AQUALIENS

Aquatic alien species - where and why will they pose a threat to the ecosystem functions and economy?

A research programme aimed at increasing our knowledge on how to assess the risks posed by introduced aquatic species and their impact on ecosystems and economy.

REVISED EDITION
2002-04-09

CONTENTS

SUMMARY

Introductions of alien species have been listed as one of the major global human influences on biodiversity and have in several cases had huge economic impact. The aquatic ecosystems imply better chances of survival and dispersal of introduced species and are more difficult to monitor than terrestrial ecosystems thus high-lightening them from a risk perspective.

The Programme will focus on:

i) Evaluating the risks on the ecosystem level for organisms having specific functions or attributes;
ii) Identifying the types of aquatic ecosystems that are most vulnerable to introductions and which kind of organism will pose the largest threat in different environments;
iii) Tools for risk analyses and assessments;
iv) Economic analyses of efficient risk management.

The emphasis of the entire Programme will be on risks at the ecosystem level to elucidate general patterns of success or failure in marine, brackish and freshwater ecosystems. Four different types of organisms will be studied: Macroalgae, vascular plants, invertebrates and fish. Those will be studied for patterns of species characteristics such as those facilitating dispersal, settling, establishment and reproduction. Patterns of site characteristics will include heterogeneity in space and time, biodiversity of recipients in comparison to non-invaded areas as well as vector influences. Ecosystem impact encompasses both ecosystem functions and services as well as utilization of our waters. The former will also be analysed from an economic perspective and utilization will emphasize aquaculture and the economic effects coupled to the spread of the American signal crayfish and outbreaks of crayfish plague. In cooperation with the MARBIPP programme potential effects of introduced species on the biodiversity of marine and brackish areas will be evaluated.

We want to stress that no field experiments will be carried out within the Programme with introduced species, unless they already are common in an area. (This must also apply to the open call).

Dissemination of the results will also emphasize the spread of information to different target groups and on different levels as an important component needed to decrease the dispersal of introduced species.

The Programme is planned to run for five years with a total budget of 30 million SEK. It will involve at least 10 senior scientists and 5+1? Ph.D. students and 3 Postdoc positions during the Programme period.

The Programme has been outlined by the

PLANNING COMMITTEE:

Prof. Inger Wallentinus, Marin botanik, Göteborgs univ., Inger.Wallentinus@marbot.gu.se

Docent Eva Willén, Miljöanalys, SLU, Uppsala, Eva.Willen@ma.slu.se

Prof. Magnus Appelberg, Kustvattenlaboratoriet, FiV Magnus.Appelberg@fiskeriverket.se

Prof. Lars-Ove Eriksson, Vattenbruk, SLU, Umeå univ., Lars-Ove.Eriksson@vabr.slu.se

Prof. Göran Bengtsson, Kemisk ekologi, Lunds univ., Goran.Bengtsson@ekol.lu.se

Prof. Ing-Marie Gren, Naturresurs- och miljöekonomi, SLU Uppsala, Ing-Marie.Gren@ekon.slu.se

Melanie Josefsson, Naturvårdsverket, SLU, Uppsala, Melanie.Josefsson@snv.slu.se

The Programme has been reviewed by a

REFERENCE GROUP:

Erik Sparrevik, Fiskeriverket, Göteborg Erik.Sparrevik@fiskeriverket.se

Johan Gråberg, Sjöfartsverket, Norrköping johan.graberg@sjofartsverket.se

Gunnar Aneer, Länsstyrelsen, Stockholm Öregrund, Gunnar.Aneer@ab.lst.se

Anders Kjellberg, Länsstyrelsen, Kalmar Anders.Kjellberg@h.lst.se

Kristina Jansson, WWF, Ulriksdal kristina.jansson@wwf.se

Comments were also received from:

Ingrid Jansson, NV. Elin Linnarsson, Nl
Jan Christiansson, Rp, Sofia Ahlroth, He, all at the SEPA

BACKGROUND

Introductions of species into new environments are probably as old as man has been travelling to other areas. However, the speed of today's transports increases the chances of survival of accidentally introduced species and makes it easier to perform deliberate imports (legal or illegal). In 1997 the SEPA published a policy document on the introduction and spread of non-native and genetically modified organisms, presenting the risks etc., as well as listing laws, international committments, directives and guidelines and concluded that a precautionary approach should be taken towards deliberate introductions of alien species, populations and genetically modified organisms. SEPA's current "Environmental Quality Objectives" contain objectives that specify that "alien species and GMOs that can threaten biodiversity are not introduced" for both "Sustainable lakes and watercourses" and "A balanced marine environment, sustainable areas and archipelagos". Introduced species were also discussed as one of the major human influences on biodiversity in the UNEP's Global Biodiversity Assessment (McNeely et al. 1995).

Aquatic environments differ from terrestrial ones in several respects concerning successful establishment of non-native species, such as more benign winter and less extreme summer climates facilitating survival; easier dispersal of propagules, larvae and even adults with currents; but not the least by the aquatic environments being much more difficult to monitor. This further dispersal is not just by means of natural vectors such as currents etc., but in many cases has been much amplified by human activities such as discharges of ballast water and sediments, transports of small pleasure boats on land to other coastal areas or to inland waters with plenty of live organisms on its hull or anchor lines etc., the usage of live baits or live plants used for packing of baits or transports of shellfish and then dumped, losses of organisms from aquaculture facilities or aquaria etc. Furthermore, it is almost hopeless to find an efficient method to eradicate species once they have become established in new waters. In aquatic environments we are often faced with the impact at a very late stage when the species might have been there for several generations and already spread its offspring to other areas.

Introductions of alien species can often be considered as "biological contamination" but may also in other cases, when constituting only a small part of the community, contribute to an increased biodiversity measured as number of species. Exotics often negatively affect natives or interfere with ecosystem function through competition, predation or ecological cascading effects. Without protection, the number of introduced aquatic species in Europe will continue to increase. For example, over the last 100 years, on average, every 7 months a new marine species was found (S. Gollasch pers. comm.). In North America new records of introduced species are even more frequent. The area which is supposed to have the highest numbers of non-native species in the world, the San Francisco Bay, today has more than 250 exotic species (e.g. Cohen & Carlton 1995). In total 74 of those listed species are believed to have been introduced by ballast water of ships (Carlton et al. 1995). There are, however, also cases of species known to be invasive in other areas and which can survive in European coastal waters, which have not or very sparsely become established (e.g. the blue crab *Callinectes sapidus*, the horse shoe crab *Limolus polyphemus*). One may also ask why is the North Pacific Seastar, being such a pest in Tasmania, not found in European waters (so far), or why different crab species of the genus *Hemigrapsus* have invaded the North American and European coasts, respectively? Thus there are huge number of questions around introduced species still waiting for answers, too many to be covered by this Programme alone. Internationally, the trend now is shifting from previously more descriptive studies to those trying to elucidate patterns and processes influencing the establishments and invasiveness of exotic species (e.g. Ruiz et al. 2000).

Legal actions generally cannot totally stop the dispersal of alien species, only reduce the risks. Thus precautionary actions must be taken to reduce the risk that the most troublesome species become established. However, to be able to optimize precautionary actions we have to know what effects can be expected and which areas most probably are at risk. Several international organisations have been involved in recommending, suggesting and implementing new guidelines, directives or laws to reduce the impact of alien marine species (e.g. IMO, ICES, EIFAC, GESAMP, OSPAR, HELCOM etc.) as well as governments (e.g. France and Spain for the tropical green alga *Caulerpa taxifolia* and outside Europe, especially regarding ballast water the US, Canada, Australia and Israel). However, to our knowledge no such mandatory guidelines or directives exist which concern the ecological impact of all alien aquatic species.

Negative economic effects caused by introduced species are for instance found among: aquaculture (e.g. introduced parasites, predators, harmful algae, fouling organisms), fishery (e.g. predation, harmful algal blooms), fouling on ships and other submersed structures (e.g. water intakes, aquaculture support systems), and recreational use (e.g. clogging of inland waters by vascular submersed plants, mass accumulations of macroalgae or mollusc shells on shores and beaches). In some cases substantial costs are incurred leading to economic losses (e.g. not being able to harvest, closure of industrial plants etc.). Furthermore, habitat modification due to erosion, fouling or dense vegetation on barren areas may restructure a complete eco-system. In some cases such costs have been estimated. During the last mass occurrence of the introduced ship worm *Teredo navalis* along the western Baltic shores wooden installations in ports and marinas were damaged. The annual costs for repair work were estimated to be 15 million US dollars (Gollasch & Rosenthal 2000). The invasion of the ctenophore *Mnemiopsis* in the Black Sea has been calculated to a reduction in fishery harvest corresponding to 30-40 million US dollars a year (Anon. 1997). One single company in Hamburg for one single year had to spend about 1.1 million US dollars to clean pipes and water intakes from the zebra mussels (Gollash & Rosenthal 1999) and in the Great Lakes area such costs have accumulated to 520 million US dollar for a period of 15 years (US Coast Guard 1997). Legal proceedings are seldom taken, but in Norway environmental authorities have been forced by court to pay 460 000 USD for releasing *Mysis relicta* in a lake with charr (Sandlund & Bongaard 2000).

However, one should not forget the profits made from all introduced species used for instance in aquaculture (e.g. the huge harvests of farmed introduced salmonid fish, that almost all “French” oysters or in fact Japanese) or for stock enhancements.

INTRODUCTION TO THE SCIENTIFIC APPROACH USED IN THE PROGRAMME

The dynamics of invasions has been suggested to follow three phases: 1) the entrainment of species in transport pathways and introduction into the environment (**arrival** phase); 2) the **establishment** of the invading species at a single location and the consequence of the growth in numbers of the invading species for other species in the community, through e.g. competition, predation, and parasitism; 3) the spatial **spread** of the invading species from a single location. For each of the phases, some broad generalisations have been suggested to delimit characteristics of the organism and the environment that are useful and quantifiable descriptors of the invasion process.

For the **arrival** phase, the characteristics of the donor region, the numbers of propagules attempting to invade, and the transport modes and speed are important. Regions with similar climates and salinity have a higher potential of successfully exchanging species (e.g. Ricciardi & Rasmussen 1998, Gollasch & Leppäkoski 1999). This is also the reason for the IMO guidelines of offshore exchanges of ballast water to minimize the risk of bringing organisms well suited for the recipient area. However, one should also bear in mind that species may show phenotypic or genotypic adaptations which may have changed their ecophysiology, as seems to be the case with the tropical green alga *Caulerpa taxifolia* in the Mediterranean Sea (suspected to be a polyploid clone from the aquaria industry). Furthermore, regions with growing economies should be considered as potential future donors of exotic species as trade and vector frequency increase. The number of arrivals may be very large, but an invasion may start with few individuals, perhaps between 10 and 20, that either eventually are eliminated in the target environment due to genetic, demographic and environmental stochasticity or may proliferate, especially if capable of asexual reproduction. The propagules may arrive randomly by diffusive transport, such as species having a planktonic phase in their life cycle or those having suitable adaptations to drift even as fertile adults. However, most successful invaders, particularly pest species, use dispersal mechanisms that involve human vectors (aquaculture, boating, shipping, fishery, ornamentals, aquaria trade, scientific experiments etc.). In fact, the global dispersal of marine organisms has been achieved primarily through transoceanic shipping (e.g. Carlton 1989, Carlton & Geller 1993, Ruiz et al. 2000) with around 3000-4000 species on the move each day (J. Carlton pers. comm.) and about one animal per litre of ballast water (Gollasch 1996). For Sweden SEPA and SSPA in 1998 published a document in which it was estimated that around 23 million tonnes of ballast water reach our harbours each year. Altogether a large number of different vectors may be involved in introductions into aquatic environments, but studies on specified vectors are no main issues in the Programme, although vectors will be included when analyzing the risks.

The prospect of **establishment** depends on interactions between the characteristics of the invading species, the community already established, and the area’s physical environment. Ehrlich (1989) suggested that the following variables of the invader are important: number of individuals, sex ratio, physiological status - are individuals mature, pregnant, healthy, acclimated, genetic composition, and behavioural status - experience of individuals, social relationships within group. Much evidence demonstrates that the probability of establishment increases both with the size of the founder population and with the number of invasion attempts. Large body size may also enhance the likelihood of successful establishment because of less harmful predation, enhanced competitive ability, and less variation in population size (Townsend 1996). Especially for a predator such as crabs, the size and behaviour of one species may determine the outcome of interactions with other crab species (Grosholz & Ruiz 1996). Introduced plants also tend to have small seeds and short juvenile periods (Kolar & Lodge 2001). Several authors (e.g. Townsend 1996, Farnham 1997, Gollasch & Leppäkoski 1999) have argued that invading species with wide tolerance limits and a broad habitat range and a polyphagous diet or being opportonists are more likely to survive and reproduce in a receiving habitat. Usually species that are abundant in their native habitats make better invaders than scarce ones (e.g. Williamson & Fitter 1996, Gollasch & Leppäkoski 1999). However, there are also examples of pest species which are not very prominent in their native countries (e.g. the European purple loosestrife *Lythrum salicaria* which is a pest in Canada, the Japanese brown alga *Sargassum muticum* which is very invasive in Europe and in the eastern Pacific).

On the physical/biological environmental side, Ehrlich (1989) considered the following variables: season, weather, size and structure of populations of resource organisms, competitors, predators, parasites, and pathogens. For geographical areas there are still contrasting views on risk areas. Brown (1989) argued that habitats of small size, contrasting markedly with the surrounding matrix, a long history of effective isolation from similar environments (e.g. oceanic islands, insular continents, insular habitats such as lakes and desert springs), and a low diversity of native species tend to be differentially susceptible to invasion. He presented evidence that a large proportion of the species of isolated oceanic islands and other long-isolated environments are invaders. Similarly, Townsend (1996) infered that species-rich communities are more resistant to invasion than species-poor communities. Both views were refuted by Simberloff (1989), who argued that most of the cases of introductions used for the comparison between mainland and island were made in agricultural land, and that the results would be different if pristine habitats were compared. Neither did he accept the view that "disturbed" habitats are more readily invaded than undisturbed, because: 1) "disturbed" habitat often means modified by man, and since they are important to us, they are more carefully studied than pristine habitats and successes more likely to be detected, and 2) opportunity was greater for introductions into man made disturbances since biological control agents were imported into those habitats. Simberloff (1989) also questioned the "rule" that invading exotics tend to be more successful when native species do not occupy similar niches (Brown 1989) mostly from the fact that consistent, measurable, and meaningful measures of "niche breadth" and "specialisation" have not been used. Even today there are different opinions/examples of that a low biodiversity of native species increases the risk of invasions (e.g. Stachowicz et al. 1999) or the risk is higher with a higher diversity (e.g. Levine 2000). The lowest percentage of establishment reviewed by various authors is about 35%, but this is certainly a gross overestimate. Williamson (1989) thought the correct number is around 10%, but focussing on average success may hinder progress in understanding what determines invasion success. The two leading causes of failure to become established are inappropriate climate and predation, but the impact of competition, disease and other factors are probably underestimated because they are more difficult to measure (Lodge 1993).

The **spreading** phase has been examined in many classical case studies. The transition between establishment and spreading is usually smooth and determined by a suite of ecological traits, e.g. reproduction and dispersal that interact in more or less subtle ways. Some modes of expansion are more important than others. For instance, vegetative reproduction is usually the commonest, and often the only method of reproduction amongst those invasive free-floating or submerged aquatic plants which have demonstrated a capacity for adventive spread into new environments as well as for many macroalgae (e.g. Ashton & Mitchell 1989, Maggs & Stegenga 1999, Wallentinus in press). Free-floating invasive aquatic plants and macroalgae have a capacity for extremely rapid vegetative multiplication, an ability to regenerate from relatively small portion of vegetative thallus, a complete or partial independence of sexual reproduction, a growth morphology that results in the development of the largest possible area of photosynthetic tissue, and an independence of substrate conditions and water levels.

What percentage of established exotics have an **impact** on the native community? Such estimates, ranging from 2 to 40% (Lodge 1993), are, like those for colonization success, fraught with uncertainty. Predation and habitat changes are the most often cited mechanisms of impact of exotics on native species. For a predator such as the crab, the size of it may determine the outcome of interactions with other crab species as well as determining the depth to which the crab may forage in soft substrate environments. Grosholz & Ruiz (1996) showed that diet preferences and ecological impacts (e.g. reduction in the abundance of predated molluscs, decline in abundance of a small crab) were qualitatively similar across sites. The habitat usage, size of individual crabs, and rate of spread were more variable among three different invasions. Brown trout, *Salmo trutta,* appeared to exert their greatest effect through predation on young fish and some invertebrates in New Zealand (Townsend 1996). For communities where predators exercise a controlling influence on their prey species, one would expect a community with a single predator to be harder to invade than one with several predator species. This means, that for a given number of prey species, communities with the most species of predator may be the easiest for prey species to invade. The introduction of a predator that feeds high in a food chain and lacks predators of its own is predicted to have a major effect. By reducing the number of grazers and the extent of their grazing, brown trout permitted an increased development of algal biomass through trophical cascading. Crayfish modified their behaviour in the presence of both trout and eels (a native predator), but a significantly greater number of defensive displays of chelae and swimming responses were made towards eels than to trout. Moreover, crayfish were able to use chemical clues to detect eels but not trout. Some studies suggest that only those species that differ sufficiently from species already present are likely to become established (Moulton & Pimm 1986a, 1986b). The view of community organisation encouraged by such studies is that species number and composition are relatively deterministic aspects of communities, and that the success or failure of invaders to establish themselves and to integrate into communities can be predicted *a priori* if enough is known about the invaders and the recipient biota. But whether or not the impact of an introduced species will be felt beyond a single trophic level is at the heart of current debates about the structure of food webs.

PROGRAMME

Organization of the Programme into Work Packages

The Programme will focus on the risk on the ecosystem level and consequences for economy more than on specific species posing a threat or not. The work will be organized in eight interacting Work Packages (WP; Fig. 1) which are described below. Both species that have successfully established and those who have failed will be examined as basis for risk assessment (WP 7). Four different types of organisms will be studied:

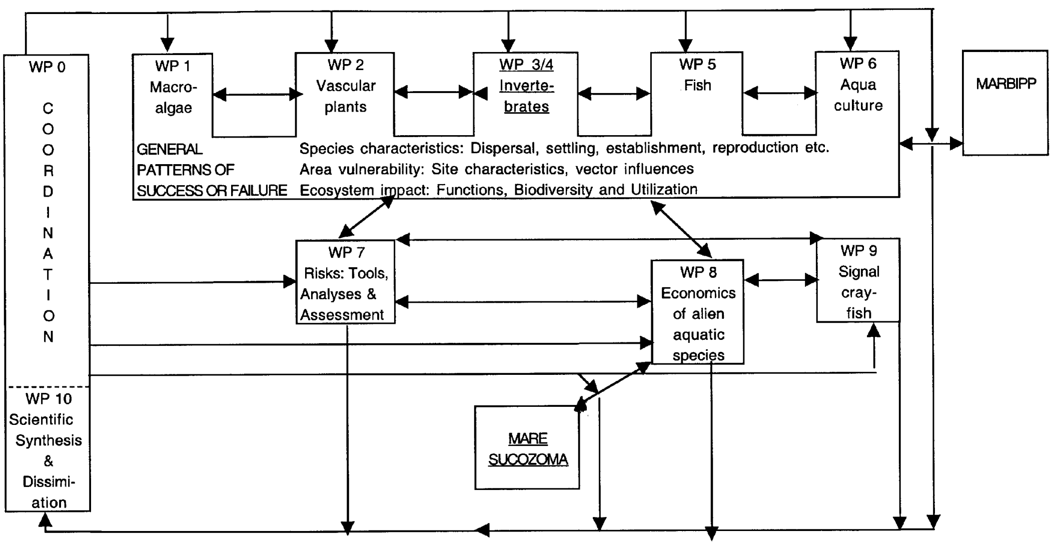

Fig. 1. The Programme structure build up of Work Packages

Macroalgae and brackish-marine macrophytes (WP 1), Vascular freshwater plants (WP 2), Invertebrates (WP 3/4) and Fish in brackish and freshwater areas (WP 5). These different types of organisms will be studied for patterns of species characteristics such as those facilitating dispersal, settling, establishment and reproduction. Patterns of site characteristics will include heterogeneity in space and time, biodiversity of recipients in comparison to non-invaded areas as well as vector influences and will be analyzed for the different types of organisms within each WP and in close cooperation with WP 7 for selected marine, brackish and freshwater areas. Ecosystem impact encompasses both ecosystem functions and services as well as utilization of our waters. The former will also be analysed from an economic perspective (WP 8) and utilization will emphasize aquaculture (WP 6) and the economic effects coupled to the spread of the American signal crayfish and crayfish plague (WP 9) based on existing data. We will cooperate with the programme MARBIPP (financed by SEPA) to estimate the impact of introduced species on biodiversity in marine and brackish waters. Also some parts of other programmes such as MARE and SUCOZOMA (both financed by MISTRA) may be rewarding co-operators.

Due to limitations in economy as well as to the few available scientists, the field of parasites and disease agents could not be included in the Programme. However, the existing data on American signal crayfish and the impact of the parasitic fungus will be used as a case study (WP 9) of economic effects (WP 8) and also provide data for risk analyses (WP 7).

The question of treatment of ballast water is now a very "hot" issue and already a subject to many studies in the US (Leppäkoski et al. in press, J. Carlton pers. comm.) as well as in several ongoing EU projects. The limited budget of AQUALIENS, unfortunately will force us to leave the matter of treating ballast outside, since one Ph.D student may not add much extra to all the studies already going on. However, the proximity of an area to a harbour where ballast water discharges occur, will be incorporated among the geographical risk factors. The question of which test organisms to choose for studying the effects of ballast water treatments is another question which will not be adressed, since we do not consider that task to be in line with the overall objectives of the Programme.

Genetically modified organisms will not be specifically addressed in the Programme. However, many of the functions and attributes listed above as criteria important for risk assessments may also apply to them and, as for new populations of existing species, fitness factors probably are the most important ones, if the species as such is not an introduction. The importance of increased fitness is also implicitly part of the risk model analyses (WP 7). Risk assessments developed for introduced species may thus also be applicable for those organisms.

For Programme management and more on links to other programmes, as well as budget and open calls see below.

Work Package 1. Macroalgae and brackish-marine macrophytes

State of the art

Only seven introduced macroalgae have so far been found along the Swedish coasts of the 113 species introduced in European coastal waters (Wallentinus 1999, in press). However, there are several examples that the ecosystem impact does not correspond to the number of introduced macroalgae, since one single species may more or less monopolize the substratum (for references see Wallentinus in press) in some regions (e.g. the green algae *Caulerpa taxifolia* and *C. racemosa* and the red alga *Womersleyella setacea* in the Mediterranean, the green alga *Codium fragile* and the red alga *Grateloupia doryphora* on the North American east coast). In such cases a single macroalgal species can have severely negative effects on the biodiversity of both other algae and vascular plants as well as on the sessile macrofauna by competition for space, light, nutrients and by hindering the sedimenting suspended particles in the water to reach the suspension- and deposit-feeding macrofauna. If growing on previously barren shores such as on stones and shells on shallow sediment bottoms they may also profoundly change the habitat by affecting water movements and light penetration to the microphytobenthic community (e.g. *Sargassum muticum*). For some Swedish regions *Sargassum muticum* and *Fucus evanescens* may occupy the main part of a zone on the shores, although on our shores mostly not as dominantly as some of the other species mentioned. Other recent introductions such as the red alga *Dasysiphonia*? sp. is spreading south along the Norwegian coast (T. Lein pers. comm.) and may well disperse to Swedish waters. Since only a short time has passed since it was first recorded in Norway, it may not yet have reached its full capacity of interacting with the other ecosystem components nor its final distribution range. As a comparison, 18 introduced macroalgae have been recorded in such a geographically close country as The Netherlands (Wallentinus in press) and by experience we know that many macroalgae recorded in that area later are dispersed by currents or other means to Scandinavia.

There is no information on any macroalgae introduced in freshwater areas in Sweden except for any possible occurrence of *Chara connivens*, which, however, mostly grows in brackish water. This species has been introduced more than hundred years ago by solid ballast and can still be found in the Öregrund archipelago (P. Snoeijs pers. comm.) but is, as many charophytes, a weak competitor and is even noted on the Swedish red list for endangered species.

Of the 203 introduced aquatic and semiaquatic vascular plants in Europe 37 species occur in brackish or marine environments (Wallentinus in press). In Swedish waters they are mainly represented by the freshwater species *Elodea canadensis*, *E. nuttallii*, presumably originating from the aquaria trade or as ornamentals. However, among introduced species recorded elsewehere in Europe some are native in regions with a climate similar to ours (e.g. *Spartina* spp., *Myriophyllum verrucosum*, *Zizannia aquatica*) and known for their weediness.

Objectives and activities

Scientific leader: Prof. Inger Wallentinus, Dept of Marine Botany, Göteborg university, P.O. Box 461, SE 405 30 Göteborg, Sweden. E-mail: Inger.Wallentinus@marbot.gu.se

The project will concentrate on:

1) Patterns based on species characters

a) To seek for patterns of species characters among successfully established macroalgae and higher plants by quantitative ranking of such characters ranked for above all: *i*) dispersal, *ii*) fecundity, *iii*) tolerance of extreme ranges of abiotic variables (desiccation, temperature, salinity, darkness) and *iv*) grazer resistence. Since the number of species introduced in Sweden is quite small this will also include literature data on species introduced and established elsewhere in Europe or European species established on other continents. Special emphasis will be on the importance of banks of propagules and the role of vegetative/asexual reproduction for further dispersal, i.e. only one inocculum plant might be enough for further dispersal, establishing clonal populations (cf. e.g. Chapman 1999, Maggs & Stegenga 1999, Wallentinus 1999). In some cases a true settling phase may not be necessary, since populations can survive lying loose on the seabed (cf. e.g. Perrone & Cecere 1994) or plants are secondarily attached by byssus threads of mussels (both these modes of life also occur among native Baltic seaweeds).

b) To use such patterns of characters (a) for species used in the aquaria trade (especially for species known to have rapid growth or being "aggressive") and aquaculture or being successfully established/nuissant in other countries of similar climate and salinity to list likely future risk species. To find out who are the grazers on those species in their native area, and if few - do similar species exist in Sweden and are they specific in choice of food?

c) To test the importance of propagulae pressure for the most likely risk species (b) (incl. asexual reproduction or large and frequent discharge of reproductive bodies or germlings) or of significantly different growth maxima periods. For WP 7 data from previous studies on the small and large scale distribution of the Japanese brown alga *Sargassum muticum* in Sweden (Johansson 1994, Karlsson & Loo 2000) will be used. Experiments studying dispersal of vegetative small fragments will be tested for introduced species already established on the Swedish west coast. Distribution ranges/rates of dispersal will be compared with invasiveness of the species in question where such data are avilable.

2) Tolerance experiments

To select some of these species (1 b) for experimental laboratory tolerance tests (salinity, temperature, darkness, desiccation), especially on young stages which presumably are more sensitive.

3) Patterns based on site characters

Patterns of site characteristics will include heterogeneity in space and time of importance for establishment such as species richness/biodiversity, disturbance, pollution, habitat fragmentation, geomorphology, as well as vector influences (proximity to harbours and shipyards where ballast is discharged, proximity to marine research stations, aquaculture sites using imported shellfish, fishing harbours visited by boats fishing in other geographical areas etc.) to assess geographical risk areas. Main currents coming from other areas may also have to be included. Patterns of site characteristics will be tested by using multivariate or other analyses.

4) Processes and ecosystem impact

Impact on ecosystem function will be documented for some areas where species have established. Furthermore, processes of importance for the function of the ecosystem will be analyzed by modelling of resource utilization as a basis for co-occurrence with most likely native plants. This will also include ranking the species preference for growing on artificial surfaces which affects both aquaculture structures and shells of molluscs as well as fouling on ships. The risk that some of these algae or vascular plants may pose a threat to the biodiversity of the marine communities will be assessed in co-opperation with MARBIPP, where the emphasis will be on the ecosystem function and structural diversity.

In cooperation with WP 7 develop models for selected species to simulate ecosystem impact, and population dynamic scenarios (incl. colonization).

It may be less easy to find examples of failed introductions among macroalgae, which are not due to too large climatic differences, since there are only a few published studies of intentional introductions which have failed and in most cases those were interupted before the plants became fertile.

Realisation of activities and deliverables

Literature data will be compiled during the first three months (some literature is already surveyed) by the scientific leader of the project, who will also select species to study further.
The Ph.D student will start with the first experimental tolerance tests during year 1, which will continue during year 2.
During year 1-2 various areas with established introduced macroalgae will be analysed for the characters listed above (mainly from literature with some complementary field studies) by the scientific leader. This phase will also include cooperation with the MARBIPP Programme .
During year 3 the Ph.D student will test vegetative dispersal of one introduced and established macroalgae and start to work with population dynamic scenarios which will continue during year 4.
Analyses of site characteristics will be started in year 2 (spring-autumn) and continue during the same periods year 3-4.
Ecosystem impact analyses will started by the scientific leader during the end of year 3 and be continued during year 4, partly in parallel to the study of site characteristics, and summarized during the beginning of year 5.

Work Package 2. Vascular freshwater plants

State of the art

Among 529 introduced vascular plants in European aquatic environments 69 are entirely linked to the water habitat as emergent, submergent or floating-leaved life-forms. Among those are 70% characterized as weedy and a majority (32 spp.) even classified as serious weeds (Wallentinus in press). There are altogether 113 non-indigenous species recorded from aquatic habitats in Sweden. Among those are eight established species considered as genuine aquatic: two submerged species (*Elodea canadensis, Elodea nuttallii*), three emergent species (*Acorus calamus, Iris versicolor, Sarracenia purpurea*), and three with floating leaves (*Nymphoides peltata, Sagittaria latifolia, Cabomba caroliniana*) (Josefsson 1999, Wallentinus in press). Two of the genuine aquatic species (*Acorus calamus, Elodea nuttallii*) are considered as weedy and two are classified as serious weeds (*Elodea canadensis, Nymphoides peltata*), while *Sarracenia* and *Cabomba* only have local distribution in Sweden, the latter species, however, being a serious weed in other countries. There are also four casual aquatic species and almost twenty other semiaquatic species (Wallentinus in press). Three of the four weedy species have no sexual reproduction and seed formation, which may occur for *Nymphoides*, is not a primary mean of reproduction in Sweden. Vegetative dispersal by rhizome fragments, or fragments of vegetative parts of the stem is the most common mode of reproduction. The species survive harsh environmental conditions by various kinds of buds (i.e. turions).

Short presentations of species with particular invasive characters in Sweden:
Elodea canadensis - the Canadian waterweed - is the species with the widest distribution. It originates from the north American continent and has spread to Europe during the 19th century. It was first recorded in the late 1870s in central Sweden and is now widely spread in meso-eutrophic alkaline lakes with fine-grained sediments in southern and central Sweden, as well as in the coastal lowlands in the northern part of the country (Mossberg et al. 1992). Its invasive character is well documented in many other European countries (Lagerberg 1956, Wallentinus in press). The main vector for its first introduction in many countries is the aquaria-trade, but it has also spread from ornamental ponds (op. cit.). Its further dispersal is facilitated by

vegetative propagation, by an easy transport of fragments due to wind and wave actions, and to human boating and fishing activities. Birds may also be a probable vector. *Elodea* species begin to grow from winter-dormant apices (buds) in the spring. Such dormant apices are produced in large numbers in the autumn just before the winter-season (up to 5000 have been recorded from 1 m^2 of sediment surface; Bowmer et al. 1984). The apices are dispersed through wind and wave-action within a lake and downstreams with running waters. Floating winter-buds start to grow when they reach the bottom layers. Good water transparency is an important environmental factor mentioned in connection with *E. canadensis*. Bicarbonate as a carbon source and supply of iron in reduced form are other prerequisites (Spicer & Catling 1988). *E. canadensis* acts as a nutrient sink because it assimilates phosphorus from the water while growing. During mineralization of large biomasses of *Elodea* considerable amounts of phosphorus are released to the water, favouring the growth of littoral and pelagic algae.

Elodea nuttallii - the Nuttall waterweed - also originates from North America and has during the 1990s invaded many waters in central Sweden and was recorded earlier in Denmark, where its occurrence still is unsufficiently known. It seems to have the same preference for hardwater lakes as *E. canadensis*, but its distribution is still restricted in Sweden. However, it has reached several sites in Lake Mälaren and occurs there in mass abundance and is a competitor to the Canadian waterweed (Anderberg 1992, Wallin 2000). There are indications that *E. nuttallii* has a competitive advantage between the two at high concentrations of NH_4-N (Dendène et al. 1993). *E. nuttallii* as well as *E. canadensis* have the potential to develop into dense submerged beds, which prevent the use of water for recreational and professional purposes. There is a need to investigate the vectors of dispersal and the differences between this recently introduced species and the Canadian waterweed both for competition and further spreading.

The floating-leaved invasive species *Nymphoides peltata* – the Yellow floating heart - another of the serious weeds, occurs in some twenty sites in southern and central Sweden´s lowland areas (Mossberg et al. 1992). Its weedy character is especially annoying in the entire water system of the River Arboga ån which drains to Lake Mälaren, and outside the town of Kungsör in the western part of Lake Mälaren (Josefsson & Andersson 2001) as well as in a number of lakes within the drainage area of Motala Ström in the county of Östergötland, S. Sweden. Some investigations have been presented on its spreading in time and space from original planting (e.g. Löfgren 1976). The attractive appearance of this species has induced to planting with devastating effects. Nuisance problems are related to the shading effects of the leaves to the underlying water and it is an obstacle to boat traffic, fishery and other recreational activities. It is dispersed via frag-mented vegetative parts (stems and rhizomes). Rhizomes and roots survive mechanical harvesting, and as a consequence of such restorations, fragments can reattach elsewhere which increases its distribution.

The above presented invasive life-forms constitute suitable test objectives of risk analysis since they correspond to some very problematic weeds on other continents such as *Eichhornia crassipes* - the Water hyacinth, which is a serious floating-leaved invader in many tropical and subtropical waters, and *Myriophyllum spicatum* - the Spiked Water milfoil, a submerged species which has caused a lot of problems during its invasion in North America (e.g. Mills et al. 1994, Mack 1996, Hall & Mills 2000).

The general impact of alien aquatic vascular plants on the ecosystem has not been investigated on a broader scale although interactions with various part of the food-web might be considerable and they may also have an evident impact on the physical and chemical environment. Norwegian studies of the Canadian waterweed came to the conclusion that an apparent decrease of biodiversity followed its invasion and mass development (Brandrud et al. 1999).

Objectives and activities

Scientific leader: Assoc. prof. Eva Willén, Dept of Environmental Assessment, Swedish University of Agricultural Sciences. P.O. Box 7050, SE 750 07 Uppsala, Sweden. E-mail: Eva.Willen@ma.slu.se

The project will focus on:

1. Patterns based on species characters

a) Explore patterns of species characters among successfully established aquatic vascular plants, and particularly those of a weedy character, by quantitative ranking of attributes decisive for dispersal, fecundity, tolerance of extreme ranges of abiotic variables and grazer resistance. An overview of the characteristics of introduced species, linked to aquatic habitats in Sweden (n=119) will be included. Special emphasis will be on the mode of reproduction since the initial number of propagules will be critical to survival and multiplication of individuals and thus to the risk of potential ecological effects. There are some recordings made of some of the serious weeds in Swedish waters which may serve as useful background material.

b) List likely future risk species causing problems mainly in Europe, considering similarities with the Swedish climate, by the use of patterns of characters for those species compared to species used in the aquaria-trade, aqua-culture and gardening. Investigate existing grazers on those species in their native areas, and if few, elucidate if similar species exist in Sweden, and their specificity in choice of food. Compilation of possible infections with an impact on the spreading of invasive species (cf. the infection causing loss of Red water-lilies in some Swedish forest lakes e.g. Fagertärn).

c) Use patterns of species characters to elucidate growth requirements and time of growth maxima of some invasive life-forms by experiments. Several of the serious weedy life-forms need a better understanding of their mode of reproduction. The Yellow floating heart has, for example, the ability to produce seeds but seems to have a vegetative propagation as an alien in Sweden. Experiments studying dispersal of vegetative fragments of some serious weeds will be performed where the prerequisites for settling, rhizome growth and further expansion are especially important to throw light upon. Distribution ranges/ rates of dispersal will be compared with invasiveness of the species in question in the case of data availability.

2. Tolerance tests
Selection of some successfully established weeds preferably representing different life-forms and with different functional roles in the ecosystem for tolerance experiments concerning water fluctuation, temperature, gas ventilation, light conditions and nutrient requirements. Introduced species may be genetically transformed and that can certainly increase the risk of ecological effects (cf. the genus *Caulerpa* in the Mediterranean Sea). Disposition among some selected species for hybridization will also be tested.

3. Patterns based on site characters
The probability of dispersal for an alien species from the site of introduction is critical to risk assessment and also depends on heterogeneity in space and time. The species impact at the first site of establishment may be negligible but if transported (intentionally or unintentionally) to a more hospitable site, it might thrive and cause major harm. Thus site characteristics are especially important to investigate. Factors such as biodiversity, influences of disturbances (wind, wave actions ice scouring etc.), pollution impact, habitat fragmentation will be considered here and compared to sites where no such introductions have occurred. Also the intensity and frequency of vectors (e.g. fishing, boating, and other outdoor human activities) as well as proximity to population and properties (incl. garden ponds) are of importance to assess the geographical risk areas. Additionally the recent Norwegian studies on Canadian water-weed which fairly recently has invaded southern Norwegian waters, will be useful complements (Brandrud et al. 1999). Patterns of site characters are suitable for multivariate statistical tests and other analyses.

4. Processes and ecosystem impact
Ecosystem impact will be documented for some areas where species have been successfully established and have proliferated. Processes of importance for ecosystem functioning will be analysed such as competition between invasive and and native species (suitable test objects are *Elodea* and *Nymphoides* species which have established in mass abundances in several places) by analysing their resource requirements in comparison to native species of equivalent life-forms. The risk that some of the vascular plants may pose a threat to the biodiversity and have an impact on the food-web of the freshwater communities will be assessed with emphasis on ecosystem functioning and structural diversity.

In cooperation with WP 7 models will be developed for selected species to simulate ecosystem impact and population dynamic scenarios (including colonization).

WP 8 will be supported with relevant data linked to human activities and ecosystem services.

Realisation of activities and deliverables
In the initiation phase of the project a thorough literature compilation will be made

In year 1 and 2 the focus will be on:

- Analyses of species and site characters as described above
- Performance of tolerance tests and hybridization capabilities of selected species
- Initiation of competition experiments with relevant aquatic life-forms which belong to the native flora

In year 3 and 4 the focus will be on:

- Continuation of competition experiments
- Experiments with vegetative dispersals
- Start on population dynamic scenarios and ecosystem impact studies include. the role of recirculation of nutrients (together with WP 7). The role of plants in water utilization (data to WP 8).

In year 5 the population dynamics and ecosystem impact studies will be finalized.

Work Package 3/4. Invertebrates (OPEN CALL)

State of the art

There are around 40 introduced benthic invertebrates in the Baltic and the Kattegat-Skagerrak area (Leppäkoski 1984, Jansson 1994, Olenin et al. 2001). Some of these are more than 100 years old (the hydrozoan *Cordylophora caspia*, the bivalve *Mya arenaria*, the zebra mussel *Dreissena polymorpha,* the mussel *Crassostera virginica*, the small gastropod *Potamopyrgus antipodarum*, the barnacle *Balanus improvisus* and the American pygmy crayfish *Oronectus limosus*), while seven species have arrived less than 20 years ago. Many probably arrived by shipping (Leppäkoski 1984, Jansson 1994, Olenin et al. 2001), others have been introduced for stocking (*Crassostera* spp.) or associated with aquaculture target species (e.g. the slipper limpet *Crepidula fornicata*, the bivalves *Tapes philippinarum* and *Petricola pholadiformis*). Some species have had a profound impact on the ecosystem such as *Dreissena polymorpha*, *Mya arenaria*, *Balanus improvisus* and the more recently introduced polychaete *Marenzelleria* cf. *viridis.* Others are quite common but seem to have a much smaller overall ecosystem impact such as the razor clam *Ensis americanus* on the Swedish west coast, *Potamopyrgus antipodarum* (occurring in marine, brackish as well as freshwater) and *Cordylophora caspia* (throughout all the Baltic basins), the athecate African hydrozoan *Clavopsella navis* (in the Baltic Sea but also established in the U.K.; Eno et al. 1997), the hydrozoan *Bouganivillea rugosa* and the small North Atlantic polychaete, *Polydora redkei*, when occurring in the Baltic Sea. Some species such as *Ficopomatus enigmatus* and *Styela clava* only have established locally, the former in discharged cooling waters and the latter seems to be spreading out of the Limfjorden area. Several species have caused socio-economic impact by destroying fish in nets (e.g. the Chinese mitten crab *Eriocheir sinensis*), by being a competitor in aquaculture (e.g. *Crepidula fornicata* on the Swedish west coast) by fouling on artificial surfaces (e.g. *Balanus improvisus, Cordylophora caspia, Styela clava, Ficopomatus enigmatus* and the bryozoan *Victorella pavida*), or by boring in wood (the ship worm *Teredo navalis*, now increasing in the southern parts of the Baltic Sea; e.g. Gollasch & Rosenthal 2000).

To the this group may also be added the six nekto-benthic amphipods introduced as fish fodder (Leppäkoski 1984, Olenin et al. 2001). These do not seem to have spread much in the Baltic, except for *Pontogammarus* which is also recorded in the Oder estuary (Gruszka 1999). On the other hand the Baikal endemic species *Gmelinoides fasciatus* has been recorded from Lake Ladoga, Karelian lakes and an Estonian lake and is considered to have had some negative impact on other species. The ballast mediated amphipod *Gammarus tigrinus* has spread along the North European coasts as well as into the Baltic.

Josefsson (1999) listed six introduced benthic invertebrates (excluding parasites) in freshwater in Sweden, most of these species also occurring in the Baltic Sea (*Dreissena polymorpha*, *Potamopyrgus antipodarum*, *Eriocheir sinensis*, the amphipod *Corophium curvispinum* and the oligochaete *Branchiura sowerbyi* (Jansson 1994, Olenin et al. 2001). *Corophium curvispinum* does not seem to has had such a profund ecosystem effect in Swedish freshwater (Josefsson 1999) as in many other European systems, where this opportunistic species is considered highly invasive (e.g. van den Brink et al. 1993, Bachmann et al. 2001). By covering stones with their muddy tubes it has had a negative impact on epilithic organisms including the introduced zebra mussel (Paffen et al. 1994). Two species of the clam *Corbicula* from southeast Asia have invaded Europe (from Germany and southwards) since the 1980s (e.g. Haesloop 1992, Rajagopal et al. 2000), but so far those are not listed for Sweden nor for the Baltic (they tolerate brackish water), but are found in the tidal parts of the river Weser and in the Rhine. In the US one species of these clams has been clogging hydroinstallations and may also have had a negative effect on native bivalves (Haesloop 1992).

In above all the Baltic Sea there are several examples of introduced and established pelagic invertebrates, which differ in their impact on the ecosystem level. Several studies have concerned the Ponto-Caspian freshwater cladoceran predator *Cercopagis pengoi*, first recorded in the Gulf of Finland and the Gulf of Riga in the early 1990s, since 1998 also occurring along the Swedish coast of the Baltic proper as well as being established in the Great Lakes since the late 1990s. It is described as a competitor to zooplanktivorous fish and may have a cascading effect on phytoplankton blooms as well as having an impact on small scale fishery through clogging of fish nets or cages by aggregations of males with long, spiny tails. This species seems to increase in abundance on the Swedish east coast (S. Hansson pers. comm.). Another introduced Ponto-Caspian cladoceran species, *Bythotrephes cederstroemi*, also having a spiny tail, so far has been recorded only from the eastern part of the Gulf of Finland, but is also established in the Great Lakes and in the Lake Vänern. This species may have similar ecosystem effects and economic impact, if dispersed to other areas.

The mysid *Hemimysis anomala* was introduced as fish fodder in the former Soviet coastal areas in the Baltic Sea, but has later spread also to the Gulf of Finland and Swedish east coast. There are no descriptions of any substantial impact on the ecosystem level of this species, but mysids are important as fish prey. Two other freshwater mysids (*Limnomysis benedeni* and *Paramysis lacustris*) are also reported from the Baltic Sea, originally introduced in freshwater, the latter also recorded from the Gulf of Finland. *L. benedeni* does not seem to have had any dispersal success in the Baltic Sea but has spread rapidly in central European freshwater apparently, however, with little ecosystem impact (Wittmann & Ariani 2000). The copepod *Acartia tonsa* is commonly distributed in the Baltic, apparently as a regular but small component of the zooplankton population. It is supposed to have arrived in ballast water and also occurs in the North Sea (Eno et al. 1997). The harpacticod *Ameira divagans* is another assumed ballast arrival. Very little is known of the hydrozoan *Maeotias inexspectata*, recently recorded in the Gulf of Riga. As a predator and if present in large populations it might have an impact on the trophic pathways and perhaps also a cascading effect on phytoplankton. Another hydrozoan with a free-living medusa stage, *Gonionemus vertens*, has been recorded from the Swedish west coast (Jansson 1994) as well as from most European Atlantic coasts (Eno et al. 1997), but not much is known of its ecosystem effects although relatives have a very potent toxin (Eno et al. 1997). There is no listing of any introduced true zooplankton in freshwater communities (Josefsson 1999). However, the cladocerans introduced in the Baltic may well migrate actively or be dispersed by human activities (fishing or ballast) into freshwater systems close to the coast and even further inland.

The species having had the most profound impact on Swedish freshwater ecosystems, no doubt is the North American signal crayfish, through carrying the fungi parasite (*Aphanomyces astaci*) and through competion with the native crayfish. The species is also occasionally recorded for the Baltic Sea. The socio-economic impact of the American signal crayfish (WP 9) will be evaluated in cooperation with above all WP 8 and WP 7.

Objectives and activities

<u>This WP will be open for other applicants</u> to study organisms of their choice and to specify their objectives. However, they should be prepared to provide the type of data required by WP 7.
Furthermore, it should be understood that no field experiments with introduced species are to be carried out unless the species in question already is established in the area.

Characterization of areas at risk depends on which type of organisms the applicant will study. Thus it may either include comparisons between the different Baltic basins or different freshwater systems and/or possiblities for transports between marine and brackish or brackish and freshwater ecosystems.
If organisms with a pelagic life strategy are to be studied they are well disposed for further dispersal, at least within e.g. the Baltic Sea basins or a freshwater system. Studies may than rather be directed towards risks of dispersal from brackish to freshwater areas or vice versa, or between marine and brackish areas. The pelagic system, in all type of waters, may also for shorter periods harbour larvae of introduced benthic species. The temporary role of these, however, is less well-known. From a risk perspective they are highly important as a dispersing phase in the life history of the species in question, though the final success of the species is depending on the establishment of parent populations.

Work Package 5. Fish in brackish and freshwater areas

State of the art

Still few non-indigenous fish species have been established in the coastal zone of the Baltic Sea (Weidema 2000), and most of non-indigenous fishes established in Swedish freshwaters are related to intentional stocking (Filipson 1994). Non-native salmonid species, such as rainbow trout (*Onchorhynchus mykiss*), which have been introduced to Swedish freshwaters, are also found along the Swedish and Finnish coast. In Estonia, cyprinid species (e.g. *Cyprinius carpio*) originating from freshwaters are moving out to the coastal areas as a possible effect of eutrophication. One of the most significant changes in the coastal fish fauna is the establishment of the Ponto Caspian round goby, *Neogobius melanostomus* in the Bay of Gdansk. This species is in the spreading phase (e.g. Olenin et al. 2001), and pose a considerable threat to the Swedish native fish fauna.

It is suggested that in unmodified habitats, fish species most likely to be successful invaders are top predators or omnivores and/or detritivores (Moyle & Light 1996). A reason to this may be that both types of fishes have unlimited resources of food during the early stages of the establishment and dispersal process. Piscivores are the most likely to cause extinction because prey fish are not adjusted to the particular type of predatory behaviour of a new species, and omnivores/detritivores use a food source that is rarely limiting in aquatic systems.

Although the most successful invaders will be those adapted to the environmental conditions, several studies imply that 'biotic resistance' does exist to a certain extent, particularly at an early stage of invasions (the establishment phase). It is therefore important to know if the habitat is 'filled' with species or if there are any obvious gaps that could be filled by invaders. Environmental disturbance creating gaps and destabilization of the native assemblage will increase the susceptibility to invasions of new (alien) species (Case 1991). With the exception of regulated rivers, the Baltic Sea is the water body most affected by anthropogenic disturbance in Sweden as it is subjected to a variety of perturbations, including fishing/harvest, physical alterations, dispersal of nutrients and chemicals, and changes related to climatic factors, as well as having a large proportion of introduced species. These changes have had substantial impact on native fish assemblages, and have increased the risks for unintentional establishment and spreading of non-indigenous fish.

Objectives and activities

Scientific leader: Prof. Magnus Appelberg, Institute of Coastal Research, National Board of Fisheries, Gamla Slipvägen 19, SE 740 71 Öregrund, Sweden. E-mail: Magnus.Appelberg@fiskeriverket.se

1. Identify phases of invasion (arrival, establishment and spreading), and characterize species, habitats and fish assemblages where non-indigenous fish species have established in the drainage area of the Baltic Sea.
2. Analyze the effects of disturbance on susceptibility to non-indigenous fishes along the coast of the Baltic Sea by:
   - assessing the effects of increased water temperature on establishment and spreading of non-indigenous fishes in coastal waters, and
   - assessing the effects of fishery and eutrophication on the susceptibility for non-indigenous fishes to establish and spread.

Realisation of activities

1. Identify phases of invasion (arrival, establishment and spreading), and characterize habitats and fish assemblages where non-indigenous fish species have established in the drainage area of the Baltic Sea

Lessons from invading fish species in the Great Lakes learn that invading species, if established, often have substantial effects on the native fish community. There are also reasons to believe that species invading the Baltic Sea may have pronounced impact on the native fish assemblages. Based on existing data from Nordic waters, retrospective analyses on the species characteristics and species distribution patterns of non-native fish species established in Nordic coastal waters and in freshwaters are performed.

Analyses will be based on existing databases for freshwater fish in lakes and streams (Institute of Freshwater Research), coastal fish (Institute of Coastal Research), data on successful establishment of new species (Filipson 1994), and species occurrence data for about 5,000 Nordic lakes compiled in late 1900s (Rask et al. 2000). By using a multivariate approach, successful and non-successful invasions will be contrasted to reveal habitat characteristics (e.g. geographical location, habitat size and heterogeneity) and assemblage characteristics (e.g. species composition and functional groups) at different situations. Data management and analyzes are coordinated with WP 6 (Aquaculture). To reveal large-scale dispersal (spreading phase) of non-native fish species in Swedish freshwaters, data on species occurrence collected in 1860-1910, 1920-1940 and 1988-2000 will be analyzed and set in relation to abiotic and biotic characteristics. Results are used as input to WP 7 (Risk assessment).

2. Analyze the effects of disturbance on fish assemblage stability and susceptibility to non-indigenous fishes along the Baltic coast

In the Baltic Sea, the most plausible invaders would be species adapted both to prevailing large-scale environmental factors such as temperature and salinity, and to habitat related factors such as substrate and exposure. In addition to environmental conditions, successful invasions are most likely to occur when native assemblages of organisms have been temporarily disrupted or depleted, as moderately disturbed systems are suggested to support groups of species that would probably not coexist under more constant conditions (Connel 1978).

- describe the possible establishment of non-indigenous fish and assess the effects of increased water temperature on life history and assemblage characteristics of native coastal fish species. Habitats with increased temperature may act as an important prerequisite during the establishment phase of alien species. Non-indigenous fish have been found in the cooling water around nuclear power plants in the Baltic region (Weidema 2000) and may act as a pool for further spreading when climatic conditions become favorable. According to regional climate studies (SWECLIM) it is reasonable to believe that increased temperature will be one of the most important changes in the Baltic region in the future, increasing the risk for invasion of non-indigenous fish species (Lodge 1993, Magnuson et al. 1997). The zoogeographical boundary for fish species will possibly move north, and increase the risk for invasions of warm water species and extirpations of cold water fishes would increase. If changes in the salinity of the Baltic basins will occur (e.g. Elmgren 2001 and references therein), this may also enhance the chances for more freshwater species to become established in the coastal waters.

The effects of increased water temperature on fish assemblage development of coastal fish are assessed by analyses of existing time series (>20 y). Complementary data are compiled from the bay Hamnefjärden, receiving cooling water from the Oskarshamn nuclear power plant. To simulate changes of life history traits (fecundity, individual growth rate and mortality) for native species in a situation with increased temperature, experimental field and laboratory studies are performed in the 'Biotest basin' at the outlet of Forsmark nuclear power plant. Results are set in relation to life history traits compiled from published data and complementary laboratory studies on potential invasive species that could be expected to pose a threat to Swedish coastal fish assemblages in a situation with increased temperature. Data on life history characteristics are used as input to WP 7 for further analyzes of risks.

- assess effects of fishery and eutrophication on the probability for non-indigenous fishes to establish and spread. The two most important types of disturbances for the coastal fish assemblages in the Baltic Sea are fishery and eutrophication (cf. Elmgren 2001). Fishery-/harvesting will increase mortality and may reduce abundance (or even cause almost extinction) of one or several fish species and/or sizes classes of species (often top predators). Reduction of species due to fishery has been shown to give rise to drastic changes in coastal fish assemblages, with a substantial increase in abundance of less competitive species. Eutrophication may change the physical and chemical environment and alter the amount and quality of resources (e.g. food, substrate), thereby affecting recruitment and competition among fish species. A pronounced increase in nutrient load has caused severe changes in the coastal fish assemblages, and caused changes from being mainly predator dominated (perch and pike) to become dominated by omnivorous/detritivorous freshwater species (cyprinid species). Recently observed decreases in recruitment among coastal fish species have also been explained by substrate degradation due to increased amount of nutrients.

Changes in life history traits of the native fishes due to disturbances can be expected to influence both the establishment and spreading of non-indigenous fish. Differences in fecundity, growth and mortality for fishes subjected to the two different perturbations are examined, and the sensitivity to different degree of predation and competition from non-indigenous fish is simulated together with WP7. For estimating differences in life history parameters, ongoing sampling programs in perturbated and 'near natural' areas are used, complemented with additional sampling of sites and characteristics not usually covered by standard monitoring. Individual growth rates, used as a proxy for competition, are estimated using field data complemented with bioenergetic modeling (Karås & Thoresson 1992). As potential invader the Ponto-

Caspian round gobio (*Neogobius melanostomus*) will be used. Life history data are collected from literature and, if necessary, from site studies in the Baltic where this species has established populations.

Deliverables

5.1 Characterization of the arrival, establishment and spreading of non-indigenous fishes in relation to habitat and native fish assemblage composition in Swedish coastal and freshwaters (coordinated with WP 6, and input to WP 7 and WP 8)

5.2.1 Predicted changes in life history characteristics of native fishes in situations with increased temperature at the Baltic coast and predicted effects on establishment and spreading of non-indigenous fishes. Input to deliverable 5.2.4, and input to WP 7.

5.2.3 Estimates of changes in life history characteristics of native fishes at different rates of mortality and competition due to fishery and eutrophication. Input to deliverable 5.2.4, and input to WP 7 .

5.2.4 Probability estimates for non-indigenous fishes to establish in coastal areas subjected to different types of perturbations (fishery, eutrophication). Input to WP 7 and WP 8.

Reasons to cooperation between WP 5 and WP **6**

Invasion of non-indigenous fishes is a complex phenomenon, and has been shown to have substantial effects on ecosystem goods and services. There are number of reports referring to invasive species that have been established in coastal areas over the world. These species (and vectors for invasions) do generally differ from species used for aquaculture purpose. We have therefore decided to treat these two problems in separate work packages. WP 5 deals with risks related to coastal areas and effects of environmental degradation, whereas WP 6 deals with fishes used for aquaculture purpose, mainly in freshwaters. The work packages will be coordinated as far as possible.

Work Package 6. Aquaculture

State of the art

Aquaculture, i.e. human effort to increase productivity of aquatic organisms, is often associated with intensive fish farming in cages, although a large part of the production are native or non-native species used for stocking in natural waters. The number of fish species used for intense food production in Sweden today is rather low (6-7 species), but is expected to rise.

The species used in aquaculture may be non-native. The most common fish used in Swedish farms is rainbow trout (*Oncorhynchus mykiss*) that originates from North America. Other non-native species used in aquaculture are brook trout (*Salvelinus fontinalis*) and lake trout (*Salvelinus namaycush*), fishes that mainly has been farmed for stocking purposes. In common for all these species used and introduced in Sweden is that their biology and ecology are rather close to the equivalents we find in our waters (i.e. brown trout, salmon, Arctic charr and grayling). Thus, there is a direct threat with releases of non-native fish basically because of their similarity with our species. Today at least 4 non-native aquaculture fish species appears to have established in the wild in Sweden.

The rapid growth of aquaculture activities in many regions around the world has raised questions about the possible ecological impacts on wild populations (Ruzzante 1994). This is particularly true for salmonids which are released in large numbers, either through intentional re-stocking programmes or as escapees from fish farms. Many thousands of stocking events, involving millions of fish take place annually in managed fisheries over the world (Hickley 1994). Beside from the stocking of 4-6 millions native salmonids per year, about 2 millions of rainbow trout is annually stocked for “put & take” angling purposes in Sweden. There are no data available for other non-native species, but considerable amounts of brook trout and to some extent lake trout are also released into natural water systems. Accidental releases of fish on a larger scale started to occur with the commencement of more intense cage culture of fish in the early 1980s (Willoughby 1999). There are no available statistics on the amount of accidental releases from fish farms in Sweden, but the number of escaped salmon and rainbow trout in Norway was estimated to be about 0.5% of the total amount produced in 1994 (Willoughby 1999). Translated into Swedish conditions, a frequency of 0.5% will give about 10 000 escapees per year, with the largest amount being rainbow trout.

Domestication represents an important step in the development of intense aquaculture activities. On the other hand domestication may result in a phenotypic divergence from the wild founder populations for a large number of biological characters (Utter et al. 1993). Domestication involves both an evolutionary response via changes in the gene frequencies between generations, and environmentally induced shifts in developmental processes and rates that occur within each generation (Price 1984). Innate behavioural responses may differ from those of wild populations after relatively few generations of culture, e.g. aggression and anti-predatory behaviours (Berejikian 1995).

When evaluating the risks with non-native fish species in Sweden, one must remember that those are not only aliens but also domesticated in many cases. For example, rainbow trout and brook trout are assumed to have been brought in from North America to Sweden in the late 1800s and since about 1930 very few new fish have been imported. Thus, these species have been held in fish farms and domesticated for many generations. Although released in very high numbers, rainbow trout does not appear to be able to establish themselves in Nordic waters, in spite of fulfilling the most important criteria (i.e. numbers released) for establishment (Kolar & Lodge 2001). One reason for this may be that the domestication process of rainbow trout is made for intensive food production, in deviation to the case with fish farmed for stocking purposes only. Brook trout on the other hand have been released, intentionally or unintentionally, to many water systems where it is established and are now spreading to new areas often at the expense of our native brown trout (Filipsson 1994, Spens unpubl.).

Reared fish escaping or in other ways entering natural waters by way of aquaculture activities represent a risk scenario in which intrinsic characters as well as the effects of domestication should be evaluated.

Objectives and activities

Scientific leader: Prof. Lars-Ove Eriksson, Dept of Aquaculture, Swedish University of Agricultural Sciences, SE 901 83 Umeå, Sweden. E-mail: Lars-Ove.Eriksson@vabr.slu.se
Co-leader: Docent Anders Alanärä (Address as above) E-mail: Anders.Alanara@vabr.slu.se

In a risk analysis of ecosystem effects of introduced exotic fish it can be of advantage to use experiences and data both from releases of exotic species in Sweden as well as doing comparative analyses on performances of ecologically similar natural and introduced fish species.
This will be done through:

i) To compile the existing data regarding aquaculture mediated introductions of alien species and to build a conceptual model regarding main factors resulting in successful establishment of alien fish and their ecological impact (together with WP 5).

ii) To analyse key characters of a successful invasive aquaculture species (Brook charr) mirrored by an unsuccessful species (rainbow trout). Analyses will be accomplished on landscape, community, population and individual levels to achieve functional key characters.

To use such patterns of characters for species used in aquaculture and fisheries management or being successfully established/nuisant in other countries of similar climate in order to list likely future risk species together with possible control measures and geographic areas of differing susceptibility/resistance.

1) Patterns of species characters will be searched for among known established alien fish species by quantitative ranking of such characters using existing data and to compare distribution ranges/rates of dispersal with invasiveness.
a) The importance of reproductive strategy, fecundity and early life history for native functional organisms (e.g. brown trout) will be evaluated in comparison with reciprocal introductions (i.e. rainbow trout and brook charr).
b) Behavioural differences and resource utilisation differences between introduced species and native, ecologically equivalent species will be studied in the laboratory and in controlled natural environments (or by modelling if utilisation patterns of native species are known).

2) Search for patterns of sites where introduced species have established in combination with site characteristics such as species richness/biodiversity, disturbance, pollution, habitat fragmentation, geomorphology, and closeness to vector receivers etc. and to test for such patterns of habitat susceptibility/resistance to invasive species.

3) Find out the role of such species in aquatic communities as predators, competitors or as parasitic hosts. The resulting impact on the ecosystem function in some areas where alien species have established will be described and analysed mainly from existing data.

Realisation of activities and deliverables

General characters of successful and non-successful introductions/escapements of reared fish are compiled from existing national and international literature data. On a landscape level patterns of species characters will be searched for among established species by quantitative ranking of abiotic and biotic ecosystem characters. A GIS linked database based on 1000 streams and 1500 lakes in Västernorrland will be used in the analysis (1a, 2 and 3).

In the field, comparative data will be collected for the North American exotic species brook charr and rainbow trout and their Scandinavian ecological equivalent brown trout. Population analyses are made including parameters such as growth rate, fecundity and age and size at maturation (1a). Please note that there are uncertainties about the occurrence of established and reproductive rainbow trout populations in Sweden. Thus, rainbow trout will be included if study populations are identified.

Comparative tests of individual behavioural characters (for example aggression, predator avoidance and competitive ability) are tested experimentally in the laboratory. A successful invasive aquaculture species (brook charr) that are spreading to numerous waters and a non-successful invasive species (rainbow trout) are compared with the natural key species of these waters (brown trout). Behavioural studies are made in semi-natural stream channels at the SLU research station in Norrbyn. The outcome of the tests will, if possible be validated in field experiments in areas where the species already are established (1b).

Year 1:
Initiation of a review of national and international literature data regarding characters of successful and non-successful introductions/escapements of reared fish. Development of contacts and co-operation with North American research.
Finalisation of an analysis regarding patterns of species characters and consequences of earlier introductions on a landscape level.
Sampling of sympatric and allopatric brown trout and brook charr populations, and brown trout and rainbow trout populations. Captured fish are analysed for determination of life history parameters in the laboratory. Life history and population parameters in relation to available habitats and environmental factors are quantified.
Preparatory and some initial work to study individual behavioural characters in the laboratory.

Year 2:
Publication of review.
Complementary sampling for an increased number of populations and (or) sample sizes in each creek. Statistical analyses are done in which the intensively studied systems are integrated with the large database.
Studies of the reproductive, territorial, foraging and anti-predatory behaviours of introduced brook charr and rainbow trout in relation to the native brown trout.

Year 3
Publication of results on comparison of life history parameters on brook charr and brown trout.
Continuation of laboratory studies of behavioural characters of native, invasive and non-invasive salmonids, especially on competitive ability under different abiotic factors (e.g., temperature, stream velocity etc).
Initiation of a short-term test of egg-to-juvenile survival of the three species in the field, depending on absence/presence of competitors.

Year 4
Finalisation of laboratory and field experiments.

Year 5
Finalisation of analyses and reports

Work Package 7. Risks: Tools, analyses and assessment

State of the art

Very few, if any, scientific reports have been published in the field of quantitative risk analysis and assessment of introduced aquatic species. Most work has been devoted to the development and application of various qualitative or semi-quantitative approaches to risk assessment, such as those represented by the cited literature in this proposal. Methodologies for quantitative risk assessments are much requested to predict the fate of invading species in agriculture and pest management (e.g. Orr et al. 1993), but few generalized analyses exist. Hayes (1997) reviewed ecological risk assessment methodologies in relation to marine invaders and later published approaches to handle ecological risk assessment for ballast water introductions (Hayes 1998, Hayes & Hewitt 2000). Although the large international programme “Global Invasive Species Programme” (GISP) has a section devoted to “Pathways of Invasives & Risk Assessment”, not much within the risk assessment part has to our knowledge been published.

Objectives and activities

Scientific leader: Prof. Göran Bengtsson, Chemical Ecology/Ecotoxicology, Dept of Ecology, Lund university, SE 22362 Lund, Sweden. E-mail: Goran.Bengtsson@ekol.lu.se

The main task within this work package is to develop a general methodology for risk analysis of invasions by alien species in aquatic environments. The general methodology will address characteristics of the three phases of invasion (see Introduction) and be used at two levels of resolutions. One is for the “if so - what” questions, that is, given certain assumptions, what will then the probabilities of certain outcomes be. The other is for the organisms and systems analysed in the Programme and will aim at adopting and applying the methodology to the specific data and situations.

Subtasks are associated with three specific research problems. The first one arises from the fact that published research has concentrated on the later transitions (establishment of alien species in invaded communities), although the early transitions (entrainment by a transport pathway, e.g. ballast water of a ship, and process of introduction by survival of transport) are the most important for management and for developments of incentives to reduce invasions. This subtask will seek to develop models for the arrival phase that allows analyses of the probabilities of species introduced in new environments. The second subtask will address models that account for heterogeneity in distribution of the invading species and in the donor habitat. The third will refine the methodology by which the impact of an invader can be evaluated.

The development of a methodology for the risk analysis is not foreseen to be the major challenge of the work but the scarcity and patchiness of the data. Where data are not available and cannot be generated, extrapolations will be made. Regardless of the methodology for extrapolations, the uncertainty of the risk analysis will be larger than if data were available.

Risk analysis

Risk indicates a degree of uncertainty about the outcome of a given action. Risk can be either objective or subjective. An objective risk can be described precisely based on theory, experiment, or common sense. Ecological risks are subjective in the sense that information about the action is normally incomplete, the action is not repeatable, or the situation is just too complex for an unequivocal answer. A risk assessment under those conditions is likely to change when more information about the situation becomes available. Disagreement can then arise about the risk assessment as such but especially about the judgement of the risk. Whether a 5 or 10% probability of a specific outcome should be defined as a risk or not is rarely possible to objectively evaluate. Once a risk is quantified, one may decide to accept it or avoid it. Some individuals may be willing to accept a certain risk, others not.

The methodology for risk analysis and assessment in this Programme will be developed based on five sequential steps: identification of assessment endpoints, model development, identification of uncertainty in data variables, model analysis with simulation, and interpretation of results. The assessment endpoints are formal expressions of the species or community values to be considered and perhaps protected, and are associated with measurement endpoints (cf Table 1). Models in ecological risk analysis are physical, statistical, and mechanistic and are used to quantify and specify the risk. Most ecological data have a certain degree of uncertainty or stochasticity that can be described by probability distributions. The characterisation and quantification of this uncertainty, as well as that of the outcome, is the most important feature of risk analysis. The model analysis has the goal to derive a probability distribution of the endpoint values. This Programme will use simulations as a basic approach to quantify the risk. The analytical approach, in which e.g. the variable distributions are described mathematically, is more complex and less practical for assessment purposes. The final interpretation of the probability distributions of the risk analysis will be made jointly within the Programme.

Ecological risk assessment will be used to characterise and quantify the uncertainty associated with an invasion. The basic sources of information for the risk assessment will be data derived from within the project and available in databases, other test data available in the literature, and models. The risk assessment will make use of a mechanistic model approach. The effects of changes in model input values, parameters, and assumptions on model outputs will be determined by sensitivity analysis. The uncertainty in the model outputs will be analysed by quantifying the uncertainty in the inputs, parameters, and model structure. The sources of uncertainties to deal with will be the inherent stochasticity of the environment (variability), the imperfect database (ignorance), and model errors.

Uncertainty of model approaches will be quantified by numerical Monte Carlo analysis, which will primarily be performed in the computer programme @Risk, which uses Excel spreadsheets as a template for data input and model solutions. @Risk is chosen as the primary tool to facilitate the transmission of risk analysis know how within the programme and to those that will be responsible for the implementation at different organisation levels, e.g. at Naturvårdsverket. Monte Carlo analyses in @Risk requires that the data can be organised and categorised as statistical distributions. This implies that also the deterministic models will sample data with a certain distribution. In case parametric probability distributions fail to fit data, non-parametric and interval analysis approaches will be used to express the variability. These procedures as well as model development and implementation will use MatLab as a template.

Table 1. Tentative examples of endpoints of a risk analysis of species invasion.

Assessment endpoints	Measurement endpoints
proportion of settlers that undergo long-distance dispersal	age-dependent dispersal
propability of invasion when optimal patches appear temporarily	growth rates of prey and consumption rate of prey by predator
proportions of prey killed by invading predator in patchy environment	growth rate of predator on prey and death rate of predator
increase in probability of establishment when some proportion of invaders tolerate environmental stress (salinity, temperature, desiccation)	predation, parasitism, and competition on native fish species by invaders
increase in invasive probability as resident fish species are reduced by fishery and eutrophication	species specific and age specific diffusion and advection rates
proportion of migrating propagules arriving in recipient habitat	intrinsic rate of growth and competition with resident species
decrease in probability of arrival when some proportion of habitats are unfavourable	arrival rate by vectors
probability of community invasion	minimum viable size in relation to Allee effects (see text)
probability of establishment with a human vector	percent mortality of arriving, settling, and spreading propagules
probability of invasion when dispersal is by vegetative fragments and reproduction asexual	number of invaders
reduction in human vector faciliated establishment by information campaign	species numbers and connectance of recipient community
	grazer resistance in algae
	dispersal and establishment of vegetative fragments of algae

Model errors will not be formally addressed in this project. There is no straightforward statistical or mathematical technique to analyse model errors, and possible approaches, such as experiments to validate the models, would be too difficult and time-consuming to manage within the project. However, if data are available for one or more WP and for more than one invasion event, a model can be pseudo-validated. As a complement, we will use probabilistic analyses to estimate the "credibility" of the assessment to help to clarify the relationship between decision making and uncertainty. Model outputs will be probability density distributions, specifying the probabilities by which certain measurement endpoint values will be realised.

Figure 2 (next page) shows the principal components and pathflows of the risk analysis. The example assumes that age specific distributions of data can be obtained on mortality, fecundity, and dispersal as a function of population density. The data represent input variables to a model, which is specified under certain conditions of population and community processes. The end result of model simulations and sensitivity analyses will be a probability distribution of age specific endpoint expressions.

The work in WP7 will be devoted to all five steps of the risk assessment mentioned. The first step will be to identify assessment and associated measurement endpoints. The following table is an illustrative example of possible endpoints for the Programme, but it should be emphasised that the identification of endpoints is a research activity within WP7, just like model development. The development of formal and unambiguous endpoint definitions is a prerequisite for testing and modelling, and the results of risk assessment tend to be as ambiguous as the endpoints.The remaining part of this WP text will describe the specific characteristics of the invasion ecology that will be addressed in the development of the methodology for risk analysis and discuss the possible approaches to model those characteristics.

Models

Arrival and establishment phase

Fisher (1937) originally proposed a framework for the process in which individuals disperse and multiply their numbers. Let N(**x**,t) denote the population density at time t and spatial coordinate **x** = (x,y) in a two-dimensional homogenous space: $\partial N/\partial t = D(\partial^2 N/\partial x^2 + \partial^2 N/\partial y^2) + (\varepsilon - \mu N)N$.
The left hand indicates the change in population density with time, caused by random diffusion and population growth. D is the diffusion coefficient, ε is the intrinsic rate of growth and μ represents intraspecific competition, such that the growth part of the equation is logistic. The diffusion part of the equation can be solved for different assumptions, including that of a random walk by an individual, in which case N(**x**,t) represents the probability density that the individual is at (x,y) and t. Since the logistic growth contains a non-linear term, numerical solutions must be derived. The range front forms a sigmoidal pattern and spreads at a constant rate, a so-called travelling wave.

If the organism has a tendency to orient itself toward external stimuli, or is carried by wind or water flow, the diffusion equation is modified to incorporate an advection term: $\partial N/\partial t = D(\partial^2 N/\partial x^2 + \partial^2 N/\partial y^2) - V(\partial N/\partial x) + (\varepsilon - \mu N)N$, where V is the advection term. As long as the per capita growth rates is positive and D is constant, the solution of the equation converges asymptotically to a travelling wave, in which the density dependence of the growth rate is insignificant near the edge of the frontal wave. The equation has been analysed for various functional forms of the diffusion and population growth parts as well as for initial distributions (Okubo 1980, Renshaw 1991, Banks 1994).

Establishment and spreading phase

The same approach can be used to describe range expansion in a heterogeneous environment in which favourable and unfavourable habitats are mixed. This habitat heterogeneity could affect the range expansion either via habitat-dependent rates of movement or habitat-dependent rates of population increase. It is possible to set up environments with a mosaic of patches varying in diffusion rate and intrinsic growth rate, but to obtain mathematical expressions that are tractable, one has to deal with special cases. One example is an irregularly varying environment in which the widths of favourable and unfavourable patches are assigned random values. For this case, computer simulation will show that, alternatively, the invaded population will become extinct so that the invasion fails, or that the population evolves into a travelling wave where the range pattern changes irregularly in time and space, reflecting the random patch widths.

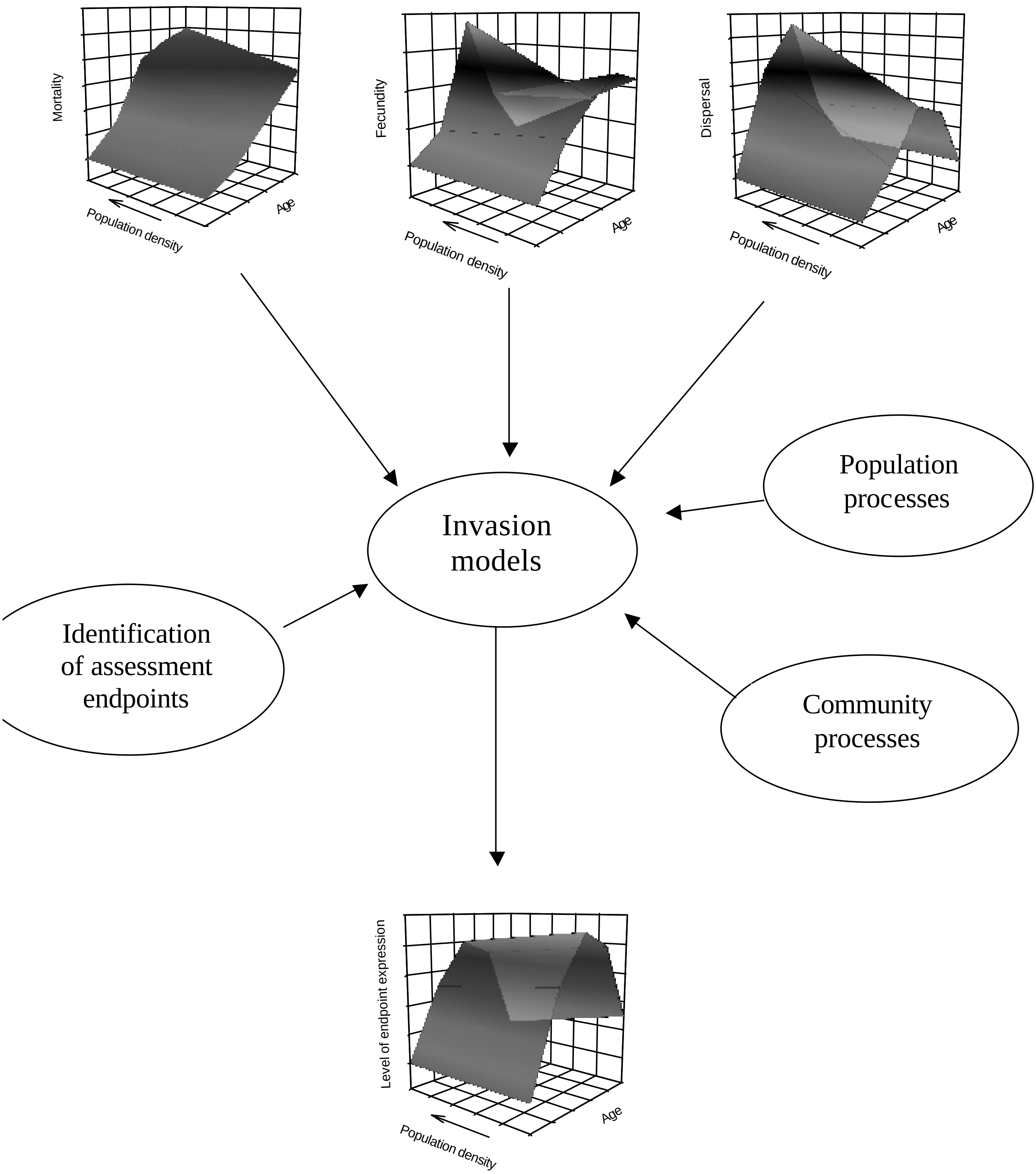

Fig. 2 Principal outline of risk analysis of species invasions. The graphs are not based on real data but used onlv for illustration.

A stochastic model is essential when the number of organisms is small, e.g. during the transition between the arrival and establishment phase and at the boundaries of the range of expansion of the population. Small population sizes or low population densities may result in negative per capita growth rate and the invasion cannot propagate unless it exceeds a critical density. This general phenomenon was referred to as undercrowding by Allee et al. (1949) and is now often known as the Allee effect. Possible effects are social effects, unable to find a mate or resources, more vulnerable to predators, and subject to competition from larger populations of other species. It is possible to derive equations for each of these effects but more difficult to find quantitative data from the field. Only epidemiological models seem to have data to test for the minimum viable size. To predict the fate of arrivals, one also has to consider extremely small individual probabilities of success, because the number of propagules attempting to invade may be very large.

Models of interacting particle systems provide a framework that includes stochasticity. In the simplest model, the environment is portrayed as a lattice of sites that are either occupied or empty. Once a site is occupied, it remains occupied for all future time. Invasion is only from the four nearest neighbours, The model has a single parameter, *p*, which enters into the probability that an unoccupied site remains unoccupied at the next time step, $(1-p)^k$, where *k* is the number of occupied neighbouring sites. A traditional sensitivity analysis is not really adequate to evaluate the robustness of the models but one also needs to know whether the results are sensitive to the form of the components (e.g. the shape of a dispersal distribution).

Species may expand their ranges by a combination of a diffusion process into surrounding areas and long-distance dispersal (stratified or hierarchical diffusion), e.g. by transportation facilities such as boats and cars. The initial expansion is then determined by neighbourhood diffusion by a founder population, and the expansion in the later phase reflecting the growth of new colonies established through long-distance dispersal. Several cases can be considered, e.g. in which the colonies established by long-distance dispersers are sufficiently removed from each other so that each one remains an independent spreading range for a long period. Similarly, populations that are age-structured may have age-dependent dispersal and reproduction. Van den Bosch et al. (1990) developed a model for range expansion that depended on life-history parameters in a homogeneous environment, but it remains to develop models addressing age-dependent range expansion in a heterogeneous environment and stratified diffusion with an accelerating travelling wave.

Impact on native community

Competition between invasive and resident species can be modelled by extending the diffusion equation with a Lotka-Volterra competition expression:

$$\partial N_i/\partial t = D_i(\partial^2 N_i/\partial x^2 + \partial^2 N_i/\partial y^2) + (\varepsilon_i - \mu_{ii}N_i - \mu_{ir}N_r)N_i$$

$$\partial N_r/\partial t = D_r(\partial^2 N_r/\partial x^2 + \partial^2 N_r/\partial y^2) + (\varepsilon_r - \mu_{ri}N_i - \mu_{rr}N_r)N_r$$

where D_i and D_r are the diffusion terms for the invasive and resident species, respectively, ε_i and ε_r are the intrinsic growth rates, and μ_{ii} and μ_{rr} are the intraspecific competition and μ_{ir} and μ_{ri} are the interspecific competition. Numerical solutions will allow the evaluation of the impact of a resident competing species on the propagation speed of the invader. A multispecies equation system can be used to evaluate the effect of an invader on species diversity, with certain simplifying conditions, e.g. every individual is assumed to interact equally with every other individual (Teramoto 1993).

The fate of the invader and resident species becomes more difficult to model when habitat conditions are assumed to vary. Rejmanek (1989) examined the invasion of a competitively inferior species into communities that were periodically disturbed, that is, an open space of a fixed size created, and found that "intermediate" disturbances promoted the coexistence between invader and resident. One can consider situations in which optimal patches for an invader occur regularly or randomly in a temporal fashion. Those conditions can be analysed by a cellular automaton model (Etter & Caswell 1994), in which each spatial location is represented as in one of a small number of states, such as high or low density of the species, or by a sink-source system. Both require data on some basic population traits, such as dispersal, mortality, and reproduction in at least two kinds of habitats for each species under consideration, and may be more or less appropriate to simulate the fate of the different systems studied in the Programme.

The invasion by a herbivore, predator, parasite, or parasitoid can be modelled by various approaches, including that of a Lotka-Volterra system. May and Hassell (1988) carried out extensive studies on mathematical models of biological control by the introduction of natural-enemy species, and several papers introducing various modifications of the conditions for establishment of natural-enemy species have been published. Here we will extend a Lotka-Volterra system to the case when a predator invades an environment in which a prey species is patchily distributed. The basic system describes the interaction for a homogeneously distributed prey species:

$$\partial H/\partial t = D_H\, \partial^2 H/\partial x^2 + (\varepsilon - \mu H)H - aHP$$

$$\partial P/\partial t = D_P\, \partial^2 P/\partial x^2 - \delta P + bHP$$

where the first term on the right side represents diffusion, the second term of the prey (H) equation the logistic growth rate of prey in absence of the predator, the third term is the consumption rate of prey by the predator, the second term of the predator (P) equation is the death rate of predators, and the last one is the growth rate of predator population due to ingested prey. This system will be used in combination with a sink-source system to evaluate the fate of the predator when both prey and predator are patchily distributed.

Models of community assembly will be used to consider impact of invaders on communities. Those models use differential equation systems to model the sequential addition of species to communities. Species numbers increase rapidly at first, but then rise to an asymptote. The final level of species numbers depends on the connectance of the community, that is, the number of actual inter-species interactions divided by the possible number. Communities with high connectance are much harder to invade than those with low connectance. This is interpreted such that a community with relatively few species is likely to be easier to invade than a community with many species. Secondly, once the community has reached its equilibrium number of species, the process of community assembly itself makes the community harder to invade. Simply, in this case each successive, successful invasion makes the community less likely to be invaded.

Realisation of activities and deliverables

The realisation of the WP will be accomplished by a group of different expertise. The Programme will support two positions. One is for a research associate ("forskarassistent"), that should have a background in mathematical modelling and preferably with experience from risk assessment/analysis and with insights in population and community ecology. The research associate will start working with the crayfish data, and then develop the food web and community connectivity models. The second position is for a PhD candidate with a background in mathematics, statistics, and ecology. The PhD candidate will spend about half of the time on scientific training activities, including courses, seminars, and literature examinations, and half of the time on the research problems specified in the WP. During the first study year, a Ph.D. candidate is normally asked to prepare a so called Introductory paper, corresponding to 10-20 weeks of work, summarising the area of research. This paper has traditionally the form of a review, and it is hoped that it can be used as a basis for qualitative risk assessment of invasive species. In addition, travelling grants will be applied for to support the stay of the PhD candidate at an European or American research facility for risk analysis to further improve the quality of the training and hopefully also add some few more results to the deliverables list. In addition to the research associate, the PhD candidate will have two formal supervisors in the group. One is the scientific leader of the WP, with a background in risk analysis and population ecology. The other is Tobias Rydén, who is professor of mathematical statistics with experience and special interest in stochastic modelling and Markov processes. Some of the work, viz. on arrival probabilities in heterogeneous landscapes, will call for support and coworking with prof Per Lundberg at Dept of Ecology after his return from sabbatical in year 2003. Per Lundberg has a special interest in the interaction between environmental stochasticity and inherent demography and in the importance of environmental stochasticity and local population dynamics on regional patterns of dispersal. The research associate will also be encouraged to apply for a grant from a research council to support another PhD candidate that can be associated with the tasks of this programme. In this way, data from WP1 through WP6 and WP9 can be considered for the risk analysis and a tight interface established to WP8.

<u>Year 1</u>

modelling vector (e.g. currents, man, birds) dependent propagule arrival

The risk analysis will use data from WP1 on likely risk species, especially *Sargassum muticum*, on *Elodea canadensis* from WP2, and freshwater and coastal fish species identified as risk species in WP5. The analysis results will be used as input to WP8.
risks associated with travelling wave behaviour, e.g. for crayfish
by end of year course on risk analysis

Year 2
modelling and estimating arrival probabilities in heterogeneous landscapes
The risk analysis will use data from WP1 on species used in aquaria trade and aquaculture, on *Elodea canadensis* from WP2, and freshwater and coastal fish species identified as risk species in WP5.
risk analysis of establishment in heterogeneous landscape and at low population density
The risk analysis will use data from WP1 on species used in aquaria trade and aquaculture, on *Elodea canadensis* and *Nymphoides pelatata* from WP2, freshwater and coastal fish species identified as risk species in WP5, and rainbow trout and brook trout in WP6.

Year 3
risk analysis based on models for range expansion by age and habitat dependent dispersal and growth
This will use data from WP1 on species used in aquaria trade and aquaculture, on *Elodea canadensis* and *Nymphoides pelatata* from WP2, freshwater and coastal fish species identified as risk species in WP5, and rainbow trout and brook trout in WP6.
building and adopting food web and community connectivity models

Year 4
risk analysis associated with community connectivity modelling
This will use data from WP1 and WP2 on invasive plant-herbivore interactions, and on predatory and competitive effects of invasive fish species in WP5 and WP6. The impact risk analysis will also be used in combination with WP8.
general methodology for risk analysis of alien species

Work Package 8. Economics of alien aquatic species

State of the art
Today there is a great concern among ecologists of the consequences from intended or unintended introduction of alien species into aquatic ecosystems. For example, the introduction of the water hyacinth into Lake Victoria has created severe problems for other lake species, and also for humans relying on fish, or electricity from water power stations (e.g. Kateregga 2001) Another example is crayfish introductions, generating damages from pests affecting other species and thereby humans. In spite of these facts, relatively little attention has been paid by economists to this environmental problem. There are a few exceptions, Perrings (2000), which mostly relate to invasive species in terrestrial ecosystem. GISP also has a section devoted to “Economic consequences of invasive species”, thus more publications may come out in the future.

A common question in economic studies is how invasion can occur. It is usually the intended or unintended consequence of economic activities, such as trade among countries and management of the sea for fish harvest enhancement (aquaculture). One important reason for this spread of invading species is the common property characteristics of the invaded aquatic ecosystems. That is, risks of damages from invasion are not paid by the economic agents – trading and shipping firms, fishery, households etc. - causing them. It thus seems as one way of mitigating the risk of species invasion is to establish payment requirements, corresponding to the costs of species invasion risks, for all activities causing the invasion. This would create incentives for the actors to be more careful about the risks of the species in questions. Other options could be to ban certain types of goods etc. with high species invasion risks, or to require strict responsibility in case of ecosystem damages (firms then have to pay for the damage irrespective of proven guilt).

Objectives and activities
Scientific leader

Prof. Ing-Marie Gren, Dept of Economics, Swedish University of Agricultural Sciences, P.O. Box 7013, SE 750 07 Uppsala, and Beijer International Institute of Ecological Economics, P.O. Box 50005, SE 104 05 Stockholm, E-mail: Ing-Marie.Gren@ekon.slu.se

An economist is not satisfied with identifying incentives correcting market failures, but aims at finding the combination of policy instruments which generate explicit invasion targets at minimum costs, or, equivalently, for a given budget generates the largest reduction in social costs from aquatic species invasion. The ultimate purpose of this WP is thus to identify the best management strategy for species risk management. This, in turn, requires three classes of interrelated theoretical and empirical analyses, which constitute the subtasks of this project:

1) Assessing risks and impacts on ecosystem functioning from invading species. Ideally, the latter can be expressed in monetary terms, such as income losses from fishery.
2) Identifying all possible means of mitigating risks and ecosystem impacts and calculating their costs. An example is reduction in trade of risky products, the cost of which is the associated losses in firms' profits and consumers' welfare from the product.
3) Compare the efficiency performance of different incentive mechanisms – information campaigns, charges on risky activities, producer responsibility etc. – in order to identify conditions for their relative advantages.

Scientific approach

The three subtasks of this WP are strongly interlinked in such a way that the first task provides the basis for the other two. However, the questions posed and methods applied differ somewhat, and are briefly described below.

<u>1. Assessing expected social costs of invading species</u>

The expected social cost of species invasion consists of three parts: the risk of invasion, risk of ecosystem damage, and social costs from associated losses in ecosystem service production. By ecosystem service production we refer to all these goods and services of direct and indirect social value, such as fish, recreation facilities, and coastal areas' pollutant cleaning for aquatic waters (see Gren et al. 1994 for a discussion of the economics value of such services in a wetland context).

Risk of species invasion is determined by the various sources of invasion such as goods transports by ships, waste disposal, and introduction of species for special purposes like aquaculture or as ornamental plants. Assessment of species invasion risk thus requires understanding of these alien species transports (see also WP 7). Impact on ecosystem service production once invasion has occurred depends on ecosystem functioning and its ability to withstand external forces. The expected social cost of ecosystem damage as expressed in ecosystem service production, thus depends on risk of damage and the value of associated service production in monetary terms. However, it may very well be the case that the ecosystem adjustment possibilities are related to other human activities, such as pollutant loads from agriculture and traffic. The higher pollutant load, the less is the resistance to withstand other impact, and, hence, larger loss in ecosystem service production. Therefore, this part of WP 8 will also investigate the total human pressure on the aquatic ecosystem.

When estimating cost of changes in ecosystem service production, the project will apply the so-called production function approach (see e.g. Gren et al. 1994). This means that the ecosystems under investigation are described as production units of relevant ecosystems services in collaboration with the other WPs. The estimation in monetary terms is then carried out by finding monetary measurement of each of the ecosystem service. For example, the social cost of commercial fish losses are calculated as the harvest decrease times the market price of fish. When market prices are not available, as in the case of water purification and recreation values, the project will use results from other studies (Gren 1999 for water purification values and Sandström 1999 for west coast recreational values). Risks of species invasion and ecosystem damage are calculated in collaboration with WP 7 for the former part and the other WPs for ecosystem impacts.

<u>2. Identifying allocation of cost effective risk management measures</u>

This can also be expressed as calculating benefits from introducing alien species for firms, households, and others. Costs of reducing the risk of damage from introducing alien species correspond to the losses in profits born by people causing the damage. Therefore, this task of the WP is very much related to the first task. By means of task 1, possible measures for reducing risk of ecosystem damage from species invasion can then be classified into: i) reduction in species transports, and ii) increase of the resistance of the invaded aquatic ecosystem by changing the pollutant stress from the catchment area.

Since the major source of unintentional species introduction occurs through shipping, obvious options would then be a decrease in shipping by reducing the amount of goods transported and /or substitute. Alternatives are improving the technology for shipping transports, already looked into by IMO and many others, and intensified monitoring of ships, if at all possible. All of these altematives imply costs for the shipping agencies and eventually also for tax payers if monitoring programmes are paid by the public sector. This is also true for the second type of measures, which aim at reducing the risk of damage by increasing the resistance of the aquatic system. Different types of measures reducing the pollution to coastal waters can then be classified into four classes: reduction in pollutant emission at the courses (agriculture, atmospheric emissions, industry, housholds, sewage treatment plants), changes land use practices reducing the leaching of pollutant into surface and subsurface waters, creation of pollutant sinks in the drainage basins, such as cultivation of reeds (for a further description of these measures see Gren et al. 1997 and Elofsson 2000 in the case of nutrient reductions).

All of the suggested measures will affect both functioning of the ecosystems and also the risk of damage. Of special interest are measures, which have relatively large impact on both, and also allow for reducing the overall risk of damage from species invasion by diversifying risks. However, it is quite likely that the susceptibility to species invasion varies for different aquatic ecosystems, and we therefore have to calculate costs for damage risk reduction at different sites. In order to avoid excessive payments for risk reduction strategies by firms and households, costs and effects of species invasion from all mentioned damage risk reduction measures are calculated and compared for different chosen aquatic sites. Operational analysis is used for optimising measures, and the chosen program code is Gams (Brooke et al. 1998).

3. Efficient incentive mechanisms for species invasion

The third task investigates how we can implement the allocation of measures identified under 2 and also from 1. In principle, there are three classes of policies influencing peoples' behaviour: *i*) information campaigns (see also WP 10 and Table 1), *ii*) economic incentives (payments by firms for risk generating activities, or subsidies for reducing measures), and *iii*) command and control (for example, bans on uses of goods, or mandatory requirements of certain transport technology).

The first option, information campaigns seem most appealing, since it equip people with knowledge necessary for making voluntary contributions, such as changing shipping transport or stop disposal waste or live specimens into waters. The desired risk damage reduction from species invasion could then be achieved without other public intervention. Why then should firms make such voluntary commitments? One obvious answer is that this will increase profits, at least in the long run, or put the firm or the sector in a better position to meet current or expected future competition.

Some recent research show that firms are more inclined to make voluntary commitment under conditions of expected governmental regulation and/or when consumers are willing to pay a higher price for the goods in question (e.g. Segersson & Li 1999). It could also imply access to relatively low costly 'environmental friendly' capital funds. In general, one would expect that firms choose voluntary commitments when the expected cost of the governmental regulation is more expensive than the voluntary commitment, and the latter can deter introduction of governmental regulation.

However, environmental impacts of voluntary agreements, such as environmental certification systems, are today unclear. This is therefore an imprecise instrument for achieving well-defined targets for species invasion. Furthermore, although they can be directed certain targets, the risk reduction achieved may not be sufficient. Then, traditional environmental policy is needed, and we can choose between two classes of instruments: command and control, and economic instruments.

It is well known, that in the most simple case without uncertainty, economic instruments generate cost-effective achievements of environmental targets, while command and control systems are more costly. The reason is that command and control systems in general do not adjust for cost differences between firms, and hence risk reduction measures are not allocated to low cost firms. One the other hand, economic instruments such as a common charge on ecosystem damage from species invasion, implies that firms with relatively low costs find it less costly to reduce risk than to pay the charge, and high cost firms instead pay the charge. In this way, cost effectiveness is achieved since risk reduction is carried out by low cost firms. The larger the differences in marginal costs among regulated firms, the more costly is a command and control system as compared to the economic systems.

Charges also have the advantages of stimulating adaptation of new risk reduction technologies since it is relatively costly to make charge payments. This gives firms an incentive to find cheaper ways of, for example, transporting goods in a more risk free way. Under a command and control systems firms pay only for the required risk reduction, and not for the remaining risk. Another advantage with charge systems is that charge incomes can be used for reducing other efficiency disturbing taxes, such as labour income, or capital taxes.

However, in practice uncertainty with regard to stakeholders preferences and behaviour, and species' ecological impact constitute constraints for implementation of efficient environmental policies. Depending on how sensitive risk reduction costs and ecosystem functioning is to changes in species exposition, either economic or command and control systems are to be preferred. Command and control system is more likely to generate a certain target, while the outcome of charge/subsidy systems are more uncertain due to the difficulty in predicting regulated firms reactions to these instruments. Therefore, when preferences are high for a safety environmental outcome, and risk reduction costs are relatively low, command and control, and permit market systems are preferred to charge/subsidy systems. On the other hand, if risk reduction costs are relatively high, and the environmental damage is regarded as less serious, economic instruments are less costly to society then command and control systems.

It is further likely that policy differ with respect to so-called transaction costs. This is defined as all types of costs needed to implement policies creating the incentives for the emission firms to undertake abatement, such as searching for information on pollutant, negotiations with involved firms and other stakeholders, and enforcement of policy instruments. With regard to enforcement costs, they may be related to profits from violation. As shown by Gren (1992), profits from violation are higher for charges than for the permit market and command and control systems.

However, insufficient understanding of the response of the aquatic ecosystems to species invasion may require adaptive management, where small changes in policies are made in order to improve understanding of the ecosystem functioning and adjustment. But, common to all type of environmental regulation, voluntary and mandatory, is that uncertainty in market behaviour and/or political decisions is likely to delay investment in environmental cleaning technologies. If there is a variation in policies, such as relaxed or tightened technology requirements, firms can gain from waiting with investment until new information appears. Frequent policy changes will probably lead to delayed and even reduced investment in environmental friendly technologies. This is thus a social cost of flexibility in policy design, which might be required for adjusting species risk management to aquatic ecosystem functioning.

In summary, this task will 1) investigate the potential of voluntary agreements, 2) simulate economic implications of economic instruments and command and control systems under different designs, and 3) analyse the role of uncertainty in the implementation of policy instruments. The method applied for the first task is based on investigation of certification in relevant sectors and information campaigns for households, the impacts of which are transferred to relevant firms and households. The Gams programming model with data from both other tasks, i.e. benefits and costs of risk reduction measures, provides the basis for simulation economic consequences of alternative policy instruments. It is complemented with estimation of at least one type of transaction cost, enforcement cost, which is based on data from current environmental regulation in Sweden.

Deliverables		Months from start of the project
1	Economic theory of alien species management	12
2	Invaded ecosystem services in monetary terms	24
3	Costs of alien species risk mitigation	36
4	Economics of crayfish invasion	48
5	Efficient management strategies (species choice to be selected within the program)	60

On each of these topics, both scientific and popular writings will be delivered.

Work Package 9. American signal crayfish

State of the art

Today there are two freshwater crayfish species in Sweden: the native noble crayfish (*Astacus astacus*) and the signal crayfish (*Pacifastacus leniusculus*). The signal crayfish was intentionally introduced into the country starting in the 1960s, to compensate for the fisheries opportunities lost due to the negative effects of crayfish plague (*Aphanomyces astaci*) on the once commercially important fishery on noble crayfish.

Both historically and today the crayfish fishery constitute a substantial social, cultural and economic value. One kilogram of crayfish was sold for an approximate price of 325 SEK for noble crayfish and 185 SEK for signal crayfish on the wholesale market in year 2000. The interest and the demand for crayfish is, however, greater than what is produced nationally so between 1500 and 2000 tons of cooked crayfish and some 40 to 50 tons of live crayfish are imported annually to meet the demand. The best estimate of the annual crayfish production in Sweden probably comes from a large-scale questionnaire about the fishing habits of the Swedish people (Fiskeriverket 2000). According to this survey 225 tons of noble crayfish and 1200 tons of signal crayfish are harvested annually in the country.

It is estimated that Sweden had 30 000 populations of noble crayfish at the turn of the last century and that only 5% or 1500 of these remain now a hundred years later (Fiskeriverket 1993). The noble crayfish is thus threatened as a species mainly because of the crayfish plague, acidification, pollution and, more recently, the introduced signal crayfish as a vector for the crayfish plague and as a strong competitor. An action plan for the conservation of the noble crayfish has been produced (Fiskeriverket & Naturvårdsverket 1998). Since May 2000 the noble crayfish is classified as vulnerable on the national Swedish red list for endangered species.

Crayfish plague is a fungal disease, spread between crayfish individuals through zoospores. The disease is primarily spread between lakes and rivers through infected crayfish, fishing gear, fish and water carrying plague spores. The disease, originating from North America, was introduced into Sweden in 1907 with a shipment of live but infected noble crayfish imported for consumption from Finland. The plague usually quickly kills a whole noble crayfish population. Despite the fact that the noble crayfish populations have decreased, many are still hit by the plague and during the time period of 1994 -1997, 150 localities with noble crayfish were struck by the plague. Although the vectors for the disease have been identified through laboratory studies no attempts have so far been made to construct an epidemiological model for the host-parasite interaction and the spread of the disease between natural waters. Likewise only a few studies have produced risk analyses for the transport and trade with freshwater crayfish. So far no treatment exists for the disease once it is established. The zoospores can, however, only survive for a couple of weeks outside the host, a freshwater crayfish, and once all crayfish are gone the disease, without new hosts, disappears.

Signal crayfish is today known from 2900 localities in Sweden. The main reason why signal crayfish is a threat to noble crayfish populations is that they carry the crayfish plague as a benign infection encapsulated by deposition of melanin in the cuticula. This means that crayfish plague becomes permanently established in a water body when signal crayfish is stocked. Since signal crayfish functions as vector for the crayfish plague the stocking of signal crayfish in Sweden has led to an accelerated spread of the plague, even when the number of populations that can be infected steadily have declined. This is well illustrated by a compilation of the plague outbreaks during ten-year periods in two counties in Sweden during the 20th century. There was a fivefold increase of the plague outbreaks during the 1980s, after a large number of signal crayfish introductions had been performed in the two counties in the 1970s. To stock fish and crayfish requires a permit from the regional administrative board, in order to control for spread of diseases. Unfortunately a great number of illegal stockings have been done and this has further increased the spread of the plague. Illegal stockings have caused the main parts of the plague outbreaks in noble crayfish populations after 1980. To conclude, even if the introduction of signal crayfish into Sweden is the basis of a good fishery today, it has been an obvious disadvantage for the noble crayfish. On the very few occasions when signal crayfish do not carry the crayfish plague, it still outcompetes the noble crayfish in the long run. It is more fecund, grows slightly faster, is less susceptible to predation, interferes sexually during the mating between noble crayfish and is more aggressive in direct interactions over resources. The different effects of the two species on the ecosystem needs more study but the differences found so far have not been so large. Signal crayfish is, however, a more severe predator than noble crayfish on amphibian eggs and tadpoles. Thus, although Sweden has enjoyed short-term benefits from the new species, including socio-economic, commercial, recreational and biological value, at the time of the introduction one was unaware of the long-term effects. Several of these negative effects are evident today.

To try to counteract the negative effects of the signal crayfish introduction on the native noble crayfish, legislative measures have been taken, including restricting permits for introductions to certain parts of the country, prohibiting movement of crayfish fishing gear without disinfection and banning movement of fish, gear and live crayfish once the plague has hit a crayfish stock. In the last years no economic support is given to stocking or management of signal crayfish.

The magnitude of illegal introductions may be estimated from comparing the permits given by the regional authorities for introduction of signal crayfish with the actual occurrence of signal crayfish in lakes and running waters. Such data are available from some of the County Administrative Boards.

Objectives and activities

Scientific leader: Senior scientist Lennart Edsman, Inst. of Freshwater Research in Drottningholm, National Board of Fisheries, SE 178 93, Drottningholm, Sweden.
E-mail: lennart.edsman@fiskeriverket.se

This workpackage is a case study of an introduced alien aquatic organism and will work in close connection to WP 7 and WP 8 and supply them with data needed for the ecological and the socio-economic analyses of the introduction of the signal crayfish. The aim is to give these two WPs data to start modelling risk and economy already at an early stage of the Programme. The experiences derived from this work can then be utilised when modelling the effects on the organism groups of the other work packages.

The general biology of the signal crayfish is quite well known from the literature with a number of experimental and field studies. It has been intensively studied since it is now quite widespread and has been introduced into many European countries and the species is also used in aquaculture.

The available knowledge about the crayfish plague is so far mainly restricted to laboratory studies but this topic is well covered in the scientific literature. The main vectors have also been identified and human activities, connected to the great economic and social interest, is probably the most important vector. There are, however, no ecological models describing the epidemiology of the plague. An ecological model that also incorporates human activities and behaviour will be the outcome of this project.

Realisation of activities and deliverables

This workpackage will run during the two first years of the main Programme and the tasks are to:

- compile the available literature on signal crayfish, noble crayfish and the crayfish plague
- collect information from the regional authorities concerning the distribution of the crayfish species, introductions, and crayfish plague outbreaks
- finalise the work that has been started with a database containing data on occurrence of the two crayfish species, results from monitoring, introductions of the two species and the registered outbreaks of crayfish plague
- deliver the compiled information to WP 7 and WP 8
- collaborate with WP 7 and WP 8 during the modelling process

The outcome of this WP may also serve as a basis for national and regional authorities, when deciding on new actions in legislation, rules, regulations and policies, and when implementing these regulations and policies. It will also serve as a scientific foundation for better codes of practice for trade, stocking and management of crayfish in Sweden. Crayfish has an important role in rural development with social, recreational, and commercial values. There is a great need and demand for knowledge based management strategies for crayfish.

Work Package 10. Public awareness, scientific synthesis and dissemination of results

State of the art and activities during the program

Intentional importation of many aquatic organisms such as fish, crustaceans and molluscs is already today strictly regulated (Fiskeriverket 2001), while for aquatic plants there are no regulations at all for private imports (Växtskyddsinspektionen pers. comm). Although the 1992 Convention on Biological Diversity (SÖ 1993:77 in SEPA 1997) states that contracting parties should take measures to prevent import of, control or extirpate those introduced species that threaten ecosystems, habitats or other species, there seems to be no fully conclusive legislation in Sweden covering all kind of species. For intentional import of aquatic invertebrates other than crustaceans and molluscs there are only recommendations such as the Agenda 21, SEPA's Policy Document (SEPA 1997), the ICES Code of Practice (Anon. 1995), the latter also giving advice to minimize the risk with species associated with aquaculture target organisms (such as epibionts, parasites, organisms in water inside the bivalves or associated in the containers). Furthermore, new trade patterns within the EU, which have not been in place before, may result in new transport routings of live marine organisms, thereby transmitting species with epibionts into other areas. Although strict EU and national regulations are in place for controlling the transfer of disease agents this is less often the case for epibionts and/or enclosed living non-disease organisms.

However, also where strict regulations apply there are still problems due to ignorance and/or lack of information on the effects an introduced species may have ecologically or by bringing parasites or disease agents. Two activities where a widespread information effort is needed are illegal releases from aquaria as well as of fish and shellfish imported live for consumption (ICES WGITMO 2000, 2001) including also various freshwater crayfish species. Such information must be short but convincing and, when addressing the general public, be presented in an easily understandable, short and "appetizing" maner. Campaigns such as production and distribution of information material of the type "You can help" are needed to make people in general to assist in reducing the further spread of alien aquatic species and thus their impact.

For totally accidental introductions the awareness within the shipping industry of the problems with organisms discharged from ballast tanks has increased, but could be higher. Some countries such as Australia (incl. also a risk analyses based on a list of target species) and the US already have laws demanding ballast water exchange before approval of ballast water release. Other countries have guidelines and the IMO voluntary guidelines of exchange of ballast water will hopefully soon be replaced by mandatory regulations for international shipping. Since exchange can never more than minimize the risks, the question of treatment of ballast water is now a very "hot" issue and already subject to many studies in the US (J. Carlton pers. comm.) as well as in several ongoing EU projects. The limited budget of AQUALIENS, unfortunately will force us to leave the matter of treating ballast outside, since one Ph.D student may not add much extra to all the studies already going on. The proximity of an area to a harbour where ballast water discharges occur, however, will be incorporated among the geographical risk factors.

Even in a smaller scale, especially for freshwater systems or between different sea areas, movements of boats and other submersible equipment (incl. fishing gear and diving bags etc.) between different water bodies may be a vector for new introductions. Thus better information on precaution measures to be taken should be distributed among e.g. boating and diving associations. However, it is more difficult to minimize the risks in gardening, with more and more new species on sale. Probably few of us would like to stop having foreign species in our gardens, but this has been emphasized in Canada and the US. Also we wish plants are hardy enough to survive in our climate and search for such strains, which increases the risk of their establishment in the wild. This is not only a problem for terrestrial ecosystems but also highly relevant for freshwater (see WP 2).

Target groups and kind of information needed

To better cover these obvious gaps in dispersal of information, the project coordinator will already in parallel to the running projects also suggest measures to be taken for better information to all the various target groups (Table 2, see next page), since in general the knowledge of the risks of introducing foreign species is meager. The Table presented here, should be seen as a first step to see which groups ought to be targeted and on which level they need information. During the work process several groups in this Table probably will be merged. However, for groups who need less detailed information, one also has to bear in mind that the information material must be presented differently, depending on the level of education and the specific interests of the groups. Unfortunately, also many biological scientists have little idea of the risks involved when moving non-established exotics or Swedish species between different geographical areas (e.g. the Swedish west coast and the Baltic Sea) for use in *in situ* experiments or laboratory studies in flow-through systems without quarantine, thus jeopardizing the surrounding aquatic ecosystems.

The activites outlined above can start already early during the project period. At the end of the project the results won, especially those within WP 7 and WP 8, will be analyzed also for the potential of new actions in legislation.

Table 2. Target groups for dissemination of information about risks with establishment of introduced aquatic species. For explanations of areas to inform on and kind of information, see below.

Target groups / Knowledge needed (for type and level see notes below)	**1** Exist	**2** Exist	**3** Exist	**4**	**5**	**6**	**7**	**8** Exist	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**
Aquaculture professionals and companies	+++	+++	++	+++	+++	+++	+++	+	+	++	+	++	+++	++	+	-
Fishery consevation associations	+++	+++	+++	+++	+++	+++	+++	++	++	+++	++	++	+++	++	+	++
Fishery authorities	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	++	+++	+++	+++	+++
Fishery organisations, professionals	+	+	+	+	+++	++	+	++	++	+	+	++	+	+	+	+
Fishermen	+	+	+	+	+++	+	-	++	++	+	+	++	+	+	-	-
Recreational fishing (organisations, clubs)	+	+	+	+	++	++	-	++	++	+	+	++	+	+	+	+
Shops selling live imported fishing baits etc.	++	+	-	-	+	++	-	-	-	-	+	-	+	-	-	+
Shops etc selling live imported shellfish	++	+	-	+	++	++	-	-	-	-	+	+	+	-		+
Maritime authorities	+++	+++	++	-	++	++	-	-	+	+	+++	++	+++	++	+++	+++
Harbour authorities	+++	+++	-	-	+	+	-	-	+	+	++	++	+++	++	+	++
Shipping companies	++	+++	-	-	+	+	-	-	-	+	++	+	++	+	+	++
Warfs	+	+	-	-	+	+	-	-	+	-	++	+++	+	-	-	-
Recreational boating organizations, clubs etc	+	+	+	-	+	+	+	+	+	++	+	++	++	+	-	++
Guest harbours and marinas	+	+	-	-	-	+	-	+	+	+	+	++	++	+	-	++
Companies selling secondhand boats	+	+	-	-	-	+	-	-	-	-	+	-	+	-	-	+
Regional authorities	+++	+++	+++	++	+++	+++	++	+++	+++	+++	+++	+++	+++	+++	+++	+++
Local authorities	+++	+++	+++	+	+++	+++	+	+++	++	+++	++	++	+++	+++	+++	+++
Water management associations	++	++	+++	++	+++	+++	+	+++	++	+++	++	++	+++	+++	++	+++
Nature organisations and NGOs	++	++	+++	+	++	+++	+	++	++	++	++	++	+++	+++	++	+++
Scientists/teachers in biology, limnology, oceanography and environmental sciences	++	++	++	+	+++	+++	++	+++	+++	++	+++	+++	+++	+++	++	+++
University students in biology, limnology, oceanography and environmental sciences	+	+	+	+	++	++	+	++	++	+	++	++	+++	++	+	++
Museums in Natural history, public aquaria etc	+	+	++	+	+	+++	+	+++	+++	++	++	+++	+++	+	+	+++
School teachers	+	+	++	+	++	+++	+	+++	+++	++	+++	+++	+++	++	+	+++
School pupils	-	-	+	+	+	++	-	+	+	+	+	+	++	+	+	+
Botanical/zoological associations	+	+	+	+	++	+++	+	+++	+++	++	++	+++	+++	+	+	++
Diving organisations and clubs	+	+	+	+	++	+++	-	+++	+++	+	++	+++	+++	+	+	++
General public	-	-	+	+	++	++	-	+	+	+	+	+	++	+	+	+
Aquaria trade (retailers and shops)	++	+	+	+++	+++	+++	+	-	-	-	++	-	++	-	-	++
Shops etc. selling aquatic ornamental plants	++	+	+	+++	++	+++	+	-	-	++	++	-	++	-	-	++

Kind of knowledge needed (+++ on a detailed level, ++ where to find details, + aware of the information, - not applicable)

1) Existing laws and regulations incl. proper quarantine regulations = *spread of existing documents*
2) Existing international guidelines and Codes of practice (IMO, ICES, EIFAC) = *spread of existing documents*
3) NV policy on introduced species = *spread of existing documents*
4) How to prevent escapes of species kept in captivity*?*
5) Risks of spreading parasites and other disease agents =*?*
6) Risks of unintentional spreading of other organisms = *AQUALIENS*
7) Knowledge of risks of hybridization with native species *?*
8) Knowledge of aquatic species already introduced in Sweden = *spread of existing documents or AQUALIENS summarizes information*
9) Species to watch for (mostly those already introduced in other northern European waters) = *AQUALIENS*
10) Areas vulnerable to introductions = *AQUALIENS*
11) Vectors of importance = *AQUALIENS*
12) How to identify non-native aquatic species or whom to ask = *List of experts to be prepared within AQUALIENS*
13) The problem with introduced species in general = *AQUALIENS summarizes information*
14) Risk assessment / analyses = *AQUALIENS*
15) Costs depending on introduced species = *AQUALIENS*
16) How to spread information / tell customers etc. of risks = *AQUALIENS to suggest information material*

PROGRAMME MANAGEMENT AND LINKS TO OTHER PROGRAMMES

Organisation

The Programme will have a co-ordinator and the scientific leaders of the Work Packages (WP) will constitute a Steering Committee. We suggest that all scientific leaders are involved in the Steering Committee due to the large geographical spreading of the partners and the diversity in scientific fields involved. The planning group has suggested that professor Inger Wallentinus should be the co-ordinator (for adminstrative experiences see personal CV, Appendix I). When the calls for the open WP is finalized it will be decided if there also should be an ad hoc group ("Arbetsutskott") of fewer persons to deal with more urgent matters, including following up that the activities match the schedules. There will not, however, be any Formal board running the Programme and it is understood that all partners will receive their own contract from the SEPA (see also Budget) and thus they have the economic responsibility for their WPs and are also committed to reserve money to cover the higher costs for the Ph.D students during the second half of the Programme.

The co-ordinator will have a position as a programme secretary for adminstrative help, the first four years budgeted for a half-time position, increased to 80% during the final year. It has not yet been decided who that person will be, but it is necessary that he/she is working in close connection to the co-ordinator. The tasks include internal information and contacts between the WPs (scientific as well as covering more practical matters), external information including producing and maintaining an active home-page as well as help developing elements on which new information material can be produced for various target groups. The programme secretary will also help formulating press releases, arranging the workshops, courses, seminars etc. and keep contact with other programmes of interest. At the end of the Programme the main task will be to make all WPs work together to produce the final results and that all promised results will be available for the synthesis.

The Ph.D. students involved in the project will be encouraged to go and also do practical work together with the Ph.D- students in other Work Packages, to get a better idea of the total aims of the project and to achieve a better consolidation of the Programme. The plan is to advertise these Ph.D student positions at the same time in one large call for new students with the intention of attracting the very best students and at the same time make the Programme more visible. Some joint Ph.D courses will be arranged within the Programme, some of which may also engage other scientific personal inolved and/or other Ph.D-students.

There will be three workshops (see Fig. 3) open also for "avnämare" such as national and regional authorities, those engaged in management, NGOs and other stakeholders. We also plan to call for some international experts on introduced species to give open seminars to keep an internationally high scientific level of the Programme. Some of the scientific leaders are already engaged in international working groups and organisations dealing with the problems caused by introduced species.

Cooperation with other large programmes

At the national level, links with other programmes in connected scientific fields will be developed with the aim of exchanging information and results. This especially concerns the MARBIPP-programme working on biodiversity in marine and brackish waters, since many introduced species have had a negative impact on native species and threaten the biodiversity e.g. through mass occurrences or trophical cascades. Examples of other programmes of interest are MARE (financed by MISTRA), the second phase of SUCOZOMA (financed by MISTRA) and the project on biofouling planned as a continuation of MASTEC, which was financed by "Strategiska Stiftelsen". Also projects dealing with GMOs are of interest from a risk perspective point of view.

The economic team within the MISTRA financed SUCOZOMA investigates and calculates economic values of fish and fishery under alternative coastal zone management options. This work will be of interest for WP8 when assessing impacts of species invasion of fishery. However, the economic analysis within SUCOZOMA does not take uncertainty into account. A complementary collaborator is therefore another MISTRA financed program, MARE, the purpose of which is to establish the scientific basis for cost effective nutrient management of the Baltic Sea. Among others, the MARE research program quantifies uncertainty in costs of nutrient abatement measures and also in nutrient transport within the Baltic Sea. This work may be of value for several WPs within AQUALIENS.

BUDGET AND OPEN CALLS

Budget

Budget calculations have been based on the total sum of 30 million SEK during a 5-year period. All sums given per WP include 18+12 % on netto for university overhead and 10 % on netto for direct costs at the departments. Any additional overhead costs need to be covered within the money allocated. For most WPs (1-3/4, 6-8) the budget will allow one Ph.D student position, starting the first two years on "utbildningsbidrag" and then having a "doktorandtjänst" the last two years. Thus all these WPs will need to reserve money during the first two and a half years to cover during the last two and a half years. It is assumed that all Ph.D students teach 10% throughout their career, paid for by money from their own university. Thus the total period for their Ph.D studies will be longer than four years. For WP 5 the same total sum will be split almost equally during the years to be able to cover the demand of the National Board of Fisheries (incl. overhead costs), which on the other hand will pay more for material and travelling. In case other positions will be used (e.g. postdoc positions) the total sum for a WP will still be the same and the time for each such position then needs to be regulated. If a Ph.D student is employed on the conditions given above, the budget also allows for material and/or travels within each WP task (except WP 5) for year 1-5 with the following sums: 200 000, 215 000, 150 000, 100 000 and 100 000 SEK (+ university and department overhead costs). If the Ph.D. student is employed on other conditions these sums may be smaller. For WP 9 a grand total of 409 500 SEK is calculated, enabling employment during 8 months for a person well acquainted with how to extrapolate and summarize the old data on American signal cray fish in Sweden needed for WP 7 and 8.

A sum of 250 000 and 150 000 SEK (+ university and department overhead costs) are reserved for courses during the first two years and for the 3 workshops (year 1, 3 and 5) 300 000, 275 000 and 500 000 SEK (+ university costs), respectively. The new budget cannot finance the co-operation with other programmes, which must be covered by the relevant WPs. Travelling for activities within the frame of the whole Programme is calculated to 900 000 SEK (+ university and department overhead costs) year 1-5. The budget for the final synthesis is 850 000 SEK (+ university and department direct costs).

To be able to co-ordinate the Programme the co-ordinator needs to allocate money to have a reduced teaching load ("friköp") corresponding to 20% year 1-4 and 40% year five amounting to a total sum of 901 400 SEK (+ university and department overhead costs). The budget for the programme secretary (50% year 1-4, 80 % year 5) is calculated to a total of 1 347 500 SEK (+ university and department overhead costs).

A detailed budget for all WPs, Programme coordination, courses, synthesis etc. is given in Appendix II. If the Programme start does not coincide with that of the fiscal year, proportions need to be calculated.

Open calls

One full WP (3/4) is totally open for other applicants corresponding to a total cost (including Ph.D-student/postdoc positions) of 2.715 million SEK for the five-year period i.e. 9%of the total budget (including university overhead and department costs). The position as research associate ("forskar-assistent) within WP 7 will also be announced as an open call by the SEPA, the salary part corresponding to 2.690 million SEK (9.7%). Together these two calls corresponds to 18.7 % of the total budget. We hope these calls can be opened very shortly after a positive decision on the Programme is taken, not to have any major delays in activities which might jeopardize the final synthesis.

Five of the other WPs will have open calls for new Ph.D students which amounts totally to 8.210 million SEK, corresponding to 27.4 % of the total budget. WP 8 may instead for a Ph.D student open a position as a postdoc, where the money available, 1.642 million SEK, only will cover a shorter time period than five years, but with plans to add additional money from other sources. This open position corresponds to 5.5 % of the total budget.

Thus totally half (51.6 %) of the Programme budget will then be open for new applicants.

SCHEDULE AND DELIVERABLES

In Fig. 3 (next page) the main activities with the different Work Packages are summarized for the five year period including main publications. Also given are the approximate times for two scheduled courses and for the three workshops. For more details on the activities see the text of each Work Package.**Fig. 3**

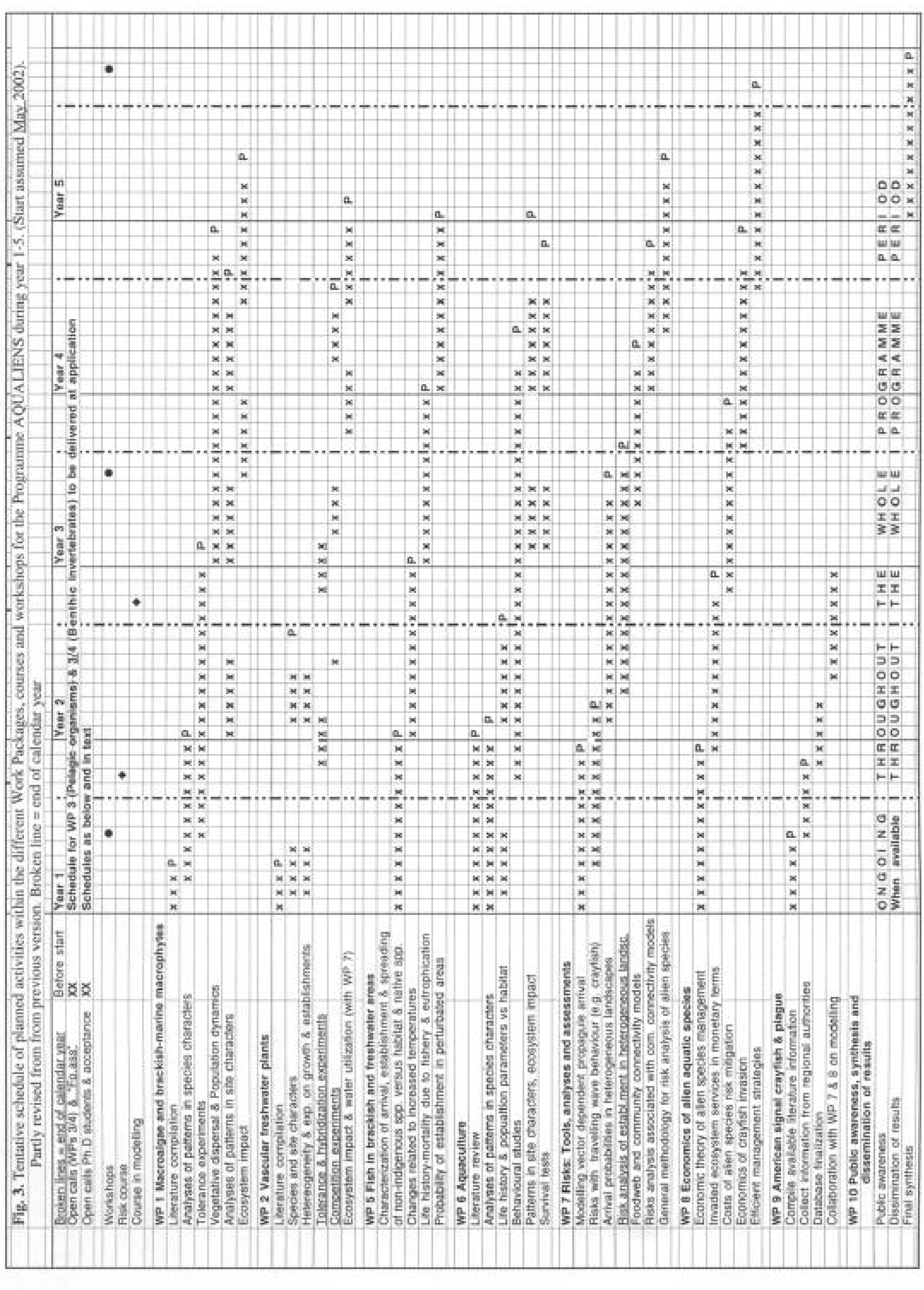

Fig. 3. Tentative schedule of planned activities within the different Work Packages, courses and workshops for the Programme AQUALIENS during year 1-5. (Start assumed May 2002). Partly revised from from previous version. Broken line = end of calendar year

REFERENCES

Allee, W.C., Emerson, A.E., Park, O., Park, T. & Schmidt, K.P. 1949. *Principles of Animal Ecology*. Saunders, Philadelphia.

Anderberg, A. 1992. Smal vattenpest, *Elodea nuttallii*, en ny vattenväxt i den svenska floran. *Svensk Botanisk Tidskrift* **86**: 43–35.

Anon. 1995. *ICES Code of Practice on the Introductions and Transfers of Marine Organisms 1994*. International Conseil for the Exploration of the Sea, Copenhagen, 12 pp.

Anon. 1997. *Opportunistic Settlers and the Problem of the Ctenophore Mnemiopsis leidyi Invasion in the Black Sea*. IMO/FAO/UNESCO-IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Pollution (GESAMP). GESAMP Reports and Studies No **58**, 84 pp.

Ashton, P.J. & Mitchell, D.S. 1989. Aquatic plants: patterns and modes of invasion, attributes of invading species and assessment of control programmes. *In* Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H. Kruger, F.J., Rejmanek, M. & Williamson, M. (eds): *Biological Invasions: A Global Perspective,* pp. 111-154. John Wiley & Sons, Chichester.

Bachmann, V., Beisel, J.N., Usseglio-Polatera, P. & Moreteau, J.C. 2001. Decline of *Dreissena polymorpha* in the River Moselle: biotic and abiotic key factors involved in dynamics of invasive species. *Archiv für Hydrobiologie* **151**: 263-281.

Banks, R.B. 1994. *Growth and Diffusion Phenomena*. Springer-Verlag, Berlin

Berejikian, B.A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 2476-2482.

Bowmer, K.H., Mitchell, D.S. & Short, D.L. 1984. Biology of *Elodea canadensis* Michx. and its management in Australian irrigation systems. *Aquatic Botany* **18**: 231–238.

Brandrud, T. E., Mjelde, M. & Johansen, S. 1999. Vasspest (*Elodea canadensis*). Effekter på biologisk mangfold, spridningsmønstre of tiltak. *NIVA Rapport LNR 4075-99*.

Brooke, A., Kendrick, D., & Meeraus, A. 1998. *GAMS. A User's Guide.* The Scientific Press, San Francisco.

Brown, J.H 1989. Patterns, modes and extents of invasions by vertebrates. *In* Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H. Kruger, F.J., Rejmanek, M. & Williamson, M. (eds): *Biological Invasions: A Global Perspective,* pp. 85-109. John Wiley & Sons, Chichester.

Carlton, J.T. 1989. Mans role in changing the face of the ocean - biological invasions and implications for conservation of near-shore environments. *Conservation Biology* **3**: 265-273.

Carlton J.T. & Geller J.B. 1993. Ecological roulette - the global transport of nonindigenous marine organisms. *Science* **261**: (5117) 78-82.

Carlton, J.T.; Reid, D.M. & van Leeuwen, H. 1995. Shipping study. *The Role of Shipping in the Introduction of Nonindigenous Aquatic Organisms to The Coastal Waters of The United States (Other than the Great Lakes) and an Analysis of Control Options*. Nat. Sea Grant Coll. Prog./Ct. Sea Grant Proj. R/ES6, USA, 213 (Appendices A-I (122 pp.)) pp.

Case, T.J. 1991. Invasion resistance, species build up, and community collapse in metapopulation models with interspecies competition. *Biological Journal of the Linnean Society* **42**: 239-66.

Chapman, A.S. 1999. From introduced species to invader: what determines variation in the success of *Codium fragile* ssp. *tomentosoides* (Chlorophyta) in the North Atlantic Ocean. *Helgoländer Meeresuntersuchungen* **52**: 277-289.

Cohen, A.N. & Carlton, J.T. 1995. *Nonindigenous Aquatic Species in a United States Estuary. A Case Study of the Biological Invasions of the San Fransisco Bay and Delta*. U.S. Fish & Wildlife Service, Arlington, VA, 272 pp.

Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science, N.Y.* **199**: 1302-1310.

Dendène, M.A., Rolland, T., Trémolières, M. & Carbiener, R. 1993. Effect of ammonium ions on the net photosynthesis of three species of *Elodea*. *Aquatic Botany* **46**: 301–315.

Ehrlich, P. 1989. Attributes of invaders and the invading processes: vertebrates. *In* Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H. Kruger, F.J., Rejmanek, M. & Williamson, M. (eds): *Biological Invasions: A Global Perspective*, pp. 315-328. John Wiley & Sons, Chichester.

Elmgren, R. 2001. Understanding human impact on the Baltic ecosystem: Changing views in recent decades. *Ambio* **30**: 222-231.

Elofsson, K. 2000 Cost effective reductions of stochastic nitrogen and phosphorous loads to the Baltic Sea. *Loads to the Baltic Sea*. Working Paper Series No. 6, Department of Economics, Swedish University of Agricultural Sciences, Uppsala.

Eno, C.N., Clark, R.A. & Sanderson, W.G. 1997. *Non-native Species in British Waters: A Review and Directory*. Joint Nature Conservation Committee, Peterborough, 152 pp.

Etter, R.J. & Caswell, H. 1994. The advantages of dispersal in a patchy environment: effects of disturbance in a cellular automaton model. *In* Eckelbarger, K.J. & Young, C.M. (eds): *Reproduction, Larval Biology and Recruitment in the Deep-Sea Benthos*, pp. 285-305. Columbia University Press.

Farnham, W.F. 1997. Invasive species on the English Channel and Atlantic coasts. *In* Actes de Colloques Septembre 1997: *Dynamics of Invasive Marine Species: Application to the Expansion of Caulerpa taxifolia in the Mediterranean*. Académie des Sciences, pp. 15-35. Lavoiser Technique & Documentation, Paris

Filipsson, O. 1994. Nya fiskbestånd genom inplanteringar eller spridning av fisk. *Information från Sötvattens-laboratoriet, Drottningholm* **2**.

Fiskeriverket 1993**.** Möjligheten att öka flodkräftbestånd i svenska vatten. *Information från Sötvattenslaboratoriet, Drottningholm*. **2**: 66 pp.

Fiskeriverket 2000. Fiske 2000: En undersökning om svenskarnas sport- och husbehovsfiske. *Finfo* **2000:1**

Fiskeriverket 2001. *Utsättning och Spridning av Fisk: Strategi och Bakgrund*.

Fiskeriverket & Naturvårdsverket 1998. *Åtgärdsprogram för Bevarande av Flodkräftan*. Stockholm. 38 pp.

Fisher, R.A. 1937. The wave of advance of advantageous genes. *Ann. Eugenics* **7**: 255-369

Gollasch, S. 1996. *Untersuchungen des Arteintrages durch den Internationalen Schiffsverkehr unter Besonderer Berücksichtigung Nichtheimischer Arten*. Ph.D. Diss., Dr. Kovac, Hamburg, 314 pp.

Gollasch, S. & Leppäkoski E. (eds) 1999. *Initial Risk Assessment of Marine Alien Species in Nordic Waters*. Nord 1999: 8. Nordic Council of Ministers, Copenhagen, 184 pp.

Gollasch, S. & Rosenthal H. 1999. National Report for Germany. *In*: *Report of the Working Group on Introductions and Transfers of Marine Organisms, Conwy, United Kingdom, 14-16 April 1999*, pp. 30-33. International Conseil for the Exploration of the Sea, Copenhagen. ICES CM 1999/ACME:1 Ref.: E+F.

Gollasch, S. & Rosenthal H. 2000. National Report for Germany. *In*: *Report of the Working Group on Introductions and Transfers of Marine Organisms, Parnu, Estonia 27-29 March 2000*, pp. 27-31. International Conseil for the Exploration of the Sea, Copenhagen. ICES CM 2000/ACME:07 Ref.: E+F.

Gren, I-M. 1999. Value of land as pollutant sink. *Ecological Economics* **30**: 419-431

Gren, I-M., Folke, C., Turner, K. & Bateman, I. 1994. Primary and secondary values of wetlands. *Environmental and Resource Economics* **4**: 55-74.

Gren, I-M., Elofsson, K. & Jannke, P. 1997. Cost effective nutrient reductions to the Baltic Sea. *Environmental and Resource Economics* **10**: 341-362.

Grosholz, E.D. & Ruiz, G.M. 1996. Prediciting the impact of introduced marine species: Lessons from the multiple invasions of the European green crab *Carcinus maenas*. *Biological Conservation* **78**: 59-66.

Gruszka, P. 1999. The river Odra estuary as a gateway for alien species immigration to the Baltic Sea basin. *Acta Hydrochimica et Hydrobiologica*. **27**: 374-382.

Haesloop, U. 1992. Establishment of the Asiatic clam *Corbicul*a cf. *fluminalis* in the tidal Weser River (N. Germany). *Archiv für Hydrobiologie* **126**: 175-180.

Hall, S.R. & Mills, E.L. 2000. Exotic species in large lakes of the world. *Aquatic Ecosystem Health & Management* **3**: 105–135.

Hastings, A. 1996. Models of spatial spread: a synthesis. *Biological Conservation* **78**: 143-148.

Hayes, K.R. 1997. *A Review of Ecological Risk Assessment Methodologies*. CSIRO, Division of Marine Research, Australia. Technical Rep. 13, 1-116.

Hayes, K.R. 1998. Ecological risk assessment for ballast water introductions: A suggested approach. *ICES Journal of Marine Science* **55**: 201-212.

Hayes K.R. & Hewitt C.L. 2000. Quantitative biological risk assessment of the ballast water vector. *In* Pederson, J. (ed.): *Marine Bioinvasions*. Proceedings of the First National Conference, January 24-27, 1999, pp 370-386. Massachusetts Institute of Technology, Cambridge, MA

Hickley, P. 1994. Stocking and introduction of fish - a synthesis. *In* Cowx, I. (ed.): *Rehabilitation of Freshwater Fisheries*, pp. 247-254. Blackwell Scientific Publications, Oxford.

ICES 2000. *Report of the Working Group on Introductions and Transfers of Marine Organisms, Parnu, Estonia 27-29 March 2000*. International Conseil for the Exploration of the Sea, Copenhagen. ICES CM 2000/ ACME: 07 Ref.: E+F, Copenhagen.

ICES 2001. *Report of the Working Group of Introductions and Transfers of Marine Organisms, Barcelona, Spain, 21-23 March 2001*, pp 47-48. International Conseil for the Exploration of the Sea, Copenhagen. ICES CM 2001/ ACME: 08, Ref. E, F, Copenhagen.

Jansson, K. 1994. Alien species in the marine environment. *Swedish Environmental Protection Agency Report* **4357**: 1-68

Johansson, B. 1994. *The Dispersal of Propagules in Aquatic Environments: an in situ Method Applied to the Brown Alga Sargassum muticum*. M.Sc. Thesis, Dept. Marine Botany, Göteborg University, 25 pp.

Josefsson, M. 1999. Introduktioner av främmande arter i svenska sjöar och vattendrag. *Naturvårdsverket Rapport* **4941**: 1-112 (In Swedish with English summary)

Josefsson, M. & Andersson, B. 2001. The environmental consequences of alien species in the Swedish lakes, Mälaren, Hjälmaren, Vänern and Vättern. *Ambio* **30**: 514-521.

Karås, P. & Thoresson, G. 1992. An application of a bioenergetics model to Eurasian perch (*Perca fluviatilis*). *Journal of Fish Biology* **41**: 217 230.

Karlsson, J. & Loo, L-O. 1999) On the distribution and the continuous expansion of the Japanese seaweed - *Sargassum muticum* - in Sweden. *Botanica Marina* **42**: 285-294.

Kateregga, E. 2001. The welfare cost of power outages: A CVM analysis on the households in the suburbs of Kampala, Jinja and Entebbe. Licentiate thesis, Department of Economics, Göteborg University.

Kolar, C.S. & Lodge, D.M. 2001. Progress in invasion biology:predicting invaders. *Tree* **16**: 199-210.

Lagerberg, T. 1956. *Vilda växter i Norden*. **Band I**. Natur och Kultur, Stockholm.

Leppäkoski, E. 1984. Introduced species in the Baltic Sea and its coastal ecosystems. *Ophelia* **Suppl. 3**: 123-135.

Leppäkoski, E., Olenin, S. Gollasch S. (eds) in press. *Invasive Aquatic Species of Europe: Distributions, Impacts and Management*. Kluwer Academic Publishers, Dordrecht.

Levine J.M. 2000. Species diversity and biological invasions: Relating local processes to community pattern. *Science* **288, 5 May**: 852-854.

Lodge, D.M. 1993. Species invasions and deletions: Community effects and responses to climate and habitat change. *In* Kareiva, P.M., Kingsolver, J.B. & Huey, R.B. (eds): *Biotic Interactions and Global Change*, pp. 367-387. Sinauer, Sunderland, Massachusetts, USA.

Löfgren, L. 1976. Sjögullet ett hot mot Mälaren. *Västmanlands Läns Natur* **1**: 26–32.

Mack, R.N. 1996. Predicting the identity and fate of plant invaders: Emergent and emerging approaches. *Biological Conservation* **78**: 107-121.

Maggs, C.A. & Stegenga, H. 1999. Red algal exotics on North Sea coasts. *Helgoländer Meeresuntersuchungen* **52**: 243-258

Magnuson, J.J., Webster, K.E., Assel, R.A., Bowser, C.J., Dillon, P.J., Eaton, J.G., Evans, H.E., Fee, E.J., Hall, R.I., Mortsch, L.R., Schindler, D.W. & Quinn, F.H. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian shield region. *In*: *Freshwater Ecosystems and Climate Change*, pp. 825-871. Hydrological Processes 11(8), Special Issue. John Wiley & Sons.

May, R.M. & Hassell, M.P. 1988. Population dynamics and biological control. *Philosophical Transactions of the Royal Society of London, Ser. B* **318**: 129-169.

McNeely, J.A., Gadgil, M., Leveque, C., Padoch, C. & Redford, K. 1995. Human influences on biodiversity. *In* Heywood V.H. (ed.): *Global Biodiversity Assessment*, pp. 711-821. UNEP and Cambridge Univ. Press, Cambridge.

Mills, E.L., Leach, J.H., Carlton, J.T. & Secor, C.L. 1994. Exotic species and the integrity of the Great Lakes. *BioScience* **44**: 666–676.

Mossberg, B., Stenberg, L. & Ericsson, S. 1992. *Den Nordiska Floran*. Wahlström & Widstrand, Stockholm, 696 pp.

Moulton, M.L. & Pimm, S.L. 1986a. The extent of competition in shaping an introduced avifauna. *In* Diamond, J.M. & Case T.J. (eds): *Community Ecology*, pp. 80-97. Harper and Row, New York.

Moulton, M L, Pimm, S L 1986b. Species introductions to Hawaii. *In* Mooney, H.A. & Drake J.A. (eds): *Ecology of Biological Invasions of North America and Hawaii*, pp. 231-249. Springer, New York.

Moyle, P.B. & Light, T. 1996. Fish invasions in California: Do abiotic factors determine success? *Ecology* **77**: 1666-1670.

Okubo, A. 1980. *Diffusion and ecological problems: Mathematical models*. Springer-Verlag, New York.

Olenin, S., Daunys, D. & Dauniene, E. 2001. *Baltic Sea Alien Species Database*. http://www.ku.lt/nemo/mainnemo.htm September 2001.

Orr, R.L., Cohen, S.D. & Griffin, R.L. 1993. *Generic Non-indigenous Pest Risk Assessment Process. "The Generic Process" for Estimating Pest Risk Associated with the Introduction of Non-indigenous Organisms*. Planning and Risk Analysis Systems, Policy and Programme development, Animal and Plant Health Inspection Service, United States Department of Agriculture, 39 pp.

Paffen, B.G.P., van den Brink F.W.B, van der Velde, G. & de Vaate, A.B. 1994. The population explosion of the amphipod *Corophiumcurvispinum* in the Dutch lower Rhine. *Water Science and Technology* **29**: 53-55.

Perrone, C. & Cecere, E. 1994. Two Soleriacean algae new to the Mediterranean: *Agardhiella subulata* and *Solieria filiformis* (Rhodophyta, Gigartinales). *Journal of Phycology* **30**: 98-108

Perrings, C. 2000. *The Economics of Biological Invasion*. Paper prepared for the workshop on "Best management practices for preventing and controlling invasive alien species", February 22-24, South Africa/United States of America Bi-National Commission

Price, E.O. 1984. Behavioural aspects of animal domestication. *Quarterly Review of Biology* **59**: 1-32.

Rajagopal, S., van der Velde, G. & de Vaate, A.B. 2000. Reproductive biology of the Asiatic clams *Corbicula fluminalis* and *Corbicula fluminea* in the river Rhine. *Archiv für Hydrobiologie* **149**: 403-420.

Rask, M., Appelberg, M., Hesthagen, T., Tammi, J., Beier, U. & Lappalainen, A. 2000. Fish status survey of Nordic lakes - species composition, distribution, effects of environmental changes. *TemaNord* **2000: 508**, 58 pp.

Rejmanek, M. 1989. Invisibility of plant communities. *In* Mooney, H.A. & Drake, J.A. (eds): *Ecology of Biological Invasions of North America and Hawaii*, pp. 369-383. Springer, New York.

Renshaw, E. 1991. *Modelling Biological Populations in Space and Time*. Cambridge University Press, Cambridge.

Ricciardi, A. & Rasmussen, J.B. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 1759-1765.

Ruiz G.M., Fofonoff, P.W., Carlton J.T., Wonham M.J. & Hines A.H. 2000. Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* **31**: 481-531.

Ruzzante, D.E. 1994. Domestication effects on aggressive and schooling behavior in fish. *Aquaculture* **120**: 1-24.

Sandlund, O.T. & Bongaard, T. 2000. The freshwater environment. *In* Weidema, I. (ed.): *Introduced Species in the Nordic Countries*, pp. 87-122. Nord Environment **2000: 13**, Copenhagen.

Sandström, M. 1996. *Recreational benefits from improved water quality: A random utility model of Swedish sea-side recreation.* Licentiate thesis. Department of Economics, Stockholm School of Economics, Stockholm.

Segerson, K. & Li, N. 1999. Voluntary approaches to environmental protection. *In* Folmer, H., and T. Tietenberg (eds): *The International Yearbook of Environmental and Resource Economics 1999/2000.* Edward Elgar, London.

SEPA 1997. *Naturvårdsverkets Policy för Introduktion och spridning av främmande organismer*. Naturvårdsverkets Förlag, Stockholm, 67 pp. (In Swedish with English summary)

SEPA 1998. *Ballast Water Transports in Swedish Waters*. NV 91-620-9860-8, 4 pp.

Simberloff, D. 1989. Which insect introductions succeed and which fail? *In* Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., M Rejmanek, M. & Williamson, M. (eds): *Biological Invasions: A Global Perspective*, pp. 61-75. John Wiley & Sons, Chichester.

Spicer, K.W. & Catling, P.M. 1988. The biology of Canadian weeds. *Elodea canadensis*. Michx. *Canadian Joumal of Plant Science* **68**: 1035–1051.

Stachowicz J.J., Whitlatch, R.B. & Osman, R.W. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* **286, 19 November**: 1577-1579

Teramoto, E. 1993. Random disturbance and diversity of competitive systems. *Journal of Mathematical Biology* **31**: 761-769.

Townsend, C.R. 1996. Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation* **78**: 13-22.

US Coast Guard 1997. *Aquatic Nuisance Species*. *In* Ballast Water Research in the United States of America, 1998-1999. UN International Maritime Organization WG on Ballast Water.

Utter, F., Hindar, K. & Ryman, N. 1993. Genetic effects of aquaculture on natural salmonid populations. *In* Heen, K., Monahan, R.L. & Utter, F. (eds): *Salmon Aquaculture*. John Wiley & Sons Inc., New York.

van den Bosch, F., Metz, J.A.J. & Diekmann, O. 1990. The velocity of spatial population expansion. *Journal of Mathematical Biology* **28**: 529-565.

van den Brink, F.W.B., van der Velde, G. & de Vaate, A.B. 1993. Ecological aspects, explosive range extension and impact of a mass invader, *Corophium curvispinum* Sars, 1895 (Crustacea, Amphipoda), in the lower Rhine (The Netherlands). *Oecologia* **93**: 224-232.

Wallentinus, I. 1999. Introductions and transfers of plants. *In* Munro, A.L.S., Utting, S.D. & Wallentinus, I. (eds): *Status of Introductions of Non-indigenous Marine Species to North Atlantic waters 1981-1991*. ICES Cooperative Research Report **231**: 1-43.

Wallentinus, I. (in press). Introduced marine algae and vascular plants in European aquatic environments. *In* Leppäkoski, E., Olenin, S. Gollasch S. (eds): *Invasive Aquatic Species of Europe: Distributions, Impacts and Management*. Kluwer Academic Publishers, Dordrecht.

Wallin, M. (ed.) 2000. Mälaren, miljötillstånd och utveckling 1965–98. *Mälarens vattenvårdsförbund*, Västerås.

Weidema, I.R. (ed.) 2000. *Introduced Species in the Nordic Countries*. Nord Environment **2000: 13**, Copenhagen, 242 pp.

Williamson, M. 1989. Mathematical models of invasion. *In* Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H. Kruger, F.J., Rejmanek, M. & Williamson, M. (eds): *Biological Invasions: A Global Perspective*, pp. 329-350. John Wiley & Sons, Chichester.

Williamson, M.H. & Fitter, A 1996. The characters of successful invaders. *Biological Conservation* **78**: 163-170.

Willoughby, S. 1999. *Manual of Salmonid Farming*. Fishing News Books, Blackwell Science, Oxford.

Wittmann, K.J. & Ariani, A.P. 2000. *Limnomysis benedeni* Czerniavsky: a Pontocaspian mysid new for the freshwaters of France (Crustacea, Mysidacea). *Vie et Milieu* **50**: 117-122.