Is the metapopulation concept applicable to the North Sea?

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Final Thesis

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Foreword

This report is the result of my final thesis project for the study Coastal Zone Management, at Hogeschool van Hall – Larenstein. The project was executed at Alterra, Wageningen UR, within the framework of IPOP (Instellings Plan/Ontwikkelings Plan) Zee en Kustzones (2007-2010) of Wageningen University and Research Center. Research on sea and coastal zones is a special focus in the policy of Wageningen UR and one of the aims is to fulfill a pioneer function in initiating and executing applied research.
For more information, see http://www.imares.wur.nl/NL/onderzoek/zee-en-kustzones/.

During this project, I went deeper and deeper into the metapopulation concept and its underlying theories. In trying to get a grip on the extensions of the concept, I had numerous conversations with many friends, colleagues and classmates, not seldom ending in a philosophic discussion. I would like to thank all people who listened to me, and contributed their own perspective.

My thanks go out to all experts from NIOZ, IMARES and Alterra I spoke with, and especially to Rob Witbaard, for his time, enthusiasm and his knowledge seeming to be endless.

I am grateful to Pieter for his good care and both him and David for providing me with the chance of working on this project.

I would like to thank Peter for his patience and time of discussing Levins' theory with me, as well as introducing me to the world of theoretic ecology.

I am grateful to Gerrit and Angelique, who read my conceptual versions through and through and provided me with very helpful comments. Wish I wouldn't have to say goodbye and that I could get more of such good supervision!

Merel den Held

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Abstract

A metapopulation is a population of populations in which extinction and recolonization regulate ongoing persistence. In the fragmented terrestrial environment, landscape ecologists have about 15 years of experience in analyzing metapopulation connectivity and persistence, and the use of this concept resulted in the development of the National Ecological Network. In the North Sea, protected areas are and will be assigned on basis of habitat type. The metapopulation concept could form an additional way of assigning protected areas by looking at habitat preferences and population dynamics. In this literature study, the applicability of the metapopulation concept on the underwater North Sea was investigated, and there was searched for possible suitable metapopulation species in the North Sea.

Requirements for a metapopulation were defined as 1) a discrete suitable habitat patch, 2) a high extinction probability and 3) a low recolonization rate, by examining the original metapopulation formula developed by Levins (1969, 1970).

The underwater North Sea clearly is a heterogeneous environment, but habitat characteristics like substratum type are more often wide ranged and no obvious physical barriers exist. Processes and structures in the seascape are mainly known over a rough scale, and even on that level, the available knowledge is only an interpretation from data. The same lack of knowledge is a bottleneck in defining connectivity among subpopulations, as dispersal capabilities of the majority of marine species are unknown. By translating the metapopulation requirements in a list of questions, the existence of metapopulation structure in marine species was assessed. The species that seems to be most suitable for use in metapopulation context in this test was grey seal. Additionally edible crab and cod are potential species to use in a metapopulation approach. Both do not have a discrete habitat patch, but are known to have a strategy to ensure their offspring recruits to their own population. For species which seemed to be suitable by having a discrete under water habitat patch, not enough knowledge was available.

Contents

1. Introduction

A metapopulation consists of subpopulations in which interaction, in the form of extinction- and recolonization processes, determine to a large extent the size and persistence of subpopulations and the metapopulation as a whole (Levins 1969, 1970, Van Dorp *et al.*1999, Foppen *et al*. 2000, Hanski 1998, Opdam & Wascher 2004). The metapopulation concept finds its origin in the dynamic theory of island biogeography established by MacArthur and Wilson (1963) (Hanski 1994), and is part of the landscape ecology field of study. In landscape ecology, the focus is on patterns and processes originating in the interaction between biotic, a-biotic and anthropogenic elements within a landscape (Van Dorp *et al.* 1999). The scale of a landscape can vary from a few square meters to tens of square kilometers and is a heterogeneous composition of interacting systems. Within a landscape, relative homogeneous landscape elements, habitats and connection zones can be distinguished (Van Dorp *et al*. 1999). On land, many species live in highly fragmented landscapes, of which suitable habitat accounts for only a small fraction (Hanski 2001). Populations of plants and animals living in a particular suitable habitat patch are often part of a network- or metapopulation (Van Dorp *et al*. 1999, Hanski 1999, Opdam & Wascher 2004), in which the metapopulation refers to the species and network refers to suitable habitat patches. The occurrence of a species at a certain moment in time thus does not mean that the species has a persistent population, as the concept of metapopulation theory tells that not every patch will be occupied in all years, but still can be an important site for a species (Verboom *et al*. 2001, Verboom & Pouwels 2004). In the terrestrial environment, loss of connection zones between suitable patches can have a major impact on a metapopulation and can eventually lead to extinction of a subpopulation or the metapopulation as a whole (Van Dorp *et al.* 1999, Foppen *et al.* 2000, Opdam & Wascher 2004). By means of simulating metapopulation dynamics in a model, insight is obtained not only in the long term development of a metapopulation in time, but different scenarios can be assessed as well (Verboom & Pouwels 2004). In a metapopulation model, parameters as habitat preferences, non habitat, habitat carrying capacity, habitat map, availability of unoccupied suitable habitat, population size, population density, population stability, number of subpopulations, dispersal capability, maximum lifespan, age at maturity, first year mortality, male/female ratio, number of offspring, life history characteristics, disastrous events and so on, are needed. These parameters are used in models of different complexities. In the relatively simple LARCH, patch size and network size determine the persistence of a species. METAPOP, a more complex model, includes population dynamics, and the very complex model METAPHOR includes life histories of each individual within a patch. In terrestrial landscape ecology, insights gained with use of the metapopulation concept are of major importance for nature development and nature conservation (Verboom & Pouwels 2004). The metapopulation concept led to adaptations of governmental policies, among others concerning Natura 2000. The concept is the basis for the development and realization of the National Ecological Network (NEN, in The Netherlands referred to as EHS, Ecologische Hoofdstructuur). Figure 1 presents a network of smaller and larger areas where nature has priority, intended to enlarge and connect protected areas.

Figure 1. The National Ecological Network in The Netherlands. Smaller and larger areas where nature has priority form a network. Figure adapted from www.pbl.nl.

Oceans and coastal zones are and will be more and more intensively used and exploited (Field *et al.* 2002, Lindeboom *et al.* 2008b). The North Sea has long been seen as an inexhaustible resource, and only in the last decades it was realized that in all economic activities, the ecology of the sea receded into the background (Raad voor Verkeer en Waterstaat 2005). In contrast to the more visible terrestrial system, relatively little is known about the structure and functioning of marine ecosystems (Field *et al.* 2002, Fraschetti *et al.* 2008, Lindeboom *et al.* 2005), although the North Sea ranks among the best studied sea areas in the world (Zijlstra 1988). In the framework of Natura 2000, protected areas are and will be assigned on the Dutch Continental Shelf (NCP) in the North Sea (figure 2). The foundation of assignment is the Habitat Directive, in which 9 coastal and halophytic habitat types and accessory species are determined for all EU marine ecosystems (North and Central Atlantic, Baltic Sea, Mediterranean Basin, Wadden- and North Sea) as a basis (Natura 2000 2007). The efficiency of assigning protected areas on the basis of abundance of species in the assumed relevant habitat types however is not undisputed, as the North Sea is a highly varying and strongly changing system (e.g. Lindeboom *et al.* 2008a). Another, or additional way to asses the North Sea ecosystem and perhaps eventually assign protected areas, could possibly be a metapopulation approach (Slim & Schippers, pers. comm., Kritzer & Sale 2006). In this approach, the consequences of assigning particular areas in the North Sea as protected, as well as the possible consequences of the systems heterogeneity, can be assessed by a spatial explicit evaluation of species habitat preferences and the natural balance of a metapopulation.

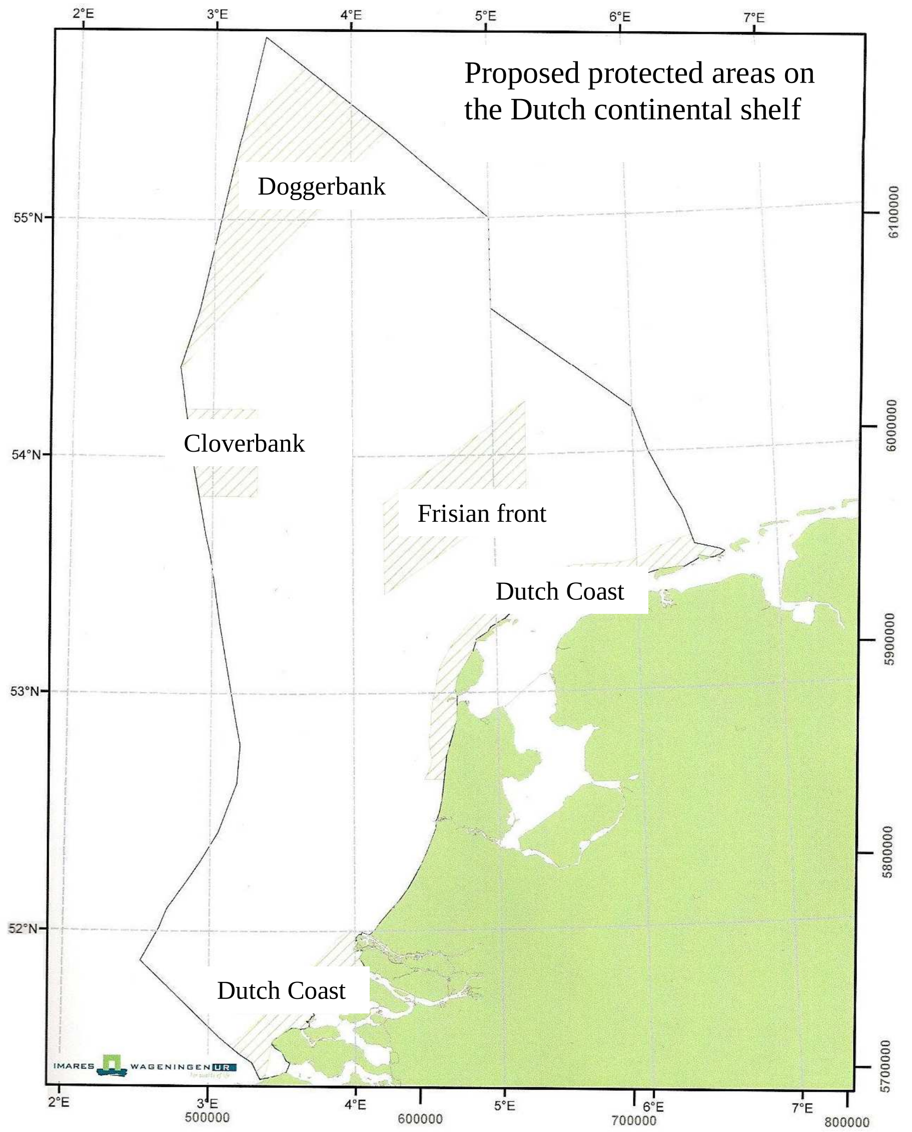


Figure 2. Shaded areas are proposed protected areas on the Dutch continental shelf.

Recently both landscape ecologists and marine ecologists on a global scale started to discover the possibilities of the metapopulation concept in the marine environment. However, non believers on both sides long resisted to use metapopulation terminology in combination with marine habitats (Kritzer & Sale 2006). Despite the effort made by those who did apply the metapopulation concept on marine ecosystems, it still does not seem to be a regularly used concept by those working on the underwater North Sea ecosystem. It seems that potential users are either not convinced or not acquainted with the possibilities of metapopulation concept in the marine environment. Arguments against the application of the concept in the marine realm could be that it is not clear what the metapopulation concept can add to the marine ecology field of study, or how it can be used in the North

Sea ecosystem. Neither is fully clear in which marine situations the metapopulation concept is or is not applicable (Kritzer & Sale 2006), and to what extent the concept should or could be adapted to the marine ecosystem. Therefore this reconnaissance focuses on the possibilities of applying the metapopulation concept in underwater North Sea research and North Sea protection. The aim of this research was to determine the extent to which the metapopulation approach can be applied to the underwater North Sea, and to find out which species could be eligible for use in marine metapopulation context.

The main question therefore was:
To what extent is the metapopulation concept applicable to fauna of the marine ecosystem of the (underwater) North Sea, and which species are suitable to use in a marine metapopulation model?

With the subquestions:

1. What is the present state of affairs in applying the metapopulation concept on marine ecosystems in the literature?

2. Which factors cause heterogeneity in the marine ecosystem?

3. What are the relevant differences between landscape ecology and seascape ecology in metapopulation context and is reference to fragmentation in the North Sea ecosystem appropriate?

4. Which marine faunal species, in the groups fish, benthos and sea mammals, are eligible for what reasons to use in a metapopulation simulation model, and are there species that can definitely not be used?

Reading guide
The requirements for being a metapopulation are defined in chapter 2, ‘Methods’. With these prerequisites in mind, a literature study and interviews with experts leads to answering sub questions 1, 2 and 3, and to the development of a scan to test species suitability to a metapopulation approach. In chapter 3, ‘Results’, the present state of affairs of applying the metapopulation concept on the marine environment is described. An overview of factors causing heterogeneity in the North Sea is followed by a comparison of land and sea in metapopulation context. The scan developed in the previous chapter is used to asses the suitability of 15 marine species for use in a metapopulation approach. The used methods and results are discussed in chapter 4, ‘Discussion’, and the answers on the research questions are given in chapter 5, ‘Conclusion’. In chapter 6, ‘Literature’, the authors referred to in the text can be found, and in appendix I, ‘Glossary’, the definitions of used terms are given.

2. Methods

2.1 Analyzing the requirements for and the existence of a metapopulation

In this study, the book 'Landschapsecologie: Natuur en landschap in een veranderende samenleving'[1] written by Van Dorp *et al*. (1999) was used to gain insight in landscape ecological aspects, in order to be able to reason from the landscape ecology point of view. For further insight in metapopulation theory ISI Web of Knowledge[2] was selected by scanning the searching term 'metapopulation' on most cited authors. Additionally, articles of scientists working on metapopulations at Wageningen Alterra were read, and some of these authors where consulted for supplementary information.

In order to be able to give an advice on species suitability for use in a metapopulation approach, requirements for suitability needed to be formulated and a decision on existence or non existence of a metapopulation structure had to be made. Therefore, the original metapopulation theory was analyzed. Levins (1969, 1970) was the first to use the term metapopulation to describe the concept of 'a population of populations which go extinct locally and re-colonize'. The mathematical description for his idea is the following:

$$\mathbf{dP/dt = mP\ (1 - P\ ) - eP}$$

Where **P** is the fraction of habitat patches occupied at time **t**, **m** is the recolonization rate, and **e** is the rate at which local populations go extinct.

According to this formula, at least (suitable) habitat patches, recolonization and extinction are criteria a species has to conform with. Parameters used in terrestrial metapopulation models, are therefore categorized in these three requirements in table 1.

Table 1. Parameters categorized in habitat, recolonization and extinction.

Criterion	**Parameters**
Habitat	e.g. habitat preferences, habitat carrying capacity, availability of unoccupied suitable habitat, number of subpopulations
Recolonization	e.g. dispersal distance, dispersal capability
Extinction	e.g. population stability, maximum lifespan, age at maturity, first year mortality, male/female ratio, number of offspring, life history characteristics, disastrous events

When setting out Levins formula for ten subpopulations in equilibrium, the balance between colonization and extinction define the fraction of occupied suitable habitat patches (figure 3).

[1] Landscape ecology: Nature and landscape in a changing society
[2] Version 4.6, logged in via Wageningen University Library

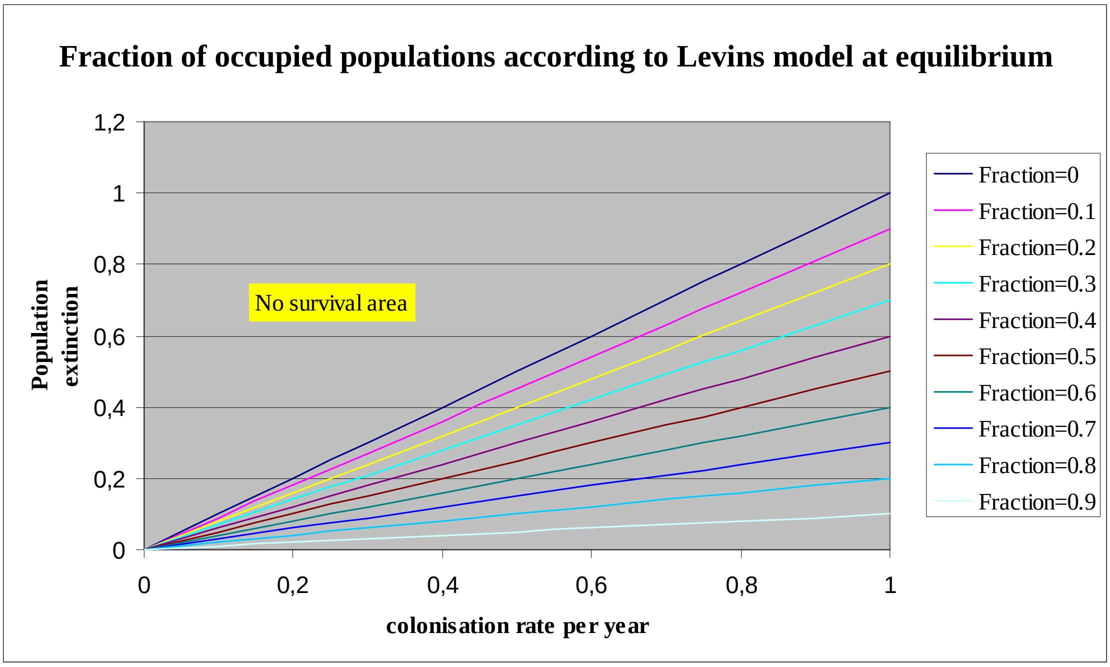
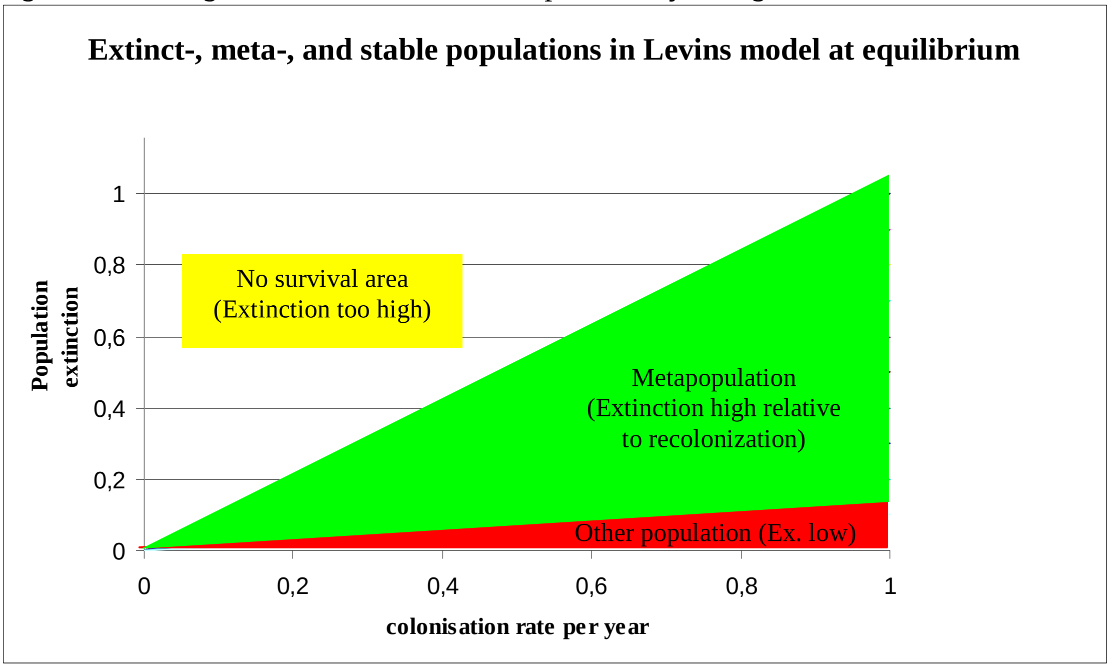


Figure 3. Fractions of occupied populations according to Levins model at equilibrium. The balance between extinction probability and recolonization rate defines the fraction of occupied suitable habitat. In the 'no survival area', recolonization rate is lower than extinction probability and fraction of occupied suitable habitat patches 0. No living species can be found here. At fraction 0.1, ten percent of the suitable habitat patches is occupied, and extinction probability is high relative to recolonization rate. In such a metapopulation, the rate of recolonization of a network patch where a local population got extinct determines the extent and ongoing persistence of the metapopulation as a whole. At fraction 0.9, ninety percent of the suitable habitat patches is occupied, and extinction probability is low relative to recolonization rate. Thus, extinction of a local population does not regularly occur, but colonization (and recolonization in case a network patch is unoccupied) does frequently occur. In such a stable population, other processes or factors (for instance competition or food availability) regulate the extent and ongoing persistence of the subpopulations and the metapopulation as a whole.

In figure 3, a metapopulation in which extinction- and recolonization processes determine to a large extent the size and persistence of subpopulations and the metapopulation as a whole, would be in between 0 and 0.9 of fractions occupied. With 0.9 or more of the suitable habitat occupied, recolonization and extinction are no longer driving forces in persistence. The no survival area would definitely not be a metapopulation. Thus, two options remain. In figure 4, the metapopulation is accentuated green, and the non-metapopulation accentuated red.

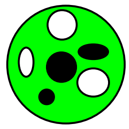
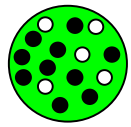
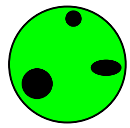
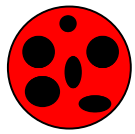
Figure 4 In the green area, the extinction probability is high relative to recolonization



rate and this area is assumed to contain metapopulations as stated in the used definition. In the red area, extinction probability is low relative to recolonization rate. In this region, populations are assumed to be regulated by other factors than extinction and recolonization.

This figure can be nuanced by combining possible rates of recolonization and probable extinction (table 2). A high extinction probability relative to a low recolonization rate in extreme would be an extinct species. In the range of living species however, this combination would be the ultimate metapopulation. High extinction relative to high recolonization would be a metapopulation, but subpopulations can probably not be distinguished by genes. Low extinction probability relative to low recolonization rate would be a metapopulation with the risk of becoming distinct subspecies as exchange of individuals is scarce. In a population with low extinction probability relative to high recolonization rate, extinction and recolonization are not the main forces regulating population persistence.

Table 2. Combining possible extinction probability and recolonization rate (with a discrete habitat as a prerequisite) results in four types of population structure. Figures represent how the possible structures might look, with white circles being unoccupied habitat patches (thus still have to be recolonized) and black circles being occupied suitable habitat patches. Green population structures are assumed to be a metapopulation, the red figure is not.

Extinction	Recolonization	Type of population
High	Low	= Ultimate metapopulation (If viable) 1 
High	High	= Metapopulation, probably with homogeneous gene flow 2 
Low	Low	= Highly isolated subpopulations, probably separated genes 3 
Low	High	= Stable populations (Recolonization and Extinction not driving forces) 4 

In figure 5, the nuanced population structures are brought back in the original figure. This illustrates even more that the 'ultimate metapopulation' only refers to viable populations, and is in extreme a dead and non existing species.

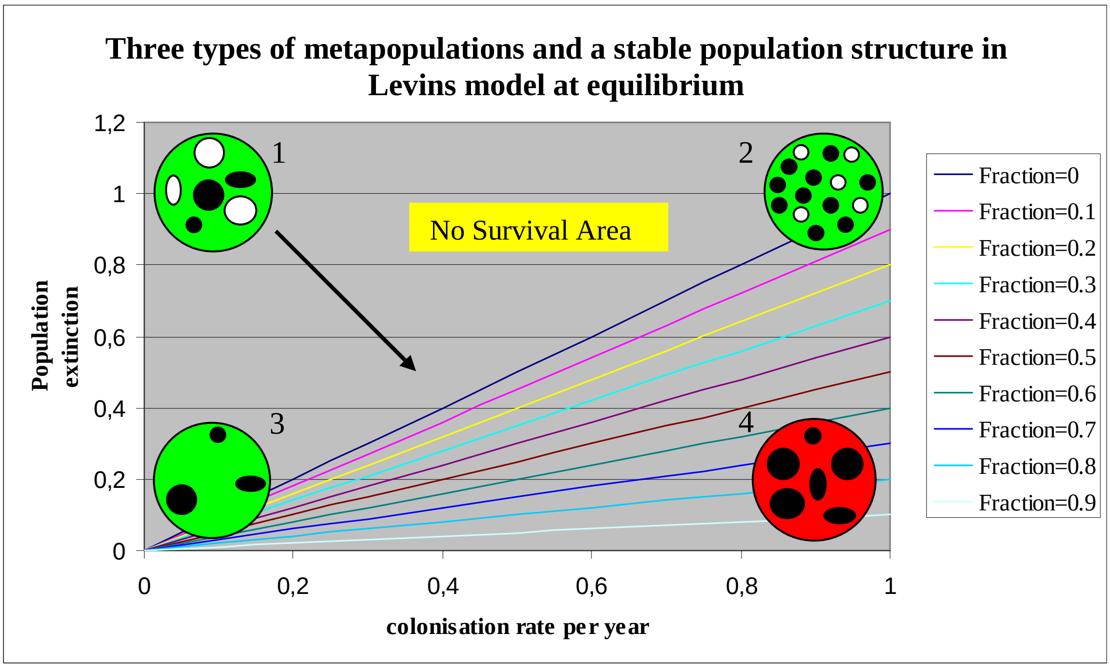


Figure 5 The three forms of metapopulations and the stable population placed back in Levins equilibrium figure. Structure 1 is only a metapopulation when the population is viable, as the upper left zone is the no survival area. The figures representing population

structures stretch out in the living area, as they comprise a balance between extinction probability and recolonization rate, and not only the extremes.

2.2 Gathering information

In order to efficiently consult marine experts later on in the research, a literature study on all research questions preceded a series of interviews. A study on research question 1 (What is the present state of affairs in applying the metapopulation concept on marine ecosystems in the literature?) was executed, using the book 'Marine metapopulations' (Kritzer & Sale 2006) as a starting point. References from this book were used as a stepping stone for a further literature study, supplemented with a literature scan on ISI Web of Knowledge. Relevant articles were selected by using the searching terms 'metapop*' combined with 'marine' / 'North Sea' etc. in the topic, resulting in a list of articles which were scanned on number of times cited. The research question was answered as far as possible, and remaining uncertainties and questions listed in order to ask them to an expert later on in the research.

A literature study on research question 2 (Which factors cause heterogeneity in the marine ecosystem?) was done by searching for 'North Sea AND ecosystem' and 'habitat AND North Sea' (etc.) on ISI. A summarized answer on this research question led to further questions to be propounded to a North Sea ecosystem expert.

Research question 3 (What are the relevant differences between landscape ecology and seascape ecology in metapopulation context and is reference to fragmentation in the North Sea ecosystem appropriate?) was answered by combining the preceding literature studies, and led to further questions to both metapopulation and marine experts. In order to prepare for the search of a suitable species (research question 4; Which marine faunal species, in the groups fish, benthos and sea mammals, are eligible for what reasons to use in a metapopulation simulation model, and are there species that can definitely not be used?), literature on terrestrial metapopulations described above was consulted again. A list of criteria / conditions which species have to meet for their suitability (in the categories habitat, recolonization and extinction) in metapopulation modeling was composed. This list was discussed with a metapopulation expert, and formed a basis for asking questions on marine species suitability to a metapopulation model.

After this base of knowledge on (marine) metapopulations was obtained, a series of interviews with marine ecologists followed. Personal conversations were held with marine ecologists from NIOZ and Wageningen IMARES, specialized in benthic communities, marine mammals, marine protected areas and population dynamics. Given the subjects wide extent and complexity, and with most questions not having a uniform answer, the aim was to leave some openness in the interviews. The consults started with an introduction in the metapopulation concept and the results found in literature study. Then, the questions aroused in the preceding literature study were used as a helping hand in structuring the conversation. In this way, the consulted scientist was able to participate in the research, adding and illuminating aspects concerning marine metapopulations which otherwise would probably not have been regarded. A digital voice recorder was used during the interviews and with every question or new subject, the time on the voice recorder was written down. After the interviews, the consults were restructured by categorizing subjects to the concerning research questions by listening back the recorded conversation. The answers on the research questions 1, 2 and 3 were supplemented with the additional information gained in the consults. The suggestions for answering research question 4 were considered for use further on in the research.

2.3 Developing a test for assessing species suitability in metapopulation context

The ultimate metapopulation thus lives on discrete suitable habitat patches, has a (relative) high chance on local extinction and a (relative) low rate of recolonization of an unoccupied network patch. To test whether it is probable that a species has a metapopulation structure or not, these requirements were translated into questions, with use of the information gathered in the literature study and the interviews. In addition, a criterion 'knowledge on species characteristics' was added, to prevent from advising to use a species on which no data exists. The developed questions needed to have a uniform answer, and needed to say something about the probability of the existence of a metapopulation structure of the tested species. The questions therefore ask for the probability that the species inhabits a discrete network patch, for a low recolonization rate and a high extinction probability, and for knowledge available. The more questions answered positively, the higher the possibility that the assessed species can be used in a metapopulation model. If the parameter asked for is unknown, the given answer is counted as no, as the suitability to use the organism in a metapopulation model decreases. The total number of questions answered with yes gives a total score between 1 and 11. This list of questions was discussed with metapopulation experts and improved on basis of their comments. In order to evaluate the developed scan for assessing suitability to a metapopulation structure, the scan was tested on four terrestrial species (replacing references to sea with 'the Netherlands' and exploitation with 'hunting').

<u>Habitat</u>
1 Does the organism live in / on discrete habitat patches?
2 Does the population return to their place of birth in order to breed?
3 Are there 2 or more (sub) populations on North Sea scale?
<u>Recolonization</u>
4 Is it probable that individuals can bridge the distances between populations occurring on North Sea scale?
5 Is dispersal active?
<u>Extinction</u>
6 Is the organism short lived (< ± 4 years)?
7 Is offspring of the organism low in number?
8 Is there a high chance on disastrous events?
9 Is the organism in the North Sea exploited by humans?
<u>Knowledge</u>
10 Is knowledge on animal characteristics sufficient (>10 articles on ISI)?
11 Is the metapopulation concept connected with this species in literature (ISI)?

2.3.1 Motivation of the individual questions

1) Some degree of isolation is needed to form a metapopulation. Habitats composed of processes and structures (e.g. substratum, fronts, eddies, upwelling of nutrients) are seen as suitable habitat when non habitat in between them can be distinguished. If no discrete

habitat patches can be distinguished, using this species in a metapopulation model will demand creative thinking.

2) If a species is known to return to its place of birth in order to breed (natal philopatry), these breeding grounds can be seen as a form of suitable habitat. The chance on recolonization then decreases, as an individual will only search for a new breeding site in case of density dependant changes or genetic predisposition in taking the risk of moving away (Kritzer & Sale 2006).

3) A metapopulation consists of subpopulations. Populations can be distinguished from each other when non habitat is in between populations (e.g. hydrodynamic forces as well as sediment structure or human induced). Genetic evidence is used when available. If there are two or less populations of the species in (or closely around) the North Sea, either the scale of the metapopulation must be sought beyond North Sea range, or the species occurs in a single, possibly spatial subdivided homogenous population. Another possibility is that there is a scale problem in distinguishing subpopulations. In all three cases, it is less probable that this species is suitable to use in a (North Sea) metapopulation model without complications.

4) Dispersal distance defines the scale on which the metapopulation lives (Kritzer & Sale 2006). Thus, subpopulations should lie within the reach of dispersal distance of the species. If dispersal distance and distance between subpopulations do not correspond (e.g. the organism can bridge 100 – 400 m, and the closest subpopulation is 10 km) it is unlikely that it concerns a metapopulation.
If dispersal distance is rather unknown, recolonization rates have to be assumed and the results of the model will show high uncertainties, meaning that the organism of subject is not (yet) the best candidate for a metapopulation model.

5) When dispersal is passive (e.g. driven by hydrodynamics), dispersal direction and distance are, in general and to some extent, chance dependant. In theory, the organism can end up anywhere in the sea, and can establish as long as suitable habitat is available (Norris 2000). Dispersal among subpopulations may happen because the organism is unable to avoid it, rather than that the species has evolved an optimal solution to the costs of dispersing relative to the benefits of moving to a new population (Kritzer & Sale 2006). This means that chances for recolonization of suitable habitat are high, because theoretically, every individual can reach every suitable habitat patch. Besides that, in most cases knowledge on for instance distances, directions and velocity of passive dispersers is scarce (Botsford & Hastings 2006). These uncertainty factors lower the reliability of a metapopulation model.
When dispersal is active (e.g. the organism is moving itself), the costs and benefits of dispersing are less chance dependant. The chance of survival is lower when leaving a habitat patch that is known to be suitable in order to wander through inhospitable habitat without the certainty if ever reaching another suitable habitat patch (Kritzer & Sale 2006). Assumed is that an individual will stay with its population / on its suitable habitat, leaving situations like density dependant changes or genetic predisposition to taking this

risk, optional for dispersing away from the population. Thus, recolonization chances in this quick scan are seen as lower for active dispersers than for passive dispersers.

6) The longer an animal lives, the smaller the chance on death per lived year (not taking mortality rates caused by human exploitation into account, they are dealt with in question 9). Short lived organisms therefore have an increased chance of local extinction.

7) If the numbers of offspring are low, the chance on recolonization decreases. Species with small numbers of descendants (1 or 2) generally give their individual young more chance of survival than species with a large amount (for instance 10.000) of young. The chance of survival of more than 2 descendants however, is higher.

8) When a species is susceptible to disastrous events (e.g. diseases, storms, extremely low temperatures, generally occurring less than once a year) which are likely to happen, the chance on local extinction is higher. This question can only be answered with yes when literature explicitly mentions such an event.

9) When the organism is exploited by humans, or affected by exploitation (e.g. by-catch or damage due to beam-trawling) the chance of extinction increases. Besides that, species of economic importance are more intensively studied in many cases, thus knowledge on the organism is probably extended. And, most species of economic relevance are in desperate need of proper management, making the metapopulation approach a welcome possible option. On the other side, capricious patterns in exploitation rates can result in unpredictable population behavior.

10) If knowledge on life history characteristics, population dynamics and habitat preferences is extremely low, it will be hard to use the organism in a metapopulation model. The more knowledge available, the more reliable the outcome of the metapopulation model. When this question is answered with no, it overrules question 11 and the species will not be advised as a probable metapopulation species.

11) If the organism was mentioned or even used by other scientists in metapopulation context before, it is likely that the species can be suitable to use, and that uncertainties can be overcome.

2.3.2 Interpretation of the quick scan results

Interpretation and analysis of the scan was worked out, using the possible population structures and a strict maintenance of the main research question.

The purpose of this quick scan is to get feeling with species which are, or are not, interesting in metapopulation context. It should be remembered that the outcome of the scan is an approach to evaluate the probability of metapopulation structure, but is not a measured value.

Step 1

Interpreting the total score is only straightforward if no questions remain unanswered. When three or more questions remain unanswered, no judgment on the population structure of the species can be passed. When one of the categories (habitat, recolonization, extinction and knowledge) is not answered with yes even a single time, the species is not (yet) interesting to use in a metapopulation model in this phase of research. In these cases, the first step of the quick scan is final and the species are not further analyzed.

Step 2

The species for which less than three question marks remain and in each category at least one question was answered with yes, are further analyzed on possible population structure. The categories recolonization and extinction has to be determined high or low. Only two questions address recolonization, since the answer on the questions should say something about the probability of a metapopulation structure in general. If one question is answered positively, recolonization is seen as high. If two questions are answered positively, recolonization is seen as low, and metapopulation structure more likely.
Four questions address extinction. One of those four addresses r-strategists, and one of them addresses K-strategists. It is not likely that both questions are answered with yes, and therefore the maximum score for the category extinction is three. (Local) extinction probability is seen as low when one question is answered positively. When two or three questions are answered with yes, local extinction probability is seen as high, and metapopulation structure more likely. For use in a metapopulation approach, there have to be more than ten articles available on the species on ISI Web of Knowledge.

2.4 Selecting species to test on suitability in a metapopulation approach

In order to asses the applicability of the metapopulation concept on the underwater North Sea, a representative set of species needed to be compiled. First, the phyla Porifera, Cnidaria, Ctenophora, Nematoda, Annelida, Mollusca, Arthropoda, Echinodermata and Chordata were selected on basis of relevance for metapopulation modeling. This selection was discussed with and approved by the initiator of this research. Secondly, it was tried to include organisms with as much species characteristics (life style, feeding mode, type of breeder etc.) and habitat preferences as possible (Table 3). With these criteria as a framework, species were selected on basis of suggestions for suitability made by marine scientists during the consults. For the remaining phyla, common species were selected and, where possible, species with distinctive characteristics not represented by others previously selected. Data on species was searched using ISI, consulting scientists and books. A maximum time of half a day was spent on searching the required information on each assessed species.

Table 3. Characteristics represented by species assessed in the quick scan for assessing species suitability for a metapopulation model. It was tried to include as many characteristics as achievable, in order to give an overview as complete as possible.

Characteristics		**At least represented by**
Position in the water column	Pelagic	Sea gooseberry
	Demersal	Cod
	Benthic	Ocean quahog
Substratum	Silt	King rag worm
	Sand	Common shrimp
	Gravel	Rayed artemis
	Hard substratum	Plumose anemone
Type of breeder	r-strategist	All except Grey seal
	K-strategist	Grey Seal
	Sexual	Moon jellyfish (medusa)
	A-sexual	Moon jellyfish (polyp)
	Oviparous	Plumose anemone
	Viviparous	Bread crumb sponge
	Semelparous	King rag worm
Type of dispersal	Passive	Horse mussel
	Active	Cod
	Both passive and active (in different stages of life)	Moon jellyfish
Adult lifestyle	Mobile	Edible crab
	Sessile	Plumose anemone, breadcrumb sponge
Human interest	Commercial important	Cod, Common shrimp
	Not (yet) commercial important	Rayed artemis
	Not commercial important but harmed by human influences	Ocean quahog Thornback ray
Feeding modes	Filter feeder	e.g. Molluscs
	Predator	e.g. Grey seal
	Scavenger	e.g. Edible crab

3. Results

3.1 Metapopulation theory applied to marine systems : Present state of affairs

The attempt of applying the metapopulation concept on marine ecosystems is represented by a strong body of literature of scientists of many research divisions from various countries. The term 'marine metapop*' in the searching database ISI Web of Knowledge results in 171 articles with the searching terms at least in the topic (18-07-2009). In the same database, the searching term 'North Sea metapop*' resulted in 34 articles with the searching term in the topic (18-07-2009).

The species to which the concept is referred to in only the North Sea ranges from e.g. fish like cod (Hutchinson 2008, Wright *et al*. 2006) herring (Mariani *et al.* 2005) and plaice (Hunter *et al.* 2003), to brittle star (Lefebvre *et al.* 2003), polychaete (Ellien *et al.* 2000), nematode (Derycke *et al.* 2007a), grey seal (Harrison *et al.* 2006) and colonial birds (Boulinier & Lemel 1996). Especially fisheries science has a long history in spatial and temporal structuring of bio complexity, although the term metapopulation has only recently been introduced (Jones 2006, Hillborn *et al*. 2003).

The many examples of the application of the metapopulation concept on the marine environment have, however, various outcomes. For instance, Hummel (2003) concludes that many bivalves in the coastal zone of Europe could better be referred to as "mega populations" instead of metapopulations. On the other hand, Gutow and Franke (2003) did find a metapopulation structure in the isopod *Idotea metallica*, although determining parameters underlying metapopulations such as migration rate and rate of patch occupancy remained difficult.

The development of adapting the metapopulation concept to marine ecosystems still is in progress and the strengths, weaknesses, gaps in knowledge and some specific situations in which it can be applied are being explored and stated (e.g. Kritzer & Sale 2006). The actual functioning of a marine metapopulation concept however, is still not fully understood and needs improvement on several aspects of it (Kritzer & Sale 2006, 2004, Grimm *et al.* 2003, Smedbol *et al.* 2002). On one side, there is a call for more strictly formulated definitions for the metapopulation concept in marine context, and a uniform use of them to prevent that the meaning of the concept becomes vague (Grimm *et al.* 2003, Smedbol *et al.* 2002, Van der Meer pers. comm.). On the other side, Kritzer and Sale (2004) and Hanski (1999) argue that strict definitions exclude a wide array of system dynamics on which the concept is applicable. And, they argue, it is more important to know the general concept and how and when it is relevant to use.

A major difficulty described in reference to marine metapopulations, is the lack of knowledge on dispersal capabilities of species. It is, for instance, extremely difficult to track dispersal of miniscule larvae in the intense volume of the ocean. The scale at which one should asses the existence of a metapopulation is dependant on dispersal distance (Bergman pers. comm., Van der Meer pers. comm., Witbaard, pers. comm., Karlson 2006, Kritzer & Sale 2006), and can vary enormously between species (Kritzer & Sale, 2006). Due to the same gap in knowledge on dispersal distances, the degree of connectivity between populations remains unsure in many cases.

The motivation to make an effort to apply the metapopulation concept to marine environments is the need to understand marine population dynamics and persistence

(Botsford & Hastings 2006), for conservation and management purposes as well as for avoiding overexploitation of marine living resources (Jones 2006, Grimm 2003). Furthermore, Hu and Wroblewski (2009) state that “for proper fisheries management, understanding the spatial and temporal population dynamics of an exploited species is fundamental”. According to Jones (2006), “the value of the metapopulation concept to fisheries management is that it reinforces finer scale regulation and harvest oversight”. Although the applicability of the metapopulation theory in marine environment is not yet completely understood, most authors referred to agree that the concept is an extremely useful framework for asking research questions addressing spatial phenomena and processes on different spatial scales.

3.2 The North Sea: a heterogeneous environment

Factors causing heterogeneity in the underwater North Sea are manifold, as can be seen in figure 6. Inflow of Atlantic water in the North and inflow of river water in coastal areas, influence both water temperature and salinity (Lindeboom *et al*. 2008a). Current velocities vary. Substratum ranges from silty sand to gravel (Groenewold & Van Scheppingen 1988). Hard substratum was formerly found at the Texel stones, but is also added to the environment by humans in the form of sunken shipwrecks oil and gaswinning platforms, and windmill parks (Lindeboom *et al*. 2008a). Depth ranges from a mean of about two hundred meters in the northern North Sea to shallow areas with a depth of twenty meters or less in the coastal areas and sandbanks. Light penetration intensities vary under influence of depth and turbidity, with turbidity itself being a function of the amount of suspended material. Where stratified waters meet mixed water, fronts develop, eventually causing the upwelling of nutrient rich water. Due to these large regional differences in substrate, depth and hydrographic conditions, the North Sea can be distinguished into functional areas (Lindeboom *et al*. 2008a), which will be illustrated by some examples on the Dutch continental shelf.

The Doggerbank (figure 7, 1), a shallow sand bank, divides the North Sea in a shallow Southern and a much deeper Northern part. The bank forms a natural border in fauna distribution, with considerable different fauna on the north and south side of it.

The Doggerbank is situated at the most northern part of the Dutch continental shelf. It stretches out about three hundred kilometer from the southwest to the northeast and covers a part of the German, English and Danish continental shelf. Tidal currents, wave forces and currents incited by wind cause intense mixing of the water column on the shallow part of the bank, whereas the long, colder waves from the northern North Sea stratify the water on the north side of the Doggerbank. At the border area of the mixed and the stratified waters develops a tidal front. Sediment on the Doggerbank consists of fine sand, with grains of 125 μm to 250 μm (Groenewold & Van Scheppingen 1988). On top of the Doggerbank the sediment contains 1%, or even less, silt. On the sides of the Doggerbank, where water depths exceed 30 m, the sediment is finer and silt percentage varies from 1 – 11% (Groenewold & Van Scheppingen 1988).

In the coastal area (figure 7, 2), water depth gradually increases within a distance of 5 to 15 km from the shoreline to 20 to 30 m. On the smooth inclined plane, grain sizes of sand vary between 250 μm and 500 μm, with silt percentages of 1 to 3 %, and patches where silt percentages are 10% of the sediment (Groenewold & Van Scheppingen 1990). In the

coastal waters of the southern North Sea, turbulences generated by strong currents and wave action result in turbidity. Rivers influence the salinity and nutrient availability in the coastal area. Salinity in the coastal area increases with enlarging depth.
Further offshore, at a distance of about 80 km north from the Wadden Islands, the Frisian front (figure 7, 3) can be distinguished. Here, stratified waters in the north and mixed waters from the coastal areas form a physical front. The area is supplied with silt and nutrients from the English coast, making an increase in primary production possible (Lindeboom *et al*. 2005).
At the western edge of the Dutch continental shelf, the Cloverbank (figure 7, 4) forms a distinguishable habitat patch, when regarding substratum. The substratum of the Cloverbank consists of gravel and stones, other than the surrounding majority of silt and sand. The Cloverbank is divided by the deeper channel Botney Cut, in which substratum consists of 50% silt (Lindeboom *et al.* 2008a).
For a detailed description of the North Sea ecosystem, see the work of Zijlstra (1988), Lindeboom *et al.* (2008a) and Janssen & Schaminée (2009).


Faeröer
(Denemarken)
50
100
200
Shetlands
Sullem Voe
Orkneys
Viking-bank
Bergen
Hardangerfjord
NOORWEGEN
ZWEDEN
Oslo
Stavanger
Noorse Geul
Skagerrak
Göteborg
Kattegat
Aberdeen
NOORD-
ZEE
Devil's Hole
Forth
Firth of Forth
Edinburgh
Jutland
DENEMARKEN
Esbjerg
Kopenhagen
Sylt
Tyne
GROOT-
BRITTANNIË
Dublin
Ouse
Doggers-bank
Duitse Bocht
Helgoland
Humber
Silver Pit
Hamburg
Emden
Bremerhaven
Trent
The Wash
WADDEN-ZEE
NEDERLAND
Amsterdam
Great Ouse
Den Haag
Ems
Weser
Elbe
Waal
Londen
Theems
Rotterdam
Maas
Antwerpen
Rijn
DUITSLAND
Nauw van Calais
Brussel
Schelde
Calais
BELGIË
Bonn
Het Kanaal
Cap de la Hague
Main
Kanaal-eilanden
Le Havre
Golf van Saint Malo
Marne
Parijs
Mont-Saint-Michel
Seine
Bretagne
FRANKRIJK
ZWITSERLAND
OOSTENRIJK
Bern
ITALIË
Currents
Deepwater currents
Depth in m.
Estuarine water
Coastal water
Atlantic and mixed water

Figure 6. Many factors and processes make the North Sea a heterogeneous environment. Figure adapted from the book De Noordzee[3], Greenpeace (1985).

[3] The North Sea.

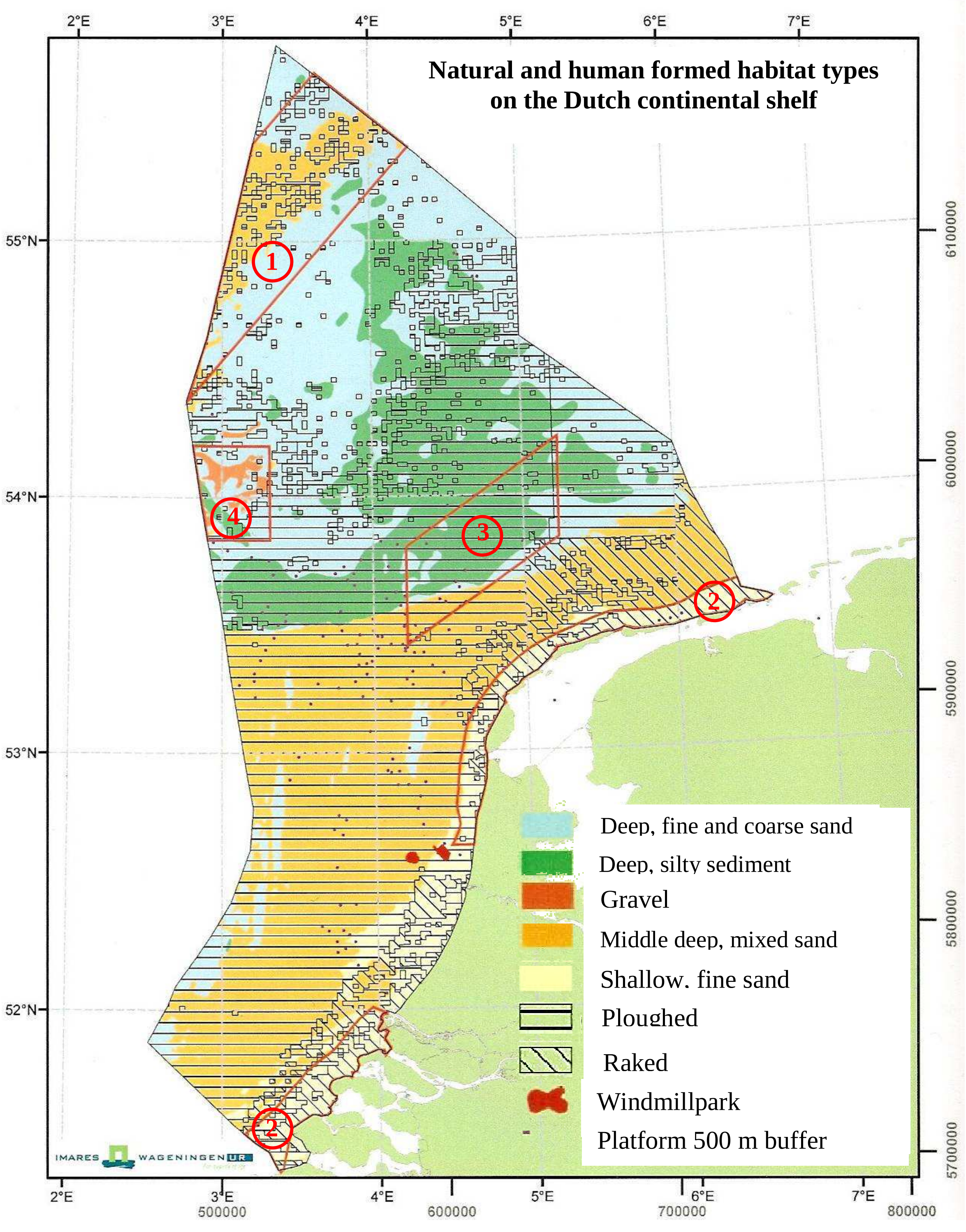


Figure 7. Habitat types in the North Sea. Areas in red lines are 1: Dogger bank, 2: Coastal area, 3: Frisian Front and 4: Clover bank. A major part of the Dutch continental shelf is strongly influenced by fisheries. On basis of depth and substratum, five habitat

types can be distinguished. Figure adapted from the Ecological Atlas North Sea (Lindeboom et al. *2008b).*

3.3 Land and Sea: Comparison in metapopulation context

3.3.1 Air versus water

Obviously the first difference between terrestrial and marine systems is the surrounding medium, air versus water. Consequently, in terrestrial systems one can easily appoint landscapes and its components by walking through it, whereas invisible underwater landscapes require far more sophisticated techniques to define structures, components and processes (e.g. Kaiser *et al*. 2005*)* Marine research, and deep water benthic research in particular, is described as "studying a black box" (Zajac *et al*. 2003) and is in most cases extremely expensive and rather fundamental. Furthermore, oceanographic processes are roughly known on a large scale, but on smaller scales uncertainty remains in many cases (Kaiser *et al*. 2005, Kritzer & Sale 2006). Existing knowledge on the North Sea bottom and its inhabitants is an interpretation from data (Lindeboom pers. comm., Kaiser *et al*. 2005) gathered by taking bottom samples along a grid or transect by either the triple-D dredge or a box core (Lindeboom pers. comm.). With these methods, patchiness in substrate structures can only be given over large scales. The lack of detailed knowledge of marine systems however, does not make it easier to profitably apply the metapopulation concept here. A consequence of the difference in the surrounding medium can also be found in a different energy budget and bottom tied ness in air and water. In an air surrounded landscape, fauna needs to move actively, and life is bottom tied in most cases; even if a species can fly, it needs a place to breed. In water, it might be harder to avoid movement than it is to move, and breeding does not essentially needs to take place on the sea bottom.

3.3.2 Human influence

Another evident difference between land and sea is the form of human influence. In the terrestrial environment, ownership is fixed, opposite to marine systems where ownership is limited. The marine system is a multi-use environment with many mobile resources while land use is largely by a single user, location specific and resources generally fixed in the long and short term (Kerr 1994). In the terrestrial environment, the results of human influence are fragmentation of landscape and habitat loss.

The human activity with most impact on the North Sea ecosystem is exploitation. Especially bottom fisheries are harmful to both organisms and their habitat (Trush *et al.* 2001). Due to the use of tickler chains in beam trawl fisheries, the bottom structure is transformed into a homogeneous field, to depth of six centimeters under the substrate surface. Infauna as well as on the bottom living fauna is seriously harmed by the chains. According to Lindeboom *et al*. (2008a), the effect of the gear can be compared to ploughed field. In figure 7, the area touched by this gear is shown as ploughed habitat. Areas touched by fishing gear which only scrapes the bottom and thereby disturbing mainly fauna living on the bottom, is shown as raked habitat in figure 7. Especially in the Dutch continental shelf, approximately 80% is changed from natural to heavily fished habitat (Lindeboom *et al*. 2008a). Less destructive but physically changing the North Sea

are human activities adding hard substratum. Shipwrecks, platforms build for oil and gas winning and windmill parks, form suitable habitat patches for species like anemones and other organisms with a sessile lifestyle. This added habitat patches might be seen as stepping stones, but do not contribute to fragmentation of the seascape (see Crossland *et al.* 2006). Shipping causes pollution of the North Sea ecosystem, by fuel use and waste dumping. Furthermore via ballast water, invasive species can be introduced. Although those influences can be harming for the ecosystem as a whole, it is not in the first place fragmenting the seascape. The noise produced by ships might be disturbing for particular species. The effects of underwater noises on organisms are not exactly known, but are thought to have a minor influence (Lindeboom *et al*. 2005).
The results of human influences in the marine realm thus rather are over exploitation and homogenization of habitat (Kritzer & Sale 2006).

3.3.3 Barriers

An important factor for the persistence of metapopulations is connectivity between subpopulations. Due to barriers (e.g. highways or urbanization) in the fragmented terrestrial landscape, individuals can not migrate to another subpopulation with extinction as a possible consequence (e.g. Hanski 1997).

In the marine environment, heterogeneity can be formed vertically and horizontally. Although the processes involved clearly induce a diverse environment, physical barriers are not that obvious, and the consequences of them are not comparable to terrestrial fragmentation. Besides the coastal zone, where the seascape is more land-like and is more patchily distributed (e.g. rocky shores, sandbars) and which is a border itself, there are very little insurmountable barriers.

In theory, the only physical barriers in the underwater North Sea are there were the bottom is not inundated, thus coastlines and sandbanks above mean high water level.

Jones (2006) appoints the difference between rather “naturally evolved” metapopulations in sea, versus the more “fragmentation induced” metapopulation on land. Heterogeneity in the North Sea clearly is “natural evolved” and not “fragmentation induced”, and species distribution patterns are adapted to the possibilities the system offers.

Patches of suitable habitat are more often widespread (comprising hundreds of square kilometers, see figure 6 and 7), opposed to patches on land (varying from some square meters to some square kilometers) which are more often isolated. Kritzer & Sale (2006) argue that there might be a fundamental difference in ecological characteristics such as stability and resilience between systems that “evolved to be patchy and interconnected as opposed to one that has recently been restructured as such”.

Of course, there are exceptions in specific habitat types and species, but marine populations in general are less isolated or fragmented than terrestrial populations. However, the question whether the factors and processes mentioned above reduce and divide a larger area of habitat into two or more fragments (thus form a barrier), is dependant on capability and habitat preference of individual species. Currents or tidal fronts can indeed form a restraint for particular species, in the strictest sense meaning that the seascape is fragmented.

3.3.4 Life history differences instead of land versus sea

Many marine fish and invertebrate have a complex lifecycle. Approximately 70% of marine invertebrates have pelagic larvae (Mileikovsky 1971) which undergo intense changes in size, morphology, physiology and behavior during dispersive stages. Most pelagic larvae are not able to avoid dispersal, as they can not move themselves for long distances horizontally (Bergman pers. comm.) They float in the water driven by ebb – and flood currents, and when a strong wind holds for a longer time, the larvae are dispersed further (Kaiser *et al*. 2005). Comparable to freely dispersing pelagic taxa, are dispersed seeds that can drift almost anywhere but are only able to complete their lifecycle in favorable habitat (Norris 2000) According to Kritzer and Sale (2006), in addition to the marine species inability to avoid dispersal, most terrestrial dispersing individuals are developmentally static, and dispersal mainly serves to get from point A to point B. Kritzer and Sale (2006) therefore state that "we might do well think about types of metapopulations in terms of life history category than whether the organisms live on land or in the sea".

3.4 Assessing species suitability for use in a marine metapopulation model

In this research, 15 species (breadcrumb sponge, moon jellyfish, plumose anemone, sea gooseberry, the nematode *Geamonhystera disjuncta*, king rag worm, rayed artemis, horse mussel, ocean quahog, edible crab, common starfish, thornback ray, cod and grey seal) were tested on suitability in a metapopulation model. In the table 4, the scores on habitat, recolonization, extinction and knowledge are shown, and if less than three questions remained open and each category was answered positively at least once, a total score was given. Individual assessment motivation, test results, number of articles on ISI, importance and prominent characteristics of species assessed using the quick scan are described below. Asterisks in the quick scan answers refer to asterisks in the species descriptions.

Porifera

Breadcrumb sponge *Halochondria panacea* (Gewone broodspons)

Total score five, three question marks remain.

124 articles on ISI.

Breadcrumb sponges live attached on algae, rocks or coarse sand (Barthel 1986). The breadcrumb sponge is viviparous; "fertilized eggs develop into swimming larvae within the mesohyle, and than leave the parent sponge through the excurrent canals and oscula" (Aman 1986). Besides sexual reproduction, sponges are famous for being able to aggregate and reorganize into a new sponge (Castro & Huber 2008). According to Witte *et al* (1994), there are several populations of breadcrumb sponges on North Sea scale.

Cnidaria

Common or Moon jelly fish *Aurelia aurita* (Oorkwal)

Total score three, no discrete habitat or homing known. Extinction probability seems to be low, and recolonization rate high.

426 articles on ISI.

In contrast to species being over exploited, the moon jellyfish is thought to be a "major limiting factor for the population growth in copepod and larval fish" (Möller 1980). The sudden mass abundance of the medusa stage may impede fishing activities, power plant cooling and local tourism.
The moon jellyfish has, as most jellyfish, a sessile polyp and a mobile medusa stage.
*Although the medusa is able to propel itself, it is dependant on hydrodynamics and therefore seen as part of plankton (Möller 1980). Reproduction is both sexual (in the medusa stage) and asexual (in the polyp stage).
Habitat seems to have a wide geographical range, mostly in shallow waters (Dawson & Hammer 2009).
*Although no discrete habitat patches are used and the exhibition of natal philopatry as well as the existence of subpopulation remains a question, the wide distribution range and passive dispersal points to the probability that individuals can bridge the distance between eventual populations.

<u>Plumose anemone *Metridium senile* (Zee anjelier)</u>
Total score four, three question marks remain.
180 articles on ISI.
All species in the class Anthozoa are marine.
Reproduction occurs asexual by pedal laceration, longitudinal or transverse fission, and sexual (oviparous), with free swimming larvae (Kenneth & Svane 1994). Occurs from the mid intertidal zone to depths of more than 100 m. Passive suspension feeder. A characteristic habitat is formed by shipwrecks, as well as rocky shores, dikes, and other hard substratum. Densities of 500 individuals per m².

Ctenophora
<u>Sea gooseberry *Pleurobrachia pileus* (Zeedruif)</u>
Total score three, three question marks remain.
81 articles on ISI.
Many articles are on anatomy of the species.
Pleurabranchia pileus is a competer for crustacean zooplankton with pelagic fish, and fish larvae (Fraser 1970). It is a non selective carnivore.
*Passive horizontal tidal movement and active day/night vertical migration (Wang *et al.* 1995). The life cycle is not completely understood. It is thought that the sea gooseberry has a lifespan of one year (Frank 1986). Spawning is "continuous while conditions are suitable but changing conditions can sometimes give the effect of two separate spawnings in a year" (Fraser 1970).

Nematoda
<u>*Geomonhystera disjuncta* (Nematode, no English or Dutch species name)</u>
Total score four. Not enough knowledge. Extinction rate seems to be low.
7 articles on ISI.
The combination of the searching terms 'Nematode' and 'Metapop*' and 'North Sea' on ISI gave three articles referring to two different nematode species, written by Derycke *et al.* (2007a, 2007b, 2006). One of these species is *Geomonhystera disjuncta.* The authors suggest that metapopulation dynamics are likely to occur in *Geomonhystera disjuncta*, as

the species is patchy distributed on algal deposits. A complicating factor however, is that the species are also observed in the sediment. Thus, when algae are completely decomposed, a local extinction will be unlikely, as the species can inhabit the sediment as well. Information below is derived from the article of Derycke *et al.* (2007a).

Geomonhystera disjuncta is a free living nematode with a endobenthic / epiphytic lifestyle. Dispersal capability is limited. The species has a short generation time (8 days) and a high reproductive output (200 – 500 eggs/female).

Only a small fraction of the total predicted nematode diversity is currently described, as species identification is complicated because important ecological features may be situated beyond the resolution of light microscopy.

Annelida

King ragworm *Nereis virens* (Zager)

Total score six. Low recolonization and high extinction. (Meta) population without discrete habitat and homing unknown.

301 articles on ISI.

The king ragworm has commercial value as bait in the sea angling sport industry and in aquaculture industries for the production of finfish and crustacea (Olive 1999). King rag worms are semelparous (individuals die immediately after breeding) (Olive *et al.* 2000). *Life span varies between one and seven years (Kristensen 1984, Olive *et al.* 2000). Annual mortality for year classes one and two are 77 and 76%, and it is assumed that an age class of king rag worms is reduced to 1.2 – 1.4% of the initial number three years after hatching (when mortality has a constant rate from hatching to reproduction) (Kristensen 1984). Natural populations are composed of several year classes and exhibit a mixed age at maturity strategy (Olive *et al.* 2000). Larval stage includes three development phases, supra benthic, pelagic and benthic.

*Settlement depends essentially on hydrodynamic processes related to the tide. Three year old individuals can migrate from upper intertidal levels downshore (Desrosiers *et al*. 1994).

Mollusca

Rayed artemis *Dosinia exoleta* (Artemisschelp)

Total score two. Six question marks remain.

9 articles on ISI.

Articles on population structure were not available (but do exist). Rayed artemis inhabits gravel and was therefore chosen to asses. The bivalve is cultivated and exploited in Spain, and is identified as a species with future market potential (Sánchez-Marín & Beiras 2008,)

Horse mussel *Modiolus modiolus* (Paardemossel)

Total score five, high recolonization and low extinction. Stable population with a discrete habitat patch.

508 articles on ISI.

The bivalve mollusk horse mussel attaches with byssus threads to the substratum or others horse mussels. The species is seriously harmed by bottom trawl fisheries (Murawski & Serchuk 1989) It is thought to have a longevity of about 20 years.

Ocean quahog *Arctica islandica* (Noordkromp)

Total score four. High recolonization and low extinction. Stable population without discrete habitat.

167 articles on ISI.

The bivalve mollusk ocean quahog is seen as an indicator for environmental health and biodiversity (Meesters *et al.* 2008, Witbaard & Bergman 2003, Rees & Dare 1993). Ocean quahog occurs in temperate and boreal shelf seas on both sides of the Atlantic Ocean (Witbaard 1997, Ropes & Murawski 1983). Distribution patterns are directly related to bottom temperatures, according to Harding *et al.* (2008). In the North Sea, ocean quahog was never collected alive in the shallow, sandy coastal sector (Witbaard & Bergman 2003). North of the 30 m depth contour it can be found virtually everywhere, although in low to very low densities (Witbaard & Bergman 2003). Ocean quahog is the longest lived (Abele *et al.* 2008) and one of the slowest growing of marine bivalves (Ropes & Murawski 1983). Ocean quahogs have clear and well defined growth lines, which makes it possible to use it in a way similar to tree rings (Witbaard 1997). By using this method, a maximum age of 400 to 405 years was recorded in Iceland quahogs (Abele *et al.* 2008). Adult ocean quahogs lives burrowed, just below the sediment – surface interface (Ropes & Murawski 1983, Rees & Dare 1993, Witbaard 1997). They feed on plankton with relatively short siphons which are extended above the surface of the substrate to pump in the water (Ropes & Murawski 1983, Cargnelli *et al.* 1999). Genetic studies suggest the existence of genetic differences and a high degree of reproductive isolation of populations within the North Sea (Holmes *et al.* 2003). According to Witbaard and Bergman (2003) it is "questionable whether the population in the Oysterground is fed by larval supply from elsewhere". The genetically distinct and geographically separated populations could however possibly be seen as part of a metapopulation. Knowledge on population structure, distribution and abundance in the North Sea remains scarce, contrary to the western Atlantic where the species is commercially important and therefore subject of studies (Witbaard 1996). Still, questions about amongst others recruitment of individuals to populations, spawning, population sizes and so on, remain unanswered (Cargnelli *et al.*1999, Mann & Wolf 1983).

Arthropoda

Edible crab *Cancer pagurus* (Noordzeekrab)

Total score seven. Low recolonization and high extinction. Metapopulation by a form of homing (see first asterisk below).

346 articles on ISI, of which one with the term 'metapopulation' and the species name in the topic: Scale effects and extrapolation in ecological experiments (Englund & Cooper 2003)[4]. Dispersal is both active (adult females can move more than 100 km) and passive (larvae remain in plankton for 2-3 months (Ungfors *et al*. 2009)).

*As "Female migrations are thought to be directed against prevailing surface currents to compensate for larval dispersal which could promote genetically distinct populations" (Ungfors *et al.* 2009), natal philopatry is given the benefit of the doubt in the quick scan. See the work of Ungfors *et al.* (2009) for a discussion on the lack on genetic structure

[4] Only an abstract was available.

which indicates a high degree of genetic mixture over a large area, and possible reasons for that. Existence of subpopulations probable (see Reyns & Eggleston 2004).
*Ageing of the edible crab is extremely difficult, as individuals grow by molting and growth rates are highly variable. Sheehy and Prior (2008) conclude that longevity of edible crab in the English channel is about 10 years.

Common shrimp *Crangon crangon* (Gewone garnaal)

Total score six, low recolonization and high extinction, but no discrete habitat and homing not known.

616 articles on ISI.

Commercial important species, with annual landings exceeding 20.000 t (Temming & Damm 2002). Surprisingly, the understanding of the lifecycle of the common shrimp is incomplete, even as knowledge on vertical migration patterns (Temming & Damm 2002, Oh & Hartnoll 2004). The maximum lifespan differs between studies, and is thought to be between 2.7 and 3.3 years (Oh & Hartnoll 2004).

Echinodermata

Common starfish *Asterias rubens* (Gewone zeester)

Total score four. High recolonization and low extinction. Stable population without a discrete habitat.

530 articles on ISI.

Common starfish have a considerable negative impact on economic important species, as it is a consumer of mussel (*Mytilus edulis*) and a competitor for food with many bottom feeding fish (Kamermans *et al*. 2009, Vevers 1949). Common starfish occur on mud to coarse and gravel to rock grounds in depths from the intertidal to > 600 m (Gemmil 1914). It is a trophic generalist predator. It is likely that there are more than 2 subpopulations in the North Sea, although the used literature only described two populations in the English channel off Plymouth (Vevers 1949). Oldest age described in the used literature was 3 years, but it is probable that Common starfish can grow somewhat older.
*Dispersal is both active and passive.

Chordata

Thornback ray *Raja clavata* (Stekelrog)

Total score seven, low recolonization and high extinction. (Meta) population without discrete habitat and homing unknown.

150 articles on ISI.

1 article refers to metapopulations (Chevelot *et al*. 2007), where the authors suggest that a “relatively high gene flow between the Irish Sea population and other source populations […] might be more relevant at the metapopulation scale”.

The thornback ray is thought to be declined with nearly 80% in the North Sea (Walker & Heessen 1996) and disappeared in some places. The species forms an unavoidable part of bycatch in demersal fisheries.

Females are mature at ages between 9 and 12 years (Chevelot *et al*. 2007) and *fecundity is called low by Chevelot *et al*. (2007), with 38-150 eggs per female per year.

*Walker *et al*. (1997) suggest the existence of 2 separate stocks; one in the Thames estuary in the North Sea and one in the English Channel. The stock in the North Sea should be seen as a “series of local concentrations with regular exchange of individuals” (Walker *et al*. 1997). Thornback rays are thought to swim a maximum distance of several 100 km, although capture – recapture measurements demonstrate distances of 60-70 km (Chevolet *et al.* 2007).

Cod *Gadus morhua* (Kabeljauw)

Total score seven, low recolonization and high extinction. Metapopulation due to natal philopatry.

5283 articles on ISI.

‘*Gadus morhua*’ and ‘metapop*’ in the topic resulted in 21 articles.

The commercially exploited, demersal cod can live up to 20 years (nowadays rare) and females produce between 500.000 and 5.000.000 eggs per year (Meesters *et al.* 2008)

* There is at least one population in the North Sea, as well as in the Barents sea and the Balthic Sea (Kijewska *et al.* 2009, Smedbol & Wroblewski 2002, Ruzzante *et al.* 2000). Given the species mobility, it is counted as positive in this scan.

Grey seal *Halichoerus grypus* (Grijze zeehond)

Total score eight. Discrete habitat patches, low recolonization rate and a high extinction probability. Ultimate metapopulation.

782 articles on ISI.

The grey seal has recolonized the North Sea only since 1970, after an absence of about 500 years (Reijnders *et al*. 1995). Reason for absence was excessive hunting. At present, four populations are established along the mainland Europe, and a link with the larger populations in the UK was indicated by tracking of movements (Härkönen *et al*. 2007).

*Table 4. Score table for assessing species suitability for use in metapopulation context. The more questions answered with yes, the more likely it is that the species can be used in a metapopulation approach. When individual categories were never answered with yes, or when three or more question marks remain, no answer can be given on the question whether this species might suitable in metapopulation context. The total score is between brackets. * Refer to species descriptions.*	**Breadcrumb sponge**	**Moon jellyfish**	**Plumuse anemone**	**Sea gooseberry**	**Nematode**	**King rag worm**	**Rayed artemis**
Habitat: 1 Does the organism live in / on discrete habitat patches?	Yes	No	Yes	No	No	No	Yes
2 Does the population return to their place of birth in order to breed?* not needed if 1 = yes	?	?	?	?	?	?	?
3 Are there 2 or more (sub) populations on North Sea scale?	Yes	?	Yes	?	Yes	Yes	?
Habitat score	**2**	**0**	**2**	**0**	**1**	**1**	**1**
Recolonization: 4 Is it probable that individuals can bridge the distances between populations occurring on North Sea scale?	?	Yes*	?	?	Yes	Yes	?
5 Is dispersal active?	Yes	No*	Yes	Yes*	?	Yes*	?
Recolonization score	**1**	**1**	**1**	**1**	**1**	**2**	**0**
Extinction: 6 Is the organism short lived (< ± 4 years)?	Yes	Yes	?	Yes	Yes	Yes*	No
7 Is offspring of the organism low in number (< 10)?	No	No	?	No	No	No	?
8 Is there a high chance on disastrous events?	?	No	No	No	No	No	?
9 Is the organism in the North Sea exploited (or affected by exploitation) by humans?	No	No	No	No	No	Yes	Yes
Extinction score	**1**	**1**	**0**	**1**	**1**	**2**	**1**
Knowledge: 10 Is knowledge on animal sufficient (>10 articles on ISI)?	Yes	Yes	Yes*	Yes	No	Yes	No
11 Is the metapopulation concept used for this species in literature (ISI)?	No	No	No	No	Yes	No	No
Knowledge score	**1**	**1**	**1**	**1**	**0**	**1**	**0**
Total score	**0** (5)	**0** (3)	**0** (4)	**0** (3)	**0** (3)	**6**	**0** (2)

Table 4 continuated.

	Horse mussel	Ocean quahog	Edible crab	Common shrimp	Common starfish	Thornback ray	Cod	Grey seal
Habitat: 1 Does the organism live in / on discrete habitat patches?	Yes	No*	No	No	No	No	No	Yes
2 Does the population return to their place of birth in order to breed?* not needed if 1 = yes	?	?	Yes*	?	?	?	Yes	?
3 Are there 2 or more (sub) populations on North Sea scale?	Yes	Yes	?	Yes	Yes*	Yes*	?	Yes
Score habitat	**2**	**1**	**1**	**1**	**1**	**1**	**1**	**2**
Recolonization: 4 Is it probable that individuals can bridge the distances between populations occurring on North Sea scale?	Yes	Yes	Yes	Yes	Yes	Yes*	Yes	Yes
5 Is dispersal active?	No	No	Yes	Yes	No*	Yes	Yes	Yes
Score recolonization	**1**	**1**	**2**	**2**	**1**	**2**	**2**	**2**
Extinction: 6 Is the organism short lived (< ± 4 years)?	No	No	Yes*	Yes	Yes*	No	No	No
7 Is offspring of the organism low in number (<10)?	No	No	No	No	No	Yes*	No	Yes
8 Is there a high chance on disastrous events?	?	?	No	No	No	?	Yes	Yes
9 Is the organism in the North Sea exploited (or affected by exploitation) by humans?	Yes	Yes	Yes	Yes	No	Yes	Yes	No
Score Extinction	**1**	**1**	**2**	**2**	**1**	**2**	**2**	**2**
Knowledge: 10 Is knowledge on animal sufficient (>10 articles on ISI)?	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
11 Is the metapopulation concept used for this species in literature (ISI)?	No	No	Yes	No	No	Yes	Yes	Yes
Score knowledge	**1**	**1**	**2**	**1**	**1**	**2**	**2**	**2**
Total score	**5**	**4**	**7**	**6**	**5**	**7**	**7**	**8**

Table 5. Score table for assessing species suitability applied to four randomly chosen terrestrial species. 'North Sea' was replaced by 'The Netherlands' and 'exploitation' by 'hunting'.

	Roe deer	**Common vole**	**Blue tit**	**Large white**
Habitat: 1 Does the organism live in / on discrete habitat patches?	Yes	Yes	Yes	Yes
2 Does the population return to their place of birth in order to breed?* not needed if 1 = yes	?	?	?	?
3 Are there 2 or more (sub) populations in the Netherlands?	Yes	Yes	Yes	Yes
Score habitat	**2**	**2**	**2**	**2**
Recolonization: 4 Is it probable that individuals can bridge the distances between populations occurring in The Netherlands?	Yes	Yes	Yes	Yes
5 Is dispersal active?	Yes	Yes	Yes	Yes
Score recolonization	**2**	**2**	**2**	**2**
Extinction: 6 Is the organism short lived (< ± 4 years)?	No	Yes	Yes	Yes
7 Is offspring of the organism low in number (< 10)?	Yes	Yes	Yes	No
8 Is there a high chance on disastrous events?	?	?	Yes	Yes
9 Is the organism in the Netherlands hunted (or affected by hunt) by humans?	Yes	No	No	No
Score Extinction	**2**	**2**	**3**	**2**
Knowledge: 10 Is knowledge on animal sufficient (>10 articles on ISI)?	Yes	Yes	Yes	Yes
11 Is the metapopulation concept used for this species in literature (ISI)?	Yes	Yes	Yes	Yes
Score knowledge	**2**	**2**	**2**	**2**
Total score	**8**	**8**	**9**	**8**

Of these 15 assessed species, 6 species (bread crumbsponge, moon jellyfish, sea gooseberry, common seastar, the nematode *Geomonhystera disjuncta* and the rayed artemis) fell out in the first interpretation step, either because too many questions remained unanswered, or because one or more categories were never answered positively.
For four of the assessed species, two or more subpopulations were described in literature, but no discrete habitat patches or homing were mentioned. This might be a scale problem (the North Sea as a whole might be a habitat patch) or simply a lack of knowledge on precise habitat preferences. According to the quick scan results, the ocean quahog populations are stable (recolonization and extinction are not driving forces) but the species does not have a discrete habitat patch. The common shrimp, king rag worm and thornback ray do show metapopulation structure, but do (as far as known) not live on discrete habitat patches. The horse mussel in the test seems to be a stable population with a discrete habitat patch. In this species however, human influence has a major role in extinction of the species, which is not shown by the results. Metapopulation structure is probable in the edible crab, as the female of this species is thought to walk opposite to the current before spawning, giving her offspring a high chance to recruit to the parent population. In cod, metapopulation structure is probable, as a stock returns to the place of birth in order to breed. Finally, the ultimate population structure is probably in grey seal population structure.

In order to compare the test results to the outcome of the test for terrestrial species, four randomly chosen land living species were chosen. ‘North Sea’ was replaced by ‘The Netherlands’ and ‘exploitation’ was replaced by ‘hunting’ (table 5).
For roe deer (*Capreolus capreolus*, Dutch: ree), the total score was eight, and with a discrete habitat patch, a low recolonization rate and a high extinction probability the species would be in the category ‘ultimate metapopulation’. The common vole (*Microtus arvalis*, Dutch: veldmuis), the blue tit (*Parus caeruleus*, Dutch: pimpelmees) and the butterfly large white (*Pieris brassicae*, Dutch: groot koolwitje) represented the same category.

4. Discussion

Besides some clear differences and similarities, complicated comparisons appear in the literature, being either nuanced or made even more complex by others. However, especially when comparing to a terrestrial landscape, the terms fragmentation, barrier and suitable habitat patches do not seem to fit the underwater North Sea. In the marine environment, exploitation and the homogenizing consequences of beam trawl fishing form major threats in population persistence for many species. Despite being a heterogeneous system, and despite the question whether the system is fragmented or not, isolation of populations is of minor importance for continued existence. This is in contradiction to terrestrial systems where fragmentation (resulting in isolation) forms the most important pressure for metapopulation persistence.

It is therefore questionable if a metapopulation approach is the most relevant one in the marine environment. Furthermore, on land, solutions for persistence problems induced by fragmentation are sought in the assignment and construction of connection zones. In the marine environment, prohibiting fisheries in assigned protected areas might stimulate persistence of populations. The feasibility of connection zones in between protected areas however, is practically unrealistic for several reasons. Hydrodynamic forces and weather influences are not geographically static, meaning that a connection zone should have such a broad margin, that it might be easier to just make one area of the areas that should be connected. Secondly, there might not be a physical barrier and thus no need for a marine organism to choose for the 'connection zone', making the actual functioning of marine connection zones questionable as well.

When looking at the wide ranging habitat types, and the theoretical lack of physical barriers, one might come to the conclusion that discrete habitat patches in the North Sea are either scarce, or that the scale of looking for patches is too small. Lack of discrete habitat however, may be a lack of knowledge, when compared to terrestrial species where much more is known from habitat preferences. Habitat uses are roughly known, but exact preferences are for most species not clear yet. Besides for instance sediment structure, water temperature or depth could be a habitat preference. Than, the underwater North Sea might actually be a patchy environment. This is however simply not known.

Furthermore, chance dependant processes play a major role in the marine environment. The medium water gives more opportunity to move than air, desired or undesired. Despite all kind of strategies species practice in order to get recruitment to the local population, it is in many cases chance dependant if young return to their parent population, or drift away and settle on another patch of suitable habitat.

The difference between land and sea inhabiting organisms is not always that simple to appoint. In many cases, an organism seems to be a perfect candidate to use in metapopulation context, but when more characteristics of this animal are set out, a complicated picture appears. The quick scan for assessing possible suitability of marine species to use in a North Sea metapopulation model is a guide to find out if it is worth the effort to focus on the particular species in metapopulation context. The questions address habitat, recolonization and extinction in such a way that the answer says something about the probability of a metapopulation structure, and are applicable for all organisms. The parameters therefore needed to be generalized, and to have a uniform answer. The

advantage of the yes / no questions used in this research is that one can relatively simply structure the different parameters a species has to conform with for being part of a metapopulation, and see the cumulative effect of those parameters together. The downside of this method is that the scan excludes the possibility to ask for species specific features. The questions on the longevity and numbers of offspring address a K-strategist and a r-strategist respectively making a score of 11 (the total number of questions) very unlikely. The question if there is a high chance on disastrous events is somewhat suggestive. It is however only answered with yes if literature appointed on such risks, other than exploitation by humans. Exploitation by humans is marked as positive for the chance on metapopulation structure, as the chance on (local) extinction gets higher. The difficulties in modeling will get larger too.
Interpretation of low or high recolonization rate / extinction probability in this scan is thus an approximation, not a measured value, and it is of major importance to keep in mind that this scan is designed as a help in structuring the different aspects a species has to conform with. When applying the test for assessing the suitability for use in metapopulation context on randomly chosen terrestrial species however, the results show the expected ultimate metapopulation structure. Despite the fact that the test might need some improvement on several aspects of it, this was seen as an indication for reliability.
The table was however not used for all terrestrial phyla.

Selection of marine species was not from a neutral point of view. Selected species were either brought under attention by scientists consulted, or they appeared to be interesting in a literature scan on ISI. Furthermore, species were selected to cover a wide range of species characteristics. The results of the quick scan might therefore not be seen as representative for all species occurring in the North Sea.
As time was restricted during this research, a maximum time to acquire data on each species was set. The question marks in the table thus do not represent all information on species available.
When looking at the three score tables, one can see some kind of parallel in the increase in score and species 'higher' in the phyla. Although the set of species is not sufficient for being able to bind any conclusion on it, this might be interesting for further research.

5. Conclusion

The attempt of applying the metapopulation concept on the marine environment is in progress. The actual functioning of a marine metapopulation concept however, is still not fully understood and needs improvement on several aspects of it. The metapopulation concept can nonetheless add a framework for asking research questions on and describe actual spatial population processes and structures.

Heterogeneity in the underwater North Sea can be formed vertically by depth related changes in light intensity and oxygen concentration, gradients in water temperature, density, salinity, nutrient concentrations and so on. Horizontally, currents, circulation patterns, surface waves, tides, longitude / latitude, substratum, salinity etcetera cause a heterogeneous environment. Although these processes clearly induce a diverse environment, physical barriers are not that obvious.

Relevant differences between land and sea comprise air versus water, fragmentation on land versus homogenization and overexploitation in sea, and the relatively straightforward terrestrial recruitment versus complex pelagic larval stages with unknown dispersal capabilities in sea.

The species that seems to be most suitable for use in a metapopulation model in the quick scan is the grey seal. Edible crab and cod are potential species to use in a metapopulation model. Both do not have a discrete habitat patch, but are known to have a strategy to ensure their offspring recruits to their own population. For species which seemed to be suitable by having a discrete under water habitat patch, not enough knowledge was present.

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Appendix I Glossary

(Re-) Colonization
A species reaching an unoccupied habitat patch, establishes and maintains (Van Dorp *et al.* 1999).

Connection zone
A zone in between habitat patches by which species can migrate from one suitable to another.

Benthic
Of, relating to or occurring at the bottom of a body of water (Merriam-Websters OnLine dictionary, 16-07-2009).

Demersal
Living near, deposited on or sinking to the bottom of the sea (Merriam-Websters OnLine dictionary, 16-07-2009).

Dispersal
The tendency of an organism to move away, either from its birth site (natal dispersal) or breeding site (breeding dispersal). Rates of regional dispersal depend on a.o. the size and shape of the source area, the dispersal ability of the organism and the influence of environmental factors such as winds or ocean currents. Dispersal may be passive, active, passive but involving an active agent or clonal (Allaby 2003). In metapopulation context, dispersal is often between subpopulations.

Disastrous event
Disasters like diseases, storms or extremely low temperatures, generally occurring less than once a year.

Ecosystem
A natural unit consisting of living and nonliving parts interacting, interacting to form a stable system. Ecosystem principles can be applied to all scales e.g. to an ephemeral pond equally to a lake, an ocean or the whole planet (Allaby 2003).

Extinction
Other than the regular definition, extinction in this context is defined as extinction of a (sub) population.

Filter feeder
Suspension feeding in which water is actively pumped or filtering structures are swept through the water (Castro & Huber 2008)

Fragmentation
The process whereby a larger, continuous living environment of a species is both reduced in area and divided into two or more fragments by obstacles or terrain that is unsuitable as habitat (see Opdam & Hengeveld 1990).

Habitat
The collection of values related to the living requirements of a species which fulfill the physiologically determined needs of that species for reproduction and survival (Ottburg *et al.* 2007).

Habitat patch
A spatially defined area where habitat for a species has been established (Ottburg *et al*. 2007), surrounded by non-habitat.

Halophytes
Salt tolerant plants.

Heterogeneity
The relative abundance (per unit volume or area) of the various structural components and their variability (Fraschetti *et al.*,2008).

Homing
The return by an animal to a particular site that is used for breeding or sleeping. The term may apply to the return of an animal to its nest after foraging, or to seasonal migrations between breeding an foraging grounds (Allaby 2003).

Isolation
Separation from surrounding environment.

K-selection / strategist
Selection for maximizing competitive ability, the strategy of equilibrium species. Most typically is a response to environmental resources. This implies selection for low birth rates, high survival rates among offspring and prolonged development (Allaby 2003).

Landscape
A landscape is a system consisting of biotic, a-biotic and anthropogenic components. A landscape can vary in scale and is a heterogeneous composition of interacting systems (Van Dorp *et al.* 1999).

Landscape ecology
The field of study focused on patterns and processes originating in the interaction between biotic, a-biotic and anthropogenic elements within a landscape (Van Dorp *et al.* 1999)

Landscape elements
The basic, relatively homogeneous ecological unit, whether of natural or human origin, on 'land' at the scale of a landscape.

Metapopulation
A metapopulation consists of subpopulations in which extinction processes and recolonization processes determine to a large extent the size and persistence of subpopulations and the metapopulation as a whole.

National Ecological Network (NEN) or Ecologische Hoofdstructuur (EHS)
The National Ecological Network is a network of areas in The Netherlands where Nature has priority.

Natura 2000
Europe-wide network of sites tasked with the preservation of natural heritage.

Networkpopulation
In the literature the term netwerkpopulation is used synonymous to the term metapopulations, although they do differ. The term metapopulation is used to refer to actual (sub) populations, and networkpopulation refers to both the actual populations and habitats where populations are (temporarily) extinct.

Ovipary

The method of reproduction in which eggs are laid and embryos develop outside the mothers body, each egg eventually hatching into a young animal. Little or no development occurs within the mothers body. Most invertebrates and many vertebrates develop this way (Allaby 2003).

Pelagic
Living in the water column, away from the bottom (Castro & Huber, 2008).

Philopatry
The tendency of an individual to return to or stay in its home area. Most animal species show some degree of philopatry (Allaby 2003).

Population
A group of organisms, all of the same species that occupies a particular area (Allaby 2003).

Population dynamics
The study of factors that influence the size, form, and fluctuations of individual species or genus populations. Emphasis is placed on change, energy flow and nutrient cycling, with particular reference to homoeostatic controls. Key factors for study are those influencing natality, mortality, immigration and emigration (Allaby, 2003).

Predator
Organism obtaining energy (as food) by consuming, usually killing, another organism, the prey (Allaby 2003).

Recruitment
The process of adding new individuals to a population or subpopulation by growth, reproduction, immigration and stocking (Merriam-Websters OnLine dictionary, 16-07-2009).

r-selection / strategist
Selection for maximizing the biotic potential (r) of an organism so that when favorable conditions occur (e.g. in a newly formed habitat) the species concerned can rapidly colonize the area. An opportunist strategy is advantageous in rapidly changing environments as in the early stage of succession (Allaby 2003).

Seascape ecology
The field of study focused on patterns and processes originating in the interaction between biotic, a-biotic and anthropogenic elements within a seascape.

Scavenger
(Detritus feeder)
Heterotroph (an organism that is unable to manufacture its own food from simple chemical compounds) that feeds on dead material (Allaby 2003).

Semelparity
(Big bang reproduction)
The condition of an organism that has only one reproductive cycle during its lifetime (Allaby 2003).

Sessile
Attached to a substrate (Allaby 2003).

Subpopulation

A population that forms a part of a metapopulation.

Terrestrial environment

Land, not inundated by water.

Vivipary

The method of reproduction in which young are produced at a stage of development in which they are active. The growth of embryos occurs within the mothers body which nourishes it (Allaby 2003).