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Is the metapopulation concept applicable to the North Sea?

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The metapopulation concept could provide an additional way of designating areas for protective measures in the North Sea, by delineating habitat preferences and population dynamics. The current study looks into the applicability of the metapopulation concept to the North Sea underwater environment. It also seeks out species in the North Sea that could possibly be suitable metapopulations for study.
The North Sea clearly is a heterogeneous environment, but habitat characteristics, like substratum type, tend to be wide ranged and without obvious physical barriers. Processes and structures in the seascape are mainly known on a rough scale, and even at 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 are unknown for the majority of marine species. The species that seems most suitable for study in a metapopulation model in this test is the grey seal. Additionally, edible crab and cod emerged as species for potential use in a metapopulation model. Neither inhabit a discrete habitat patch, but both are known to have a strategy to ensure that their offspring recruits into their own population. For species that at first seemed to suitable because they have a discrete underwater habitat patch, insufficient knowledge was available to apply the theory further.

Keywords: Metapopulation, Underwater, North Sea, Coastal zone, The Netherlands, Seascape, Connectivity, Dispersal capabilities, Marine species, Grey seal *Halichoerus grypus,* Edible crab *Cancer pagurus,* Cod *Gadus morhua.*

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Preface

This report is the result of my final thesis project for the Coastal Zone Management program at the Van Hall Larenstein University of Applied Sciences. The project was executed at Alterra, Wageningen University and Research Center, within the framework of the Wageningen UR Strategic Plan on Sea and Coastal Zones (2007–10). Research on sea and coastal zones is a special focus of the Wageningen UR, in which it aims to play a pioneer role in initiating and executing applied research. For more information, see 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 colleagues, classmates and friends, not seldom ending in philosophic discussions. I thank everyone who listened to me and contributed their own perspective.

My thanks also go to all of the experts at NIOZ, Wageningen IMARES and Alterra Wageningen UR with whom I spoke, especially to Rob Witbaard, for his time, enthusiasm and his knowledge seeming to be endless.

I am grateful to Pieter Slim, initiator of this project, for his care and to both him and David Goldsborough for providing me the chance to work on this project. I also thank Peter Schippers for his patience and time in discussing Levins' theory with me, as well as for his introducing me to the world of theoretic ecology.

I am grateful to Gerrit Karssenberg and Angelique Kuiper, who read my drafts through and through and provided me with helpful comments. I wish I didn't have to say goodbye and that I could get more of such valuable supervision!

Merel den Held

Arnhem, July 2009

Abstract

A metapopulation is a population of (sub)populations in which processes of local extinction and recolonization regulate ongoing persistence. For the past 15 years, landscape ecologists have applied this theory in the Netherlands to analyze populations' connectivity and persistence in the fragmented terrestrial environment. This has resulted in development of the Dutch National Ecological Network.

In the North Sea, conservation areas are assigned based on habitat type. Here too the metapopulation concept could provide an additional way of designating areas for protective measures, by delineating habitat preferences and population dynamics. The current study looks into the applicability of the metapopulation concept to the North Sea underwater environment. It also seeks out species in the North Sea that could possibly occur in a metapopulation structure.

Referring to the original metapopulation formula developed by Levins (1969, 1970) three requirements are defined for a species to be considered to have a metapopulation structure:

- inhabiting discrete suitable habitat patches,
- exhibiting a relatively high probability of (local) extinction,
- having a low recolonization rate.

The underwater North Sea clearly is a heterogeneous environment, but habitat characteristics, like substratum type, tend to be wide ranged and without obvious physical barriers. Processes and structures in the seascape are mainly known on a rough scale, and even at 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 are unknown for the majority of marine species. The current study translated the three metapopulation requirements above into a list of questions, by which the existence of metapopulation structure in marine species could be assessed. The species that seems most suitable for study in a metapopulation model in this test is the grey seal. Additionally, edible crab and cod emerged as species for potential use in a metapopulation model. Neither inhabit a discrete habitat patch, but both are known to have a strategy to ensure that their offspring recruits into their own population. For species that at first seemed to suitable because they have a discrete underwater habitat patch, insufficient knowledge was available to apply the theory further.

1 Introduction

A metapopulation consists of spatially separated subpopulations in which processes of (local) extinction and recolonization largely determine the size and persistence, both of the individual subpopulations and of 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 originated in the dynamic field of island biogeography established by MacArthur and Wilson (1963) (Hanski 1994), and it is part of the landscape ecology field of study. In landscape ecology, the focus is on patterns and processes emanating from the interactions between biotic, a-biotic and anthropogenic elements within a landscape (Van Dorp *et al.* 1999). Landscapes vary in scale from a few square meters to tens of square kilometers and form a heterogeneous composition of interacting systems. Within a landscape, relatively homogeneous elements, habitats and connection zones can be distinguished (Van Dorp *et al.* 1999).

Many land-dwelling species live in highly fragmented landscapes, where suitable habitat is available only in a small fraction of the area (Hanski 2001). Populations of plants and animals living in a particular patch of suitable habitat often form part of a 'network population' or 'metapopulation' (Van Dorp *et al.* 1999, Hanski 1999, Opdam & Wascher 2004). Here, 'metapopulation' refers to the actual population of the species and 'network' refers to the suitable habitat patches regardless of whether they are all currently inhabited (see also the glossary in the appendix). The occurrence of a species at a specific habitat patch at a particular point in time does not necessarily mean that the species population is persistent. Metapopulation theory predicts that not every patch will be occupied in all years, but that patch nonetheless may still be an important habitat site for a species (Verboom *et al.* 2001, Verboom & Pouwels 2004). In the terrestrial environment, loss of connection zones between suitable patches can greatly impact a metapopulation and eventually lead to extinction of a subpopulation or of the entire metapopulation (Van Dorp *et al.* 1999, Foppen *et al.* 2000, Opdam & Wascher 2004). Insight into the long-term development of a metapopulation can be obtained by using models to simulate metapopulation dynamics, whereby a variety of scenarios can be assessed (Verboom & Pouwels 2004).

Metapopulation models require information on parameters such as habitat preferences, carrying capacity and maps; presence of unoccupied suitable areas; population size, density and stability; number of subpopulations; dispersal capability; maximum lifespan; age at maturity; first-year mortality; male/female ratio; number of offspring; life history characteristics; probability of a disastrous event; and so on. The models differ in complexity. In the relatively simple LARCH model, habitat patch size and network size determine the persistence of a species. METAPOP, a more complex model, includes population dynamics, and the even more intricate METAPHOR model includes the life histories of each individual at a patch.

In terrestrial landscape ecology, insights gained through the use of the metapopulation concept have been of major importance in nature development and conservation (Verboom & Pouwels 2004). Findings have even led governments to revise conservation policies, such as those concerning Natura 2000. In the Netherlands, the concept provided the basis for development and realization of the National Ecological Network. Figure 1 depicts this country-wide system of smaller and larger areas where nature has policy priority. The network is intended to stimulate the enlargement and linking of conservation areas.

Figure 1. The National Ecological Network of the Netherlands. A network is formed by smaller and larger government-designated areas where nature has policy priority. Figure adapted from www.pbl.nl.

Oceans and coastal zones are being more and more intensively used and exploited (Field *et al.* 2002, Lindeboom *et al.* 2008b). The North Sea was long seen as an inexhaustible resource, and only in recent decades has concern for the ecology of the sea come more to the fore (Advisory Council for Transport, Public Works and Water Management 2005). Unlike the more visible terrestrial ecosystems, 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 world's most studied sea areas (Zijlstra 1988). In the framework of Natura 2000, conservation areas are being designated on the Netherlands Continental Plate (NCP) in the North Sea (figure 2). These are chosen based on the EU Habitats Directive, which defines nine coastal and halophytic habitat types and accessory species for all EU marine ecosystems (North and Central Atlantic, Baltic Sea, Mediterranean Basin, Wadden- and North Sea) (Natura 2000 2007). However, the efficiency of assigning protected areas based on abundance of species in the assumed relevant habitat types is not undisputed, as the North Sea is a highly dynamic and changeable system (see e.g. Lindeboom *et al.* 2008a). Another, or additional way to assess the North Sea ecosystem, and perhaps ultimately to assign conservation areas, could be application of the metapopulation approach (Slim & Schippers, pers. comm.; Kritzer & Sale

2006). Using this approach, the consequences of designating particular areas in the North Sea as protected, as well as the possible effects of the system's heterogeneity, can be assessed by means of a spatially explicit evaluation of species habitat preferences and the natural balance of a metapopulation.

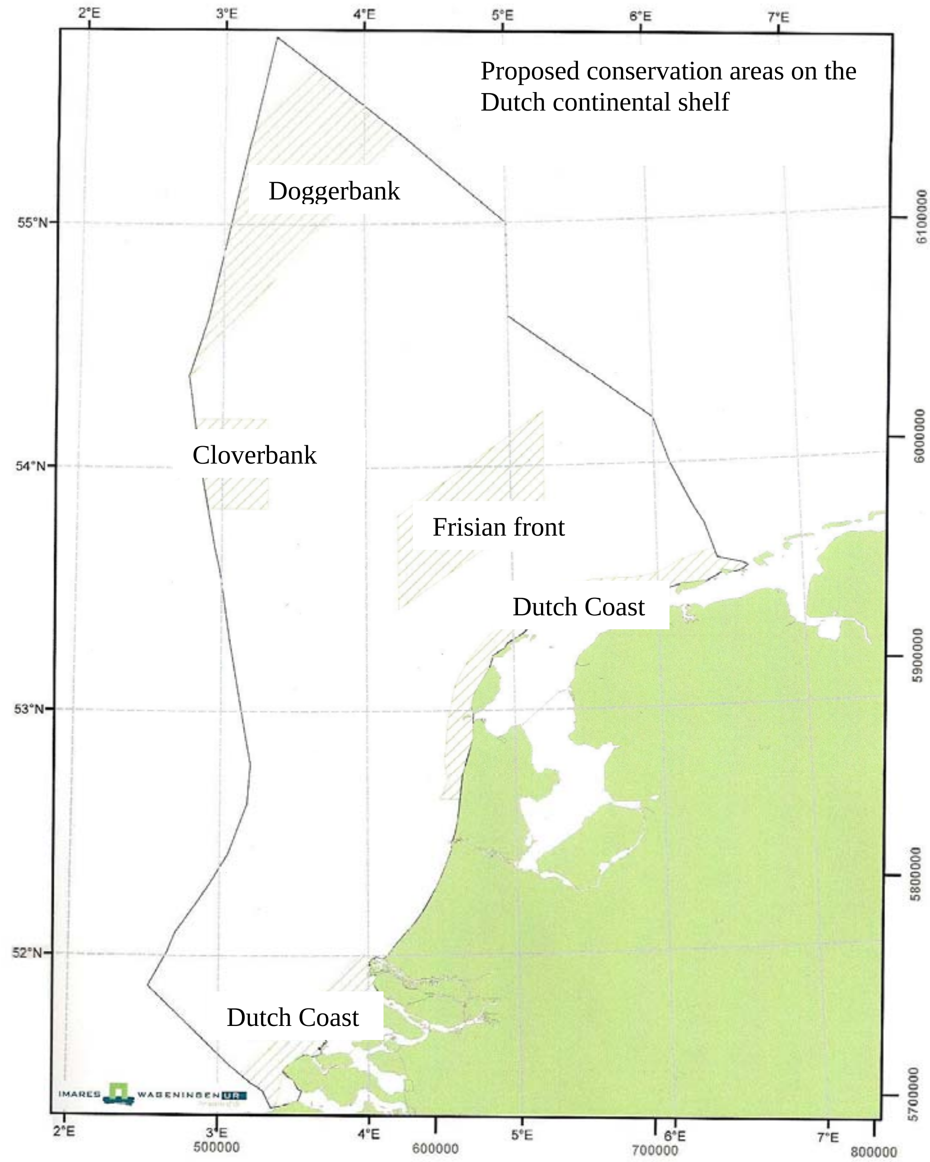


Figure 2. Shaded areas are proposed conservation areas on the Dutch continental shelf.

Both landscape ecologists and marine ecologists on a global scale are discovering the possible applications of the metapopulation concept in the marine environment. However, doubters on both sides have long resisted use of metapopulation terminology in combination with marine habitats (Kritzer & Sale 2006). Despite the efforts of those who have applied the metapopulation concept to marine ecosystems, it still does not seem to be a concept used regularly by those studying the underwater

North Sea ecosystem. Potential users appear either unconvinced or unfamiliar with the possibilities of metapopulation concept in the marine environment. Arguments against application of the concept in this marine realm are that it is unclear what the metapopulation concept can contribute to the marine ecology field of study and it is uncertain how the theory can be used to study the North Sea ecosystem. Neither is known in which marine situations the metapopulation concept is and is not applicable (Kritzer & Sale 2006), and the extent to which the concept should and could be adapted to apply to the marine ecosystem.

The current investigation focuses on the possibilities of applying the metapopulation concept in underwater North Sea research and North Sea conservation. Specifically, this research aims to determine the extent to which the metapopulation approach can be applied to the North Sea ecosystem, and to learn which species could be suitable for study from a marine metapopulation perspective. This leads to the following main research question:

> *To what extent is the metapopulation concept applicable to fauna of the marine ecosystem of the North Sea bottom and waters, and what species are suitable for study using a marine metapopulation model?*

Related to this are four subquestions:
1. What is the present state of the literature on applying the metapopulation concept in marine ecosystems?
2. What factors cause heterogeneity in marine ecosystems?
3. What are the relevant differences between landscape ecology and seascape ecology from a metapopulation perspective, and is fragmentation a relevant factor in the North Sea ecosystem?
4. What marine faunal species, in the groups fish, benthos and sea mammals, are suitable for study using a metapopulation simulation model and for what reasons, and are there species that definitely cannot be used?

Chapter 2 defines further the requirements for designating a group as a metapopulation. With these prerequisites serving as a backdrop, the chapter goes on to present the results of a literature study and interviews with experts. These provide answers to subquestions 1, 2 and 3 and lead into development of a scan to test species suitability for study using the metapopulation approach. Chapter 3 describes the present situation regarding marine applications of the metapopulation concept. Factors causing heterogeneity in the North Sea are then reviewed, followed by a comparison of land and sea from a metapopulation perspective. The scan developed in chapter 2 is employed to assess the suitability of 15 marine species for study using a metapopulation approach. Chapter 4 delves deeper into the research methods and the results. Chapter 5 presents the study conclusions, answering our main research question. Appendix I contains a glossary of the terms used.

2 Methods

2.1 The requirements for and the existence of a metapopulation

The author used Van Dorp *et al.* (1999) to gain insight into relevant aspects of landscape ecology and to learn to reason from a landscape ecology point of view. Knowledge on the metapopulation theory was gained via the ISI Web of Knowledge database,[1] searching using the term 'metapopulation' on the most-cited authors. Additionally, articles by scientists working on metapopulations at Alterra, Wageningen UR, were read, and some of these academics were consulted for supplementary information.

To provide a recommendation on the species most suitable for study using the metapopulation approach, requirements for suitability had to be formulated and decisions made on the existence or nonexistence of a metapopulation structure. 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 of his idea is as follows:

$$dP/dt = mP\,(1 - P) - eP$$

where P is the fraction of habitat patches occupied at time t, m is the recolonization rate, and e is the probability of a local population going extinct. Terrestrial metapopulation models define these terms using species-specific parameters (table 1).

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

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

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

Figure 3 relates to metapopulations for which extinction and recolonization processes largely determine the size and persistence of subpopulations and of the metapopulation as a whole. With 90% or more of the suitable habitat occupied, recolonization and extinction are no longer the driving forces in persistence. In the no-survival area no metapopulation is possible. Thus, two options remain. In figure 4, the area where a metapopulation structure is possible is marked green, and that where no metapopulation structure is possible is colored red.

[1] Version 4.6, logged in via Wageningen University Library

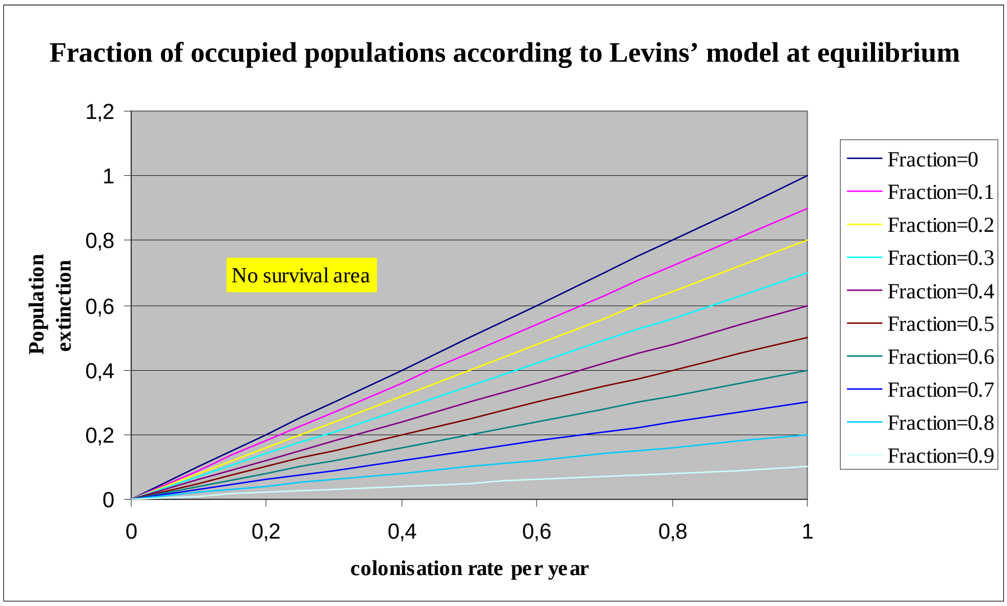


Figure 3. Fraction of suitable habitat patches occupied at a particular point in time according to Levins' model at equilibrium. The balance between extinction probability at a patch and recolonization rate of unused suitable patches defines the fraction of suitable habitat occupied. In the 'no-survival area', the recolonization rate is lower than the extinction probability and the fraction of suitable habitat patches occupied is thus 0. No living individuals of the species can be found here. At 0.1, 10% of the suitable habitat patches is occupied, and the extinction probability is high relative to the recolonization rate. Here, the rate of recolonization of patches where a local population went extinct determines the ongoing persistence of the metapopulation as a whole. At 0.9, 90% of the suitable habitat patches is occupied, and the extinction probability is low relative to the recolonization rate. Therefore, extinction of a local population is not a regular occurrence, but colonization (and recolonization in cases where a patch is unoccupied) does frequently occur. In such a stable population, other processes or factors (for instance, competition or food availability) regulate the persistence of the subpopulations and of the metapopulation as a whole.

Table 2 expands on this figure by combining various rates of recolonization and extinction probabilities. At one extreme, a high extinction probability combined with a low recolonization rate would mean an extinct species. In the realm of living species however, this combination would be the 'ultimate metapopulation' (i.e. one that lives in discrete suitable habitat patches, has a relatively high chance of local extinction and a relatively low rate of recolonization of unoccupied network patches). High extinction probability combined with a relatively high recolonization rate would indicate a metapopulation, but one whose subpopulations are probably genetically indistinguishable. Low extinction probability combined with a relatively low recolonization rate would indicate a metapopulation at risk of becoming a distinct subspecies, since exchange of individuals is rare. In a population with low extinction probability and a relatively high recolonization rate, extinction and recolonization are not the main forces regulating the population's persistence.

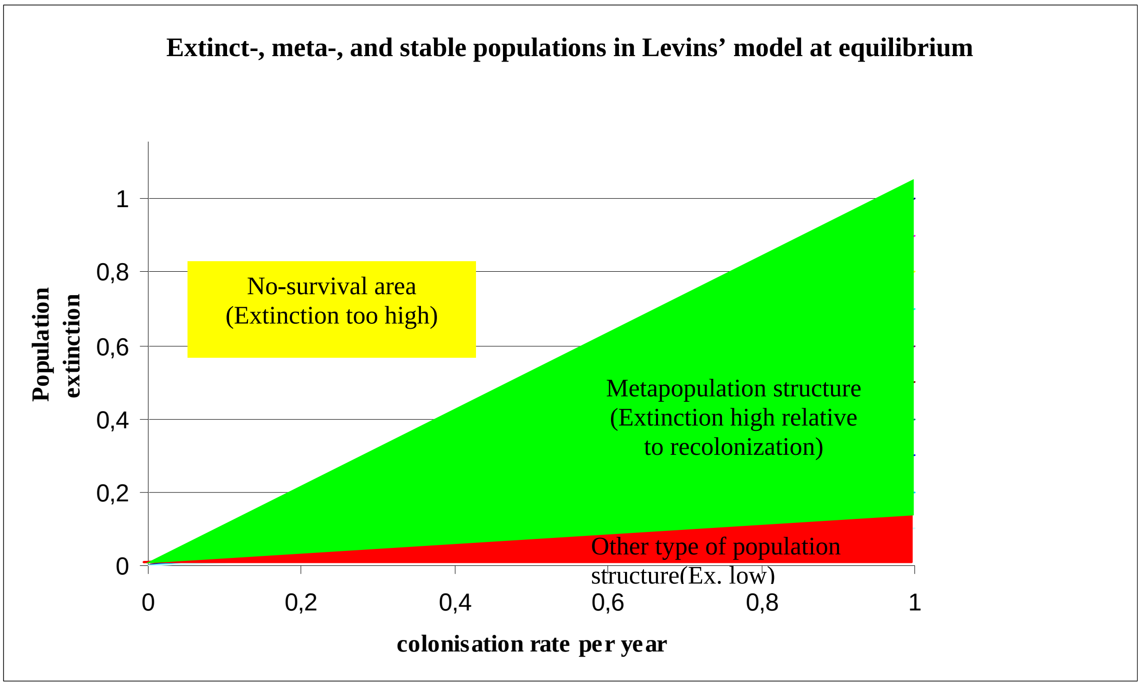
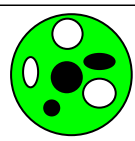
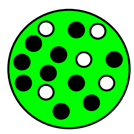
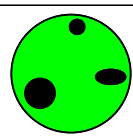
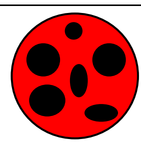


Figure 4. In the green area, the local extinction probability is high relative to the recolonization rate and this area is assumed to contain metapopulations as stated in our definition. In the red area, extinction probability is low relative to recolonization rate. In this region, populations are assumed to be regulated by factors other than extinction and recolonization.

Table 2. Four types of population structure resulting from combining the different levels of extinction probability and recolonization rate (with a discrete habitat as a prerequisite). The figures on the right represent the possible structures, with white circles indicating unoccupied habitat patches (those still to be recolonized) and black circles being occupied habitat patches. Green population structures are assumed to have a metapopulation structure, the red figure is not.

Extinction	**Recolonization**	**Type of population**		
High	Low	= Ultimate metapopulation (if viable)	1	
High	High	= Metapopulation, probably genetically homogeneous	2	
Low	Low	= Highly isolated subpopulations, probably genetically dissimilar	3	
Low	High	= Stable populations (recolonization and extinction are not driving forces)	4	

The population structures as presented in the table can be placed back into the graph in figure 3 (figure 5). This illustrates once again that the 'ultimate metapopulation' refers only to viable populations, and at this extreme are only dead or nonexistent species.

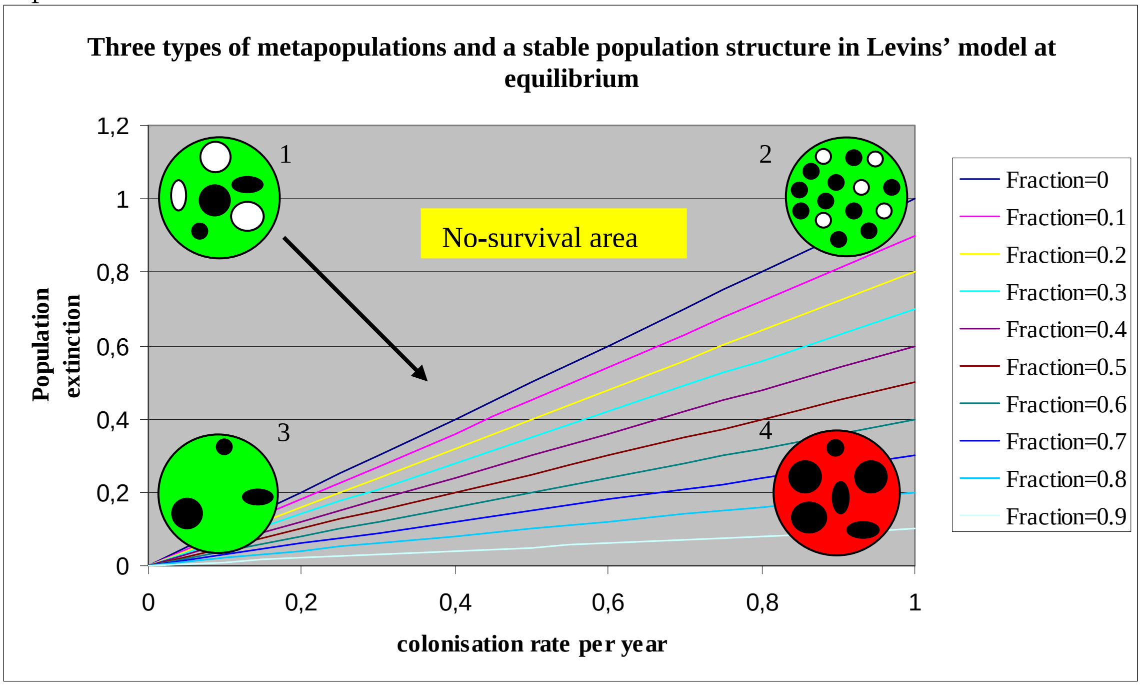


Figure 5. The three types of metapopulation and the stable population placed back into Levins' equilibrium figure. Structure 1 is only a metapopulation if the population is viable, as the upper left zone is the no-survival area. The figures representing population structures overlap into the survival area, as they represent a balance between extinction probability and recolonization rate, and not only the extremes.

2.2 Gathering information

This research began with a review of the literature related to each of the study questions, followed by interviews with marine experts. Question 1, relating to the present state of the literature on application of the metapopulation concept to marine ecosystems, was investigated starting with the book *Marine Metapopulations* (Kritzer & Sale 2006). References from this book provided a stepping stone for further literature study, supplemented by a scan of the literature using the ISI Web of Knowledge database. Relevant articles were selected using the search term 'metapop*' combined with 'marine', 'North Sea' and the like, resulting in a list of articles which in turn were scanned according to the number of times cited. Using this information, the first question was answered in as far as possible, and remaining uncertainties and questions were listed to present to an expert later in the research.

Question 2, on the factors that cause heterogeneity in the marine ecosystem, was investigated by searching the ISI database for terms such as 'North Sea AND ecosystem' and 'habitat AND North Sea'. A summarized answer to this research question similarly led to a list of further questions to be posed to a North Sea ecosystem expert.

Question 3, on the relevant differences between landscape ecology and seascape ecology from a metapopulation perspective and on fragmentation in the North Sea, was answered by combining the preceding literature studies. This also led to further questions to be posed to metapopulation and marine experts.

To prepare for the search for species suitable for study using a metapopulation simulation model and to learn why certain species are more suitable than others (question 4), the literature on terrestrial metapopulations described above was again consulted. A list was composed of criteria and conditions that species would have to meet to be suitable for metapopulation modeling (in the categories 'habitat', 'recolonization rate' and 'extinction probability'). This list was discussed with a metapopulation expert and formed a basis for further questions on marine species suitability for use in a metapopulation model.

This base of knowledge on (marine) metapopulations provided background for a series of interviews with marine ecologists. These included personal conversations with marine ecologists from NIOZ and Wageningen IMARES specialized in benthic communities, marine mammals, marine conservation areas and population dynamics. Given the subject's breadth and complexity, and because most of the questions lacked a uniform answer, the aim was to leave some openness in the interviews. The interviews started with an introduction to the metapopulation concept and the results of the literature study. The questions emerging from the literature study then served to structure the remainder of the conversations. As such, the scientists consulted expanded on and illuminated aspects concerning marine metapopulations which otherwise might have been disregarded. A digital voice recorder was used during the interviews and with every question or new subject the time on the voice recorder was noted. After the interviews, the researcher reorganized the responses by playing back the recordings and categorizing what was said according to the research questions. Notes from the literature study relating to questions 1, 2 and 3 were supplemented with the information from the interviews. The suggestions for answering research question 4 were considered for use later in the research.

2.3 Developing a test of species suitability for use in a metapopulation model

The ultimate metapopulation thus lives in discrete suitable habitat patches, has a (relatively) high chance of local extinction and a (relatively) low rate of recolonization of unoccupied network patches. To test whether it is probable that a species has a metapopulation structure, these requirements were translated into questions using the information gathered during the literature study and interviews. In addition, a criterion 'knowledge on species characteristics' was added, to prevent advising use of a species on which little data exists. The questions had to have a uniform answer and supply information about the probability of the tested species having a metapopulation structure. The questions therefore inquire into the probability that the species inhabits a discrete network patch, exhibits a low recolonization rate and has a high local extinction probability; also knowledge on the species must be available. The greater the number of questions answered positively, the higher the possibility that the assessed species could be used in a metapopulation model. An unknown answer to one of the questions is given a question mark and then counted as 'no', as it would reduce the organism's suitability for use in a metapopulation model. The total number of questions answered in the affirmative yields a score between 1 and 11. This list of questions was discussed with metapopulation experts and refined based on their comments. To evaluate the scan it was first tested on four terrestrial species, replacing references to the sea with 'the Netherlands' and exploitation with 'hunting' (see table 5).

Habitat
1. Does the organism live in discrete habitat patches?
2. Does the population return to its place of birth to breed?
3. Are there two or more (sub)populations on a North Sea scale?

Recolonization
4. Is it probable that individuals can bridge the distances between populations occurring on the scale of the North Sea?
5. Is dispersal active?

Extinction
6. Is the organism short lived (< ± 4 years)?
7. Are offspring of the organism few in number?
8. Is there a high chance of disastrous events?
9. Is the organism in the North Sea exploited by humans?

Knowledge
10. Is knowledge of animal characteristics sufficient (>10 articles on ISI)?
11. Is the metapopulation concept associated with this species in literature (ISI)?

2.3.1 Logic behind the individual questions

1. Does the organism live in discrete habitat patches? Some degree of isolation is needed for a metapopulation to exist. Local habitats are composed of processes and structures (e.g. substratum, fronts, eddies, upwelling of nutrients) and nonhabitat should be distinguishable between them. If no discrete habitat patches can be distinguished, use of this species in a metapopulation model will demand creative thinking.

2. Does the population return to its place of birth to breed? If a species is known to return to its place of birth to breed (natal philopatry), these breeding grounds can be seen as a suitable habitat. For these species the chance of recolonization decreases, since an individual searches out a new breeding site only in cases of density-dependent changes or a genetic predisposition to risk moving away (Kritzer & Sale 2006).

3. Are there two or more (sub)populations on a North Sea scale? A metapopulation consists of subpopulations. Subpopulations are distinguishable from one another when nonhabitat exists between them (e.g. hydrodynamic forces as well as sediment structure or human influences). When available, genetic evidence can also be used to distinguish subpopulations. If there are two or fewer subpopulations of the species in (or in the vicinity of) the North Sea, either the scale of the metapopulation must be sought beyond North Sea range, or the species occurs as a single, possibly spatially subdivided homogenous population. In these cases, the species is unlikely to be suitable for straightforward use in a (North Sea) metapopulation model.

4. Is it probable that individuals can bridge the distances between populations occurring on the scale of the North Sea? Dispersal distance defines the scale at which the metapopulation exists (Kritzer & Sale 2006). To exchange individuals, subpopulations must lie within reach of one another. If the distance between subpopulations is larger than the species' dispersal distance (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 unknown, recolonization rates have to be assumed and model results become highly uncertain, meaning that the organism is not (yet) the best candidate for use in a metapopulation model.

5. Is dispersal active? When dispersal is passive (e.g. driven by hydrodynamics), dispersal direction and distance are, in general, dependent on chance to some extent. In theory, the organism could end up anywhere at sea, and could establish as long as suitable habitat is available (Norris 2000). Passive dispersal thus occurs because the organism is unable to avoid it, rather than because the species has evolved an optimal solution to the costs relative to the benefits of moving to a new patch (Kritzer & Sale 2006). For passive dispersers, the chance of recolonization of suitable habitat is high because theoretically every individual can reach every patch of suitable habitat. Nonetheless, knowledge tends to be scarce on, for instance, distances, directions and velocity of passive dispersers (Botsford & Hastings 2006). These uncertain factors reduce the reliability of the use of such organisms a metapopulation model. When dispersal is active (e.g. the organism is moving itself), the costs and benefits of dispersing are less chance-dependent. The probability of survival is lower when leaving a habitat patch that is known to be suitable to wander through inhospitable areas without the certainty of ever reaching another suitable patch (Kritzer & Sale 2006). This study assumes that an individual will stay with its population/in its suitable habitat, unless stimulated to move by, say, density-dependent changes or a genetic predisposition to take this risk. Thus, this quick scan assumes recolonization rate to be lower for active dispersers than for passive dispersers.

6. Is the organism short lived (< ± 4 years)? The longer an animal lives, the smaller the chance of death per live year (not taking into account mortality rates caused by human exploitation, as these are dealt with under question 9). Short-lived organisms therefore have an increased chance of local extinction.

7. Are offspring of the organism few in number? If offspring are few, the chance of recolonization is also relatively low. Species with few descendants (1 or 2) generally give their individual young more chance of survival than species with many young (e.g. 10,000). However, the chance of survival is still higher for species with more than 2 descendants.

8. Is there a high chance of disastrous events? When a species is susceptible to disastrous events (e.g. disease, storm, extremely low temperature) generally occurring less than once a year, the chance of local extinction is relatively high. This question can only be answered in the affirmative if the literature explicitly mentions such susceptibility.

9. Is the organism in the North Sea exploited by humans? When the organism is exploited by humans, or affected by exploitation (e.g. due to being bycatch or damaged by beam-trawling) the chance of extinction increases. Besides that, economically important species tend to be more intensively studied, thus extensive knowledge on such organisms is likely to be available. Most economically relevant species are in desperate need of improved management, making the metapopulation approach a welcome possible option. Nonetheless, capricious patterns and rates of exploitation can produce unpredictable population behavior for these organisms.

10. Is knowledge of animal characteristics sufficient (>10 articles on ISI)? If little knowledge is available on life history characteristics, population dynamics and habitat preferences, it will be difficult to use the organism in a metapopulation model. The more knowledge is available, the more reliable the outcome of the metapopulation model will be. If this question is answered with a 'no', question 11 is moot and the species cannot be recommended for use in a metapopulation model.

11. Is the metapopulation theory associated with this species in literature (ISI)? If the organism has been mentioned or even used by other scientists in metapopulation context, the species is considered a candidate for use and the assumption is made that uncertainties can be overcome.

2.3.2 Interpretation of the quick scan results

Interpretation and analysis of the scan were accomplished using the types of population structure possible and strict maintenance of the main research question. The purpose of the quick scan is to get a feeling for which species are and are not of interest from a metapopulation perspective. The scan is a means to evaluate the probability of a species having a metapopulation structure, not to provide a measured value.

Step 1
Interpreting the total score is straightforward only if all questions are answered. If three or more questions remain unanswered, no judgment can be made on the population structure of the species. At least one question in each of the categories (habitat, recolonization rate, extinction probability and knowledge of the species)

must be answered in the affirmative for the species to be considered for use in a metapopulation model. Otherwise, the first step of the quick scan is the final one and the species is not further analyzed.

Step 2
Species for which fewer than three question marks remain and in each category at least one question is answered with a 'yes' are further analyzed for population structure. The categories 'recolonization rate' and 'extinction probability' must be classified as high or low. Only two questions address recolonization. If one question is answered positively, recolonization rate is considered to be high. If two questions are answered positively, recolonization is seen as low and a metapopulation structure is more likely.

Four questions address extinction. One addresses r-strategists, and one addresses K-strategists. It is unlikely that both these questions will be answered 'yes', and therefore three is the maximum score for the extinction probability category. (Local) extinction probability is considered to be low if one question is answered positively. If two or three questions are answered 'yes', local extinction probability is high and a metapopulation structure is more likely.

For use in a metapopulation model, more than ten articles must be available on the species from the ISI Web of Knowledge database.

2.4 Selecting species to test for suitability for a metapopulation approach

To assess the applicability of the metapopulation concept for study of the North Sea underwater environment, a representative set of species was compiled. First, the phyla Porifera, Cnidaria, Ctenophora, Nematoda, Annelida, Mollusca, Arthropoda, Echinodermata and Chordata were selected based on their assumed relevance for metapopulation modeling. This selection was discussed with and approved by the initiator of this research. Second, attempts were made to include organisms with a maximum of known species characteristics (lifestyle, feeding mode, type of breeder, etc.) and habitat preferences (table 3). With these criteria providing a framework, species were selected based on suggestions made by marine scientists during the interviews. For the remaining phyla, common species were selected as well as species with distinctive characteristics not yet present in the selection. Data on the species was sought using the ISI database, by consulting scientists and by reading books. A maximum time of half a day was spent searching for the required information on each assessed species.

Table 3. Characteristics represented by species subjected to the quick scan to assess suitability for study using a metapopulation model. As many characteristics as feasible were included to provide as complete an overview 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	Commercially important	Cod, common shrimp
	Not (yet) commercially important	Rayed artemis
	Not commercially 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

Attempts to apply the metapopulation concept to marine ecosystems are documented in a strong body of scientific literature with contributions from diverse research divisions and countries. The term 'marine metapop*' in the ISI Web of Knowledge database yielded 171 articles with the search term appearing at least in the subject (18 July 2009). In the same database, 'North Sea metapop*' returned 34 articles with the search term in the topic (18 July 2009).

Species for which the concept is referred to only in the North Sea range from fish such as 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), the grey seal (Harrison *et al.* 2006) and colonial birds (Boulinier & Lemel 1996). Fisheries science, in particular, has a long tradition of spatial and temporal structuring of biocomplexity, though the term 'metapopulation' has only recently been introduced (Jones 2006, Hillborn *et al.* 2003).

Outcomes of the numerous marine applications of the metapopulation concept vary. Hummel (2003) concluded that many bivalves in the coastal zone of Europe were better referred to as 'megapopulations' instead of metapopulations. Yet Gutow and Franke (2003) did find a metapopulation structure in the isopod *Idotea metallica*, although it remained difficult to determine parameters underlying metapopulations, such as migration rate and patch occupancy rate.

The adaptation of the metapopulation concept for marine ecosystems is still in progress, and the strengths, weaknesses, knowledge gaps and specific situations in which the theory can be applied are being explored and documented (e.g. Kritzer & Sale 2006). Neither is the actual functioning of a marine metapopulation concept however, is still not as yet fully understood, and improvements are required in several respects (Kritzer & Sale 2006, 2004; Grimm *et al.* 2003; Smedbol *et al.* 2002). First, there is a call for more strictly formulated definitions for the metapopulation concept in the marine context, and for a uniform use of concepts to prevent the meaning of the concept from becoming blurred (Grimm *et al.* 2003; Smedbol *et al.* 2002; Van der Meer, pers. comm.). At the same time, however, Kritzer and Sale (2004) and Hanski (1999) argue that strict definitions would exclude a wide array of system dynamics for which the concept is applicable. They underline further that it is most important to know the general concept and how and when it is relevant.

A major difficulty related to marine metapopulations is the lack of knowledge on dispersal capabilities of species. It is, for instance, extremely difficult to track the dispersal of miniscule larvae in the immense volume of the ocean. Yet the scale at which one should assess the existence of a metapopulation is dependent 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 knowledge gap on dispersal distances, the degree of connectivity between populations remains uncertain in many cases.

Efforts to apply the metapopulation concept to marine environments are motivated by the need to understand marine population dynamics and persistence (Botsford & Hastings 2006) for conservation and management purposes, as well as to avoid overexploitation of marine life (Jones 2006, Grimm 2003). According to Hu and Wroblewski (2009), "[F]or proper fisheries management, understanding the spatial and temporal population dynamics of an exploited species is fundamental." Jones (2006) writes, "[T]he value of the metapopulation concept [for] fisheries management is that it reinforces finer scale regulation and harvest oversight." Although unknowns remain regarding the applicability of the metapopulation theory in the marine environment, most authors agree that the concept provides a useful framework for research addressing spatial phenomena and processes at different spatial scales.

3.2 The North Sea: A heterogeneous environment

Factors causing heterogeneity in the North Sea waters are many (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). Flow velocities also vary. The substratum ranges from silty sand to gravel (Groenewold & Van Scheppingen 1988). Hard substratum was found at the 'Texel stones', and has also been added to the environment by humans in the form of sunken shipwrecks, oil and gas drilling platforms and windmill parks (Lindeboom *et al.* 2008a). Depth ranges from a mean of about 200 m in the northern North Sea to shallow areas with a depth of 20 m or less in the coastal areas and near sandbanks. Light penetration varies according to depth and turbidity, with turbidity being a function of the amount of suspended material. Where stratified waters meet mixed waters, fronts develop, eventually causing an upwelling of nutrient-rich water. Due to these large regional differences in substrate, depth and hydrographic conditions, functional areas in the North Sea can be distinguished (Lindeboom *et al.* 2008a). These are illustrated by some examples on the Dutch continental shelf.

The Dogger bank (number 1 in figure 7) divides the North Sea into a shallow southern part and a much deeper northern part. The sandbank is located at the northernmost part of the Dutch continental shelf. It extends some 300 km from southwest to the northeast, covering part of the German, British and Danish continental shelf. The sandbank forms a natural border for fauna distribution, with considerably different fauna on the northern and southern sides. Tidal currents, wave forces and currents incited by wind cause intense mixing of the water column on the shallow side of the bank, whereas the long, colder waves from the northern North Sea stratify the water on the north side. Where these stratified waters from the north meet the mixed waters from the south a tidal front develops. Sediment on the Dogger bank is fine sand, with grains ranging from 125 μm to 250 μm (Groenewold

& Van Scheppingen 1988). The sediment on top of the sandbank contains 1% or less silt. On the sides of the Dogger bank, where water depths exceed 30 m, the sediment is finer and the silt percentage varies from 1% to 11% (Groenewold & Van Scheppingen 1988).

In the coastal area (number 2 in figure 7), water depth gradually increases to 20–30 m 5–15 km from the shoreline. On the smooth inclined plane, sand grain sizes vary between 250 µm and 500 µm, with silt percentages of 1–3%, and patches where silt makes up 10% of the sediment (Groenewold & Van Scheppingen 1990). In the coastal waters of the southern North Sea, turbulence generated by strong currents and wave action cause turbidity. Rivers influence the salinity and nutrient availability along the coast. Salinity here increases with depth.

Further offshore, at a distance of about 80 km north from the Wadden Islands, lies the Frisian front (number 3 in figure 7). Here, stratified waters from 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 possible an increase in primary production (Lindeboom *et al.* 2005).

Along the western edge of the Dutch continental shelf, the Clover bank (number 4 in figure 7) forms a distinct habitat patch with regard to substratum. The substratum of the sandbank consists of gravel and stones, unlike its surroundings, which are mainly silt and sand. The Clover bank is divided by the deeper Botney Cut sea channel, in which the substratum consists of 50% silt (Lindeboom *et al.* 2008a). For a detailed description of the North Sea ecosystem see Zijlstra (1988), Lindeboom *et al.* (2008a) and Janssen & Schaminée (2009).

Figure 6. Many factors and processes make the North Sea a heterogeneous environment. Figure adapted from the book The North Sea (in Dutch) by Greenpeace (1985).

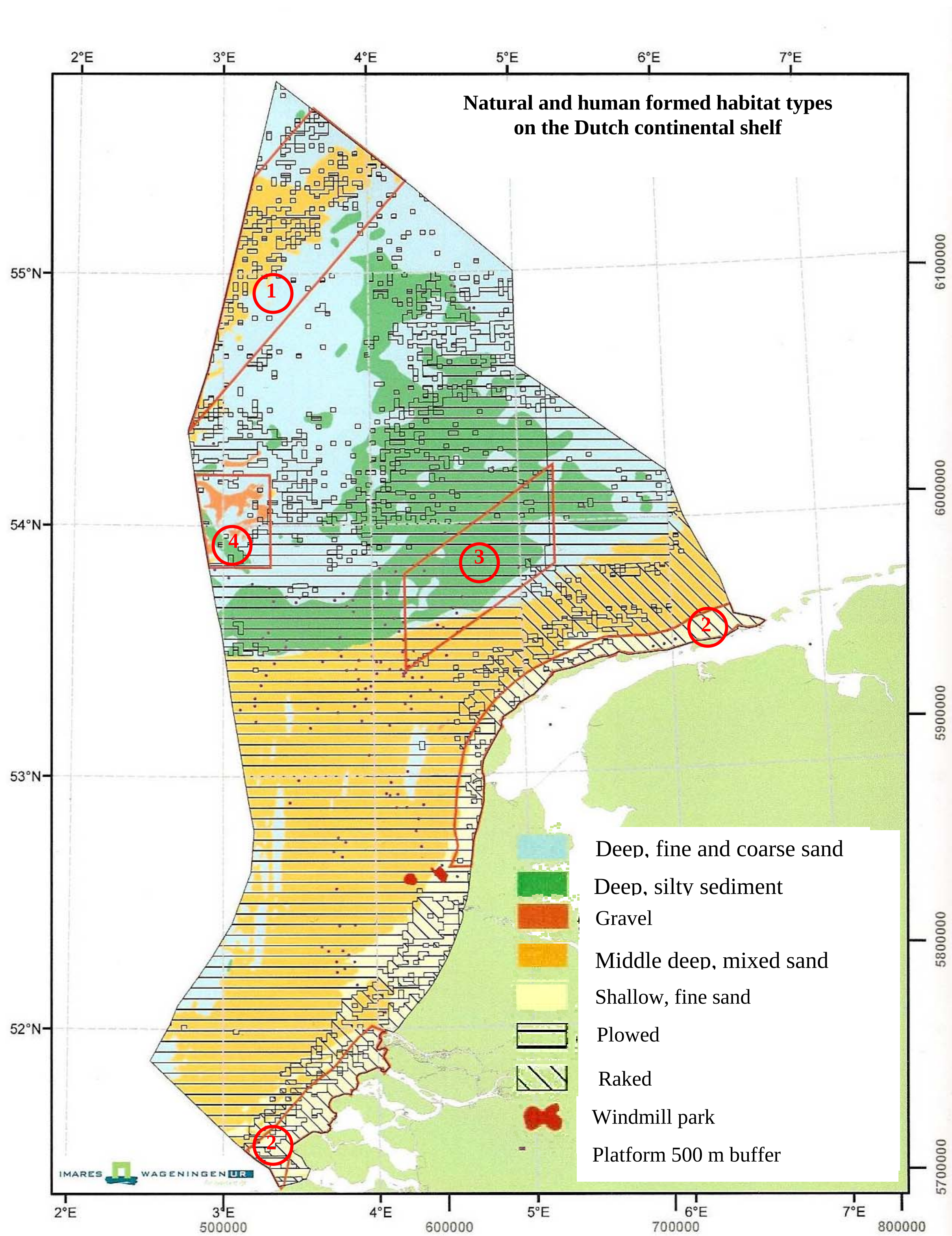


Figure 7. Habitat types in the North Sea. Areas within the red lines are (1) Dogger bank, (2) the coastal areas, (3) the Frisian front and (4) Clover bank. A major part of the Dutch continental shelf is influenced by fisheries. Based on depth and substratum, five habitat types can be distinguished. Figure adapted from the Ecological Atlas of the North Sea (Lindeboom et al. *2008b).*

3.3 Land and sea: Comparison from a metapopulation perspective

3.3.1 Air versus water

The most obvious difference between terrestrial and marine systems is the surrounding medium: air versus water. In terrestrial systems, one can easily appoint landscapes and their components, for example, by walking through them. However, invisible underwater landscapes require far more sophisticated techniques to define structures, components and processes (see 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: 829) and is in most cases extremely expensive and rather fundamental. Furthermore, though oceanographic processes are roughly known on a large scale, on smaller scales uncertainty remains in many cases (Kaiser *et al.* 2005, Kritzer & Sale 2006). As such, existing knowledge of the North Sea bottom and its inhabitants is an interpretation (Lindeboom, pers. comm.; Kaiser *et al.* 2005) of data gathered by taking bottom samples along a grid or transect either by triple-D dredge or box core (Lindeboom, pers. comm.). These methods can indicate patchiness in substrate structures only on a large scale. This lack of detailed knowledge of marine systems makes it more difficult to profitably apply the metapopulation concept here.

Another consequence of the surrounding medium is the different energy budget and bottom-tiedness in air and water. In an air-surrounded landscape, fauna must move actively, and life is bottom-tied in most cases; even species that can fly need a place to breed. In water, avoiding movement might be harder than moving, and breeding need not take place on the sea bottom.

3.3.2 Human influence

Another obvious difference between land and sea is the form of human influence. In the terrestrial environment ownership is fixed, unlike 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 with resources generally fixed in the long and short term (Kerr 1996). In the terrestrial environment, the results of human influence are fragmentation of landscapes and habitat loss.

The human activity that most impacts the North Sea ecosystem is exploitation. Bottom fisheries is especially harmful, both to organisms and to habitat (Trush *et al.* 2001). The use of tickler chains in beam-trawl fisheries transforms the bottom structure into a homogeneous mass to a depth of six centimeters under the substrate surface. Infauna as well as bottom-dwelling fauna are seriously harmed by the chains. According to Lindeboom *et al.* (2008a), the effect of the gear is comparable to the plowing of a field. Figure 7 shows the area affected by this gear as 'plowed habitat'. Areas affected by fishing gear that only scrapes the bottom (rather than plowing it) and thereby disturbs mainly bottom-dwelling fauna is shown as 'raked habitat' in figure 7. On the Dutch continental shelf in particular, some 80% of the area has been transformed from natural to heavily fished habitat (Lindeboom *et* *al.* 2008a). Less destructive but still physically changing the North Sea are human activities adding hard substratum. Shipwrecks, oil and gas drilling platforms and windmill parks provide suitable habitat for anemones and other organisms with a sessile lifestyle. These added habitat patches can be viewed as stepping stones, however, and not as contributing 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, invasive species can be introduced via ballast water. Although these influences can be harmful to the ecosystem as a whole, they do not lead to fragmentation of the seascape in the first place. The noise produced by ships might be disturbing to particular species, but the influence, though not exactly known, is thought to be minor (Lindeboom *et al.* 2005).

The human influences with the largest effect in the marine realm are thus overexploitation and homogenization of habitat (Kritzer & Sale 2006).

3.3.3 Barriers

An important factor for the persistence of metapopulations is connectivity between subpopulations. In the fragmented terrestrial landscape, barriers (e.g. highways and urban areas) prevent individuals from migrating to another subpopulation, with extinction as a possible consequence (see e.g. Hanski 1997).

In the marine environment, heterogeneity can be found both vertically and horizontally. Although the processes involved clearly induce diversity in the environment, physical barriers are not as obvious as in terrestrial landscapes, and their consequences are not comparable to terrestrial fragmentation. Few insurmountable barriers are found outside of the coastal zone, where the seascape is more land-like and distributed in a patchy fashion (e.g. with rocky shores and sandbars forming barriers in themselves).

In theory, the only physical barriers in the North Sea underwater are where the bottom is not inundated, that is to say, coastlines and sandbanks above the mean highwater level. Jones (2006) points out the difference between 'naturally evolved' metapopulations in the sea and the more 'fragmentation induced' metapopulations on land. Heterogeneity in the North Sea clearly is 'naturally evolved' and not 'fragmentation induced', and species distribution patterns are adapted to the possibilities offered by the marine system.

At sea, patches of suitable habitat are often widely spread, comprising hundreds of square kilometers (see figures 6 and 7), as opposed to patches on land, which vary from a few square meters to a few square kilometers and tend to be isolated. Kritzer and Sale (2006: 520) 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 types of habitat and for certain species, but marine populations are generally less isolated and fragmented than terrestrial populations. However, whether the factors and processes mentioned above reduce and divide a larger area of habitat into two or more fragments (thus forming a barrier) is dependent on the capabilities and habitat preferences of individual species. Currents and tidal fronts 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 species have a complex lifecycle. Approximately 70% of marine invertebrates have pelagic larvae (Mileikovsky 1970) which undergo intense changes in size, morphology, physiology and behavior during dispersive stages. Most pelagic larvae are unable to avoid dispersal, as they cannot move themselves horizontally over long distances (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). Similar 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), most terrestrial dispersing individuals are developmentally static, and dispersal serves mainly to get them from point A to point B. These authors therefore state, "We might do well to think about types of metapopulations in terms of life history categories rather than whether the organisms live on land or in the sea" (Kritzer & Sale 2006: 519).

3.4 Assessing species' suitability for use in a marine metapopulation model

This research tested the suitability of 15 marine species for use in a metapopulation model. These are the breadcrumb sponge, the 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 the grey seal. Table 4 presents these species' scores on habitat, recolonization, extinction and knowledge. A total score is given only where fewer than three questions remained open and each category was answered positively at least once. This section describes for each species the assessment motivation, test results, number of articles in the ISI database, importance and prominent characteristics. Asterisks (*) in the quick scan answers refer to asterisks in the species descriptions.

Porifera

<u>Breadcrumb sponge, *Halochondria panacea* (in Dutch '*Gewone broodspons*')</u>
Total score five, three question marks remain.
124 articles in the ISI database.
The breadcrumb sponge lives attached to algae, rocks or coarse sand (Barthel 1986). The organism is viviparous (Amano 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 in the North Sea.

Cnidaria

Common or moon jelly fish, *Aurelia aurita* (in Dutch '*Oorkwal*')
Total score three, no discrete habitat or homing known. Extinction probability seems to be low and the recolonization rate high.
426 articles in the ISI database.
Unlike overexploited species, the moon jellyfish is thought to be a "major limiting factor for the population growth of copepod and larval fish" (Möller 1980: 123). Sudden mass abundance of moon jellyfish in 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, its motion is dependent on hydrodynamics. It is therefore seen as part of plankton (Möller 1980). Reproduction is both sexual (in the medusa stage) and asexual (in the polyp stage). Habitat appears to be wide in geographical range but mostly in shallow waters (Dawson & Hammer 2009).

*No discrete habitat patches are used and natal philopatry as well as the existence of subpopulations of the species are questionable. Nonetheless, the wide distribution range and passive dispersal indicate a probability that individuals could bridge distances between populations if they exist.

Plumose anemone, *Metridium senile* (in Dutch '*Zee anjelier*')
Total score four, three question marks remain.
180 articles in the ISI database.
All species in the class *Anthozoa* are marine. Reproduction is both asexual, by pedal laceration and longitudinal or transverse fission, and sexual (oviparous), with free swimming larvae (Kenneth & Svane 1994). *Metridium senile* occurs from the mid intertidal zone to depths of more than 100 m. It is a passive suspension feeder. Shipwrecks provide a characteristic habitat, as do rocky shores, dikes, and other hard substrata. Densities are some 500 individuals per square meter.

Ctenophora

Sea gooseberry, *Pleurobrachia pileus* (in Dutch '*Zeedruif*')
Total score three, three question marks remain.
81 articles in the ISI database. Many of the articles are on the anatomy of the species.
Pleurabranchia pileus competes with pelagic fish for crustacean zooplankton and fish larvae (Fraser 1970). It is a nonselective carnivore.

*It displays passive horizontal tidal movement and active day/night vertical migration (Wang *et al.* 1995). The lifecycle of the organism is not completely understood. The sea gooseberry is thought to have 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

Geomonhystera disjuncta (nematode, no common English or Dutch species name)
Total score four. Insufficient knowledge available. Extinction probability seems low.
7 articles in the ISI database.
Combining the search terms 'nematode', 'metapop*' and 'North Sea' in ISI produced three articles written by Derycke *et al.* (2007a, 2007b, 2006) referring to two nematode species. One of these species is *Geomonhystera disjuncta*. The authors suggest that metapopulation dynamics are likely to occur in *Geomonhystera disjuncta*, as the species is patchily distributed on algal deposits. A complicating factor, however, is that the species is also observed in sediment. Thus, even when algae are completely decomposed, local extinction is unlikely since the species can inhabit the sediment as well. According to 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 per 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* (in Dutch '*Zager*')
Total score six. Low recolonization rate and high extinction probability.
(Meta)population without discrete habitat, homing unknown.
301 articles in the ISI database.
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).

*Lifespan varies between one and seven years (Kristensen 1984, Olive *et al.* 2000). Annual mortality for year classes one and two are 77% and 76%, respectively, 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). The larval stage includes three development phases: supra benthic, pelagic and benthic.

*Settlement depends 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* (in Dutch '*Artemisschelp*')

Total score two. Six question marks remain.

9 articles in the ISI database.

Articles on population structure were unavailable (but do exist). Rayed artemis inhabits gravel and was chosen for assessment based on this characteristic. The bivalve is cultivated and exploited in Spain, and it is identified as a species with future market potential (Sánchez-Marín & Beiras 2008).

Horse mussel, *Modiolus modiolus* (in Dutch '*Paardemossel*')

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

508 articles in the ISI database.

The bivalve mollusk horse mussel attaches with byssus threads to the substratum or to other horse mussels. The species is seriously harmed by bottom-trawl fisheries (Murawski & Serchuk 1989). Longevity is thought to be about 20 years.

Ocean quahog, *Arctica islandica* (in Dutch '*Noordkromp*')

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

167 articles in the ISI database.

Occurrence of the bivalve mollusk ocean quahog is often considered an indicator of environmental health and biodiversity (Meesters *et al.* 2008, Witbaard & Bergman 2003, Rees & Dare 1993). Ocean quahog is found 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 have never been collected live in the shallow, sandy coastal sector (Witbaard & Bergman 2003). North of the 30 m depth contour it is found virtually everywhere, though 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 marine bivalves (Ropes & Murawski 1983). Ocean quahogs have clear and well defined growth lines, which makes it possible to estimate age in a way similar to the use of rings in trees (Witbaard 1997). With this method, a maximum age of 400 to 405 years has been recorded in Iceland quahogs (Abele *et al.* 2008). Adult ocean quahogs live 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 water (Ropes & Murawski 1983, Cargnelli *et al.* 1999). Studies suggest genetic diversity and a high degree of reproductive isolation of populations within the North Sea (Holmes *et al.* 2003).

According to Witbaard and Bergman (2003: 22) it is "questionable whether the population in the Oyster Ground is fed by larval supply from elsewhere". The genetically distinct and geographically separated populations, however, could be seen as part of a metapopulation. Knowledge on population structure, distribution and abundance in the North Sea remains scarce, unlike the western Atlantic where the species is commercially important and therefore the subject of more studies (Witbaard 1996). Still, questions remain, for example, about recruitment of individuals to populations, spawning and population sizes (Cargnelli *et al.* 1999, Mann & Wolf 1983).

Arthropoda

Edible crab, *Cancer pagurus* (in Dutch '*Noordzeekrab*')

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

346 articles in the ISI database, of which one with the term 'metapopulation' and the species name in the subject (Englund & Cooper 2003).[2]

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)).

* Natal philopatry is given the benefit of the doubt in the quick scan, as it is thought that females migrate against the currents and spawn there, giving their larvae a larger chance to return to the parent population (Ungfors *et al.* 2009).. Ungfors *et al.* (2009) discuss the lack of genetic structure indicating 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 to estimate, 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* (in Dutch '*Gewone garnaal*')

Total score six, low recolonization rate and high extinction probability, but no discrete habitat, homing unknown.

616 articles in the ISI database.

This is a commercially important species, with annual catch exceeding 20,000 t (Temming & Damm 2002). Surprisingly, our understanding of the lifecycle of the common shrimp is incomplete, as is knowledge of vertical migration patterns (Temming & Damm 2002, Oh & Hartnoll 2004). The maximum lifespan found differs across studies, and is thought to be 2.7–3.3 years (Oh & Hartnoll 2004).

Echinodermata

Common starfish, *Asterias rubens* (in Dutch '*Gewone zeester*')

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

530 articles in the ISI database.

Common starfish have a considerably negative impact on economically 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

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[2] Only an abstract was available.

are found in mud and in gravelly and rocky grounds in depths from the intertidal zone to more than 600 m (Gemmil 1914). It is a trophic generalist predator. More than two subpopulations in the North Sea are likely, though the literature consulted described only two populations in the English Channel off Plymouth (Vevers 1949). The oldest age found in the literature was three years, but the common starfish can probably reach a somewhat older age.

*Dispersal is both active and passive.

Chordata

Thornback ray, *Raja clavata* (in Dutch '*Stekelrog*')

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

150 articles in the ISI database. One article refers to metapopulations (Chevelot *et al.* 2007), in which 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".

Occurrence of the thornback ray is thought to have declined by nearly 80% in the North Sea waters (Walker & Heessen 1996) and it has even disappeared in some places. The species is an unavoidable bycatch in demersal fisheries. Females are mature between 9 and 12 years of age (Chevelot *et al.* 2007) and *fecundity is classified as low by Chevelot *et al.* (2007), with 38–150 eggs per female per year.

*Walker *et al.* (1997) suggest the existence of two separate stocks; one in the Thames Estuary of 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 hundred kilometers, although capture-recapture measurements have shown distances of just 60–70 km (Chevolet *et al.* 2007).

Cod, *Gadus morhua* (in Dutch '*Kabeljauw*')

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

5,283 articles in the ISI database. '*Gadus morhua*' and 'metapop*' in the topic resulted in 21 articles.

The commercially exploited, demersal cod can live up to 20 years (though nowadays this is rare), and females produce between 500,000 and 5 million 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 species mobility, it is counted as positive in this scan.

Grey seal, *Halichoerus grypus* (in Dutch '*Grijze zeehond*')

Total score eight. Discrete habitat patches, low recolonization rate and high extinction probability. Ultimate metapopulation.
782 articles in the ISI database.
The grey seal has recolonized the North Sea only since 1970, after an absence of about 500 years (Reijnders *et al.* 1995). Excessive hunting was the reason for the absence. At present, four populations have become established along mainland Europe, and tracking studies indicate a link with the larger populations in the United Kingdom (Härkönen *et al.* 2007).

Of the 15 assessed species, 6 species (breadcrumb sponge, moon jellyfish, sea gooseberry, common seastar, the nematode *Geomonhystera disjuncta* and the rayed artemis) were eliminated in the first interpretation step, either because too many questions remained unanswered or because one or more of the categories had no affirmative answer.

For four of the assessed species, two or more subpopulations were described in the 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 reflect 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 discrete habitat patches. The common shrimp, king rag worm and thornback ray do show a metapopulation structure, but do not (as far as known) live in discrete habitat patches. The horse mussel in the test seems to be a stable population with discrete habitat patches. For this species, however, human influences have played a major role in local extinctions, which is not shown by the results. Metapopulation structure is probable for the edible crab, as the female of this species is thought to walk against the current before spawning, giving her offspring a high chance of recruiting into the parent population. For cod, a metapopulation structure is probable, as stock returns to the place of birth to breed. Finally, the grey seal likely represents an ultimate metapopulation structure.

In order to compare the test results for the marine species with the test outcome for terrestrial species, four randomly chosen land-dwelling species were chosen. The 'North Sea' was replaced by 'the Netherlands' and 'exploitation' was replaced by 'hunting' (table 5).

For roe deer (*Capreolus capreolus*, in Dutch '*ree*'), the total score was eight, with discrete habitat patches, low recolonization rate and high extinction probability, the species would belong in the category 'ultimate metapopulation'. The common vole (*Microtus arvalis*, in Dutch '*veldmuis*'), the blue tit (*Parus caeruleus*, in Dutch '*pimpelmees*') and the large white butterfly (*Pieris brassicae*, in Dutch '*groot koolwitje*') represent the same category.

*Table 4. Score table for assessing species suitability for use in a metapopulation model. The greater the number of questions answered with a 'yes', the more likely it is that the species can be used in a metapopulation model. When individual categories had no yes answers, or when three or more question marks remained, no answer could be given on the question of whether the species might be suitable for study using a metapopulation approach. The total score is in 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 discrete habitat patches?	Yes	No	Yes	No	No	No	Yes
2. Does the population return to its place of birth in order to breed?* not needed if 1 = yes	?	?	?	?	?	?	?
3. Are there two or more (sub)populations on a 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 the scale of the North Sea?	?	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. Are offspring of the organism few in number (< 10)?	No	No	?	No	No	No	?
8. Is there a high chance of 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 the 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 continued.

	Horse mussel	Ocean quahog	Edible crab	Common shrimp	Common starfish	Thornback ray	Cod	Grey seal
Habitat								
1. Does the organism live in discrete habitat patches?	Yes	No*	No	No	No	No	No	Yes
2. Does the population return to its place of birth in order to breed?* not needed if 1 = yes	?	?	Yes*	?	?	?	Yes	?
3. Are there two or more (sub)populations on a 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 the scale of the North Sea?	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. Are offspring of the organism few in number (<10)?	No	No	No	No	No	Yes*	No	Yes
8. Is there a high chance of 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 the 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 discrete habitat patches?	Yes	Yes	Yes	Yes
2. Does the population return to its place of birth in order to breed?* not needed if 1 = yes	?	?	?	?
3. Are there two 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 on the scale of 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. Are offspring of the organism few in number (< 10)?	Yes	Yes	Yes	No
8. Is there a high chance of disastrous events?	?	?	Yes	Yes
9. Is the organism in the Netherlands hunted (or affected by hunting) by humans?	Yes	No	No	No
Score extinction	**2**	**2**	**3**	**2**
Knowledge				
10. Is knowledge on the 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**

4 Discussion

Besides the straightforward differences and similarities between terrestrial and marine environments, the literature contains complex comparisons of applications of the metapopulation theory in the two contexts. However, especially compared with a terrestrial landscape, the terms ‘fragmentation’, ‘barrier’ and ‘suitable habitat patch’ seem less relevant to the North Sea bottom and waters. In the marine environment, exploitation and the homogenizing effects of beam-trawl fishing constitute major threats to the persistence of many species. Despite being a heterogeneous system, and regardless of whether the system is or is not fragmented, isolation of populations is of minor importance for continued existence. This contrasts with terrestrial systems, where fragmentation (resulting in isolation) exerts the most pressure on metapopulation persistence.

It is therefore questionable whether a metapopulation approach is the most relevant basis for studying the North Sea. 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 designated conservation areas might stimulate persistence of some populations. However, maintaining connection zones between protected areas is unfeasible for at least two reasons. First, hydrodynamic forces and weather influences are not geographically static, meaning that a connection zone would require such a broad margin that it might be easier to just make one contiguous area enclosing the zones that need to be connected. Secondly, there might be no physical barrier and thus no need for a marine organism to choose the ‘connection zone’, making the actual functionality of marine connection zones questionable as well.

Looking at the wide range of habitat types, and the theoretical lack of physical barriers, one might conclude that discrete habitat patches in the North Sea are either scarce, or that the North Sea scale is too small to look for patches. Lack of discrete habitat, however, may be merely a function of lack of knowledge of marine life, compared to terrestrial species on which much more is known about habitat preferences. Marine habitat is roughly understood, and for most species exact preferences are not yet clear. If, for instance, sediment structure, water temperature and depth are factors in habitat preferences, then the North Sea waters might actually be a patchy environment. This is simply not known.

Furthermore, chance-dependent processes play a major role in the marine environment. The medium water, more than air, gives additional opportunities for motion, both desired and undesired. Despite the many strategies species practice in order to get recruitment to the local population, in many cases whether young return to their parent population, or drift away and settle at another patch of suitable habitat is purely a function of chance.

Neither is the difference between land- and sea-inhabiting organisms always simple to appoint. Even if an organism at first appears to be a perfect candidate for use in a metapopulation model, when more characteristics of the species are set out the picture often blurs. The quick scan presented here to assess the suitability of marine species for use in a North Sea metapopulation model provides a guide from a metapopulation perspective to learn whether such modeling is indeed worth the effort. The questions posed in the scan address habitat, recolonization rate and extinction probability in such a way that the answers give information about the probability of there being a metapopulation structure. The questions are applicable to all organisms. The parameters therefore needed to be generalized and have uniform answers. The advantage of the yes/no questions used in this research is that it is relatively simple to structure the different parameters a species has to conform with to be considered part of a metapopulation, and one can grasp the cumulative effect of those parameters together. The downside of this method is that the scan excludes the possibility of asking for species' specific features. Also, the questions about longevity and number of offspring address K-strategists and r-strategists, respectively, making a score of 11 (the total number of questions) unlikely. The question of whether there is a high chance of disastrous events occurring is somewhat suggestive. However, it is answered 'yes' only if the literature explicitly points to such a risk, other than exploitation by humans. Human exploitation is marked as positive for the chance of a metapopulation structure, as it increases the probability of (local) extinction. Nonetheless, it increases the modeling difficulties too.

Interpretations of recolonization rate and extinction probability as low or high in this scan are approximations, not measured values. The scan was designed as an instrument to help structure the various aspects that a species has to conform with to be considered a metapopulation. Applying the test to randomly chosen terrestrial species resulted in the expected ultimate metapopulation structure. Despite the fact that the test might need refinement in some respects, this can be viewed as an indication of its reliability. The test, however, was not used for all terrestrial phyla.

The marine species tested were not selected from a neutral point of view. They were either brought to the researcher's attention by the scientists consulted, or they emerged as candidates from the literature review. Furthermore, species were chosen to cover a wide range of characteristics. The results of the quick scan therefore might not be representative of all species occurring in the North Sea.

Because time was limited during the research, a maximum time was set to acquire data on each species. With more time invested some of the question marks in the table might be resolved.

Looking at the three score tables, some parallels are evident in the increase in the scores of species towards the 'higher' end of the phyla. Although our set of 15 species is not sufficient to draw conclusions, this association provides an interesting subject for further research.

5 Conclusion

Attempts to apply the metapopulation concept to the marine environment are still in progress. However, the way a marine metapopulation concept functions, is still not fully understood, and improvements are required in several respects. The metapopulation concept nonetheless, provides an additional framework for asking research questions and describing spatial population processes and structures.

Heterogeneity in the North Sea underwater is found vertically (in depth-related changes in light intensity and oxygen concentration, gradients in water temperature, changes in density, salinity and nutrient concentrations and so on) and horizontally (in currents, circulation patterns, surface waves, tides, longitude/latitude, substratum and salinity). Although these processes clearly induce diversity in the marine environment, physical barriers are not obvious.

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

The quick scan developed in this research showed the grey seal as the marine species that appears most suitable for use in a metapopulation model. The edible crab and cod are species that could potentially be used in a metapopulation model. Neither has a discrete habitat patch, but both have known strategies for ensuring that their offspring recruits into the parent population. For species that appeared to be suitable because they have a discrete underwater habitat patch, insufficient knowledge was available.

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Appendix 1 Glossary

(Re)colonization
A species reaching an unoccupied habitat patch, becoming established and maintaining a presence there (Van Dorp *et al.* 1999).

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

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

Demersal
Living near, deposited on or sinking to the bottom of the sea (Merriam-Websters OnLine dictionary, 16 July 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 e.g. 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, or passive but involving an active agent or clonal (Allaby 2003). In a metapopulation context, dispersal is often between subpopulations.

Disastrous event
Disasters like disease, storm or extremely low temperature, generally occurring less than once a year.

Ecosystem
A natural unit consisting of living and nonliving parts interacting to form a stable system. Ecosystem principles can be applied at all scales. E.g., it is equally applicable to an ephemeral pond, a lake, an ocean and 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 by 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 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 to maximize competitive ability, the strategy of equilibrium species. It is typically a response to environmental resources. This implies selection for low birth rates, high survival rates among offspring and prolonged development (Allaby 2003).

Landscape
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
A 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 largely determine their size and persistence, both of the individual subpopulations and of the metapopulation as a whole.

National Ecological Network (NEN) or *Ecologische Hoofdstructuur* (EHS)
The National Ecological Network is a governmentally designated network of areas in the Netherlands where nature has priority.

Natura 2000
Europe-wide network of sites designated for the preservation of natural heritage.

Network population
Much of the literature uses the term 'network population' as synonymous with 'metapopulation', although they do differ. Metapopulation refers to actual (sub)populations and network population 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 July 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 mother's body which nourishes it (Allaby 2003).