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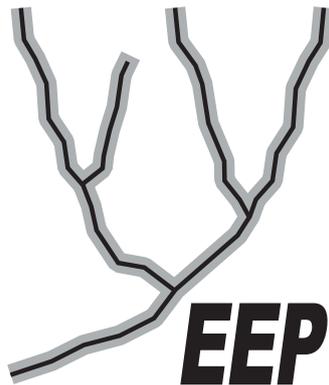
Five Research Projects

Evolution and Ecology Program
International Institute for Applied Systems Analysis
Laxenburg, Austria

EEP

Fisheries-induced evolution of metamorphosis

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Goal

To understand which ecological conditions favor the evolution of metamorphosis and to understand how this is in influenced by the harvesting of large individuals.

Background and motivation

In commercially exploited fish populations fishing is a major source of mortality and can therefore induce phenotypic adaptive responses in the population. Harvesting of fish is often size selective because larger individuals of the population are often the target. Therefore fishing will alter the genetic composition of the population because individuals are removed selectively. It has been shown that fisheries-induced evolution may occur over time scales of just a few generations (Heino and Dieckmann 2009). The best documented case of fisheries-induced evolution is evolution towards earlier maturation (Heino and Dieckmann 2009). However, it is expected that harvesting will also lead to an evolutionary response in other important life-history traits.

Many fish species that are of commercial interest undergo metamorphosis in order to change diet and habitat during their life (e.g., smoltification in salmon; McMenamin and Parichy 2013). It is thought that ontogenetic changes in diet were the first steps in evolutionary history towards life cycles with metamorphosis. Because different resources require different morphologies (Werner 1977), it is expected that species with an ontogenetic diet shift may adapt their morphologies over life to the utilized resource. However, independent evolution of traits may be prevented by genetic correlations between the different life stages (Schluter et al. 1991). Increasing fitness in one stage can in this case be disadvantageous for another stage, leading to a trade-off between juvenile and adult performance.

It is thought that metamorphosis decouples traits between different life-stages, allowing the stages to evolve independently from each other under different selection regimes (Moran 1994). It is unclear to what extent metamorphosis can decouple different life stages. Some studies have reported independent evolution of larval and adult traits (e.g., Saenko et al. 2012) while others found strong correlations of traits between different stages (e.g., Fellous and Lazzaro 2011). While metamorphosis may break up the correlations between different life stages, it is also a costly process. Species often lose body mass during metamorphosis and are more vulnerable to predation (Wassersug and Sperry 1977; Geffen et al 2007). This poses the question under which ecological conditions the potential benefits of metamorphosis can outweigh the disadvantages.

Harvesting of large individuals may alter if the costs of metamorphosis will outweigh the benefits. Since harvesting of fish can lead to earlier maturation and therefore smaller fish, this might change the optimal timing of metamorphosis and also the optimal amount of energy individuals should invest in metamorphosis. It is therefore of interest to understand how size selective harvesting will affect the evolution of metamorphosis in order to get insight in the natural-resource management options that could be taken in order to manage fish populations in a sustainable way.

The proposed research aims to understand which ecological conditions favor the evolution of metamorphosis in species that change their diet over their life cycle. Furthermore, it aims to understand how size-selective harvesting affects the evolution of metamorphosis.

Research questions

I will address the following questions:

- When will the benefits of metamorphosis outweigh the costs and therefore evolve?
- How does harvesting of large individuals in a fish population affect the timing of metamorphosis?
- How does harvesting of large individuals in a fish population affect the extent of metamorphosis?
- When will the costs of metamorphosis outweigh the benefits and therefore disappear in a population that is being harvested?

Methods and work plan

Ecological dynamics

The population dynamics will be modeled using a fully size-structured population model with continuous reproduction. The model is an extension of the consumer-resource model described by Persson et al. (1998). In fish metamorphosis occurs between the larval and the juvenile stage, before sexual maturation and is often associated with a change in diet and habitat. It is therefore assumed that the population feeds on two resources that are located in two different habitats. One resource, the original resource, is available for all individuals, while the alternative resource is only available after an individual has reached a certain size (juvenile and adult phase). Both resources follow semi-chemostat dynamics.

The feeding, growth, reproduction and mortality of an individual are assumed to be functions of its body mass. The body mass of an individual consists of irreversible mass (such as bones and organs) and reversible mass (such as fat, muscle tissue and gonads) and are referred to as x and y, respectively. The ratio between x and y is a measure of the condition of an individual. It is furthermore assumed that there is a maximal ratio of reversible mass to irreversible mass $y^* = q_j x$. Larvae are born with irreversible mass x_b and maximum condition. Individuals become juveniles when reaching the critical irreversible mass x_j, and mature into adults when reaching x_f. Handling time and attack rate depend on x through the quantity $w = x(1 + q_j)$. Resource intake follows a Holling type 2 functional response for any given size. It is assumed that individuals have the same size-specific handling time ($h(w)$) on both resources. The resource ingestion will therefore be written as

$$I(R_1, R_2, w) = \begin{cases} \dfrac{a_1(w)R_1}{1+h(w)a_1(w)R_1}, & \text{if } x < x_j, \\ \dfrac{\varphi a_1(w)R_1 + (1-\varphi)a_2(w)R_2}{1+h(w)\varphi a_1 R_1 + h(w)(1-\varphi)a_2(w)R_2} & \text{otherwise.} \end{cases}$$

In this equation φ is the fraction of time individuals spend in the original habitat and $a_1(w)$ and $a_1(w)$ are the size specific attack rates on the original and alternative resource, respectively. Large individuals will allocate their time in each habitat in such a way that they maximize the food intake and minimize the mortality rate. The energy individuals get from foraging is initially used to pay maintenance costs. Metabolic demand per unit of time is a function of body mass ($x + y$) and can be described by a power function,

$$E_{\mathrm{m}}(x, y) = m_1(x + y)^{m_2},$$

where m_1 and m_2 are positive constants. The net energy production ($E_{\mathrm{g}}(x, y, R_1, R_2)$) equals the difference between the energy intake rate ($E_{\mathrm{a}}(w, R_1, R_2)$) and the maintenance requirements ($E_{\mathrm{m}}(x, y)$) per unit of time,

$$E_{\mathrm{g}}(x, y, R_1, R_2) = E_{\mathrm{a}}(w, R_1, R_2) - E_{\mathrm{m}}(x, y),$$

where $E_{\mathrm{a}}(w, R_1, R_2)$ equals the ingestion rate $I(R_1, R_2, w)$ multiplied by a conversion factor σ. Larvae and juveniles allocate a fraction $\kappa_j(x, y)$ to growth in irreversible mass and the remaining fraction into growth of reversible mass. Adults allocate a smaller fraction ($\kappa_{\mathrm{a}}(x, y)$) to growth of irreversible mass, a fraction $1 - \kappa_j(x, y)$ to growth of reversible mass and the remainder ($\kappa_j(x, y) - \kappa_{\mathrm{a}}(x, y)$) to reproduction.

The number of eggs b that an adult produces per time step equals

$$b(x, y, R_1, R_2) = \begin{cases} (\kappa_j(x, y) - \kappa_{\mathrm{a}}(x, y))E_{\mathrm{g}}(x, y, R_1, R_2)\eta, & x > x_{\mathrm{f}}, \\ 0, & \text{otherwise,} \end{cases}$$

where η is a conversion factor.

It is assumed that the two resources require two different morphologies to be effectively utilized. This means that a morphology that is optimal for feeding on the original resource, is not very efficient in feeding on the alternative resource. The trade-off between the two morphologies is given by

$$m_1^{\frac{1}{s}} + m_2^{\frac{1}{s}} = 1,$$

in which s determines the strength of the trade-off. A value of 1 for m_1 (m_2) means that individuals have the optimal morphology for the original (alternative) resource, while a value of 0 means that they are not adapted at all to this resource.

Initially it is assumed that all individuals have a morphology completely adapted on the original resource and thus $m_1 = 1$ and $m_2 = 0$.

Evolutionary dynamics

The model will be extended with a metamorphosis between the larval stage and the juvenile stage. It is assumed that metamorphosis involves an energy investment and allows for the independent evolution of traits between different life stages and will thus weaken the trade-off between the juvenile/adult morphology and the larval morphology. Metamorphosis will be modeled as a continuous trait. The decoupling of the different life stages because of metamorphosis is given by

$$\begin{cases} m_1^{\frac{1}{s - \omega y_{\mathrm{invest}}}} + m_2^{\frac{1}{s - \omega y_{\mathrm{invest}}}} = 1, & x < x_j, \\ m_1^{\frac{1}{s}} + m_2^{\frac{1}{s}} = 1 & \text{otherwise,} \end{cases}$$

where y_{invest} is the amount of reversible mass individuals invest in metamorphosis and ω a scaling factor. It is assumed that the maximum amount of energy individuals can invest in metamorphosis equals $y_{\mathrm{invest}} = q_s x$. Individuals that do not invest in metamorphosis will have the same morphology over their lifetime. Individuals that invest a lot in metamorphosis can adapt their morphology to the original resource while small and to the alternative resource when large.

The framework of adaptive dynamics (e.g., Geritz et al. 1998) will be used to study how much energy individuals will invest in metamorphosis, if they will adapt to the alternative resource or not and the timing of the metamorphosis. Because harvesting large individuals will presumably also change the optimal timing of maturation, it will be assumed that this trait can evolve as well in order to understand the interplay between the optimal timing of metamorphosis and maturation in an evolutionary context.

Tools

Because explicit expressions for the equilibrium densities cannot be obtained for the model, model analysis will be based on numerical simulations using Matlab, Maple, and C-based programs.

Work plan

- Formulate model and implement metamorphosis in the model
- Parameterization of model
- Understand when metamorphosis can evolve
- Study the effect of size selective harvesting on the evolution of metamorphosis.

Relevance and link to EEP's research plan

The project aims to understand a very fundamental question in evolution and ecology and will lead to a better understanding of the eco-evolutionary dynamics of living systems. Furthermore, it will contribute to the ongoing research at EEP on fisheries management.

Expected output

The results of this project are intended for publication as a coauthored article in an international scientific journal and will also be a chapter in my PhD thesis.

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Disruption risks in adaptive inter-firm networks

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Goal

To investigate how firm-level attitudes towards risks of supply disruption affect trade network structure, using agent-based modeling and adaptive dynamics theory.

Background and motivation

The globalization and interconnectedness of economic activities seem to carry with them new types of risks, often termed systemic risks. Business organizations and international institutions, such as Lloyd's or the World Economic Forum, have recently called for a better understanding of these new types of risks (Goldin 2010; World Economic Forum 2012). The recent financial crash is a prototypical example of systemic crisis, in which an exogenous shock has a disproportionate impact on the economy. This has sparked vivid research on financial contagion; see for instance Battiston et al. (2007).

When an economy is hit by an exogenous shock, such as an extreme climate event, we usually first focus on the direct output losses that are due to the direct damages on some firms. But a significant part of the output losses are also indirect, resulting from interactions between businesses. In the context of hurricane Katrina, Hallegatte (2008) suggested that indirect costs increase nonlinearly with respect to direct damages.

One of the main shock amplification mechanisms is shock propagation along supply chains via input-output relationships, either forward (from supplier to buyer) or backward (from buyer to supplier) (Carvalho 2014). A relationship seems to exist between the structure of an economy, captured by the trade input-output network, and its vulnerability to exogenous shocks. This was empirically documented in the case of the East Japan Earthquake by Todo et al. (2013).

At a theoretical level, Acemoglu et al. (2012) have underlined the role of the input-output structure on macro-level fluctuations using a multi-sector general equilibrium framework, a finding that has sparked a rich discussion in the macro-economic literature. The availability of some firm-level trade data have led to empirical insights on the structure of regional and national production network, see for instance Fujiwara and Aoyama (2010) for the Japanese economy.

The structure of the network itself results from agent-level interactions. The behavior of firms—e.g., their inventory and supply policies, their price or quantity adjustment decisions—determines trade relationships, and *in fine* influences the network structure. This, in turn, affects the overall economic resilience to shocks.

The purpose of the proposed project is to better understand how firm-level knowledge and attitude towards supply risk aggregate to system-level risks, and how these micro-behaviors shape the network structure. In turn, we are interested in examining how the emerging network structure and systemic risk affect firm-level strategies. We intend to tackle this topic using a firm-based theoretical model. This study will contribute to the emerging research field of adaptive inter-firm networks.

Research questions

The aim is to investigate how firm-level attitudes towards risks of supply disruption affect systemic risk and trade network structure. Using a stylized dynamic model of firms interacting through supplier–buyer relationships, in which supply disruptions can originate from exogenous shocks and propagate through the network, the following questions will be addressed:

- Do we observe aggregate losses that (a) are larger than the initial direct perturbations, and (b) that scale nonlinearly with the intensity of the shocks? These relationships characterize the level of systemic risks.

- Suppose that, given their degree of risk aversion, firms can rewire their supplier network to manage supply disruption risks, what are the possible resulting structures of the overall network?

- How does the distribution of risk aversion among firms affect (a) the resulting network structure and (b) the relationship between shock intensity and aggregate losses?

- Suppose that firms have an imperfect knowledge of the overall network there are embedded in, what is the effect on systemic risk?

- At the firm level, which risk strategy yield highest long-term profit?

- Suppose that firm, imitate the risk strategy of the best performers. Can we observe co-existing risk strategies within the same economy?

Methods and work plan

The project involves the formulation, exploration, and analysis of an agent-based model, using the theory of dynamical system. Numerical simulations will be carried out, along with, when possible, analytical treatments. The model description will follow the Overview, Design concepts, Details (ODD) protocol of Grimm et al. (2006, 2010).

Model entities, state variables and macro-level indicators

The model describes an economic system. Individual firms are represented as nodes, and trade relations as edges, directed from the supplier to the buyer. The edges thus represent the flows of goods or services, rather than financial flows. All households are represented as a single terminal node, with incoming edges from the firms.

Within each sector of the economy, all firms are identical in terms of production technology: they produce the same good, and use for that the same proportions of inputs. We will first consider a single-sector economy. For multi-sector economies, an input-output matrix W will be used. Its coefficients w_{ki} represent how much of output of sector k a firm belonging to sector i needs to produce one unit of output. At least one sector is primary: it use inputs that are not produced by any other sectors, and that are available in unlimited quantity.

The following factors will be excluded from this model: firm entry and exit, savings and investment, and labor and dividends. Price are fixed and set to 1, so that we can interchangeably describe a quantity in physical units of goods or monetary value.

At time t, each of the N firms is characterized by its current level of available input from sector k, $u_{ki,t}$, its output $x_{i,t}$ and its total demand received $d_{i,t}$.

The overall state of the economy is monitored through three aggregate indicators: total production, total unsatisfied final demand, and the average connectivity. These indicators will be observed in relation to the severity of the shocks, measured as the direct output loss.

Overall dynamics of the model

The model will be formulated in discrete time. At each time step, the following sequence of event unfolds:

- Production and exogenous shocks: firms use the goods they received at the last time step to produce. Some firms a subject to an exogenous shock and cannot produce.
- Demand anticipation: firms evaluate the demand that will be addressed to them at the next time step
- Production planning: firms evaluate their needs based of the anticipated demand
- Rewiring: firms evaluate their goal-function and maximize it through rewiring
- Ordering: households and firms place orders to meet their needs
- Trade: goods produced at the last time step are transferred to the buyers, and paid to the suppliers
- Learning: firms observe each other and adapt their strategy towards risk disruption

The initial conditions are:

- The initial budget of the households M_0.
- The initial endowment of output of each firm $x_{i,0}$.
- The initial trade relationships, i.e. the network structure, represented as a $N * N$ matrix denoted $A_{t=0}$ with coefficients $a_{ki,0}$. Here, $a_{ki,0} = 1$ if firm k is supplying firm i, while $a_{ki,0} = 0$ otherwise.

Modules

1. Production and exogenous shocks

Production is represented via a Cobb-Douglas production function. In the case of one sector, with constant return to scale, this function is simply

$$x_{i,t} = z_{i,t} \, u_{1i,t}.$$

where z_i is the productivity of firm i and $u_{1i,t}$ the stock of available input. With S sectors and a rate of return to scale b, for firm i belonging to sector $s_i = k$, this function becomes

$$x_{i,t} = z_{i,t} \, \prod_{j=1}^{S} \left(\frac{u_{ji,t}}{w_{jk}} \right)^{b \, w_{jk}}.$$

A possible extension would be to use the so-called constant elasticity of substitution (CES) production function, given by

$$x_{i,t} = z_{i,t} \, \left[\sum_{j=1}^{S} w_{jk} \left(\frac{u_{ji,t}}{w_{jk}} \right)^{-h} \right]^{-b/h}.$$

When $h \to 0$, this reduces to the Cobb-Douglas production function, while for $h \to \infty$ one recovers the Leontief production function. The use of CES function allows us to tune the degree of substitutability between the inputs.

The productivity of firms is stochastically perturbed. To begin with, we will consider random perturbations independently affecting all firms. At each time step, there is a probability q_i that $z_{i,t}$ temporarily falls to 0. We suppose that firms observe each other and know the observed failures rates $f_{i,t}$ of each firm.

2. Demand anticipation

Demand is composed of two terms: the final demand from household and the intermediary demand from firms. Firms anticipate the demand that will have to meet at the next time step using a simple myopic rule: future demand is equal to current demand $d_{i,t}$.

3. Production planning

Using the production function, firms evaluate the most cost-effective combination of inputs they need to meet the anticipated demand.

4. Ordering

Households consume a fixed budget $B_t = B_0$ at each time step, spent equally on each firm. Firms order their necessary inputs to their suppliers. When a firm has several suppliers, the quantity ordered is split equally among them. We denote by $v_{ki,t}$ the amount of goods ordered by firm i from firm k at time t.

5. Trade

Suppliers sell output to their clients. For each firms, if the demand exceeds the supply, goods are rationed equally among all buyers. If the supply exceeds the demand, the excess goods are lost.

6a. Firm decision-making process

The short-term objective of the firms is to maximize their expected profits while preventing risks of supply chain disruptions. Expected profits are the difference between expected sales, i.e., the anticipated demand, and expected costs in the next time step.

With constant returns to scale and in the absence of a price signal, firms maximize their expected profits by meeting the anticipated demand $d_{i,t}$ while minimizing the costs. Costs are composed of input costs, proportional to the amount of inputs ordered $v_{ki,t}$, and supply chain costs, proportional to the number of suppliers $m_{i,t}$. The latter represent the transaction and administrative costs of maintaining supply relationships, which amount to c for each supplier. Thus, the expected profit in the next time step is given by

$$P_{i,t} = d_{i,t} - \sum_{k=1}^{N} v_{ki,t} - cm_{i,t}.$$

The risk of supply chain disruption is the risk that one or several suppliers fail to deliver the inputs, which will consequently hamper production and undermine future profit. This risk is estimated by firms as their expected loss of sales, denoted by $L_{i,t}$, evaluated by firms given its knowledge of the hazards and the network.

At first we assume that firms are not aware of potential trade links between their suppliers. In this case, for a firm i buying only from firm j, the expected loss of sales is the expected amount of sales that is expected to be missed, taking into account the observed failure rate of the supplier,

$$L_{i,t} = z_{i,t}\, f_{j,t}\, v_{ji,t}.$$

The relative importance of these two quantities, expected profits and disruption risks, is mediated through a parameter representing risk aversion denoted by r_i, which will be used as an evolving trait. The goal of the firm is to maximize its utility, expressed as the following goal-function,

$$G_{i,t} = P_{i,t} - r_i L_{i,t}.$$

6b. Rewiring

With constant return to scale and in the absence of price signals, the only way firms can optimize the goal function is to modify their supplier network. Changing suppliers will affect supply chain costs and disruption risks.

At each time step, each firm considers a certain number of other configurations: the addition of a new supplier, the deletion of a current supplier, and the replacement of a current supplier by a new one. They compute the anticipated outputs of the goal-function for each one of these new configurations, and choose the configuration that yields the highest utility. To give more flexibility to the system, we can also consider mapping these utility quantities into a probability of rewiring, using a sigmoidal function.

7. Firm long-term objective and learning process

The long-term performance of firms is measured through their realized profits over a certain period of time T. To improve their performance, firms adapt their strategy towards risks through a learning process, based on the Fermi rule. A firm observes the strategy of another firm, i.e. its degree of risk aversion, with a certain error term, represented by a Gaussian white noise of standard deviation σ, along with its performance. The observed performance is mapped onto a probability of adopting the observed strategy through a sigmoidal function. The adoption occurs with a certain friction parameter.

Work plan

To begin with, we will consider the model without learning and with homogenous firms. We will thoroughly characterize the equilibrium state without perturbations. The dynamical response to single perturbations will be studied, for varying degrees of substitutability in supplies, i.e., over a range of h values. Then, the full perturbation regime, i.e., failures of a firm with probability q_i, will be introduced. Its consequence on the network topology will be analyzed. At this stage it will be interesting to analyze whether total loss is proportional to the severity of the perturbation regime.

The next step will be to introduce heterogeneous risk aversion r_i and observe how this heterogeneity affect firms profit and the macro-level state of the economy. We will start by defining two type of firms: type A is risk adverse, type B is risk tolerant, and observe the aggregate variables for different #B/(#A + #B) ratio.

Finally, the learning mechanism will be added, with r_i endogenously changing. The objective will be to observe the attractor of the r_i, and its dependence on the perturbation regime.

Further perspectives

After the completion of the work plan, there is a wide spectrum of options to deepen the analysis of the model. A very interesting question is to examine whether increasing firms' knowledge about their supply network, in particular about potential linkages between suppliers, decrease the aggregate vulnerability of the economy. Such knowledge would translate into a more accurate disruption risk evaluation in their goal function.

Second, in the multi-sector case, the use of CES production function could allow to test the role of substitutability between inputs.

Third, the economic plausibility of the model could be strengthened via the introduction of endogenous pricing. This could be implemented by applying decreasing return to scale, i.e.,

setting $b < 1$: firms would then be able to decide their production plan through a profit maximization process, taking into account their expectation about future price, instead of merely following the demand. Prices will be determined through market clearing. The objective will be to examine whether the findings are robust to this change of modeling assumptions. In the same vein, the number of sectors could be increased.

Another avenue of research will be to test and evaluate different mechanisms that alleviate systemic risks, e.g., compulsory inventory for highly exposed firms, private insurance, and collective investment to decrease the vulnerability the most exposed firms.

Relevance to EEP's research plan

The proposed research is closely connected to EEP's ongoing project *Systemic Risk and Network Dynamics*. In particular, some EEP researchers are investigating the response of ecological networks and trade networks to external shocks. Exploring the application of the theory of adaptive dynamics, which is a key area of expertise at EEP, to a non-ecological topic is also a recent and insightful agenda for EEP.

The project additionally links with topics of the research plan of IIASA's Advanced System Analysis (ASA) program. Namely, an ongoing project at ASA uses an agent-based approach to better understand how external shocks propagate throughout an economic system to other sectors and households. Other ASA scholars are currently looking at the influence of the network structure, in particular redundancy, on the response to shocks in the context of past economic networks. These close topical connections are expected to lead to fruitful interactions within EEP, and, more broadly, within IIASA.

Expected output and publications

The work from this project is expected to result in a coauthored publication in a peer-reviewed international scientific journal. In addition, I expect this manuscript to be a chapter in my PhD thesis.

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Fisheries-induced evolution of cannibalism

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Goal

To understand the effects of cannibalism in fisheries stock assessment models, the evolution of cannibalism in dependence on ecological environments, and the impact of fisheries on the evolution of cannibalism.

Background and motivation

Natural populations respond to mortality by showing demographic, plastic and evolutionary changes. From observational, experimental and modeling studies on multiple fish stocks it is currently well established that the evolutionary response to fisheries can be rapid (Heino and Dieckmann 2009). Research on fisheries-induced evolution mainly focuses on a limited set of life history traits, such as age and size at maturation or growth and reproductive investments. This revealed that fisheries impose selective pressures for higher reproductive investments, slower growth and maturation at smaller sizes (Marty et al. 2015).

Besides changes in the mentioned life history traits fisheries-induced evolution might also select for other traits. Harvesting inevitably changes standing stock biomass and might also alleviate competition between the remaining individuals and thereby impact the population size-distribution. Such changes in the size-distribution will affect resource availabilities through the ecological feedback of the species with its environment. Hence, resource profitability will shift and this might lead to adaptive responses in traits related to feeding. Currently, research on fisheries-induced evolution has not considered selective change in such trophic traits, as opposed to life-history traits.

A trophic interaction frequently observed among fish species is cannibalism (Polis 1981; Smith and Reay 1991). As fish species often grow considerably in size during their life they are especially prone to the effects of cannibalism, since this is mostly a size-dependent interaction. While most fish species are cannibalistic to some extent there is substantial variation in the importance of cannibalism for population dynamics. Some species only suffer from egg cannibalism for which the energetics gains of the cannibals are limited, while in other stocks a major part of the diet in terms of biomass is derived from cannibalism. Moreover, even interpopulational differences exist, such that individuals from some populations are more prone to cannibalize than individuals of other populations of the same species (Amundsen et al. 1999). The mechanism behind this variation is currently not well understood, but the variation itself suggests that the cannibalistic behavior should be regarded as adaptive and possibly has a genetic basis.

To include the effects of cannibalism in fisheries assessment models and understand the selective changes that fisheries might impose on cannibalistic behavior it is crucial to first understand which ecological factors enhance or inhibit the evolution of cannibalism. From an ecological point of view the evolution of cannibalism is predicted to depend on the profitability of cannibalistic prey in relation to the availability of alternative prey types (Getto et al. 2005). As argued above harvesting can lead to changes in these prey availabilities, possibly mediated

by ecological feedbacks. However, there is currently no clear understanding of how these feedbacks might change the evolution of traits related to cannibalism.

My project aims to elucidate this by studying the evolution of cannibalism and its dependence on the ecological environment. Subsequently, I will assess the effect of cannibalism on predictions of fish stock assessment models and study how fisheries affect the evolutionary success of cannibalistic individuals.

Research questions

- Which ecological factors explain variation in cannibalism?
- How does cannibalism effect predictions of fish stock assessment models?
- How do fisheries change evolution of cannibalism in natural population?

Methods and work plan

Ecological dynamics

In order to understand the effects of ecological feedbacks and harvesting on the evolution of cannibalism the model species Arctic char *Salvelinus alpinus* (L.) is used. This species is commercially harvested in some parts of its circumpolar distribution and has a variable life style and ecology in which cannibalism is expressed in several instances (Klemetsen et al. 2003). Cannibalism was especially important for structuring high Arctic and alpine populations of Arctic char, in contrast to the more temperate ones (Griffiths 1994; Klemetsen et al. 2003). The combination of variation in the extent of cannibalism and commercial fisheries makes Arctic char an ideal species for studying fisheries-induced evolution of cannibalism.

The model of Claessen and De Roos (2003) is used to describe the ecology and cannibalistic feeding of Arctic char. The model describes key life history processes such as growth, reproduction, maturation and mortality on an individual basis. The processes of feeding, growth and reproduction depend both on individual length l and on the state of the environment, which is represented by zooplankton resource R. Body length can be converted to body mass w by using $w(l) = \lambda l^3$. The attack rate of Arctic char on zooplankton is a hump-shaped function of body size, as confirmed by several experiments (Jansen et al. 2003; Byström and Andersson 2005). All individuals feed from this zooplankton and therefore compete for a common resource. The cannibalistic feeding depends on both prey and predator size and the cannibalistic attack rate is maximal at the prey-predator length ratio ϕ. Deviations from this optimal ratio leads to discounting of the attack rate. This discounting is done by a tent shaped function that decreases with increasing distance from the optimal predator-prey ratio. The lower limit of the cannibalistic predation window is given by δ and the upper limit is represented by ε. In Claessen and De Roos (2003) the maximum attack rate on cannibalistic prey increases quadratically with predator length. In this relationship the proportionality constant β indicates the cannibalistic voracity. Because the size-scaling of this relationship is uncertain the parameter θ is used in order to study the effects of deviations from the quadratic relationship. A Holling type II functional response describes the joint feeding on cannibalistic prey and zooplanktivory. Internal handling time is assumed inversely proportional to body mass with proportionality constant ξ. The acquired energy from cannibalism and zooplanktivory is assimilated with efficiency σ_a. Claessen and De Roos (2003) use a kappa-rule model for energy allocation. Instead, I follow the approach taken by Persson et al. (1998) who use a similar model to study population dynamics of roach, but instead use a net production allocation scheme. Assimilated energy E_a is

hence first used for maintenance costs E_m, which is proportional to body mass with proportionality constant m. Assimilated energy left from maintenance is used for growth in juveniles and for growth and reproduction in case of adults. Individuals mature at a fixed size l_f. Adult allocation towards growth is represented by parameter κ. Note that this parameter differs from the one used in Claessen and De Roos (2003), because of the difference in energy allocation scheme. A fraction of $1 - \kappa$ is hence allocated towards reproduction. Allocation towards reproduction is multiple by egg respiration efficiency σ_r and divided by the mass at birth $w(l_\mathrm{b})$ to represent to reproductive rate of an adult. Mortality is composed of size-independent background mortality μ_0, size-dependent mortality $\mu_\mathrm{d}\exp(-l/l_m)$ and cannibalistic mortality $\mu_\mathrm{c}(l)$. All model equations and parameters are shown in the tables below.

The population level functions are composed of an ordinary differential equation that describes semi-chemostat growth of resources and resource ingestion of all individuals in the population. The change in the size-distribution $n(l)$ is represented by a partial differential equation, which is accompanied by a boundary condition that represents the population level reproduction rate.

Evolutionary dynamics

Evolutionary dynamics are studied by using the framework of adaptive dynamics (Metz et al. 1995; Dieckmann and Law 1996; Geritz et al. 1998). The main evolutionary parameter of interest is β, the cannibalistic voracity. Other evolutionary parameter to be studied are the optimum predator-prey ratio ϕ and the lower and upper limits of the cannibalistic window, δ and ε respectively. Furthermore, in response to harvesting the size at maturation l_b and the reproductive/growth investment parameter κ are also allowed to evolve.

Evolutionary dynamics are initially studied without explicitly considering trade-offs, since a time trade-off is already incorporated in the functional response function. Next the evolutionary effects of other kind of trade-off could be studied. One existing trade-off in Arctic char is the zooplankton intake rate and predation risks, as the better feeding spots are also the most dangerous in terms of the risks of falling victim to cannibalism (Klemetsen et al. 2002).

Tools

Recently a numerical software package has been developed for equilibrium and evolutionary analysis of PSPMs, called PSPM-analysis (https://staff.fnwi.uva.nl/ a.m.deroos/PSPManalysis/index.html). This package will be used to perform equilibrium analysis of the ecological model and can furthermore be used to detect and classify evolutionary singular points and create pairwise invasibility plots. In order to perform equilibrium analysis with the PSPM-analysis package the model should have a finite-dimensional environment. In case of the size-dependent cannibalism function as presented by Claessen and De Roos (2003) the environment is infinite-dimensional, because every l-sized predator has its own prey availability and the length axis is infinite-dimensional. To circumvent this problem and still use the equilibrium analysis a cannibalistic function that depends on predator and prey sizes in a separable way should be derived. The possibility to use such an implementation while simultaneously adhering the size-dependent nature of cannibalism will be explored.

To analyze non-equilibrium dynamics a numerical package called EBT-tool will be used (https://staff.fnwi.uva.nl/a.m.deroos/EBT/index.html). This package is specifically developed to study population dynamics of PSPMs. In addition, the canonical equation of adaptive dynamics can be used to study evolutionary dynamics of cannibalism as a function of time.

Work plan

Model parameterization

Model parameter for Arctic char can be derived from the literature or from experts working in this field. Furthermore, statistical models can be used to estimate the cannibalistic interaction and its size-dependency in a separable way.

Model analysis

Model analysis will constitute the largest part of this project and should focus on understanding the qualitative and quantitative behavior of the model and its dependency on the other model parameters.

Writing

When the model analysis is finished and the results are interpreted in a biological context the aim is to write a paper for publication in a scientific journal.

Relevance and link to EEP's research plan

The IIASA Evolution and Ecology Programaims at understanding how ecological and evolutionary dynamics shape population, communities and ecosystems. The current research proposal strongly relates to this objective since it involves ecological and evolutionary dynamics of a complex systems with multiple non-linear feedbacks. Furthermore, studying the evolutionary response of (size-selective) harvesting can result in a better understanding of how the manage natural fish populations.

Expected output

The results of this research will be submitted for publication in an international scientific journal and will form a chapter in my dissertation.

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Variables

a	i-state age	days
l	i-state length	mm
R	resource biomass	g / l

Individual level functions

$w(l) = \lambda l^3$

Body mass

$$I(l) = \frac{\gamma_R(l) + \gamma_C(l)}{1 + h(l)(\gamma_R(l) + \gamma_C(l))}$$

Type-II ingestion rate

$\gamma_R(l) = a_R(l)R$

Zooplankton encounter rate

$$a_R(l) = A\left(\frac{l}{l_0}\exp\left(1 - \frac{l}{l_0}\right)\right)^\alpha$$

Zooplankton attack rate

$$\gamma_C(l) = \int_0^\infty v(l)T(l,y)n(y)\mathrm{d}y$$

Cannibalistic encounter rate of predator with size l for prey with size y

$$T(c,v) = \begin{cases} \dfrac{v - \delta c}{(\phi - \delta)c} & \text{if } \delta c < v \leq \phi c \\ \dfrac{\varepsilon c - v}{(\varepsilon - \phi)c} & \text{if } \phi c < v \leq \varepsilon c \\ \quad 0 \ \text{ otherwise} \end{cases}$$

Cannibalism tent function

$h(l) = \xi l^{-3}$

Digestion time prey biomass

$v(l) = \beta l^\theta$

Cannibalistic maximum attack rate

$E_a(l) = \sigma_a I(l)$

Assimilation rate

$E_m(l) = m l^3$

Maintenance rate

$g(l) = \frac{1}{3\lambda l^2}\max\big(\kappa(E_a(l) - E_m(l)), 0\big)$

Growth rate

$b(l) = \begin{cases} \sigma_r(1-\kappa)\big(E_a(l) - E_m(l)\big)w(l_b)^{-1} & \text{if } l > l_f \\ \quad\quad 0 & \text{otherwise} \end{cases}$

Reproduction rate

$\mu(l) = \mu_0 + \mu_d\exp(-\frac{l}{l_m}) + \mu_c(l)$

Total mortality rate

$$\mu_c(l) = \int_0^\infty \frac{v(l)T(y,l)}{1 + h(y)(\gamma_R(y) + \gamma_C(y))}n(y)\mathrm{d}y$$

Cannibalistic mortality

Population-level functions

$$\frac{\mathrm{d}R}{\mathrm{d}t} = r(K - R) - \int_l^\infty \frac{\gamma_R(l)}{1 + h(l)(\gamma_R(l) + \gamma_C(l))} n(l)\mathrm{d}l$$ Resource dynamics

$$\frac{\partial n(l)}{\partial t} + \frac{\partial g(l)n(l)}{\partial l} = -\mu(l)n(l)$$ PDE for size-distribution

$$g(l_b)n(l_b) = \int_{l_f}^\infty b(l)n(l)\mathrm{d}l$$ Boundary Condition

Parameters	Units	Definition
l_b	mm	Length at birth
l_f	mm	Length at maturation
l_0	mm	Length at maximum zooplankton attack rate
l_m	mm	Mortality size
λ	g mm^{-3}	Length-weight scaling constant
α	-	Zooplankton attack rate scaling
A	l day^{-1}	Maximum zooplankton attack rate
ε	-	Upper limit of cannibalism window
δ	-	Lower limit of cannibalism window
ϕ	-	Optimum of predation window
ξ	day g^{-1} mm^3	Digestion time scaling constant
m	g day^{-1} mm^{-3}	Maintenance scaling constant
β	l day^{-1} mm$^{-\theta}$	Cannibalism maximum attack rate
θ	-	Cannibalistic size-scaling
σ_a	-	Assimilation efficiency
σ_r	-	Efficiency of offspring production
μ_0	day^{-1}	Size-independent background mortality
μ_d	day^{-1}	Size-dependent background mortality
κ	-	Allocation constant

Ecological public goods in spatially heterogeneous environments

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Goal

To understand the evolutionary dynamics of public goods in spatially heterogeneous environments and devise policies for the sustainable harvesting of renewable resources.

Background and motivation

A public good that is freely accessible to everyone, but limited in quantity, can be optimally used if everyone cooperates in using no more than their fair share. However, those who consume more than their share obtain a greater benefit. This leads to overexploitation of the public good which eventually results in a suboptimal state of resource availability for all individuals, a phenomenon called "the tragedy of commons" (Hardin 1968; Hauert et al. 2008). Therefore, the evolution of cooperation is of widespread interest and an active area of research not only in evolutionary biology but also in economics and social sciences. Indeed, mechanisms to avoid the tragedy of commons could inform important policy decisions, negotiated treaties, etc.

Several mechanisms (Nowak 2006) have been proposed to explain how cooperators can resist invasion by defectors. The key ingredient in the evolution of cooperation is positive assortment (Hamilton 1975), wherein cooperators interact more often with other cooperators than expected by chance. Theoretical studies of public goods games typically assume a single resource which is equally accessible to all actors. This assumption is rarely fulfilled under realistic circumstances. In this project, we account for spatial heterogeneity in resource availability. Indeed, there has been a lot of focus in recent years on spatial mechanisms of positive assortment, which include local dispersal (Queller 1992), collective movement (Garcia et al. 2014; Joshi 2015), spatial heterogeneity (Wakano et al. 2009), and patchy resource distributions (Baalen and Sabelis 1995; Kun and Dieckmann 2013). In particular, spatial heterogeneity can have a strong influence on individuals' strategies of dispersal and on local adaptation (Berdahl et al. 2015). It is thus natural to ask whether and to what extent spatial heterogeneity help avert the tragedy of commons. Previous studies have shown that spatial heterogeneity alone is unable to select for dispersal (Hastings 1983), and that other biological factors are necessary. To this end, we consider the evolution of exploitation rates in conjunction with the dispersal rates.

Spatial public goods games can be understood in terms of the milker–killer dilemma (Baalen and Sabelis 1995). Given that each consumer of resources has a choice to be a milker (a prudent consumer who seeks to maximize long-term payoffs by lowering immediate harvesting rates) or a killer (a selfish consumer who quickly exploits resource at a high harvesting rate to maximize immediate payoff), the killer strategy can clearly invade the milker strategy, in a well-mixed population (although killers may eventually themselves go extinct). By contrast, if there is spatial structure, for example, on account of the resource being heterogeneously distributed over a landscape and harvested by selfish individuals at different spatial locations, it is plausible that the resource can be sustainably maintained across a wide area even if resource densities occasionally collapse locally. Accounting for spatial structure in public goods games is thus likely to bring about qualitative changes in the evolutionary dynamics. I will explore

public goods games in spatially heterogeneous environments and investigate how social learning and resource-conditional dispersal of consumers influence realized harvesting rates. I will also test whether specific policy interventions, such as restricting the amount resource consumption in certain areas, or declaring certain areas as no-go areas, etc, can help in attaining a sustainable harvest.

Research questions

We will use an individual-based model of consumers harvesting a spatially distributed resource. The exploitation and dispersal rates of the consumers are allowed to coevolve. Based on this model, we will aim to answer the following questions:

- How do the evolved exploitation and dispersal rates change with the density of individuals? How do these results compare with previous studies in the milker–killer dilemma framework?

- Starting with a monomorphic population, does spatial heterogeneity lead to evolutionary branching, leading to two or more stable dispersal / exploitation strategies?

- If we start with two distinct exploitation rates (dimorphism in exploitation strategies), how do the dispersal strategies evolve?

- How do specific policy interventions (such as declaring protected areas, capping the consumption rate in certain areas) impact the dynamics? Is it possible to devise policies to ensure sustainable harvest?

Methods and work plan

Model overview

We model consumer and resource populations on a continuous two-dimensional space. The resource grows logistically with a spatially varying growth rate (and/or carrying capacity). Consumers exploit the resource in their neighborhood at an individual specific consumption rate, and disperse to other sites when local conditions become adverse, at an individual specific dispersal rate. Both the resource exploitation rate and the dispersal strategy can evolve over time through imitation of successful individuals.

Resource dynamics

The resource R at each point in space z grows logistically, with the harvesting term H depending on the number of consumers exploiting that site and their rates of consumption,

$$\frac{\mathrm{d}R}{\mathrm{d}t} = r(z)R\left(1 - \frac{R}{K(z)}\right) - H(z),$$

where r and K are the growth rate and carrying capacity as a function of the spatial location, respectively. To begin with, we assume that only the growth rate is spatially heterogeneous, while the carrying capacity is constant. The growth rate can be modelled using Perlin noise with different grain parameters.

Consumer dynamics

Consumers exploit the resource around them according to an exploitation kernel $E(z)$, given by a Gaussian function with zero mean and variance σ_{E}^2. Thus, the total resource available for consumer i at location z, per unit time is given by

$$R_i = h_i \int R(z)E(z_i - z)\,\mathrm{d}z,$$

in which z_i is the spatial position of the ith individual, and h_i is its harvesting rate. Thus, the resource harvested per unit area from location z can be written as

$$H_i(z) = h_i R(z)E(z_i - z).$$

Consequently, the amount of resource being harvested at location z by all consumers together can be written as

$$H(z) = \sum_{i=1}^{N} H_i(z),$$

in which the index i runs over all the individuals. In this derivation, we have assumed a so-called Holling type-I functional response.

When the local conditions become adverse, individuals leave the site. The new site is drawn from a Gaussian distribution with zero mean and variance σ_{D}^2. The condition for leaving consists of a measure of the local resource conditions, and a "dispersal response function" that maps the local condition onto a dispersal rate. We will initially use a simple measure of the local condition, given by the local resource availability as compared with a certain individual specific threshold ($R_{\mathrm{T},i}$). The leaving rate is given by a sigmoidal function,

$$r_{\mathrm{D},i} = S_{\mathrm{D}}\big(R_i - R_{\mathrm{T},i}\big),$$

in which S is the dispersal response function defined as

$$S_{\mathrm{D}} = \frac{1}{1 + e^{-k_{\mathrm{D}} t}}.$$

Evolution

Noticing the payoffs of the other individuals (either globally or in their local neighborhood), consumers can choose to imitate the dispersal strategies (defined in terms of the threshold resource level R_{T}), of those with highest payoff (along with a small copying error). The payoff V is calculated as the benefit from cumulative resource consumption accounting for the cost of dispersal c_{D} (the cost of dispersal in a single dispersal event is assumed to be constant, as a single dispersal consists of a random walk with fixed number of steps),

$$V(T) = \frac{1}{T}\left(\int H_i \mathrm{d}t - nc_{\mathrm{D}}\right),$$

in which n is the number of times dispersal occurred during time T. Thus, the probability of copying the strategy of an individual with payoff V_j, given the payoff to self is V_i, can be

$$p = S_{\mathrm{I}}(V_j - V_i),$$

in which S_{I} is the imitation response function. It can also be modelled as a sigmoid curve so that the probability can be constrained between 0 and 1. In this way, the dispersal rates are allowed to be subject to evolutionary dynamics.

Work plan

The broad idea is to start with a simple system and sequentially add more complexities:

- To begin with, we introduce two types of consumers with fixed (non-evolvable) resource consumption rates (prudent consumers with a low harvesting rate, and selfish

consumers with a high harvesting rate), and investigate the evolved dispersal strategies.

- Next, we will allow both the parameter traits (h_i and $R_{T,i}$) to evolve, and investigate the evolutionary outcome. We will repeat this for different densities of individuals.

- Next, we test the impact of constraining the resource consumption in designated areas and other such external interventions, with an aim to determine effective policy interventions to achieve sustainable harvest of the resource.

- Finally, we will allow imitation of strategy based on spatial distance (using an imitation kernel).

Further extensions

Some obvious further extensions would involve relaxing the various assumptions in the above model to incorporate more realistic processes. In order to test the robustness of the results, we will consider the following model variants:

- Test robustness to different measures of local resource condition. For example, compare local abundance to cumulative resource already consumed.

- Letting multiple parameters of the dispersal response function evolve.

- Allowing both growth rate and carrying capacity to be spatially heterogeneous.

Relevance to EEP's research plan

Evolution of cooperation, especially in human societies, is one of the key interests of EEP. Indeed, effects of grouping and spatial heterogeneity on the evolution of cooperation have been the focus of some of the YSSP projects in previous years. Many resources in the real world are heterogeneously distributed, ranging from biotic ones like forests to abiotic ones like water and air. The present work may reveal valuable insights into management and policy decisions aimed at avoiding the tragedy of commons.

Expected output and publications

The work from this project is expected to be published as a coauthored article in an international scientific journal.

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Trait-based community dynamics of a North-Sea ecosystem

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Goal

To establish an ecological model for trait-specific biomasses in benthic communities in the North Sea, to infer the functionally most important trait.

Background and motivation

Bottom macrofauna plays an important role in marine ecosystem processes such as biogeochemical processing (e.g., nutrient cycling, pollutant metabolism) and energy flow (secondary production, food-web dynamics). Furthermore, benthic communities are a favorite target of impact and conservation studies, since their structure reflects environmental conditions over longer periods of time (Warwick et al. 2002).

Long-term changes in marine ecosystems are often assumed to be related to climate change (Schlüter 2010). Although various other aspects can potentially explain the observed changes in the ecosystems (for example, aspects related to physiological and ecological processes, such as autonomous changes in behavior or changes in population dynamics), the climate hypothesis is often the most obvious and most invoked one (Schlüter 2010), because it assumes that marine organisms respond to changes in the environment they live in, and because this response is to some extent proportional to the environmental variability. It is also the most popular assumption because it can be easily tested, and it holds the hope for a better understanding of the biological variations in the system under investigation, once the relationships with the environment have been identified and quantified (Schlüter 2010).

Apart from climate factors, anthropogenic influences like fisheries, eutrophication and pollution have been made responsible for major change in the North-Sea ecosystem (Schröder 2003). For instance, bottom fishing gears impact on the sea floor, causing mortality and injury to surface-living and shallowly-buried fauna, altering physical habitat features, sedimentation, nutrient cycling and suspending particulate matter into the water column (Riemann and Hoffmann 1991).

Studies undertaken at various special scales across the North Sea have demonstrated a role of climatic change in the structuring of benthic communities (Kröncke et al. 1998; Warwick et al. 2002). Previous analyses of the German Bight time series datasets have revealed some trends that parallel the pattern of variation in the climatic indices (Schröder 2003).

Ecological experiments and theoretical considerations indicate that ecosystem functioning depends on biodiversity in terms of the "functional characteristics" (biological traits) of organisms present in the ecosystem and on their distribution and abundance over space and time (Díaz and Cabido 2001).

The traits and their interactions both define the functioning, dynamic and stability of communities and ecosystems (Loreau et al. 2001), and provide information about how communities respond to environmental stress (Díaz and Cabido 2001).

Several recent papers (Díaz and Cabido 2001; Hooper et al. 2002; Petchey and Gaston 2002) highlight that a better understanding of the determinants of local-scale community dynamics

may result from considering the biological trait values of species. The critical question here, that of which traits are important in terms of community dynamics and structure as some traits may play a crucial role in constructing functional groups that are relevant to the provisioning of ecosystem services. We believe that the identification of fundamental traits would provide some evidences to understand the benthic community structure. Additionally, prediction of benthic functioning and its performance in interaction with environmental variability are expected to be more realistic.

Research questions

I will address the following questions:

- Which traits are important for ecosystem dynamic and functioning in the North Sea benthic ecosystem (i.e., "fundamental traits")?
- How well can we predict the ongoing warming effects on benthic community dynamic and functionality in the North Sea using the trait-based community dynamics model?
- What are the possible changes in the North Sea benthic functioning under various warming scenarios?

Methods and work plan

During my stay at IIASA, I will set up an ecological model for trait-specific biomass. This model has to be calibrated to infer importance of interactions among traits, and thus the most important traits, from estimated interaction coefficients. Then, we reduce system in some manner with the goal of retaining predictability using information criteria; finally – if time permits – use model to investigate warming scenarios.

Time series data

A database was generated from a long-term macro-zoobenthos time series at four sites in the German Bight (Fig 1). Benthos samples were collected each spring from 1981 to 2011 (i.e., "taxa by station" matrix). The sites covered the dominant sediment types (FSd = fine sand, Slt = silt, SSd = silty sand and WB = White Bank with silty sand in deeper waters) in the southeastern North Sea with the corresponding typical benthic associations (Salzwedel et al. 1985). At each station and sampling date, five 0.1 m^2 Samples were taken with a van Veen grab. The samples were sieved over 0.5 mm mesh and fixed in 4% buffered formalin. Macro-zoobenthic organisms were identified to species level as far as possible, counted and weighed (wet weight). In total we identified 334 species belonging to 235 genera and 157 families, respectively. After computing average densities per sampling date and station from the five replicate samples, our basic data matrix consisted of 334 species times four stations times 31 sampling dates. From these data, we computed average abundance per species and station over the complete sampling period (1981–2011).
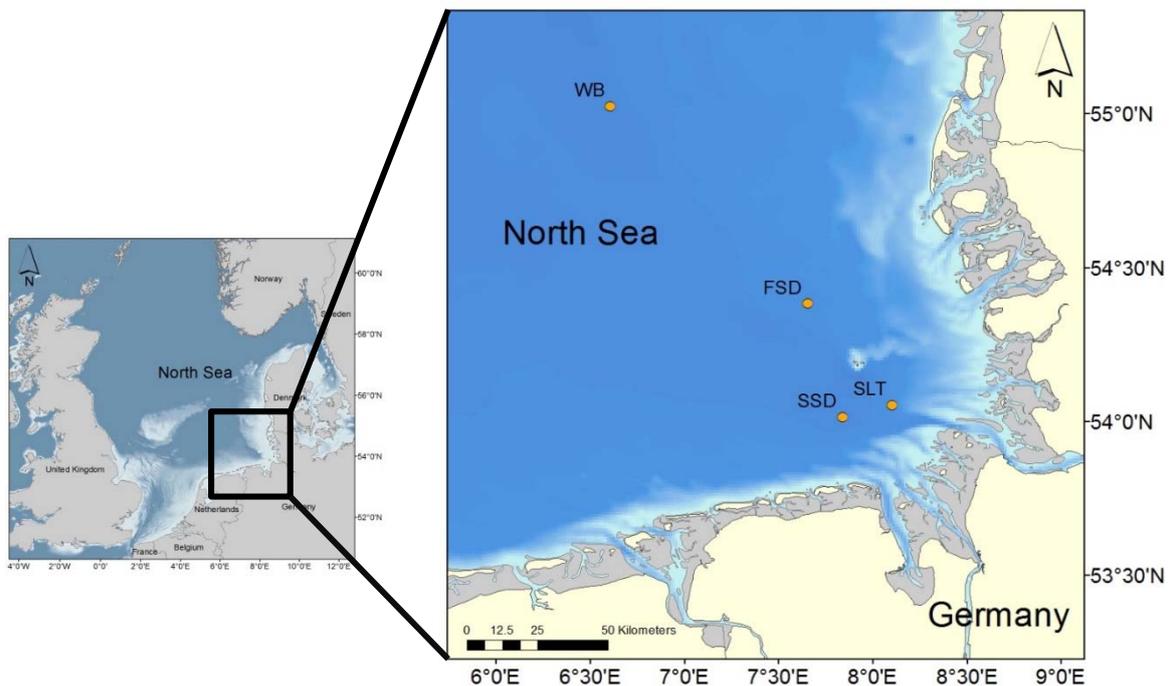
Fig 1. Location of the four long-term monitoring sites (i.e., Slt = silt; SSd = silty sand, FSd = fine sand, WB = White Bank) for macro-zoobenthos in the German Bight.

Biological trait model description

An autecological database (i.e., "trait by species" matrix) was generated from ten different traits covering life history, behavioral characteristics, morphological attributes and environmental preferences of benthic species. Traits were selected either for their importance for the structure and functioning of the benthic system or for their sensitivity to changes in environmental variables. Each trait comprised qualitative or quantitative modalities, which allow for a functional characterization of individual taxa. Specific trait modalities were assigned to individual taxa (i.e., species or genus) using a "fuzzy coding" procedure (Chevene et al. 1994) with a scoring range for affinities of zero to three. An affinity score of zero indicates no association of a taxon with a modality, whereas a score of three indicates highest affinity. Information on biological traits of taxa was compiled from peer-reviewed literature, species identification guides, online databases (e.g., BIOTIC, 2012) and from personal expert consultations. Missing data were supplemented by using information referring to closely related species. To give the same weight to each taxon and trait, the scores were standardized by scaling the sum of all scores for each trait of a taxon equal to 100. The standardized modality scores for each taxon were multiplied by the average species abundance at each station and summed up over all taxa. The results are a "trait by station matrix" providing the frequencies of occurrence of modalities in each year and at each station.

MARSS model description

The core functionality of MARSS 'Multivariate Autoregressive State-space Model' is based on likelihood maximization using the Kalman filter, combined with an EM algorithm (Holmes et al. 2014). The MARSS allows a wide variety of model structures to be specified (such as fixed or shared parameters). In addition to model-fitting, the package provides bootstrap routines for

simulating data and generating confidence intervals, and multiple options for calculating model selection criteria (e.g., AIC)

A MARSS model takes the form

$$x_t = B_t X_{t-1} + u_t + C_t c_t + w_t, \text{ where } w_t \sim MVN\ (0, Q_t),$$
$$y_t = Z_t x_t + a_t + D_t d_t + v_t, \text{ where } V_t \sim MVN\ (0, R_t),$$
$$x_1 \sim MVN\ (\pi, \Lambda) \text{ or } x_0 \sim MVN\ (\pi, \Lambda).$$

The equation for x is termed the state process and the equation for y is termed the observation process. Data enters the model as y, although there may be missing data; c and d are input (exogenous variables, covariates or indicator variables). For more information see Holmes et al. (2014).

Work plan

- Generate the first time series of "trait-specific-biomass" vectors from the data.
- Gain familiarity with MARSS model structure, coding, and execution.
- Set up the model using first "trait-specific biomass" and abiotic data to obtain the matrix of interaction coefficient.
- Quantify how the predictability changes by excluding trait categories.
- Refine this method by considering the linear combination of traits as suggested by eigenvalues analysis of interaction matrix.
- Decide on criteria for the trade-off between good predictability and few traits.
- Time permitting, predict community dynamics and structure of benthic macrofauna with variations in sea surface temperature due to ongoing warming.

Relevance and link to EEP's research plan

My work will contribute to EEP's "Eco-evolutionary Dynamics of Living Systems" project by developing a trait-based community dynamics model (TCDM) to provide better predictions of future developments resulting from rising sea temperatures.

Expected output and publications

The results of this project are intended for publication as a coauthored article in a peer-reviewed journal. It will also be a part of my Ph.D. thesis.

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