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# Relative performance of salmonid phenotypes across environments and competitive intensities

Thesis for the degree of Philosophiae Doctor

Trondheim, April 2011

Norwegian University of Science and Technology  
Faculty of Natural Sciences and Technology  
Department of Biology



**NTNU – Trondheim**  
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Grethe Robertsen  
Trondheim  
April 2011



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## LIST OF STUDIES:

- I. Robertsen, G., Armstrong, J.D., Nislow, K.H., Herfindal, I., McKelvey, S & Einum, S. Phenotype performance depends on local environmental conditions in juvenile Atlantic salmon. *Manuscript*.<sup>1</sup>
- II. Skoglund, H., Einum, S. & Robertsen, G. (2011). Competitive interactions shape offspring performance in relation to seasonal timing of emergence in Atlantic salmon. *Journal of Animal Ecology* **80**, 365-374.<sup>2</sup>
- III. Robertsen, G., Skoglund, H. & Einum, S. Competitive regimes shape the spatio-temporal patterns of offspring size effects in Atlantic salmon. *Manuscript*.<sup>3</sup>
- IV. Robertsen, G., Kvingedal, E. & Einum, S. (2011). Is there genetic variation in the response to competition intensity in juvenile brown trout, *Salmo trutta*? *Journal of Fish Biology* **78**, 635-646.<sup>4</sup>

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## **INTRODUCTION**

### **Environmental conditions and selection patterns**

According to life-history theory, optimal trait values that maximize fitness should evolve in a given environment. Hence, genetic variation in fitness-related traits should erode (e.g. Roff, 1992). Yet, genetic variation in such traits is common, even within populations (Weigensberg and Roff, 1996). The mechanisms responsible for maintaining this variation have received much attention in evolutionary ecology and a number of hypotheses have been developed (reviewed in Roff, 2002). Among the explanations proposed are spatial and temporal variations in selection pressures. These hypotheses are founded on that natural environments commonly vary. Since it is unlikely that one genotype can produce phenotypes that are superior under all conditions, this can result in variable selection pressures. Theoretically, spatial variation in selection pressures may be an important factor in preserving genetic variation (Levene, 1953; Bulmer, 1971; Gillespie & Turelli, 1989). Temporal variation in selection pressures may also be important, although, under a narrower set of assumptions (e.g. overlapping generations, Ellner & Hairston, 1994; Ellner, 1996; Ellner & Sasaki, 1996). Thus, my main focus will be on spatial heterogeneity, although temporal variation in selection pressures will also be discussed.

The relationship between a trait and success in different environments is of general interest since it may provide information regarding the evolution of fitness-related traits. However, it is also important in an applied context. Firstly, for preserving genetic variation within populations and secondly for identifying environmental factors that may influence the phenotype-fitness function in species that are subject to anthropogenic disturbances. Such knowledge could prove invaluable for assessing the consequences of human interference as well as providing a framework for mitigating the negative effects of human impacts.

### **Spatial variation in environmental conditions in general**

Environmental factors like latitude, temperature and other climatic factors are often found to vary spatially over large scales, causing selection gradients to vary among populations (Williams & Moore, 1989; Weber & Smidt, 1998; Bronikowski, 2000; Koskinen et al., 2002). Uncovering spatial variation in environmental factors across scales small enough to induce variation in selection pressures within populations may be more difficult. Still, due to certain characteristics of their biology, this may be easier to study in some organisms. For instance, juveniles of Atlantic salmon (*Salmo salar* L.), one of the model species employed in this

thesis, from the same population can grow up in tributaries that vary in several environmental factors (e.g. altitude, predators and shelter, Armstrong et al., 2003; Finstad et al., 2011). Thus, selection pressures are not likely to be constant across tributaries.

#### **.. and competitive intensity in particular**

Population density is one biotic environmental factor which is easy to identify and may vary over small spatial scales in both sessile (Rees et al., 1996; Law et al., 1997) and mobile organisms (Hassell, 1987; Brown et al., 1995; Ray & Hastings, 1996). According to theories of density-dependent natural selection, the performance of an individual at a given density depends on its competitive ability when competition is asymmetric (reviewed in Joshi et al., 2001). Specifically, having traits connected with high competitive ability should be advantageous when density, and thereby competition, is high. Under low population densities, with lower levels of competition, such traits may be of less importance. Since traits conferring high competitive ability are frequently associated with costs, they may even be detrimental at low population densities. Hence, if such traits are heritable different genotypes may be optimal at different densities (e.g. Charlesworth, 1971; Roughgarden, 1971; reviewed in Joshi et al., 2001). Selection pressures may, accordingly, be expected to vary spatially within a population depending on local levels of conspecific density.

#### **Temporal variation in competitive intensity**

Variation in selection pressures may also be caused by temporal fluctuations in population densities. In many organisms, abundance, and thus densities, varies substantially among years (e.g. Calsbeek & Smith, 2007; Svanbäck & Persson, 2009). Also, in species with seasonal reproduction, densities are expected to increase over the season as more juveniles enter the population, resulting in an increase in competition intensity (Svennson & Sinervo 2000; Plaistow et al., 2007). Specifically, offspring entering the population late in the season will experience higher levels of competition than those entering early. Thus, selection for traits associated with competitive ability may be expected to vary among offspring entering the population at different times.

#### **Trade-offs in fitness-related traits**

To study the impact of environmental conditions on selection pressures we selected a number of fitness-related traits which are known to vary within populations and where the relative advantages of different trait values are expected to depend on environmental conditions (level

of competition or harshness). In my thesis I focus on the following traits: 1) metabolic rate, 2) offspring size, 3) age and size at maturation, and 4) timing of breeding.

#### *1) Metabolic rate*

Maintenance metabolism is the minimum energy required to support basic life functions (McNab, 1988). Although metabolic rate is expected to be closely linked to fitness (Konarzewski et al., 2005) it varies considerably within-populations (Metcalf et al., 1995; Burness et al., 1998; Nespolo et al., 2003). There is at least some genetic component to it (Sadowska et al., 2005; Nilsson et al., 2009; Tieleman et al., 2009, but see Dohm et al., 2001) and it is linked to both physiological (Rezende et al., 2006) and behavioural traits (Bryant & Newton, 1994; Mathot et al., 2009). For instance, salmonid individuals with high metabolic rates have higher dominance ranks and are more aggressive than individuals with low metabolic rates (e.g. Metcalfe et al., 1995; Lahti et al., 2002). This may be expected to be advantageous under high levels of competition. However, having a high metabolic rate may entail cost in terms of high energy output (Milidine et al., 2009). Indeed, the correlation between metabolic rate and survival has been found to be negative under restricted food conditions and neutral when food was abundant (Bochdansky et al., 2005). Thus, selection on metabolic rates may be expected to vary depending on environmental conditions, such as overall food availability (Boratynski & Koteja, 2010; Larivée et al., 2010; Armstrong et al., in press).

#### *2) Offspring size*

Offspring size is a maternal effect known to vary substantially within populations. Maternal effects have been defined as ‘the causal effect of maternal genotype or phenotype on the phenotype of the offspring’ (Wolf & Wade, 2009). Accordingly, they can result from pure environmental effects on the maternal phenotype which, in turn, influence the phenotype of the offspring. Many maternal effects, however, have a genetic basis. For instance, in salmonids, there is a substantial genetic component to egg size ( $h^2 = 0.3 - 0.6$ , Gall and Huang, 1988; Su et al., 1997). Thus, egg size depends on the mother’s phenotype, which may be partly ascribed to environmental conditions, but it also depends on maternal genes. Selection for a particular egg size could, therefore, lead to an evolutionary response in the population. Offspring size is typically traded off with offspring number: fecundity correlates negatively with offspring size (e.g. Ferguson & Fox, 1984; Carrière & Roff, 1995). Offspring size is of profound importance for offspring success (Ferguson & Fox, 1984; Stanton, 1984; Rius et al., 2010), for instance because of its effect on competitive ability (large offspring size

may infer competitive advantages, Marshall et al., 2006). Thus, potential fitness gains in highly fecund mothers may be counter-balanced by lower survival of smaller offspring. Furthermore, the optimal offspring size maximizing female fitness may depend on environmental conditions (Smith & Fretwell, 1974; Parker & Begon, 1986; Lloyd, 1987; McGinley, 1987). In fact, the relative strength, and even direction, of selection on offspring size can depend on environmental conditions, with large offspring size often being advantageous when conditions are harsh or when the level of competition is high (Sinervo et al., 1992; Einum & Fleming, 1999; Fox, 2000; Joshi et al., 2001; Gregersen, 2008; Monro et al., 2010).

### *3) Age and size at maturation*

Age and size at maturation is highly associated with fitness, varies substantially among and within populations and may be partly governed by a genetic component (e.g. Atlantic salmon,  $h^2 = 0.1-0.48$ , Gjerde et al., 1994; Wild et al., 1994). Delayed maturity may provide an advantage in terms of increased fecundity in organisms with indeterminate growth. Also, offspring size, and hence survival, may be positively correlated with parental age (e.g. Fleming & Gross, 1990; Dearborn et al., 2008). Hence, costs of delayed maturation (e.g. pre-adult mortality) may be offset by both increases in fecundity and offspring success. If the correlation between maturation age and offspring size is pleiotropically based, selection on offspring size may be accompanied by selection on age at maturation.

### *4) Timing of breeding/hatching*

Timing of breeding is another maternal trait that can be associated with substantial additive genetic variation (e.g. suggested heritability in salmonids is 0.65, Su et al., 1997). Timing of breeding can be an important determinant of offspring fitness because it influences the timing of offspring birth or hatching (correlated with timing of emergence from the gravel in salmonid juveniles) (e.g. Landa, 1992; Einum & Fleming, 2000; Warner & Shine, 2007). For example, emerging early may provide competitive advantages in terms of prior access to favourable locations (Huntingford & Garcia De Leaniz, 1997; Cutts et al., 1999) and larger body size (Cutts et al., 1999; Johnsson et al., 1999). Conversely, it may entail costs in terms of increased susceptibility to predation (Brännas, 1995) and unfavourable environmental conditions. However, the role of competition intensity on the relationship between emergence date and offspring success is uncertain. For example, when levels of competition are high, the competitive advantages of arriving early may prove beneficial despite the potential for being exposed to harsh environmental conditions. Whereas at low levels of competition intensity,

competitive ability may be of less importance. Accordingly, the relative success of breeding early versus late may depend on the level of competition experienced by offspring (Iwasa & Levin, 1995).

### **Study organisms**

In my thesis I used stream dwelling members of the family Salmonidae, Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) as study organisms. These display a remarkable variation with regard to biology and life-history traits, both among and within the species (Klemetsen et al., 2003). Adults commonly spawn in streams where the juveniles hatch and spend some time before potentially migrating into the sea (anadromous) or a lake (freshwater resident) for feeding. Anadromous fish may stay in the sea from some months (brown trout) to one year (one-sea-winter fish) or several years (multi-sea-winter fish), where the majority of growth occurs, before returning to the stream to spawn (Klemetsen et al., 2003). Hence, both age and size at maturation may vary considerably within populations.

Juveniles of stream-dwelling salmonids are ideal study organisms for investigating the relationship between environmental heterogeneity and the relative fitness of different phenotypes. They often inhabit small manageable streams, where environmental conditions may vary spatially and temporally (e.g. Arnekleiv et al., 2006; Finstad et al., 2009; Parra et al., 2009). During the early juvenile stage density dependence is commonly pronounced (Elliott, 1989; Jonsson et al., 1998; Armstrong & Nislow, 2006) and high mortality rates make strong selection pressures likely (e.g. brown trout juveniles experience up to 98% mortality within 2-3 months of emergence from the nest, Elliot, 1994). Large spatial variation in density during the early stages of development is likely due to patchy egg distribution and limited juvenile movement (Einum & Nislow, 2005, Einum et al., 2008a). The timing of emergence can also vary considerably among nests, because females may spawn at any time during the breeding season that may last up to 10 weeks in some populations (Fleming, 1996; Garcia de Leaniz et al., 2007). Thus, levels of competition may also vary temporally within one season because juvenile density increases with the number of juveniles emerging from nests and entering the population.

## **AIMS OF THE THESIS**

The main objective of this thesis was to assess the potential for environmental conditions in general, and levels of competition in particular, to influence adaptive landscapes in stream-dwelling salmonid fish. Specifically, I am interested in the potential for spatial and temporal variation in selection pressures to maintain genetic variation within populations. To do this, a range of questions connected to these issues were formulated and experimentally tested:

- 1) Can the success of different maturation strategies, or of different trait values for egg size and metabolic rate, vary within a population depending on local environmental conditions (Study I)?
  
- 2) Is the relative performance of juveniles with different seasonal timing of emergence influenced by local levels of competition (Study II)?
  
- 3) Does the relationship between egg size and juvenile performance vary spatially or temporally depending on competitive intensity (Study III)?
  
- 4) Is there genetic variation in competitive ability in juvenile salmonids (Study IV)?

## **METHODOLOGICAL APPROACH**

### **Among-stream variation in environmental conditions**

To ensure sufficient among-stream variation in the study concerned with effects of general environmental conditions on phenotype performance (Study I) we selected streams located at a wide range of altitudes. In addition, we planted out either a relatively low or high number of eggs in each stream. All this led to variation among streams with regard to growth conditions, overall mortality and movement away from the nest sites. The level of environmental harshness was quantified for each stream as the average growth or movement distance or as the overall mortality, which is expected to cumulatively represent the influence of a range of un-measured environmental factors.

### **Manipulating competition intensity**

We manipulated levels of competition in the field (Study II and III) by planting out juveniles at either of two spatial configurations, yielding one low and one high density stream reach. In the semi-natural streams (Study IV) and the stream channels (Study II) either a relatively low or high number of juveniles were released, creating channels with either low or high competition intensities. In the tank experiments (Study IV) competition intensity was manipulated by applying different feeding regimes. Juveniles were either given a restricted ration of monopolizable food (high competition) or feed to excess (low competition).

### **Performance proxies**

Three performance proxies were used in this thesis: movement (Study I, II and IV), growth (Study I, II, III and IV) and apparent survival (Study I, II, and III). Movement at early stages is frequently considered a result of territorial individuals displacing subordinates that do not manage to hold territories. Being displaced has also been linked to high mortality (Elliott, 1994). In the semi-natural streams, an individual was classified as a mover if it was caught at the trap outlet. In natural streams we used the absolute distance away from the nest site where a juvenile was captured as a measure of movement. Rapid growth can be advantageous because a large body size may increase the prospects of juvenile survival in stream salmonids (e.g. Einum & Fleming, 2000; Biro et al., 2004; Finstad et al., 2004, but see Hendry et al., 2003; Carlson et al., 2008). Growth rate and body size may also influence traits important for fitness, e.g. parr maturation and size and age at smoltification (e.g. Forseth et al., 1999; Pichè et al., 2008; Paez et al., 2010). Recapture rates were used as a proxy for survival.

## **KEY RESULTS**

### **Phenotype performance depends on local environmental conditions (Study I)**

To assess whether the success of different phenotypes can be shaped by local environmental conditions, we stocked Atlantic salmon eggs from 10 different families across 10 tributaries within a single watershed. Parental age differed among the families (1 sea-winter vs. multi-sea-winter) as did mean trait values for egg metabolism and mass. The tributaries were sampled and the performance of the resulting juveniles assessed. Relative family performance in terms of growth or movement did not differ significantly among tributaries. However, the relative survival of offspring from the two parental age-classes was found to depend on environmental conditions. Specifically, multi-sea-winter offspring had a survival advantage compared to one-sea-winter offspring when the overall mortality in a tributary was high. There was also variation among the tributaries in the manner in which survival was related to mean family egg mass and metabolic rate. The relationship between egg mass and apparent survival changed from being positive in tributaries with high overall mortality to neutral in tributaries where it was low. For egg metabolic rate, however, the relationship was positive in tributaries with low overall mortality and negative when the mortality was high. These results suggest that within a population variation in environmental conditions can shape the relationship between a phenotype and performance.

### **Effects of emergence timing on performance depends on spatial levels of competition (Study II)**

In this study we tested whether local levels of competition can influence the performance of juveniles with different emergence timing. This was done by manipulating the timing of emergence of Atlantic salmon juveniles, resulting in offspring emerging early, normal and late. We subjected these juveniles to either high or low conspecific densities, under both controlled environments (stream channels) and in the wild, and recorded their performance. Even though the early group emerged under conditions expected to be highly sub-optimal, they had the overall highest survival and largest final body size in the wild. The effect on survival was strongest at high density where the early emerging offspring had significantly higher survival than both normal and late emergers. At low density, survival did not differ significantly between early and normal offspring, but both early and normal emergers had significantly higher survival than late ones. In the stream channels, the early offspring outperformed the later ones when density was high, whereas at low density there was no significant difference in survival among the emergence groups. Furthermore, the relative performance of the different groups was not sensitive to water discharge regimes in semi-



natural streams (temporally stable vs. fluctuating). These results suggest that timing of hatching/birth relative to each other may be more important for offspring success than emerging under optimal conditions in species like Atlantic salmon, particularly when juvenile densities, and thus competitive intensities, are high.

### **Performance effects of egg size varies spatially and temporally with competitive regime (Study III)**

Offspring size is a trait which is commonly strongly linked to competitive ability (e.g. Marshall et al., 2006). Thus, offspring size performance patterns may be expected to depend on early juvenile competitive regimes. These may possibly be shaped both by spatial heterogeneity in local densities and temporal fluctuations in densities due to variable seasonal timing of reproduction. In this study we simultaneously manipulated the spatial distribution and the timing of emergence of Atlantic salmon juveniles. To test for influences of egg size on offspring performance we used recapture data and family assignments. An overall positive correlation between egg size and final body mass was revealed. We did, however, not find any effect on growth rates. More importantly, the effect of mean family egg size on juvenile survival depended both on density and emergence timing. Specifically, there was only a survival advantage of large egg size at high density and when competition occurred among juveniles emerging at a similar time. Thus, the relationship between egg size and juvenile performance can depend on competitive intensity and can vary both temporally and spatially within one season.

### **Genetic variation in the response to competition (Study IV)**

We tested whether spatial variation in population density can influence selection pressures by recording effects of competition intensities on performance (growth and dispersal) of juveniles from nine brown trout families. This was done in both tank experiments and semi-natural streams using juveniles of an age where maternal effects were expected to be weak (maternal effects are generally assumed to be limited to the period after hatching in fishes, Heath & Blouw, 1998). The families differed consistently with regard to both growth and dispersal, which indicates genetic variation in these traits. However, family origin and level of competition did not interact significantly in either of the experimental set-ups. Hence, we found no variation in the response to competition among the families. Yet, studies of maternal effects in salmonid fishes have shown certain trait values to be particularly favourable under high levels of competition (Hutchings, 1991; Einum & Fleming, 2000). It would therefore be surprising if offspring genetics in general plays no role in determining their response to

competition. One possible explanation to these results is that the wild trout population which our population originate from might have evolved under ecological conditions with limited spatial variation in levels of early-life competition (e.g. large and highly fecund adults breed within restricted areas).

## DISCUSSION

The finding that relative phenotype performance (i.e. apparent survival) varied across tributaries depending on overall local environmental conditions (stream harshness) suggests that selection pressures varied spatially within the geographic range of this population (Study I). Moreover, since the relative survival of juveniles with different phenotypes varied temporally and spatially with the levels of conspecific density (Study II and III), population density likely has an important role in shaping the adaptive landscape. Thus, my research has demonstrated that spatial and temporal variation in density is likely to result in variable patterns of selection. Given genetically based phenotypic variation, this provides support for the hypothesis that spatial and temporal variation in selection pressures can contribute to conserve within-population genetic variation in fitness-related traits (as proposed by e.g. Levene, 1953; Bulmer 1971; Gillespie & Turelli, 1989; Ellner & Hairston, 1994).

Even though this thesis highlights the potential for conspecific density to shape selection patterns, the results were not entirely as predicted. We did, for instance, not find genotype differences in the response (movement rate and growth) to competition among brown trout parr in tanks and semi-natural streams (Study IV). One possible explanation to this can be that the fish used in this specific study came from a population with stable spatio-temporal selection pressures for competitive ability, and thus no variation existed. In addition, in Study I there was a lack of interactions between environmental conditions (stream harshness) and egg metabolic rate and egg size on movement, and of egg metabolic rate on growth. This may be due to the fish re-distributing themselves after the initial period of high mortality (Einum et al., 2006). Hence, the resulting density gradients around the nest sites (generally high close to a nest site and declining with distance away from it, e.g. Einum et al., 2008a; Foldvik et al., 2010) may have counter-balanced the effects of other environmental conditions. Finally, the absence of an effect of initial density on growth rate in Study II and III could have been caused by a period of high mortality in the high density stream decreasing the difference in density in comparison to the low density stream.

The effect and direction of environmental harshness and density on the apparent survival of different phenotypes also differed among the fitness-related traits that I measured. First, Study I indicated that selection for delayed age at maturation increased with natal environmental harshness. Selection patterns for egg size and metabolic rate were also suggested to depend on

environmental harshness. This shows that environmental conditions for juveniles in freshwater, may have variable effects on the evolution of fitness-related traits in salmonids. Second, the finding that juvenile density can be an important factor shaping phenotype selection patterns (Study II and III) is according to density-dependent selection theory (e.g. Einum et al., 2008b) and points to the possibility for population density to act as a link between population dynamics and evolution. Thus, a decrease in population abundance may lead to decreased juvenile competition resulting in relaxed selection for traits associated with competitive ability, such as large egg size and early emergence timing. Hence, human interference, whether non-selective, or selective in themselves, leading to decreased population abundances (e.g. exploitation or environmental disturbance) may have secondary evolutionary consequences.

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# **STUDY I**

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## **STUDY II**

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## **STUDY III**

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## **STUDY IV**

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**Doctoral theses in Biology**  
**Norwegian University of Science and Technology**  
**Department of Biology**

<b>Year</b>	<b>Name</b>	<b>Degree</b>	<b>Title</b>
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos Zoology	Breeding events of birds in relation to spring temperature and environmental phenology
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i>
1982	Dag Dolmen	Dr. philos Zoology	Life aspects of two sympatric species of newts ( <i>Triturus, Amphibia</i> ) in Norway, with special emphasis on their ecological niche segregation
1984	Eivin Røskaft	Dr. philos Zoology	Sociobiological studies of the rook <i>Corvus frugilegus</i>
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos Zoology	Biochemical genetic studies in fish
1985	John Solem	Dr. philos Zoology	Taxonomy, distribution and ecology of caddisflies ( <i>Trichoptera</i> ) in the Dovrefjell mountains
1985	Randi E. Reinertsen	Dr. philos Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds
1986	Bernt-Erik Sæther	Dr. philos Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach
1986	Torleif Holthe	Dr. philos Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna
1987	Helene Lampe	Dr. scient Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires
1987	Olav Hogstad	Dr. philos Zoology	Winter survival strategies of the Willow tit <i>Parus montanus</i>
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway

1987 Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i>
1987 Bjørn Åge Tømmerås	Dr. scient. Zoolog	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction
1988 Hans Christian Pedersen	Dr. philos Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care
1988 Tor G. Heggberget	Dr. philos Zoology	Reproduction in Atlantic Salmon ( <i>Salmo salar</i> ): Aspects of spawning, incubation, early life history and population structure
1988 Marianne V. Nielsen	Dr. scient Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels ( <i>Mytilus edulis</i> )
1988 Ole Kristian Berg	Dr. scient Zoology	The formation of landlocked Atlantic salmon ( <i>Salmo salar</i> L.)
1989 John W. Jensen	Dr. philos Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth
1989 Helga J. Vivås	Dr. scient Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose <i>Alces alces</i>
1989 Reidar Andersen	Dr. scient Zoology	Interactions between a generalist herbivore, the moose <i>Alces alces</i> , and its winter food resources: a study of behavioural variation
1989 Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture
1990 Bengt Finstad	Dr. scient Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season
1990 Hege Johannesen	Dr. scient Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung
1990 Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990 Arne Johan Jensen	Dr. philos Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon ( <i>Salmo salar</i> ) and brown trout ( <i>Salmo trutta</i> ): A summary of studies in Norwegian streams
1990 Tor Jørgen Almaas	Dr. scient Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues
1990 Magne Husby	Dr. scient Zoology	Breeding strategies in birds: Experiments with the Magpie <i>Pica pica</i>
1991 Tor Kvam	Dr. scient Zoology	Population biology of the European lynx ( <i>Lynx lynx</i> ) in Norway
1991 Jan Henning L'Abée Lund	Dr. philos Zoology	Reproductive biology in freshwater fish, brown trout <i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> in particular
1991 Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991 Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991 Trond Nordtug	Dr. scient Zoology	Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods

1991 Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991 Odd Terje Sandlund	Dr. philos Zoology	The dynamics of habitat use in the salmonid genera <i>Coregonus</i> and <i>Salvelinus</i> : Ontogenic niche shifts and polymorphism
1991 Nina Jonsson	Dr. philos	Aspects of migration and spawning in salmonids
1991 Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992 Torgrim Breiehagen	Dr. scient Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher
1992 Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy ( <i>Phleum pratense</i> L.)
1992 Tycho Anker-Nilssen	Dr. scient Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i>
1992 Bjørn Munro Jenssen	Dr. philos Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks
1992 Arne Vollan Aarset	Dr. philos Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993 Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O <sup>6</sup> -methylguanine-DNA methyltransferase in mammalian cells
1993 Tor Fredrik Næsje	Dr. scient Zoology	Habitat shifts in coregonids.
1993 Yngvar Asbjørn Olsen	Dr. scient Zoology	Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993 Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993 Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993 Thrine L. M. Heggberget	Dr. scient Zoology	Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> .
1993 Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993 Kåre Haugan	Dr. scient Botany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994 Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe ( <i>Gallinago media</i> ): Male mating success and female behaviour at the lek
1994 Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994 Nils Røv	Dr. scient Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i>
1994 Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry ( <i>Rubus idaeus</i> L.)
1994 Inga Elise Bruteig	Dr. scient Botany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses



1994 Morten Bakken	Dr. scient Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i>
1994 Arne Moksnes	Dr. philos Zoology	Host adaptations towards brood parasitism by the Cuckoo
1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply
1994 Torbjørn Forseth	Dr. scient Zoology	Bioenergetics in ecological and life history studies of fishes.
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions
1995 Hanne Christensen	Dr. scient Zoology	Determinants of Otter <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i>
1995 Svein Håkon Lorentsen	Dr. scient Zoology	Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition
1995 Chris Jørgen Jensen	Dr. scient Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport
1995 Vidar Moen	Dr. scient Zoology	Distribution patterns and adaptations to light in newly introduced populations of <i>Mysis relicta</i> and constraints on Cladoceran and Char populations
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae
1996 Ola Ugedal	Dr. scient Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjörg Einarsdóttir	Dr. scient Zoology	Production of Atlantic salmon ( <i>Salmo salar</i> ) and Arctic charr ( <i>Salvelinus alpinus</i> ): A study of some physiological and immunological responses to rearing routines
1996 Christina M. S. Pereira	Dr. scient Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation
1996 Jan Fredrik Børseth	Dr. scient Zoology	The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics
1996 Gunnar Henriksen	Dr. scient Zoology	Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region
1997 Gunvor Øie	Dr. scient Bothany	Eevaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture

1997 Per Gustav Thingstad	Dr. scient. Zoology	Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher
1997 Torgeir Nygård	Dr. scient Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitor
1997 Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper <i>Cinclus cinclus</i> in southern Norway
1997 Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil ( <i>Hylobius abietis</i> ), analysed by gas chromatography linked to electrophysiology and to mass spectrometry
1997 Rolv Lundheim	Dr. scient Zoology	Adaptive and incidental biological ice nucleators
1997 Arild Magne Landa	Dr. scient Zoology	Wolverines in Scandinavia: ecology, sheep depredation and conservation
1997 Kåre Magne Nielsen	Dr. scient Botany	An evolution of possible horizontal gene transfer from plants to soil bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i>
1997 Jarle Tufto	Dr. scient Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997 Trygve Hesthagen	Dr. philos Zoology	Population responses of Arctic charr ( <i>Salvelinus alpinus</i> (L.)) and brown trout ( <i>Salmo trutta</i> L.) to acidification in Norwegian inland waters
1997 Trygve Sigholt	Dr. philos Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon ( <i>Salmo salar</i> ) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997 Jan Østnes	Dr. scient Zoology	Cold sensation in adult and neonate birds
1998 Seethaledsumy Visvalingam	Dr. scient Botany	Influence of environmental factors on myrosinases and myrosinase-binding proteins
1998 Thor Harald Ringsby	Dr. scient Zoology	Variation in space and time: The biology of a House sparrow metapopulation
1998 Erling Johan Solberg	Dr. scient. Zoology	Variation in population dynamics and life history in a Norwegian moose ( <i>Alces alces</i> ) population: consequences of harvesting in a variable environment
1998 Sigurd Mjøen Saastad	Dr. scient Botany	Species delimitation and phylogenetic relationships between the Sphagnum recurvum complex (Bryophyta): genetic variation and phenotypic plasticity
1998 Bjarte Mortensen	Dr. scient Botany	Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro
1998 Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach
1998 Bente Gunnveig Berg	Dr. scient Zoology	Encoding of pheromone information in two related moth species
1999 Kristian Overskaug	Dr. scient Zoology	Behavioural and morphological characteristics in Northern Tawny Owls <i>Strix aluco</i> : An intra- and interspecific comparative approach
1999 Hans Kristen Stenøien	Dr. scient Botany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)

1999 Trond Arnesen	Dr. scient Botany	Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway
1999 Ingvar Stenberg	Dr. scient Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker <i>Dendrocopos leucotos</i>
1999 Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis
1999 Trina Falck Galloway	Dr. scient Zoology	Muscle development and growth in early life stages of the Atlantic cod ( <i>Gadus morhua</i> L.) and Halibut ( <i>Hippoglossus hippoglossus</i> L.)
1999 Marianne Giæver	Dr. scient Zoology	Population genetic studies in three gadoid species: blue whiting ( <i>Micromisistius poutassou</i> ), haddock ( <i>Melanogrammus aeglefinus</i> ) and cod ( <i>Gadus morhua</i> ) in the North-East Atlantic
1999 Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lokeus</i>
1999 Ingrid Bysveen Mjølnerød	Dr. scient Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon ( <i>Salmo salar</i> ) revealed by molecular genetic techniques
1999 Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces
1999 Stein-Are Sæther	Dr. philos Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999 Katrine Wangen Rustad	Dr. scient Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999 Per Terje Smiseth	Dr. scient Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat ( <i>Luscinia s. svecica</i> )
1999 Gunnbjørn Bremset	Dr. scient Zoology	Young Atlantic salmon ( <i>Salmo salar</i> L.) and Brown trout ( <i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999 Frode Ødegaard	Dr. scient Zoology	Host spesificity as parameter in estimates of arthropod species richness
1999 Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000 Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000 Ingar Jostein Øien	Dr. scient Zoology	The Cuckoo ( <i>Cuculus canorus</i> ) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000 Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000 Sigbjørn Stokke	Dr. scient Zoology	Sexual segregation in the African elephant ( <i>Loxodonta africana</i> )
2000 Odd A. Gulseth	Dr. philos Zoology	Seawater tolerance, migratory behaviour and growth of Charr, ( <i>Salvelinus alpinus</i> ), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000 Pål A. Olsvik	Dr. scient Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout ( <i>Salmo trutta</i> ) in two mining-contaminated rivers in Central Norway

2000 Sigurd Einum	Dr. scient Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001 Jan Ove Evjemo	Dr. scient Zoology	Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species
2001 Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forest systems
2001 Ingebrigt Uglem	Dr. scient Zoology	Male dimorphism and reproductive biology in corkwing wrasse ( <i>Symphodus melops</i> L.)
2001 Bård Gunnar Stokke	Dr. scient Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002 Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> )
2002 Mariann Sandsund	Dr. scient Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002 Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002 Frank Rosell	Dr. scient Zoology	The function of scent marking in beaver ( <i>Castor fiber</i> )
2002 Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A <sub>2</sub> in Monocytes During Atherosclerosis Development
2002 Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002 Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002 Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002 Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and the Ral GTPase from <i>Drosophila melanogaster</i>
2002 Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003 Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003 Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatus</i> L.
2003 Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003 Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003 Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo ( <i>Syncerus caffer</i> ) in Chobe National Park, Botswana
2003 Marit Stranden	Dr. scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species ( <i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i> )
2003 Kristian Hassel	Dr. scient Biology	Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i>
2003 David Alexander Rae	Dr. scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments
2003 Åsa A Borg	Dr. scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective

2003 Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon ( <i>Salmo Salar</i> L.) parr and smolt
2004 Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004 Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004 Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i>
2004 Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004 Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species ( <i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i> )
2004 Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004 Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004 Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming
2004 Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry ( <i>Fragaria x ananassa</i> ): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i>
2004 Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005 Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005 Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005 Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005 Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005 Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005 Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal ( <i>Halichoerus grypus</i> ) pups and their impact on plasma thyroid hormone and vitamin A concentrations
2005 Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005 Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005 Åslaug Viken	ph.d Biology	Implications of mate choice for the management of small populations
2005 Ariaya Hymete Sahle Dingle	ph.d Biology	Investigation of the biological activities and chemical constituents of selected <i>Echinops</i> spp. growing in Ethiopia
2005 Anders Gravbrot Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge

2005 Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005 Kjartan Østbye	Dr.scient Biology	The European whitefish <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation
2006 Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutants (POPs) in seabirds Retinoids and $\alpha$ -tocopherol – potential biomarkers of POPs in birds?
2006 Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006 Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on <i>Calanus finmarchicus</i>
2006 Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006 Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006 Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity
2006 Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout ( <i>Salmo trutta</i> ) from mining contaminated rivers in Central Norway
2006 Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006 Jafari R Kideghesho	ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006 Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish <i>Syngnathus typhle</i> : when and how to invest in reproduction
2006 Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006 Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006 P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007 Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle <i>Tenebrio molitor</i> - a study on possible competition for the semi-essential amino acid cysteine
2007 Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007 Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007 Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth <i>Heliothis virescens</i>
2007 Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, ( <i>Mamestra brassicae</i> L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007 Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes

2007 Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007 Vedasto Gabriel Ndiralema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007 Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007 Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007 Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod ( <i>Gadus morhua</i> L.) Focus on formulated diets and early weaning
2007 Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008 Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> ) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008 Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008 Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich ( <i>Struthio camelus massaicus</i> ) in the Serengeti Ecosystem, Tanzania
2008 Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, ( <i>Taeniopygia guttata</i> )
2008 Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008 Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod ( <i>Gadus morhua</i> ): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008 Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008 Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008 Anna Kusnierczyk	ph.d Biology	<i>Arabidopsis thaliana</i> Responses to Aphid Infestation
2008 Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008 John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008 Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in <i>Cyclamen persicum</i> . Biological investigations and educational aspects of cloning
2008 Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes

2008 Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009 Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease
2009 Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth <i>Heliothis virescens</i> : Physiological and morphological characterisation, and integration into a standard brain atlas
2009 Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009 Johan Reinert Vikan	ph.d Biology	Coevolutionary interactions between common cuckoos <i>Cuculus canorus</i> and <i>Fringilla</i> finches
2009 Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009 Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009 Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions ( <i>Panthera leo</i> ) in Tanzania
2010 Huy Quang Nguyen	ph.d Biology	Egg characteristics and development of larval digestive function of cobia ( <i>Rachycentron canadum</i> ) in response to dietary treatments -Focus on formulated diets
2010 Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010 Sverre Lundemo	ph.d Biology	Molecular studies of genetic structuring and demography in <i>Arabidopsis</i> from Northern Europe
2010 Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania
2010 Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis
2010 Anders Lyngstad	ph.d Biology	Population Ecology of <i>Eriophorum latifolium</i> , a Clonal Species in Rich Fen Vegetation
2010 Hilde Færevik	ph.d Biology	Impact of protective clothing on thermal and cognitive responses
2010 Ingerid Brønne Arbo	ph.d Medical technology	Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans
2010 Yngvild Vindenes	ph.d Biology	Stochastic modeling of finite populations with individual heterogeneity in vital parameters
2010 Hans-Richard Brattbakk	ph.d Medical technology	The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits
2011 Geir Hysing Bolstad	ph.d Biology	Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy
2011 Karen de Jong	ph.d Biology	Operational sex ratio and reproductive behaviour in the two-spotted goby ( <i>Gobiusculus flavescens</i> )
2011 Ann-Iren Kittang	ph.d Biology	<i>Arabidopsis thaliana</i> L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS:– The science of space experiment integration and adaptation to simulated microgravity



2011 Aline Magdalena Lee	ph.d Biology	Stochastic modeling of mating systems and their effect on population dynamics and genetics
2011 Christopher Gravingen Sørmo	ph.d Biology	Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in <i>Arabidopsis thaliana</i>

