance to the nearest forest edge is associated with the ease of finding suitable hibernating sites. Both forms hibernate in woodlands, below the surface to avoid extremely low air temperatures (Fog et al. 1997, Holenweg and Reyer 2000, Voituron et al. 2005).

The positive relationship of sun exposure and the negative relationship of distance to nearest forest egde are not considered to be conflicting, because the interference of the forest edge at distances greater than 15 meters were negligible on the sun exposure.

Water colour was found to be a limiting factor to the presence of *R.* kl*. esculenta* and the relationship was negative. This effect was unexpected as water colour often reflects the humic content of a lake (Juday and Birge 1933) and humic content is generally believed to have ameliorating effects on the presence of amphibians because of the ability of humic acids to bind and detoxify aluminium (Skei and Dolmen 2006).

pH was found to be a possible limiting factor for reproduction and the relationship was positive. The lowest pH value in which reproduction was observed on Finnøy was 6.6. Few studies exist on the pH tolerance in the green frogs complex, but several studies on amphibians as a group support the positive relationship between pH and tadpole survivorship, stating that pH around 4 and 5 is lethal for amphibian larvae (Pierce 1985, Freda and Dunson 1986, Sadinski and Dunson 1992, Pierce 1993, Horne and Dunson 1995, Skei and Dolmen 2006). Comparatively, the frogs on Finnøy have a relatively low tolerance towards low pH. It must be mentioned that in the sample used for the habitat requirements of reproduction there were only two localities with lower pH that could be suitable for reproduction (i.e. with *R. lessonae* present and sun exposure above 80%) suggesting that the distinction of the lower pH tolerance level for reproduction had little statistical power. If the observed low tolerance towards pH is tangible, it may become a strong limiting factor for the invasion success on the mainland. The nuance between acidic and acidified waters is consequential, and this is further discussed below in the context of the Aust-Agder population.

Aluminium content was found to possibly be important for reproduction and seemed to have either a negative effect on reproduction or interactive effects with pH. Both effects had low statistical power, but trended in agreement with relationships discussed in the literature: Aluminium toxicity in freshwater organisms is related to decreased respiratory efficiency due aluminium precipitation and mucus accumulation on gills and osmoregulatory disturbances caused by increased loss and decreased uptake of ions (Rosseland and Staurnes 1994). Generally, aluminium becomes more soluble and toxic in acid environments, and different components of aluminium have different toxicity on freshwater organism (Brönmark and Hansson 1998, Walker and Hopkin 2006), for instance, the hydroxides $Al(OH)^{2+}$ and $Al(OH)_2^{+}$ are the most toxic at 5.3 and 5.9, repectively (Lydersen 1991). As even native Norwegian amphibians show different tolerance towards aluminium content and pH (Skei 1991, Dolmen et al.

2004, Skei and Dolmen 2006, Skei et al. 2006) it is not informative to correlate the green frogs' tolerance with native Norwegian amphibians. Further experimental studies including broad range of aluminium concentration and pH would be fruitful for the prediction of habitat requirement and invasiveness of the green frogs.

The interaction effect between pH and Na^+ (NaCl) with the relationship of reproduction would have been interesting to investigate for the frogs on Finnøy as it was found relevant for native Norwegian amphibians. The relationship associated increased contents of Na^+ with a higher tolerance towards low pH linked to the ion transport mechanism primarily through the gills and skin of amphibians (Dolmen et al. 2004, Dolmen et al. 2008).

Predatory fish is known to be a strong regulating factor on the green frog complex (Semlitsch 1993). Although not investigated statistically, the presence of predatory fish was observed in several breeding localities on Finnøy and is not believed to be a strong limiting factor in the study area.

The continuum from highly specialized to broadly generalist species has been associated with the level of invasiveness of introduced species (Moyle and Marchetti 2006). The interpretation of statistical analyses, especially the importance of the principle of parcimony is significant in concluding the degree of habitat eurytopy of the green frogs on Finnøy and their invasiveness. To avoid oversimplifying or making erroneous predictions of habitat suitability, the two extremes of habitat requirement found for the green frogs on Finnøy were used to predict habitat suitability on the mainland close to Finnøy. .

In the case of reproduction, which may be the most informative predictor of invasiveness, one scenario predicts only one locality to be suitable on the mainland, while the other predicts all localities to be suitable for breeding. The real habitat suitability on the mainland may be anywhere between these two predictions. Further studies are needed to see if the second hypotheses can be rejected (mainland localities near Finnøy are homologous to breeding localities on Finnøy). Among the investigated variables, pH was the main determinant of the different predicted habitat suitabilities. Experimental studies and field observations have shown contrasting results on amphibians' ability to respond to acidic stress by rapid evolutionary responses (Andrén et al. 1989, Dolmen, D, Räsänen et al. 2003, Merilä et al. 2004, Personal communication D. Dolmen 2011) ergo studies on the pH tolerance and ability for adaptations of the green frogs may be helpful to discern mainland suitability and the invasiveness of the green frogs.

The degree of climate matchability is recognized as an important determinant in modelling an alien species' anticipated potential range (Pearce and Lindenmayer 1998, Duncan et al. 2001, Forsyth et al. 2004, Thuiller et al. 2005). Turning the equation around, it is evident that Finnøy, provided the necessary degree of climate matchability compared to the donor region of the propagule (Krakow, Poland) since the alien population on Finnøy is thriving. The climate in Krakow can be characterized as more extreme compared to Finnøy, with colder winters and hotter summers (Figure 14). Any climate within the range Finnøy/Krakow is therefore believed suitable for the frogs. The climate in five areas in the county Rogaland (Forsand, Klepp, Sola, Stavanger and Ålgård) were within the temperature ranges Finnøy/Krakow (Appendix 7) thus, climate is not assumed to have negative impact on the invasiveness of the frogs if further introduced to the mainland.

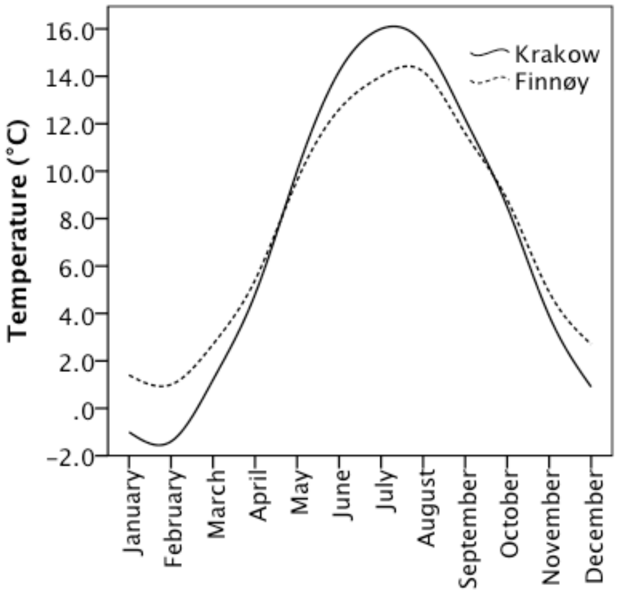

Figure 14. Mean monthly temperatures on Finnøy (modified from Norwegian Meteorological Institute) and Krakow (modified from Anon. 2011).

In the absence of additional limiting environmental variables, there is no reason to believe that the green frogs would thrive less on the mainland close to Finnøy than what they have done on Finnøy.

6.4. Fitness

The yearlings of the northern clade of *R. lessonae* in Aust-Agder were larger in body size than the yearlings of the southern clade of the introduced *R. lessonae* on Finnøy, thus the third null-hypothesis may be rejected. The direction of the effect was unexpected for several reasons. Firstly, recent reports on anurans provide conflicting support to the tendency for organisms to be larger in cooler climates (Ashton 2002, Adams and Church 2007). Secondly, larger size and vigour is often found in successful invaders compared to conspecifics in the native range (Elton 1958, Jakobs et al. 2004, Bossdorf et al. 2005). Thirdly, because of the general association between body size and fitness stating that "bigger is better" (Kingsolver and Huey 2008). On the other hand, studies have concluded that individuals inhabiting range edges are often larger than core-area conspecifics (Meiri et al. 2009 and references therein).

Although larger in yearling body size, the native Aust-Agder population has undoubtedly less vigour than the alien Finnøy population (based on the number of breeding localities, population growth and range in relation to residence time).

A population at the edge of its natural range, like the Aust-Agder population, must be constricted by at least one niche axis, or it would expand its range (Caughley et al. 1988).

Less suitable climate have been postulated to be such a limiting factor (Brown 1984, Pitt et al. 2008). On average, Arendal/Grimstad, which is the area in Aust-Agder where *R. lessonae* occurs, has a more extreme climate compared to Finnøy, with colder winters and warmer summers (Figure 15). As warmer summer temperatures are considered positive for the development of frogs (Smith 1976, Sjögren et al. 1988, Sanuy et al. 2008), other components of climate should have negative impact if the reasoning of less suitable climate being a limiting niche axis holds true.

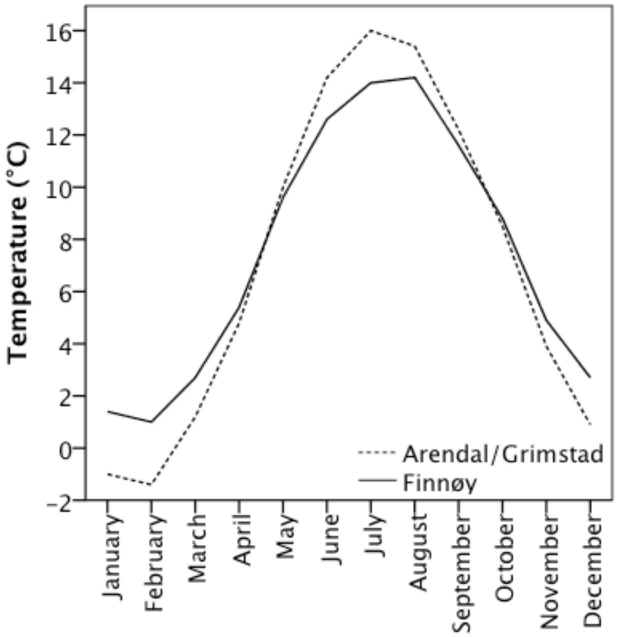

Figure 15. Monthly mean temperatures at Finnøy and Arendal/Grimstad calculated from weather normal 1961-1990 (modified from Norwegian Meteorological Institute).

Another niche axis limiting the Aust-Agder population, could be the prevalent acidification of surface waters in Southern Norway (Wright and Henriksen 1978). Although slowly recovering, the acidified waters have led to current breeding problems for amphibians in Norway (Skei 1991, Skei and Dolmen 2006, Skei et al. 2006). The only three breeding localities known for *R. lessonae* in Aust Agder have pH values of 5.4, 5.8 and 5.9 and according to Henriksen's acidification line (Henriksen 1979) the localities are either acidified or close to being acidified (Figure 16). Whether it is acidic waters per se or the acidification of them that limit the distribution of *R. lessonae* in Southern Norway is difficult to discern. On Finnøy, however, the conditions of the freshwater localities are better; with both higher pH in general and a high number of non-acidified localities (when Henriksen's acidification line is extrapolated).

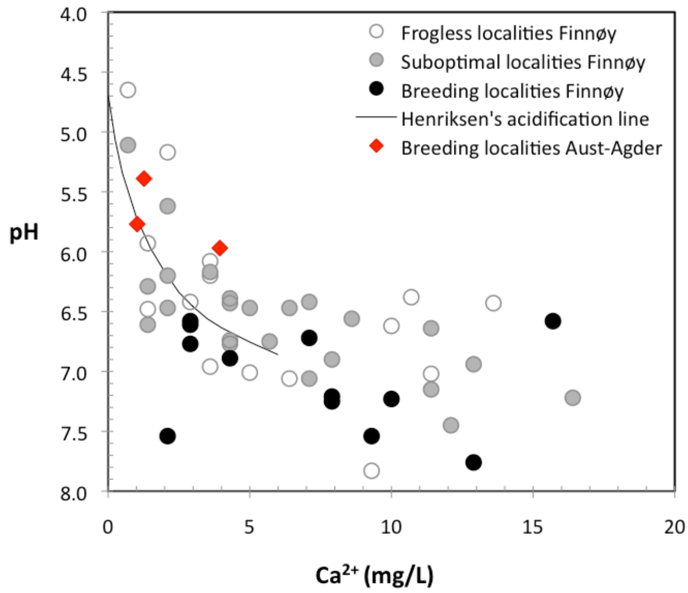

Figure 16. The relationship between Ca^{2+} and pH in frogless, suboptimal (only metamophosed frogs) and breeding localities on Finnøy and Aust-Agder. Localities above Henriksen's acidification line are characterized as acidified.

If either climatic or acidity (and/or acidification) differences constitute explanation on the relative difference in fitness of the two populations, it allows for two implications:

- The native population of the northern clade of *R. lessonae* in Aust-Agder could possibly prevent its impending extinction if some individuals from Aust-Agder were relocated to areas with a more benign climate or less acidic/acidified waters, for instance islands adjacent to Finnøy.
- The invasion success of the Finnøy-frogs may decrease together with the degree of acidified surface waters in the unwanted, but probable event of secondary introductions to the mainland.

7 Conclusion

This project has provided evidence that the green frogs introduced to Finnøy have great invasion success and may be a valid conservation problem in Norway:

- The population on Finnøy has increased the number of occupied and breeding localities every year and is rapidly expanding its geographical range.
- The frogs exist in high numbers at optimal localities and therefore have the ability to have major impact on the invaded ecosystem.
- Although vigorous and seemingly healthy, the population could still be disease vectors.
- The green frogs have broad habitat tolerances, with either only sun exposure as a limiting factor or distance to forest, water colour, pH and aluminium as additional limiting factors.
- Investigated freshwater localities on the mainland provide suitable habitats for the green frogs.

Although the complex long-term consequences of the introduction on Finnøy remain unknown and irreversible, the formidable invasion success of the green frog population provides a perfect example of what could happen on the mainland.

According to the Nature Diversity Act (2009) and the cross-national strategy on invasive alien species (Miljøverndepartementet) the natural management authorities should not chance secondary green frog introductions and possible subsequent invasion on the mainland. The window of opportunity during which eradication of an incipient population on the mainland can potentially succeed is narrow. Failure to act before this window closes would mean that the frogs could rapidly become so dense and widespread that effective action becomes impossible very fast. A proactive approach focusing on prevention, early-detection and rapid-response is hereby advised.

Finally, the comparison between the introduced population on Finnøy and native population in Aust-Agder have prompted possible conservation efforts to prevent the extinction of the northern clade of *R. lessonae*.

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Appendix 1. Raw data Finnøy (1/3)

Locality		Position		2010			2009		2011		
#	Name	E	N	RL	RE	REP	RL	RE	RL	RE	REP
1	Stranddam Vestre	318888	6566754	0	0	0	0	0	0	0	0
2	Stranddam Midt	318888	6566754	1	1	1	0	0	1	1	1
3	Stranddam Ost	318888	6566754	1	1	1	0	0	1	1	1
4	Hopen	317797	6565793	0	0	0	0	0	0	0	0
5	Landa	318381	6565787	1	1	0	0	1	1	1	0
6	Mjolnesdammen	318877	6565856	1	1	1	1	1	1	1	1
7	Nedre Stemmen	318966	6565728	1	0	0	0	1	1	0	0
8	Ovre Stemmen	319000	6560000	0	0	0	0	0	0	0	0
9	Dam ved vei Sor for Mjolnesfjell	318792	6565395	1	1	0	0	0	1	1	0
10	D1 Sor for Mjolnesfjellet	319006	6565230	1	0	0	1	0	1	0	0
11	D2 Sor for Mjolnesfjellet	319028	6565353	1	1	0	1	0	1	1	0
12	Myrpytt Sor for Mjolnesfjellet	319018	6565137	1	0	0	1	1	1	0	0
13	Brekkemyr	317438	6564345	0	1	0	0	1	1	1	1
14	Liten Skogsdam ved Fylling	319164	6564200	0	0	0	0	0	0	0	0
15	Lang Skogsdam	319118	6564234	1	0	0	1	0	1	0	0
16	Dam ved Raskdeponi	319300	6564200	1	1	1	1	1	1	1	1
17	Sump ved Vegkryss	319400	6564100	0	0	0	0	0	0	0	0
18	Dam Vest for Vestbo Varde	318700	6563900	1	1	1	1	0	1	1	1
19	Dam ved grind Nord for Nokjevann	319000	6563900	1	0	0	1	1	1	0	0
20	Stolpedam	319520	6563998	0	1	0	0	0	0	1	0
21	Nokjevann	319100	6563600	1	1	1	1	1	1	1	1
22	Nokjevannsdam	319100	6563700	1	1	1	1	1	1	1	1
23	Spannevann	319998	6564347	1	1	1	1	1	1	1	1
24	Lauvsnesvann	320347	6564330	1	1	1	1	1	1	1	1
25	Hauskjevann	320149	6563844	1	1	1	1	1	1	1	1
26	Fiskedam Sor for Haras	319700	6563400	0	0	0	0	0	0	0	0
27	Dam ved Falkeid	318816	6563226	1	1	0	1	1	1	1	0
28	Dam Ost for Firedamsump	319081	6563120	1	1	0	1	1	1	1	0
29	Firedamsump Forlengelse	319549	6563253	1	1	1	1	1	1	1	1
30	Dam i Skogen ved Idrettsanlegg	319447	6563134	0	0	0	0	0	0	1	0
31	Firedamsump	319625	6563187	1	1	0	1	1	1	1	0
32	Dam1ved Flesjo	318522	6562744	0	1	0	0	1	0	1	0
33	Bekkedam 1 Sor for Flesjo	318415	6562501	0	1	0	0	0	0	1	0
34	Bekkedam 2 Sor for Flesjo	318503	6562342	0	1	0	0	0	0	1	0
35	Oppdemt Dam Sor for Flesjo	318555	6562433	1	1	1	0	0	1	1	1
36	Dam Nord for Kuhammar	318671	6562520	1	1	0	0	0	1	1	0
37	Olamyra	319259	6562523	1	1	1	0	0	1	1	1
38	Oppdrettsdam	320236	6562663	0	1	0	0	0	0	1	0
39	Dam ved Grind Iglemyra	318900	6561800	0	0	0	0	0	0	0	0
40	Dam sentralt pa Iglemyra	318973	6561855	0	1	0	0	1	1	1	0
41	Øvre Bergdam	318356	6561265	0	0	0	0	0	0	1	0
42	Nedre Bergdam	318447	6561168	0	0	0	0	0	0	0	0
43	Dam SorVest for Kingestad	317617	6561114	0	1	0	0	0	0	1	0
44	Dam pa myr NordOst for Bleievann	317200	6561000	0	0	0	0	0	0	0	0
45	Bleievann	316992	6561020	0	1	0	0	0	0	1	0
46	Myrdam SorOst for Savheimsvann	317023	6561329	0	0	0	0	0	0	0	0
47	Dam ved myr Sor fpr Savheimsvann	316624	6561317	0	1	0	0	0	0	1	0
48	Savheimsvann	316623	6561627	0	1	0	0	0	0	1	0
49	Grunn Dam SorVest for Bleievann	316800	6560600	0	0	0	0	0	0	0	0
50	Dam SorSorVest for Bleievann	316800	6560400	0	0	0	0	0	0	0	0
51	Lasteinvann	316500	6560600	0	0	0	0	0	0	0	0
52	Dam 1 Vigenes Sor	316145	6563296	0	0	0	0	0	0	0	0
53	Dam 2 Vigenes Nord	316141	6563296	0	0	0	0	0	0	0	0

Appendix 2. Raw data Finnøy (2/3)

	elevation	dist.mjølnes	2010 Range		dist.forest	bott.veg.	Ca	Mg	NaCl	Al	P
#	m.a.s.l.	m	RL	RE	m	%	µg/L	µg/L	µg/L	mg/L	µg/L
1	2	908	1	1	60	1	5.00	9.10	8.62	353.72	40.43
2	2	900	1	1	50	10	2.14	3.03	5.65	558.43	14.87
3	4	894	1	1	50	10	9.28	5.64	8.21	320.46	10.20
4	1	1082	1	1	300	1	NA	NA	NA	8.99	11.82
5	60	500	1	1	1	70	4.28	1.73	1.77	84.95	20.40
6	80	0	1	1	150	5	2.86	2.17	2.27	87.38	15.26
7	100	155	1	1	1	60	0.71	2.17	3.67	331.71	59.39
8	104	208	1	1	1	5	1.43	1.73	1.94	215.36	59.01
9	111	469	1	1	50	30	8.57	3.47	3.01	93.98	12.45
10	120	639	1	1	3	5	11.42	4.77	3.09	37.13	37.26
11	126	525	1	1	5	5	4.28	3.47	3.01	105.27	24.13
12	120	733	1	1	30	50	3.57	3.03	3.26	219.10	9.72
13	15	2087	1	1	50	20	12.85	5.20	2.52	41.52	185.25
14	100	1681	1	1	1	5	11.42	4.77	1.53	120.77	50.50
15	100	1640	1	1	1	5	5.71	2.60	1.44	128.76	33.40
16	100	1709	1	1	50	40	15.71	6.94	1.44	179.62	155.00
17	101	1832	1	1	1	70	13.57	3.90	2.43	89.71	56.18
18	140	1964	1	1	10	70	2.86	2.17	2.76	83.94	69.84
19	138	1960	1	1	100	50	7.14	5.64	2.76	723.80	112.11
20	101	1966	1	1	10	85	2.14	0.87	2.19	125.44	367.52
21	120	2267	1	1	1	20	7.85	4.34	2.52	50.83	12.61
22	120	2196	1	1	50	30	12.85	5.20	2.60	69.70	21.74
23	100	1880	1	1	1	5	2.86	2.60	2.27	107.04	29.66
24	80	2119	1	1	1	10	7.85	3.90	2.02	33.79	13.15
25	80	2380	1	1	1	25	10.00	3.90	2.10	26.68	30.05
26	120	2590	1	1	300	5	6.43	3.47	1.86	41.19	31.51
27	45	2631	1	1	1	50	2.14	1.30	1.53	243.40	70.16
28	71	2744	1	1	10	2	4.28	2.60	1.86	544.97	109.04
29	140	2688	1	1	20	30	7.14	2.60	2.02	74.70	62.52
30	120	2781	1	1	1	5	10.00	3.90	2.19	228.26	49.24
31	140	2772	1	1	10	10	12.14	5.64	2.02	82.29	56.85
32	40	3132	1	1	150	75	6.43	2.60	1.44	224.27	40.99
33	50	3387	1	1	1	1	7.85	3.90	2.27	63.16	19.83
34	78	3534	1	1	5	1	4.28	2.17	1.86	73.65	14.92
35	70	3438	1	1	20	1	2.86	1.73	1.61	119.82	23.09
36	60	3342	1	1	20	40	16.42	5.64	2.10	277.27	78.30
37	80	3355	1	1	50	40	4.28	3.03	2.02	59.69	16.53
38	50	3470	1	1	1	1	11.42	5.20	2.35	78.69	31.44
39	80	4056	0	1	30	0	3.57	2.17	2.10	63.00	17.35
40	80	4002	0	1	40	85	5.00	2.17	1.94	70.97	10.55
41	115	4620	0	1	300	2	9.28	4.34	2.35	384.44	49.11
42	107	4708	0	1	1	5	6.43	3.90	2.10	246.65	9.98
43	76	4907	0	1	100	10	7.14	3.03	2.10	75.83	16.92
44	114	5137	0	1	50	40	2.14	1.30	2.19	174.27	10.28
45	100	5190	0	1	1	5	1.43	1.30	3.09	8.23	3.50
46	92	4892	0	1	30	30	3.57	1.73	3.09	110.47	5.90
47	72	5067	0	1	25	40	2.14	1.30	2.93	56.34	5.57
48	60	4792	0	1	1	1	1.43	1.73	3.01	43.13	9.39
49	89	5651	0	0	10	50	0.71	1.30	3.42	91.96	49.22
50	100	5838	0	0	10	10	1.43	3.03	2.43	129.28	33.22
51	80	5768	0	0	1	1	2.86	1.73	2.85	54.05	55.26
52	20	6528	0	0	500	40	10.71	5.20	2.52	69.93	27.72
53	20	6774	0	0	500	50	3.57	2.17	2.19	452.11	70.17

Appendix 3. Raw data Finnøy (3/3)

	Tot.N	Tot.Hard	konduk	pH	pH	W.Col	sun
#	ppm N	°dH	K25	el.	col.	Pt	%
1	1.14	2.8	251	7.01	6.9	100	99
2	0.79	1	166	7.54	6.7	125	99
3	0.87	2.6	248	7.54	7.2	125	99
4	1.16	0	1070	8.82	NA	60	99
5	0.40	1	81.3	6.39	5.8	80	60
6	0.46	0.9	82.4	6.61	6.5	45	80
7	1.16	0.6	99	5.11	4.7	60	60
8	0.61	0.6	64.7	5.93	NA	80	10
9	2.47	2	135.2	6.56	6.1	45	90
10	0.84	2.7	150.2	6.64	6.3	50	50
11	0.92	1.4	108.7	6.43	5.9	50	40
12	0.61	1.2	79.3	6.17	6.0	100	99
13	2.43	3	166.5	6.94	6.0	125	99
14	0.57	2.7	137.5	7.02	NA	85	10
15	1.06	1.4	89.7	6.75	5.9	50	30
16	1.04	3.8	76.2	6.58	5.9	90	99
17	0.98	2.8	107.8	6.43	NA	160	10
18	0.78	0.9	93	6.59	5.9	70	90
19	7.48	2.3	160.2	6.42	6	180	75
20	1.72	0.5	67.6	6.2	5.3	70	90
21	1.17	2.1	130.5	7.25	6.5	40	90
22	0.72	3	155	7.76	6.3	70	99
23	0.80	1	85.9	6.77	7.2	45	80
24	1.49	2	83.3	7.21	7.1	35	90
25	1.41	2.3	91.2	7.23	7.0	40	95
26	2.06	1.7	98.3	7.06	NA	50	95
27	1.11	0.6	60.7	6.47	6.1	100	50
28	1.22	1.2	89.1	6.74	6.1	100	80
29	0.56	1.6	51.1	6.72	6.2	100	90
30	0.47	2.3	106.8	6.62	5.3	150	5
31	0.95	3	140.7	7.45	6.3	45	90
32	1.23	1.5	90.4	6.47	5.9	70	50
33	0.91	2	125.5	6.9	6.3	40	50
34	0.34	1.1	86.5	6.77	6.2	50	50
35	0.64	0.8	71.2	6.58	6.6	50	80
36	0.98	3.6	172.4	7.22	6.7	70	60
37	0.77	1.3	89.7	6.89	6.3	60	90
38	2.66	2.8	107.2	7.15	7.2	50	90
39	0.33	1	74.1	6.2	NA	80	20
40	0.31	1.2	86.2	6.47	6.1	70	70
41	2.76	2.3	141.1	7.83	7.0	40	99
42	1.65	1.8	120.4	9.69	6.7	70	80
43	1.04	1.7	114.6	7.06	6.6	50	70
44	0.34	0.6	68.2	5.17	NA	100	99
45	0.10	0.5	76.9	6.29	6.5	15	80
46	0.34	0.9	98.4	6.08	5.8	70	90
47	0.20	0.6	88	5.62	5.6	60	99
48	0.23	0.6	85.6	6.61	6.7	40	80
49	0.62	0.4	92.8	4.65	NA	70	10
50	0.81	0.9	85.3	6.48	NA	70	40
51	1.28	0.8	92.5	6.42	NA	15	80
52	0.60	2.7	134.2	6.38	NA	90	99
53	1.18	1	78.9	6.96	NA	100	99

Appendix 4. Raw data mainland localities.

#	Name	Pos. E.	Pos. N.	Pt-value	pH	K25	Sun (%)	Distance Forest (m)	Vegetation cover %
1	Skoratjørna	33175	656040	40	6.4	61.6	90	1	5
2	Vest for Skoråsen	33135	656010	50	5.9	83.9	80	1	60
3	Åsatjernet	33720	656180	50	5.3	143	80	1	60
4	Erekjeret	33080	655210	40	6.4	55.2	95	10	5
5	Vestlige d.n.f.østrehus	32970	655190	100	6.4	68.5	80	1	10
6	Vardlandstjern	32690	655315	80	6.1	66	90	2	60
7	Seldalsmsmyr	32585	655270	90	5.3	77.8	95	1	90
8	Dam vd Prestegård	32375	655010	300	5.4	59.6	95	2	50
9	nord for Vaule	30800	652265	150	5.8	88.1	90	5	90
10	Øksnavad	30760	652240	70	6.5	207	99	2	5
11	Dam vd Kvernaland fabri	30855	652050	50	6.7	206	99	1	40
12	Heiatja	30925	651850	70	6.1	67.8	90	1	10
13	Bekk vd Dobleveiene	31325	651840	70	6.2	72.9	NA	NA	NA
14	Mississipi ved Stokkava	31015	654140	15	6	207	85	1	30
15	Mosvann	31150	653980	25	5.8	220	80	1	90
16	Dam ved Mosvann	31150	654030	20	5.8	286	90	1	40
17	Littlevannsåsen	31220	653820	35	5.3	86.8	85	1	40

Appendix 5. Hydrology Aust-Agder breeding localities.

Lok.	pH	K25	Pt-verdi	Na23(MR)	Mg25(MR)	Al27(MR)	P31(MR)	S34(MR)	Cl35(MR)	Ca43(MR)	Total-N
				µg/L	µg/L	µg/L	µg/L	µg/L	µg/L	µg/L	ppm N
Lok. 1	5.39	35.5	100	3 555	542	176	4.7	1 002	6 261	1 268	0.155
Lok. 2	5.77	29.9	55	3 497	571	133	6.2	739	5 370	1 026	0.156
Lok. 3	5.97	44.1	95	3 949	863	175	4.9	886	5 579	3 943	0.214

Appendix 6. Correlation matrix Finnøy hydrology.

		Ca	Mg	NaCl	Al	P	Tot.N	Tot. hardness	K25	pH
Mg	r	.750**								
	P	0								
	N	52								
NaCl	r	-0.102	.382**							
	P	0.473	0.005							
	N	52	52							
Al	r	-0.078	0.206	.313*						
	P	0.58	0.143	0.024						
	N	52	52	52	53					
P	r	0.125	0.045	-0.138	0.192					
	P	0.377	0.753	0.331	0.168					
	N	52	52	52	53					
Tot.N	r	0.226	.349*	-0.005	.497**	.317*				
	P	0.107	0.011	0.97	0	0.021				
	N	52	52	52	53	53				
Tot. hard.	r	.959**	.906**	0.098	0.069	0.116	.283*			
	P	0	0	0.49	0.622	0.409	0.04			
	N	52	52	52	53	53	53			
Conductivity	r	.461**	.765**	.723**	-0.034	-0.094	0.089	-0.053		
	P	0.001	0	0	0.808	0.502	0.525	0.707		
	N	52	52	52	53	53	53	53		
pH	r	.450**	.476**	0.052	0.057	-0.124	0.17	.354**	.465**	
	P	0.001	0	0.716	0.683	0.377	0.224	0.009	0	
	N	52	52	52	53	53	53	53	53	
Water colour	r	0.192	0.262	0.235	.583**	0.267	.306*	0.24	0.031	-0.076
	P	0.173	0.06	0.093	0	0.054	0.026	0.084	0.823	0.587
	N	52	52	52	53	53	53	53	53	53

Appendix 7. Mean monthly temperatures (°C) in five areas in Rogaland county (data generated from eklima.net).

	Forsand	Klepp	Ålgård	Sola	Stavanger
January	0.2	-0.1	0.6	0.8	1.2
February	0.2	-0.2	0.4	0.6	1.1
March	2	1.9	2.6	2.7	2.8
April	5.5	4.8	5.5	5.5	5.5
May	9.8	9.1	9.8	9.9	9.9
June	12.8	12.1	12.7	12.8	12.8
July	14.3	13.4	14	14.2	14.1
August	14.2	13.6	14.2	14.4	14.4
September	11.3	11.1	11.7	11.7	11.7
October	8.3	8.1	8.6	8.8	8.8
November	4.2	3.8	4.5	4.6	4.8
December	1.5	1.4	2.1	2.2	2.5

Appendix 8. Abnormalities on yearlings on Finnøy.