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Corrigendum to: North Sea coastal ecology: Future challenges Journal of Sea Research 127 (2017) 227–230

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The authors regret that in the summary the acknowledgement is missing which should read:

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Summary

North Sea coastal ecology: Future challenges

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1. Introduction

This special volume on "North Sea coastal ecology" contains a number of contributions stressing the interactions between the open North Sea and its surrounding shallow coastal zones. The focus is on soft-sediment systems, such as large parts of the European coastal zone and estuarine systems including the Wash at the north-west corner of East Anglia, and the Wadden Sea bordering the coastline of The Netherlands, Germany and Denmark. The aim of this volume is not to get an exhaustive overview of all ongoing research and of present ecosystem knowledge, but to capture representative results of state-of-the-art ongoing research, with an emphasis on long-term trends, to be able to define future challenges.

North Sea coastal ecology implies studying a large-scale system with substantial interannual variability, among others due to variations in wind climate (e.g. Tiessen et al., 2014), in addition to long-term trends resulting from overfishing, climate change (e.g., warming, acidification, deoxygenation), habitat destruction and pollution (Bijma et al., 2013; European Marine Board, 2013). In order to capture this variation in time and space, present studies more and more rely on high-resolution data and an integration over large spatial scales. Data from local field observations can still, however, aid in resolving cause-effect relationships, see for instance in this volume Neumann et al. (in this volume, in this volumeb), Courtens et al. (in this volume) and Nordberg et al. (in this volume). The study on exposure times of intertidal flats by Nauw et al., in this volume, which relies largely on modelling, demonstrates the need for more synoptic observations for validation of models.

The paper by Tiessen et al. (in this volume) on suspended particulate matter transport in the East Anglian plume is illustrative of combining in situ measurements (field sampling) with remote sensing. The importance of high-resolution multi-annual observations is also reflected in the paper by van der Hout et al. (in this volume) on dynamics of suspended matter and chlorophyll-a and by Witbaard et al. (in this volume) on the effects of *Ensis directus* on the transport and burial of silt. Both studies rely on automated sensor information deployed from "lander" frames at different seasons collecting high-resolution abiotic data, whilst Witbaard et al. (in this volume) additionally performed in-situ experiments to determine the response of biota to their abiotic environment.

For large-scale observations, innovative technologies have become available such as, for instance, underwater gliders and satellite observations. Especially long-term monitoring efforts pay off with respect to the understanding of ecosystem functioning. Jung et al. (in this volumeb), for example, analysed long-term data of nitrogen [N] and phosphorus [P] concentrations for the western Dutch Wadden Sea between 1976 and 2012 to construct nutrient budgets and were able to show that the system switched from net annual import to export during this period. The contribution by Compton et al. (in this volume) illustrates that two macrozoobenthos surveys conducted 30 years apart in the Ems Dollard estuary provided a unique opportunity to compare changes over time. However, the data also show that continuous (annual) long-term field observations would even provide a fuller understanding of the complex dynamics of the macrozoobenthos. The contributions on changes in fish phenology in the Dutch Wadden Sea (Tulp et al., in this volume; van Walraven et al., in this volume) and on long-term temporal and spatial changes in the inshore fish community of the British North Sea coast (Henderson, in this volume) also all rely on long-term field data.

Various papers focus on the complex interactions of environmental abiotic and biotic factors and the distributions of top predators, whereby also long-term (monitoring) data are used, including changes in distributional patterns of plaice (Støttrup et al., in this volume), distribution of three sandeel species (Tien et al., in this volume) and habitat use and foraging ecology of breeding Sandwich terns (Fijn et al., in this volume).

For data processing and integration, more and more complex (eco) system models are implemented, such as those used in van der Molen et al. (in this volume) and Hufnagl et al. (in this volume). van der Molen et al. (in this volume) showed that their model was able to produce reasonable simulations of field measurements of seasonal suspended (mineral) particulate matter concentrations at the northwest European continental shelf. On the other hand, Hufnagl et al. (in this volume) came with a clear warning. In comparing various hydrodynamic ocean circulation models and Lagrangian particle tracking models for the North Sea, they concluded that variability between models is generally high and using absolute values from only one single model might be biased and results or conclusions drawn from such studies need to be treated with caution. These model studies also underline the importance of and need for more long-term synoptic validation data, both spatially and temporally.

2. Future challenges

The combination of increasing high resolution, large-scale

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observations with model simulations shows us the enormous complexity and variability of the system and the challenges we face to unravel this. Nevertheless, some promising fields for future coastal research can be identified, here illustrated by the connections between the North Sea and the Wadden Sea.

2.1. Setting the stage: dynamics of water and sediments

Studies in this volume repeatedly illustrate that hydrodynamics and sediment transport are at the basis of many biological processes. In spite of the major sediment fluxes in this area, there is still much debate on the nature of the most dominant transport processes and on the values of the long-term mean fluxes (e.g. Sassi et al., 2015). Hydrodynamic processes that underlie sediment transport also affect transport of nutrients and biological material in the pelagic phase and are thus essential for the connectivity within coastal areas and between the coastal zone and adjacent North Sea. Using the state-of-the art numerical models, such as the GETM/GOTM system, the hydrodynamics can be simulated accurately (Duran-Matute et al., 2014; Gräwe et al., 2016).

Additionally, an effort is needed to introduce more sophisticated methods/modules to determine the sediment concentration, nutrient distribution and biological and benthic processes. Knowledge of these processes is essential in determining their susceptibility to anthropogenic climate change and the carrying capacity of the (sub)systems. Apart from that, the already existing monitoring system needs to be evaluated and expanded both spatially and in terms of measured parameters to be able to calibrate and validate the simulations with coupled hydrodynamic - biogeochemical models.

2.2. Fuelling the food web: microalgae

In many shallow coastal systems, pelagic and benthic microalgae are the main primary producers. The benthic and pelagic compartments are closely coupled and primary production by microphytobenthos may rival or even exceed that of the phytoplankton (e.g. MacIntyre et al., 1996). Changing benthic and pelagic productivity may have overarching consequences on the entire food web, as these microalgae provide a key food source for all higher trophic levels (Christianen et al., 2017), whereby the interaction with offshore ecosystems cannot be neglected (Jung et al., in this volumea).

However, studies on the overall carrying capacity of shallow estuaries and the coastal zone in general and on benthic primary production in particular are scarce. New measuring techniques include satellite information and automated sensor networks. The recent launching of the Sentinel satellites is particularly expected to strongly enhance the temporal resolution of information on bathymetry and sediment composition, e.g. once every 5 days (Sentinel 2) to daily (Sentinel-3), provided that images are cloud-free (Vihervaara et al., 2017). In combination with ground-truth derived from automated sensors such as hyperspectral radiometers and fast repetition rate fluorometry (FRRF), we should be able to monitor state variables (such as phytoplankton biomass) as well as ecosystem process (such as phytoplankton productivity) at a proper time scale throughout the area (e.g. Schuback et al., 2017).

Although the transport of microalgae is relatively passive as the result of their small size, their movement can also have an active component. Pelagic flagellates expose vertical migration in the water column to move to a niche optimal for their growth and reproduction, controlled by external factors such as light and gravity. During daylight hours, benthic diatoms migrate upwards when tidal flat sediments are exposed at low tide (Underwood and Kromkamp, 1999). Key issues to be explored include the contribution of passive and active components to the distribution of microalgae in the water and the sediment, and the consequences of these movements for the availability of microalgae as a food source for pelagic and benthic grazers.

2.3. The turntable in the foodweb: macrozoobenthos

Benthic macrofauna are central to the maintenance of many ecosystem services in estuarine and shallow coastal systems (Norling et al., 2007). Defined as sediment-dwelling animals greater than 1 mm in size, the macrozoobenthic organisms recycle nutrients, decompose organic matter, regulate nutrient cycles and are an important food source to many species including humans. For example, suspension feeders transport sediments across the sediment–water interface, bioturbators increase the turnover in nutrients and sediments, and biogenic builders generate structure and consolidate sediments (e.g. van der Zee et al., 2012).

Describing the assemblage composition of the macrozoobenthos can thus be considered fundamental to understanding a system and can provide a basis for determining the influence of anthropogenic activities, e.g. eutrophication, species introduction, habitat alteration, gas extraction, dredging for shellfish or combinations of these factors. For example, median grain size, followed by biomass of phytoplankton and microphytobenthos, organic carbon content of the sediment and exposure time are important variables describing differences in assemblage composition on tidal flats (Compton et al., 2013).

The coastal zone forms a heterogeneous landscape where assemblage composition varies across multiple gradients, which has repercussions for ecosystem functions, including structuring of abiotic environmental conditions (e.g. hydrodynamics, geomorphology) and provisioning of food and shelter to other coastal organisms.

2.4. Loading factors and invisible connectors: parasites

Parasites are an important but little known compartment of (coastal) ecosystems. Via their complex life cycles, involving trophic transmission, parasites intricately link different trophic levels (primary consumers and invertebrate, fish and bird predators) (e.g. Goedknegt et al., 2016; Schade et al., 2016). They do not only directly affect the fitness of their hosts but can also generate indirect effects on species interactions and ecosystem functioning (e.g. by reducing secondary production). Parasites are thus hidden but potentially forceful players of high ecological, conservation and economic importance. Their relevance is expected to increase in the near future due to climate change (warming, acidification) and increasing introductions of species (new hosts and parasites). However, to date, our knowledge on the role of parasites in coastal ecosystems and on how anthropogenic changes will affect their impact is very limited. Also this special volume lacks contributions on parasites. So far, studies have been limited to a few localities and parasite-host systems and future research will be needed along several lines to fully identify the role of parasites.

2.5. Visible connectors: seabirds and fish

Coastal seabirds live at the interface of the coastal zone and North Sea, while concentrating on benthic and/or pelagic resources (various invertebrates and fish species). Characteristic species include a variety of seaducks (Anatidae), gulls (Laridae) and terns (Sternidae). The populations of the most typical taxa breeding or wintering within the southern North Sea and the western Wadden Sea fluctuate in response to resources, availability of breeding habitat, and are often strongly influenced by anthropogenic factors and the effects of climate change (e.g. Fluhr et al., 2017). Several North Sea populations are currently threatened or under severe ecological stress (e.g. Harris et al., 2016), and the factors leading to population declines need further study.

Many fish species rely on shallow coastal habitats for at least one of their life stages (Zijlstra, 1972; Elliott et al., 2007). Naturally, such coastal areas support large numbers of fish that make use of the suitable habitats characterised by a high food availability and shelter from predators. Many fish species have declined in population size. The causes of the observed declines in population size are still not fully clear but point towards fisheries, climate change and habitat destruction (van der Veer et al., 2015). Both from a fundamental scientific as well as a societal point-of-view, understanding these mechanisms and population declines are important.

To understand the mechanisms behind the declining population sizes and assess the roles of anthropogenic and natural impacts, we need to know more about the basic biology of the species, their ecology and community dynamics. Moreover, the central North Sea and its surrounding coastal zones should be seen as a meta-ecosystem connected to the adjacent tributaries of main rivers such as Elbe, Meuse, Rhine and Thames. Therefore, there is a need to understand the connectivity within North Sea metapopulations, whereby it is important to understand the functional relationships (e.g. food, safety) between fish species and their specific needs during particular life phases (e.g. habitats). Currently, such data are mostly lacking. The unresolved key-issues include lacks of knowledge on the spatial scale of the various ecological processes of importance for the life cycle and the consequences of this for population regulation. In addition, the physiological performance of most of the species and food web structure of the coastal zone including species interactions (e.g. pelagic-benthic interactions, predator-prey relationships) is required to predict the consequences of environmental change on fish populations and communities.

2.6. *Visible intercontinental connectors: migratory shorebirds*

A specialized group of birds (the shorebirds or Charadrii) has as its core survival strategy the use of seasonal resources at (sometimes) opposite ends of the globe. The species breeding on the Arctic tundra almost without exception rely on coastal resources during the non-breeding season, concentrating in masses on the few places that offer extensive sea beds that, by tidal forcing, become available to them once or twice each day. Shorebirds have become a predominant secondary consumer on mudflats worldwide, in the process affecting the survival strategies of secondary producers and connecting mudflat systems that may be 1000s of kilometres apart (van Gils et al., 2016).

Building on half a century of research investments, ongoing research programmes on the long-term demography and microevolution of a few key species (red knot, bar-tailed godwit, sanderling), in which an understanding of distribution and abundance are embedded in programmes measuring both the resources and predator landscapes (i.e. the bottom-up and top-down processes), should be continued. An attention for organismal detail (physiological and personality characteristics of individuals) should be married with a solid understanding of the hemispheric processes affecting these individuals and in turn their populations (climate change, changing ecosystem properties at connected sites).

3. The integration, movement ecology of plankton, fish and birds

Many organisms such as bivalves, fish, crustaceans, polychaetes, seagrasses and invasive species (e.g. Pacific oysters) have a complex life cycle, i.e. sessile benthic adult stages and juvenile pelagic dispersive phase. During their dispersive phase, currents transport propagules from their sources to potential settlement destinations. To understand distributions and developments of populations, knowledge about the distribution of habitat and populations and the way in which populations and habitats are connected via pelagic spread is required. High-resolution Lagrangian hydrodynamic transport models have been found to be useful for simulating dispersal kernels in complex marine seascapes to obtain estimates of connectivity in metapopulations (see for instance Bolle et al., 2009; van der Molen et al., 2015; Hufnagl et al., 2013, in this volume).

Movement of individual organisms, one of the most fundamental features of life on Earth, is a crucial component of almost any ecological and evolutionary process, including major problems associated with

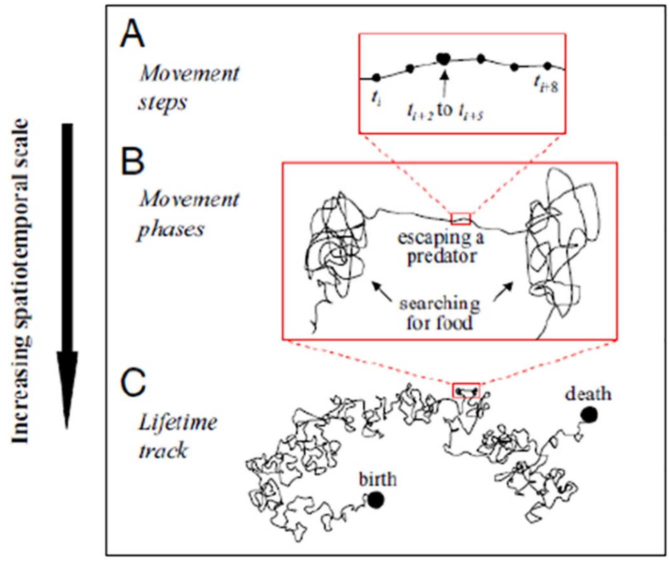

Fig. 1. Spatiotemporal scales of movement and spatial distributions.
Taken from Nathan et al. (2008).

habitat fragmentation, climate change, biological invasions, and the spread of pests and diseases. A key challenge in ecological research is identifying the key processes that shape movement decisions and distributional patterns at different spatial and temporal scales (Fig. 1). On small spatiotemporal scales, among-individual differences affect movement decisions. These are reflected on an intermediate spatiotemporal scale where the key processes that shape an individual's movement and consequently the distributional patterns of populations are: the a-biotic environment, social interactions (competition, co-operation), escaping predation, and finding resources. All these processes come together on the largest spatiotemporal scale, where they affect lifetime reproductive success, survival, large-scale distributions and population dynamics (demography).

Teasing apart the mechanisms that drive movement decisions (processes) and spatial distributions (patterns) requires measuring the relevant variables in the field, as well as indoors under controlled experimental conditions. Such experiments allow scaling up these mechanisms to free-living individuals, and allow a comprehensive understanding of the causes and consequences of movement in the field.

Measuring resource landscapes in the field, however, is notoriously difficult in large marine ecosystems. Researchers often use multi-step remotely sensed proxies to indicate resource abundance. For instance, to understand Blue Shark movements and distributions, Humphries et al. (2010) mapped chlorophyll concentrations that, via primary production and secondary production, correlate with availability of food for these sharks. At large spatial scales such proxies can be informative. However, understanding the choices that individuals make (and how these movement decisions ultimately result in spatial distributions) requires measuring food landscapes at small spatiotemporal scales.

Main research themes include the coupling between the abiotic and biotic environments, spatiotemporal variation within this ecosystem, the role of (passive/active) movements in species' distribution and population dynamics and trophic interactions (including predation, facilitation and the role of parasites). Long-term time series measurements are considered crucial for characterizing and understanding trends and variability in the system and for identification of key causal relationships, which control this ecosystem and the large-scale spatial and temporal variability that occurs.

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