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An ecotope map of the trilateral Wadden Sea

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ABSTRACT

Here we present the first digital, publicly available, ecotope map of the trilateral Wadden Sea covering the Netherlands, Germany and Denmark. This ecotope map, representative for the time period 2008–2012, was developed on the basis of bathymetry, salinity, flow velocity, exposure time, sediment composition, hard substrates and salt marshes. Ecotopes are discrete classes of the physical environment based on the distributions of communities in an ecosystem. An ecotope map can give a first–order estimate of the potential spatial distribution of species and communities. The use of a single, consistent and well-defined ecotope system made it possible to compare the proportions of the different ecotopes and compare properties of the tidal basins over the entire trilateral Wadden Sea. The 39 tidal basins within the Wadden Sea were clustered in four distinct types, using an unsupervised clustering algorithm. These four types included: 1) basins that are characterised by a large proportion of low-dynamic low-littoral ecotopes, 2) basins with a high proportion of high-dynamic sublittoral ecotopes, 3) shallow basins with over 50% low-dynamic mid-littoral ecotopes and 4) basins with an equal distribution of low-dynamic low-littoral and low-dynamic mid-littoral ecotopes. The clustering in four major tidal basin types gives clear guidance for comparative ecological and morphological studies between tidal basins. The ecotope map can be used for environmental research, policy and conservation purposes of the trilateral Wadden Sea in an integrated manner.

1. Introduction

1.1. The Wadden Sea

The trilateral Wadden Sea is the largest connected system of intertidal sand flats, mud flats and salt marshes of the temperate world. It is located in northwestern Europe stretching over 500 km along the coasts of the Netherlands, Germany, and Denmark between the towns of Den Helder and Esbjerg (Fig. 1). Since June 2009, the Wadden Sea has been listed as UNESCO World Heritage site because of its outstanding universal value on geological and ecological processes and high biodiversity (Reise et al., 2010). The Wadden Sea is a mesotidal barrier island system in which almost all of the sediments are supplied from the North sea with only minor contribution from rivers, contrary to most intertidal systems worldwide. In contrast with deltaic coasts, the tidal flats near the inlets are predominantly sandy and those near the coast are muddy (Van Straaten, 1954). The Wadden Sea consists of a series of tidal basins, filled and emptied by tidal channels and separated by tidal divides where flood waters of adjacent tidal inlets meet (Postma, 1954). The proportion of channels and tidal flats in a tidal basin depend on the morphology and local hydrodynamics. Renger and Partenscky (1974) established an empirical relation for the area of tidal channels as a function of the total basin area $A_c = 2.5{\cdot}10^{-5}{\cdot}A_b^{1.5}$, where A_b is the basin area (m^2) and A_c is the channel area (m^2). Cleveringa and Oost (1999) found that the channel systems in the Dutch Wadden Sea can be regarded as 'statistical self-similar fractal' networks, where the channel-system circumference length is logarithmically related to the tidal prism and drainage area. Above mean high-tide level the largest system of (partially man-made) salt marshes in Europe is found on the Wadden islands and along the mainland coast of the trilateral countries Netherlands, Germany and Denmark (Dijkema, 1983; Dijkema et al., 1984; Kamps, 1962).

1.2. The ecotope concept

For environmental research, policy and conservation purposes, it is useful to classify ecosystems or geographic areas into distinct spatial units on the basis of geographical and ecological criteria (Dankers et al., 2012; Frissell et al., 1986). Klijn and Udo de Haes (1994) discussed various existing - predominantly terrestrial - ecosystem classifications

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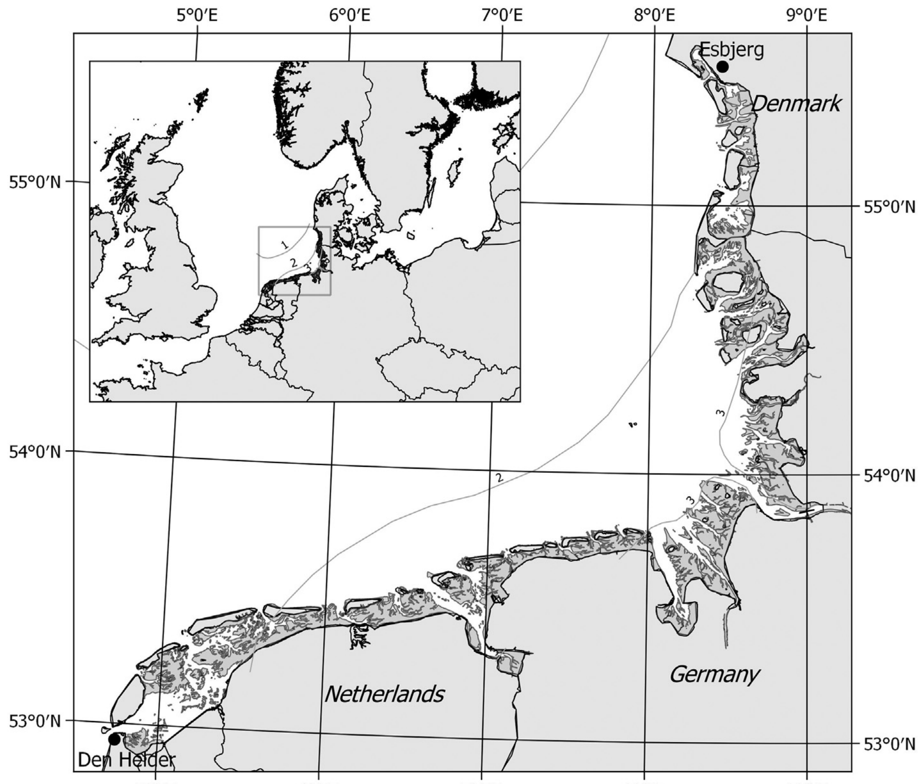

Fig. 1. The trilateral Wadden Sea tidal flat area ranging between the towns of Den Helder and Esbjerg and isolines of tidal range (m).

and concluded that the Anglo-American and Canadian land classifications were the best examples of a systematic hierarchical approach. Elaborating on these examples they formulated the hierarchical ecosystem classification (HEC) framework for classifying and mapping ecosystems. HEC distinguishes the following homogeneous geographical units at various spatial scales from large to small: ecozone, ecoprovince, ecoregion, ecodistrict, ecosection, ecoseries, ecotope and eco-element. Verdonschot et al. (1992) used the HEC for a classification of freshwater ecosystems in which units were distinguished on the basis of abiotic and biotic variables that determine the species composition. The end-units used were called aquatic ecotopes, where an ecotope was defined as: "*a geographical unit homogeneous within limits for the most important hydromorphological and physical-chemical environmental factors that are relevant for biota*." Based on this practical ecotope definition and Frissell et al. (1986), a practical typology for Dutch river systems was designed by Rademakers and Wolfert (1994). This formed the onset for the development of an ecotope typology for all Dutch waters managed by the national government, i.e., the large lakes, large rivers, estuarine and coastal waters and the North Sea (Wolfert, 1996). A typology for estuarine and coastal waters was subsequently proposed by De Jong (1999), Dankers et al. (2001) and further specified by Bouma et al. (2005) resulting in the ecotope system for coastal waters, abbreviated as ZES.1 that was applied in this study.

The definition of the ecotope concept has changed in time. It originates from Arthur Tansley, a British ecologist who also introduced the ecosystem concept (Tansley, 1935). He defined an ecotope as a particular portion of an ecosystem by joining the term eco- (from the Greek "oikos" meaning home) with -tope (from the Greek "topos" meaning place) (Tansley, 1939, p. 228). The term "ecotope" is often confused with similar concepts such as "habitat", "niche", "biotope" and "biocoenosis". Whittaker et al. (1973) attempt to sort out these concepts. According to their definitions, the term "niche" applies to the species' functional role in a "community" and the term "habitat" applies to the range of physical environments over which a species occurs. A practical definition for "community" is given by Mills (1969): 'a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups.' Whittaker et al. (1973) point out that the term "habitat" has been used interchangeably with "biotope", the former more in English and the latter more in other European languages, and that when distinction is desired "biotope" should apply to the community's physical environment and "habitat" to the species' physical environment (Udvardy, 1959). This is in accordance with the original definition of biotope by Dahl (1908), describing the physical conditions for the existence of a "biocoenosis", where a "biocoenosis" is defined as a complex superorganism in which animals and plants live together in an interdependent biological community, as described by Möbius (1877). Recently however, the UK Joint Nature Conservation Committee 'rediscovered' the term biotope and produced a new interpretation "biotope = habitat + community", combining the physical environment and its distinctive assemblage of conspicuous species (Olenin and Ducrotoy, 2006). The community is interpreted as a biotic element of a biotope and the habitat as the physical environment of a community. Not only is this new definition essentially different from the traditional meaning of biotope, it is also deviating from the traditional meaning of habitat, since this is referring to a species, not a community. Nonetheless, the new understanding of "biotope" now dominates in the international scientific and applied environmental literature, such as those for the CORINE and EUNIS maps (Olenin and Ducrotoy, 2006) and the new use for "habitat" applying to communities instead of species, as it is also applied in the European Habitats Directive, is further infringing the original definition (Dauvin et al., 2008). Whittaker et al. (1973) also give a description for the "ecotope" concept being "ecotope = habitat + niche". They suggest to describe an ecotope as the species' relation to both its physical environment (its habitat) and its role within a given community (its niche), thus representing the full range of environmental and biotic variables affecting the species. Whittaker's ecotope definition is not in accordance with the modern ecotope definition (Klijn and Udo de Haes, 1994; Verdonschot et al., 1992). In this study an ecotope is defined as the physical environment for communities, which is the same as the traditional meaning of biotope and the modern meaning of habitat.

1.3. Wadden Sea ecotope maps

A first map of the vegetation and landscapes of the islands and mainland coastal areas of the complete trilateral Wadden Sea was composed by Dijkema (1980). This was followed by the first and only ever made map of the entire trilateral Wadden Sea including the sublittoral, littoral and supralittoral parts by Dijkema (1991). This map represents the situation of the Wadden Sea at the end of the 1970s and was produced in printed hard-copy on 24 separate sheets on 1:100,000 scale. It distinguishes tidal channels, subtidal flats and a tidal flat typology based on the combination of emersion time and sediment composition. The map also shows low, intermediate and highly elevated salt marsh zones, salt marsh pioneer zones and areas where seagrass beds and mussel beds occurred. Later ecotope maps were produced only for parts of the trilateral Wadden Sea. An ecotope map of the Dutch Wadden Sea following the typology of Bouma et al. (2005) was composed by Wijsman and Verhage (2004). A map in print, following as far as possible the typology of Bouma et al. (2005), was produced by Dankers et al. (2006). Shortly hereafter Herrling and Niemeyer (2007) composed a map with a relatively limited number of ecotopes for the Dutch and German Ems-Dollard area. More recently a digital ecotope map of the Dutch Wadden Sea was published online by Christianen et al. (2015). Finally, updated maps following the typology of Bouma et al. (2005) for the Ems-Dollard (Ysebaert et al., 2016a, 2016b) and the entire Dutch Wadden Sea (Baptist et al., 2016) were produced and digitally made public. To sum up, since the first hard-copy map of Dijkema (1991) representing the ecotope composition of the trilateral Wadden Sea at the end of the 1970s no updated map was made, nor was any trilateral ecotope map digitally available. The objective of this paper was to describe the development of a new and improved ecotope map of the trilateral Wadden Sea, which is representative for the time period 2008–2012.

2. Methods

2.1. Ecotope classification system

Our ecotope map of the trilateral Wadden Sea area followed the ecotope system for coastal waters ZES.1 typology (Bouma et al., 2005; Kers et al., 2013). This ecotope system is based on the notion that local physical environmental factors and processes are main determinants of communities. Since this ecotope system was about tidal environments the emphasis was on benthic fauna and salt marshes. The main physical environmental factors and processes in the ZES.1 system were mean and variability of salinity, substratum type, mean water depth, and hydrodynamics. Class boundaries were used to classify the continuous variables in order to define the ecotopes. The ZES.1 ecotype system hierarchically arranges the ecotope variables on the basis of the dominance of the physical environmental factors and processes in determining community composition (Table 1).

The ZES.1 hierarchic system's first level distinguishes mean salinity and salinity variability. Distinct benthic communities can be observed along a salinity gradient (Ysebaert et al., 1998). The mean salinity is classified into three classes, Fresh, Brackish and Marine. Class boundaries for salinity are founded on the Venice system, named after the 1958 Symposium for the Classification of Brackish Waters held in Venice (Anonymous, 2003). Differing from the ZES.1 typology made by Bouma et al. (2005) we included oligohaline waters into the Brackish class of the ecotope system, which is therefore defined as having a mean salinity between 0.5 and 18 ppt. A seasonally fluctuating salinity regime has a marked effect on the distribution of the benthic fauna (Sanders et al., 1965; Wolff, 1973). Therefore, in addition to the Venice system, attempts have been made to classify salinity fluctuations (Heerebout, 1970). In the ZES.1 ecotope system the salinity variability is calculated from time series data which may be observed or modelled. When the coefficient of variation (CV = standard deviation / mean) is larger than 0.25, the salinity is considered variable, else it is considered stable.

Table 1
Variables, classes and class boundaries to describe the ecotopes of the trilateral Wadden Sea. Code denotes the final coding used in the digital map.

Variables	Classes	Class boundaries	Code
Mean salinity	Fresh	Yearly mean < 0.5 ppt	0
	Brackish	0.5 ppt ≤ yearly mean < 18 ppt	1
	Marine	Yearly mean ≥ 18 ppt	2
Salinity	Stable	st. dev./mean ≤ 0.25	0
Variability	Variable	st. dev./mean > 0.25	1
Substratum	Sediment	Soft sediment	0
	Hard	Dikes, dams, quays, etc.	1
Depth	Deep sublittoral	Depth < −5 m MLWS	0
	Shallow sublittoral	−5 m MLWS ≤ depth < 4% mean exp.	1
	Low littoral	4% ≤ mean exposure < 25%	2
	Middle littoral	25% ≤ mean exposure < 75%	3
	High littoral	75% ≤ mean exposure < 85%	4
	Supralittoral	Mean exposure ≥85%	5
	Salt marsh	Vegetated	6
Hydrodynamics	Low dynamic	max. current velocity < 0.8 m/s	0
	High dynamic	max. current velocity ≥ 0.8 m/s	1
Sediment	Undetermined	No data	0
Composition	Silt	Silt content ≥25%	1
	Fine sand	D50 < 250 μm	2
	Coarse sand	250 μm < D50 < 2000 μm	3
Salt marsh	No vegetation	TMAP coastal vegetation S.0	0
	Pioneer zone	TMAP coastal vegetation S.1	1
	Low salt marsh	TMAP coastal vegetation S.2	2
	Brackish marsh	TMAP coastal vegetation S.5	3
	High salt marsh	TMAP coastal vegetation S.3	4
	Other marsh	TMAP coastal vegetation other S	5
	Dune slack	TMAP coastal vegetation D.1	6
	Fresh grassland	TMAP coastal vegetation S.6	7

The second level distinguishes between artificial hard substrata and sediments. A notable difference exists between flora and fauna on hard substrata compared to soft sediments (Peterson, 1991). Moreover, hard substrata in the Wadden Sea are known to have many non-native species (Buschbaum et al., 2012). Wadden Sea hard substratum consists mainly of dams and dikes made of stones or concrete elements, possibly with an asphalt layer and are usually found along the Wadden Sea coasts. Natural hard substrata formed by mussel beds are added to the ecotope map as an eco-element. Sediment beds cover considerably larger areas than hard substrata. Sediments are further subdivided at the sixth hierarchic level of the ecotope system based on sediment composition.

The third level discerns between three depth classes, i.e. the sublittoral zone (permanently under water), the littoral zone (flooded each tide), and the supralittoral zone (not flooded each tide), based on mean tidal levels. The sublittoral zone is defined beneath mean low water spring tide (MLWS), the littoral zone is in between MLWS and mean high water neap tide (MHWN) and the supralittoral zone is above MHWN. However, the application of the ecotope system in the Western Scheldt estuary made clear that the theoretical class boundaries used (MLWS and MWHN) could be better replaced by the more practical limits of 4% and 85% exposure frequency respectively (Kers et al., 2013). The three depth classes are further subdivided at the fifth level.

The fourth level of the hierarchic ecotope system is hydrodynamics. Tidal currents are a major determinant of benthic distribution and production (Wildish and Peer, 1983). At locations where the current or orbital velocity is high enough to stir up and transport sediments frequently, most benthic organisms cannot survive. A maximum, depth-averaged current velocity at spring tide of 0.8 m/s was taken to distinguish between low and high dynamic ecotopes. At this velocity the formation of sandwaves and megaripples on the bed is initiated (Boothroyd and Hubbard, 1975).

At the fifth level, the three depth classes of the third level are subdivided. The sublittoral class is subdivided into a deep sublittoral and a shallow sublittoral at a water depth of 5 m below MLWS. Many juvenile fish, adult fish and crustaceans commute with the rising and ebbing tide between approximately 5 m below low water to the littoral zone (e.g. Kuipers, 1973). The littoral class is subdivided into three zones based on mean exposure time (%). The exposure time of tidal flats determines a benthic zonation through processes such as desiccation, foraging times of sessile benthos prey and their predators such as fish and shorebirds (Folmer et al., 2010; Reise, 1985). The following ranges were used for subdivision of the littoral class: low littoral zone between 4% and 25% exposure, a middle littoral zone between 25% and 75% exposure, and a high littoral zone between 75% and 85% exposure. The supralittoral class above 85% exposure time is further described by Bouma et al. (2005) by its vegetation with salt marsh flora. This is classified by the inundation frequency (number of times inundated per year), distinguishing the pioneer zone and low, middle and high marsh. For our application in the trilateral Wadden Sea we applied the TMAP salt marsh classification (Petersen et al., 2014) with added classes for Other marsh, Dune slack and Fresh grassland (Table 1).

The final, sixth, ecotope level is sediment composition. Sediment composition is a main factor determining the occurrence and distribution of benthos (Beukema, 1976; Ysebaert et al., 1998). The sediment composition partly reflects a combination of the availability of sediment, its erodability and hydrodynamic conditions but is also affected by the presence and density of microphytobenthos and macrozoobenthos (Reise, 2002). Bouma et al. (2005) chose median grain size (D50) of the sand fraction and silt content (weight percentage of particles < 63 μm) to classify sediment composition into gravel (D50 > 2000 μm, silt% < 25%), coarse sand (250 μm < D50 < 2000 μm, silt% < 25%), fine sand (D50 < 250 μm, silt% < 25%), and silt (silt% > 25%).

2.2. Simplified ecotope typology

The combination of all ecotope classes deliver 5376 theoretically possible combinations, of which 255 form logical combinations for ecotopes. A more practical, simplified ecotope typology with 11 types was therefore developed by Bouma et al. (2005). The simplified typology ignores salinity and sediment composition and consists of two salt marsh types (pioneer and salt marsh), one supralittoral zone, three low dynamic littoral zones (low, middle and high), one high dynamic littoral zone, two high- and low-dynamic sublittoral zones, one hard substrate type and one ‘other’, consisting the remaining salt marsh types, Table 2.

2.3. Data base

To provide hydrodynamic input fields for the classification of ecotopes, we used output from a baroclinic three-dimensional numerical model. The model output data were generated using the General Estuarine Transport Model (GETM) that was set-up for the entire Wadden Sea. A horizontal resolution of 200 m was used with terrain-following vertical coordinates with 26 depth layers. The time step of the model was 40 s. Model output for salinity and current velocity comprised the years 2009–2011, for which meteorological forcing, freshwater discharge, and boundary conditions for tidal forcing and storm surges were imposed. For a detailed description of the model set-up and performance we refer to Gräwe et al. (2016). Depth-averaged monthly mean salinity values (based on hourly model output) for 36 months were averaged to obtain yearly mean salinity as input variable for the ecotope map. Standard deviations were divided by the means in each computational cell over each of the 36 months. It was subsequently evaluated if the maximum value was larger than 0.25 to classify the salinity variability. The ecotope map is based on rather average hydrological conditions for 2009–2011. Extreme hydrological years will change the ecotope composition. Depth-averaged maximum current velocity values over the 36-months period (based on hourly model output) were obtained to classify hydrodynamics as input variable. The data on salinity, current velocity and bathymetry from the GETM model were applied as point data with a grid spacing of 200 m. These point datasets were polygonised in ArcGIS by applying the Buffer builder using a buffer distance of ½√2 times the grid spacing and where relevant “Dissolve by Field” into one multipart polygon. Subsequently, the Integrate tool was applied on these polygons with a xy-tolerance of ~1/4 of the buffer distance yielding correctly adjacent polygons without overlaps while retaining an area around single or dual points of a given input class.

Model bathymetry in the Wadden Sea GETM model was based on data provided by the Dutch Rijkswaterstaat (resolution 20 m), the German project AufMod (resolution 50–200 m), and the Danish Maritime Safety Administration (resolution 200 m). These datasets were combined to construct a computational grid for the entire Wadden Sea with a resolution of 200 m on a Cartesian coordinate system. The coordinate system was rotated anticlockwise by 18° to align the coastline in east-west direction to reduce the number of grid cells. The Dutch bathymetric data applies Amsterdam Ordnance Datum (NAP) as vertical reference and is comprised of a composition of tidal basin surveys from several years, mainly from the years 2008 until 2012 (Duran-Matute et al., 2014). The German bathymetric data is a reconstruction of the bathymetry close to 2008 using the NHN (Normalhöhennull) - also known as the German Mean Height Reference System (DHHN92) - as vertical datum. The Danish bathymetric data of around 2008 applies the Dansk Vertikal Reference 1990 (DVR90) as vertical datum. There is a small offset of maximum 2 cm between the three vertical datums (Strykowski et al., 2011) for which no correction was made since the bathymetric differences between survey years due to morphodynamics are much larger. Based on the composite map for the bathymetry (2008–2012) and the numerical model years (2009–2011) we dated our Wadden Sea ecotope map as representative for the time period 2008–2012.

The vertical reference to determine the planimetric areas for channels and flats used by Renger and Partenscky (1974) was mean low water (MLW), whereas Yu et al. (2014) applied mean sea level (MSL), so including part of the littoral zone. In the ecotope typology the vertical reference for the subtidal area is MLWS, which is lower than MSL and MLW and this would therefore lead to smaller planimetric areas for the tidal channels. To calculate channel areas we used the simplified ecotope typology and summed the areas for the low dynamic sublittoral, the high dynamic sublittoral and the high dynamic littoral. The last category consists only of low littoral parts below 25% mean exposure time, which is in between MSL and MLW. We also combined the tidal basin Schatzkammer with the Elbe basin since Schatzkammer does not contain any sublittoral ecotopes, yielding a total of 38 tidal basins to apply the Renger and Partenscky (1974) relationship.

The bathymetric data was used to classify between shallow sublittoral and deep sublittoral in three regions of the Wadden Sea. A first region is the Dutch and German Wadden Sea excluding the Ems-Dollard for which a value of 6.3 m below vertical reference height was applied in accordance with the earlier ecotope map of the Dutch Wadden Sea by Wijsman and Verhage (2004). A second region is the Danish Wadden Sea for which a value of 6.0 m below vertical reference height was applied since the tidal amplitude is smaller in the Danish Wadden Sea. The third region is the Ems-Dollard estuary for which a value of 7.0 m below reference height was applied, similar to the class boundary in the Westerschelde estuary, and in accordance with Ysebaert et al. (2016b).

Folmer et al. (2016a,b) computed the mean exposure time of tidal flats on the basis of simulations with the above described numerical Wadden Sea model (Gräwe et al., 2016). The GeoTIFF raster data set

Table 2
Translation table for the relevant ecotope classes in the simplified ecotope typology.

Variables	Classes	1 salt marsh	2 pioneer zone	3 supralittoral	4 low dyn. high littoral	5 low dyn. mid littoral	6 low dyn. low littoral	7 high dyn. littoral	8 low dyn. sublittoral	9 high dyn. sublittoral	10 hard substrate	11 other
Substratum	Sediment	■	■	■	■	■	■	■	■	■		■
	Hard										■	
Salt marsh	No vegetation			■	■	■	■	■	■	■	■	
	Pioneer zone		■									
	Low salt marsh	■										
	Brackish marsh	■										
	High salt marsh	■										
	Other marsh	■										
	Dune slack											■
	Fresh grassland											■
Depth	Deep sublittoral								■	■		
	Shallow sublittoral								■	■		
	Low littoral						■	■				
	Middle littoral					■		■				
	High littoral				■			■				
	Supralittoral			■								
Hydrodynamics	Low dynamic				■	■	■		■			
	High dynamic							■		■		

was downloaded from the Dryad Digital Repository https://doi.org/10.5061/dryad.q9c54.2 (Folmer et al., 2016b). The continuous exposure data, ranging between 0 and 100%, were classified based on the boundaries of 4%, 25%, 75% and 85%. The raster data were then polygonized with Raster to Polygon.

Data on hard substrates, i.e. dikes, groynes and dams, were obtained from various sources. Hard substrate data for the Netherlands were obtained from Rijkswaterstaat, data for Schleswig-Holstein were provided by the Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein (LKN.SH), data for Lower Saxony were bought from the Landesamt für Geoinformation und Landesvermessung Niedersachsen (LGLN), data for Neuwerk (Hamburg) were provided by Behörde für Umwelt und Energie (BUE) and data for Denmark were provided by the Danish Coastal Authority and Danmarks Miljøportal. All data were joined in one polygon layer.

High-resolution sediment data covering the Dutch and German Wadden Sea were provided by the German Federal Maritime and Hydrographic Agency (BSH). The sediment data was compiled of many datasets gathered and analysed within the AufMod project (Zeiler et al., 2014). The sediment data consisted of two datasets, one for median grain size D50 (in µm) and one for silt content (weight percentage of sediment particles < 63 µm). Missing data for the Danish Wadden Sea were obtained from Folmer et al. (2016a,b) who imputed the sediment data with a K-nearest neighbour model on the basis of known environmental variables. The resulting sediment distribution in the Danish Wadden Sea was relatively noisy with many small patch sizes compared to the German and Dutch dataset. The ArcGIS-tool Boundary Clean was applied with default settings to obtain smoother data. The point data on sediment classes were then polygonised in ArcGIS using the Buffer builder and Integrate tool, in a similar way as for the bathymetry, salinity and velocity point data.

Salt marsh data for the trilateral Wadden Sea were obtained from the Trilateral Monitoring and Assessment Programme (TMAP), expert group salt marshes & dunes, and covered the Netherlands, Niedersachsen and Schleswig-Holstein (Esselink et al., 2017). Additional data on the Hamburg salt marshes were provided by the Behörde für Umwelt und Energie (BUE) and for the Danish salt marshes by Danmarks Miljøportal. The Danish data were not yet classified in TMAP classes. We therefore translated the known Natura 2000 classification codes into TMAP codes following the translation table of Petersen et al. (2014). Ultimately, all saltmarsh data for the entire trilateral Wadden Sea were classified into seven salt marsh classes (Table 1) and joined in one polygon dataset.

2.4. Eco-elements and tidal basins

Within the scale level of ecotopes, typical ecological communities with structuring characteristics may occur in smaller areas, deviating from the general ecological communities that are present elsewhere in the ecotope involved. These are called eco-elements. The occurrence of eco-elements depends partly on coincidental processes and partly on small-scale factors that are not adequately described by the ecotope variables. The trilateral map of the Wadden Sea contains two of such eco-elements, i.e. mussel/oyster beds and seagrass meadows. The eco-element mussel/oyster beds shows the frequency of occurrence of blue mussel, Pacific oyster and mixed beds/reefs in the Dutch and German Wadden Sea. These data were assembled by Folmer et al. (2017) for the Quality Status Report. The eco-element seagrass presence shows all known intertidal seagrass occurrences between the 1970s and 2015. These data stem from Folmer et al. (2016a), and were downloaded as a GeoTIFF raster data set from the Dryad Digital Repository https://doi.org/10.5061/dryad.q9c54.2 (Folmer et al., 2016b).

The boundaries of the 39 tidal basins in the trilateral Wadden Sea were added to the ecotope map and used in further analyses. A digital map of tidal basins was originally compiled by Kraft et al. (2011). Careful examination showed that four tidal basins of the Danish sector (1: Graadyb, 2: Knude Dyb, 3: Jyvre Dyb, 4: Lister Tief) were misaligned by some tenths of metres. In ArcGIS these boundaries were repositioned and thus made fit to existing fixed features such as coastlines, dikes and quays. Additional editing was carried out to remove internal gaps from within the tidal basin extents. The gaps (donut holes) were mainly flood-free unprotected islands and also some diked islands that we wanted to include in the tidal basin area. Five diked islands in human/agricultural use were assigned to tidal basins, i.e. Hooge, Langeneß, Oland, Grode (all SH) and Neuwerk (HH). The larger enclosed islands Pellworm, Föhr and Mandø have been excluded from tidal basin areas. Finally, salt marsh areas that drain into a tidal basin, but are located outside its boundaries, were assigned to the basin they drain into manually. Not all charted vegetation have been assigned to a tidal basin since some were located on the North Sea side of the islands.

3. Results

All data of this study are available at Mendeley Data http://dx.doi.org/10.17632/2rvtxpjtfg.1. The resulting ecotope map is the first digital, publicly available trilateral Wadden Sea ecotope map. Fig. 2 presents a typical example of an ecotope map defined by the combination of depth, exposure and hydrodynamics, and salt marsh types. For the sake of brevity, the mean salinity, salinity variability, substratum and sediment classes were omitted in this example.

The use of a single, consistent and well-defined ecotope system made it possible to compare the properties of tidal basins over the entire trilateral Wadden Sea. Table 3 presents the ecotope areas for each tidal basin according to the simplified ecotope typology and Fig. 3 shows a bar chart for the relative ecotope areas in all 39 tidal basins. There is a large size difference between basins and moreover, the relative distribution of ecotopes is not uniform. Based on the relative distribution of sublittoral, littoral and supralittoral ecotopes within each tidal basin, a cluster analysis was performed in R (R Core Team, 2013) using Ward's hierarchical clustering on an euclidean distance matrix. Results show four major clusters, Fig. 4, further depicted as clusters 1–4. The first cluster (8 basins covering 35% of the area) consists of tidal basins that are characterised by a large proportion, often > 50%, of low-dynamic low-littoral ecotopes often in combination with low-dynamic sublittoral ecotopes. These tidal basins are located at both ends of the Wadden Sea, where the tidal ranges are relatively low (Fig. 1). The one exception is the Otzumer Balje. According to empirical relationships for the volume of the tidal flats and for the volume of the channels in a tidal basin the equilibrium state of a short basin (i.e. one without estuarine outflow) is determined by two basic parameters: the total basin area A_b and the tidal range H (Renger and Partenscky, 1974; Van Goor et al., 2003; Wang et al., 2018), and the average level of tidal flats measured relative to low water relates well to the mean tidal range (Dieckmann et al., 1987; Wang et al., 2012). Remarkably, the names of the tidal basins in this cluster often refer to a 'deep' basin, such in Graadyb & Knude Dyb (Denmark), Lister Tief & Hörnum Tief (Germany), and Borndiep & Marsdiep (the Netherlands). The second cluster (7 basins covering only 4% of the area) consists of tidal basins with over 50% low-dynamic mid-littoral ecotopes, so these are the very shallow basins. Since large basins have relatively more channels than small ones, the small basins in cluster 2 consequently have a relatively large proportion of tidal flats (Eysink, 1990; Renger and Partenscky, 1974). The third cluster (5 basins covering 31% of the area) is characterised by a large proportion of high-dynamic sublittoral

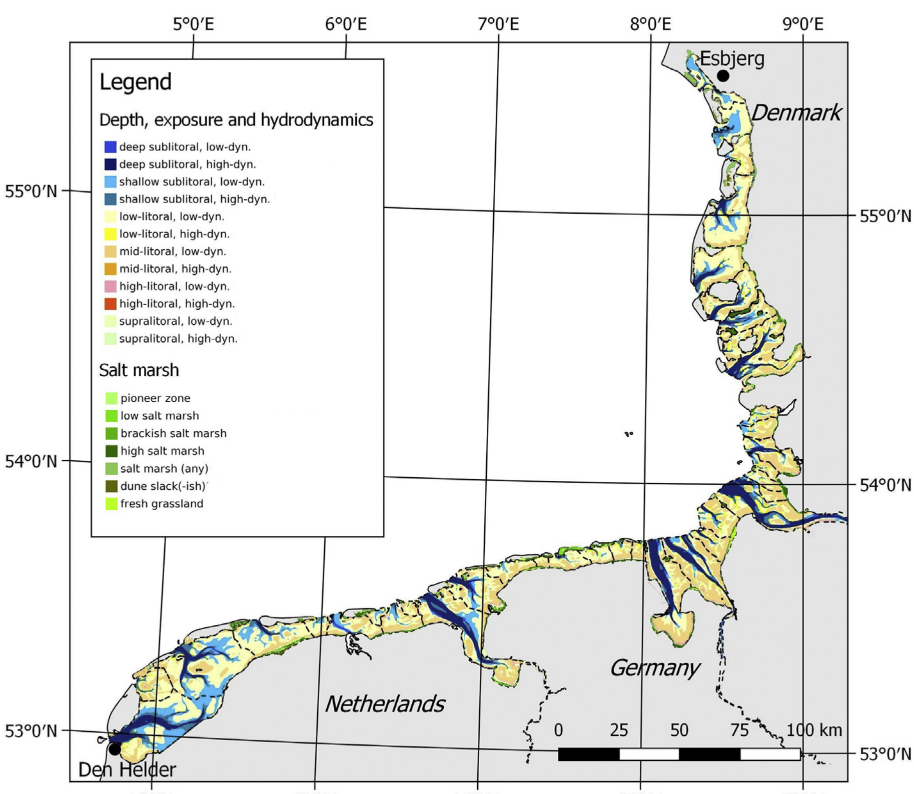

Fig. 2. Ecotope map of the trilateral Wadden Sea as defined by the combination of depth, exposure and hydrodynamics, and salt marsh types. Salinity, substratum and sediment classes were omitted for brevity; complete maps can be downloaded as zipped shapefile at Mendeley Data http://dx.doi.org/10.17632/2rvtxpjtfg.1.

Table 3
Ecotope area (ha) per tidal basin according to the simplified ecotope typology.

Tidal basin	Salt marsh	Pioneer zone	Supralittoral	Low dyn. high littoral	Low dyn. mid littoral	Low dyn. low littoral	High dyn. littoral	Low dyn. sublittoral	High dyn. sublittoral	Hard substrate	Other
1. Marsdiep	87	15	179	86	5009	24,803	907	18,387	19,892	33	0
2. Eijerlandse Gat	60	18	54	167	5838	7437	937	219	1242	0	
3. Vlie	288	51	555	188	8644	32,770	1412	14,141	11,629	49	
4. Borndiep	2665	1030	253	71	6345	15,492	179	4879	2728	12	770
5. Pinkegat	460	23	61	146	1893	2944	87	603	383	4	6
6. Zoutkamperlaag	1235	276	458	343	5408	5697	160	2924	509	9	30
7. Eilanderbalg	409	33	93	88	1265	1334	176	596	143		
8. Lauwers	595	354	436	577	5622	4473	148	1226	775	2	40
9. Schild	133	10	182	158	1743	1275	135	76	66	1	0
10. Eems-Dollard	1607	159	2949	1115	15,965	13,518	878	6081	13,709	196	118
11. Osterems	1453	295	976	594	8496	11,888	479	2986	3685	154	3
12. Norderneyer Seegat	629	91	167	14	4763	4724	187	658	257	86	181
13. Wichter Ee	348	39	108	36	1267	681	75	1	20	45	118
14. Accumer Ee	1630	96	163	27	3422	4684	203	324	600	38	110
15. Otzumer Balje	682	199	152	110	1592	4166	443	272	511	17	12
16. Harle	502	72	323	227	2590	2318	523	64	373	3	
17. Blaue Balje	144	18	307	218	2307	944	313	40	88	9	
18. Jade/Jadebusen	1878	282	1169	1844	16,459	10,696	695	2470	11,451	205	16
19. Weser	664	40	1497	777	18,386	7907	1913	2908	10,888	158	178
20. Robinbalje	157	80	146	29	6162	2712	678	258	941	51	361
21. Westertill/Nordertill	310	142	104	61	7662	6021	1478	744	1863	13	469
22. Elbe	779	181	4420	920	10,395	8004	3927	6464	20,889	222	86
23. Schatzkammer	452	158	17	0	3149	1086	238				4
24. Neufahrwasser	562	198	147	18	2964	2861	243	459	78	8	2
25. Flackstrom	167	86	71	3	2578	1507	572	383	653	2	0
26. Piep/Meldorfer Bucht	575	179	395	249	8974	4624	816	975	2956	30	9
27. Wesselburener Loch	170	256	61		5155	2178	463	956	185		0
28. Eidermündung	261	96	2	203	2629	1986	566	1078	435		1
29. Tümlauer Bucht	303	245	347	105	368	107	13	4		14	
30. Norderhever-Heverstrom	2023	1031	1278	221	15,236	9657	2405	1037	9118	58	4
31. Rummeloch West	110	31	35		3280	3306	722	243	464	0	1
32. Hoogeloch	0	0	22	5	963	410	112	9	3	1	1
33. Süderaue	1956	207	495	2	5462	5506	357	2125	2924	47	76
34. Norderaue	565	293	359	33	8453	8727	1014	964	3861	19	2
35. Hörnum Tief	795	255	202	104	6496	14,208	575	2012	4449		0
36. Lister Tief	1310	245	285	29	8800	21,198	661	4195	3893	10	0
37. Jyvre Dyb	1868	238	85		4142	6086	461	460	240	0	
38. Knude Dyb	852	420	78		631	9957	152	5550	2078	0	
39. Graadyb	2664	358	57	1	698	7101	382	3751	1313	4	
Grand total	31,347	7800	18,685	8772	221,211	274,987	25,682	90,521	135,292	1501	2598

ecotopes, or in other words, deep tidal gullies with high flow velocities. The tidal basins of the third cluster often belong to estuarine systems, such as the Eems-Dollard, Jade, Weser, and Elbe for which the basin morphology is characterised by the river channel (De Haas et al., 2018). The fourth cluster (19 basins covering 30% of the area) is characterised by a large proportion of low-dynamic low-littoral and low-dynamic mid-littoral ecotopes in equal distribution. Many Dutch tidal basins such as Pinkegat, Zoutkamperlaag, Eilanderbalg, Lauwers & Schild are part of the fourth cluster, as well as many tidal basins in the German Bight.

We applied the Renger and Partenscky (1974) relationship for relative area of tidal channels on the completed consistent mapping of all tidal basins in the trilateral Wadden Sea, Fig. 5. We indeed found that the channel area A_c is proportional to the 1.5 power of the basin area A_b and found $A_c = 2.0 \cdot 10^{-5} \cdot A_b^{1.5}$ with a high $R^2 = 0.951$.

4. Discussion

In principal the hierarchy and class boundaries of the Ecotope System for Coastal Waters are chosen in such a way that they have a direct ecological meaning, explaining the density and biomass of benthic species and salt marsh vegetation. However, only limited validation of the ecotope typology has been undertaken. Van Wesenbeeck et al. (2010) made a first attempt at validation of the ecotope system using macrozoobenthos monitoring data of the Western Scheldt estuary, the Netherlands. They found that salinity is indeed the major component explaining species distribution, but current velocity is more important in explaining species composition over depth and sediment composition and should therefore be placed higher in the hierarchical ecotope system. They note that depth and sediment composition are strongly correlated with current velocity. The most distinct deviation in class boundaries compared with the ZES.1 ecotope typology found by Van Wesenbeeck et al. (2010) was for silt percentage, which could be set at 7% rather than 25%, showing pronounced effects on the benthic composition at much lower silt percentages than implemented in the ZES.1 typology. An optimal class boundary for salinity of 24.1 ppt was found instead of 18 ppt, but they point out that salinity variability was not included in their analyses. With regard to the class boundary for current velocity, they established a slightly lower velocity boundary in the range of 62.5–75.5 cm/s instead of 80 cm/s, but they question the reliability of the numerical flow model that tended to under-predict velocities in intertidal areas. A later, comparable study by Ysebaert et al. (2016a,b) confirmed the importance of hydrodynamics in determining benthic communities. They established a class boundary for velocity applying to sublittoral ecotopes of 95–110 cm/s, and to littoral ecotopes of 43–58 cm/s. The latter could be due to model underestimation since mathematical modelling of wetting and drying in shallow intertidal zones is notoriously difficult (Balzano, 1998). In

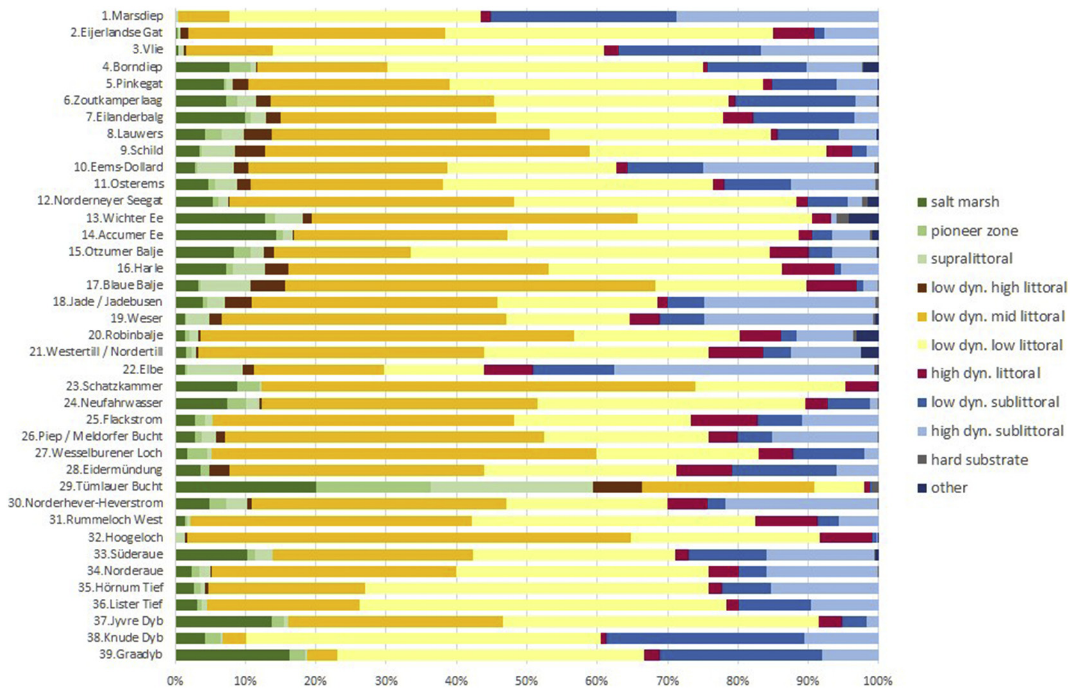

Fig. 3. Proportion of ecotope areas (%) for all 39 tidal basins in the trilateral Wadden Sea, defined according to the simplified typology.

addition to flow velocity, Bouma et al. (2005) proposed to apply wave orbital velocity as a class boundary as well, since wave action is an important determinant for hydrodynamics in the littoral zone. We expect that by including wave action more areas will be classified as 'high dynamic', specifically shallow locations that generally have low current velocities but can have high wave orbital velocities. However, the computation of orbital velocities on tidal flats is even more challenging, so this was abandoned in further ecotope applications (Kers et al., 2013). Instead, a more detailed mapping of hydrodynamics without the use of numerical modelling can be made by interpretation of morphological features on aerial photographs taken during low tide. The importance of hydrodynamics as explanatory variable in benthic distribution underlines the recommendation that more knowledge, data and model instruments should become available on the relation between hydrodynamic energy and benthos, particularly in the shallow wave breaking intertidal zone.

The application of the Renger and Partenscky (1974) relationship for relative area of tidal channels gives a practical example of the use of the trilateral ecotope map. Yu et al. (2014) analysed the empirical equation of Renger and Partenscky (1974) for 13 tidal basins in Schleswig-Holstein and found $A_c = 2.36{\cdot}10^{-5}{\cdot}A_b^{1.5}$ with an $R^2 = 0.753$. We established $A_c = 2.0{\cdot}10^{-5}{\cdot}A_b^{1.5}$ with a high $R^2 = 0.951$ for all 39 tidal basins, further deviating from the theoretical value of $3.95{\cdot}10^{-5}$ for the coefficient in the power relationship as established by Yu et al. (2014). Using the ecotope map in a similar manner, the fractal-network geometry found in the Dutch Wadden Sea by Cleveringa and Oost (1999) can now be studied for the entire trilateral Wadden Sea.

Further use of ecotope maps in the ecological domain is to describe habitat suitability for species of benthos, birds or other flora and fauna. This can be achieved through habitat suitability modelling, a technique that is founded in the U.S. Fish and Wildlife Service publication "Habitat Evaluation Procedures Handbook" (U.S. Fish and Wildlife Service, 1980). Habitat modelling is based on the preferences of flora and fauna for the physical characteristics of their living environment, i.e. the ecotopes or habitats. Univariate or multivariate functions link the abiotic characteristics to a proportional index for habitat suitability. Subsequently, based on the assessment of the carrying capacity and supply of suitable habitat, potential population sizes of the species reviewed may be calculated. Care should be taken because fundamental problems in relating habitat attributes to the quantification of population abundance due to ill-selected variables, errors in measurement of variables and missing correlation of abundance with habitat exist (Mitchell and Lindström, 2005). Most habitat suitability models are unable to address issues related to habitat fragmentation, connectivity, and contiguity, unless an assessment of the connectivity of suitable habitats into ecological networks is carried out as well. Biological interactions, such as predator-prey relationships are usually neglected. Further, behavioural attributes such as territoriality, competition and predation, which can influence utilization of available (suitable) habitats, are rarely included as well, although progress has been made (Hirzel and Le Lay, 2008). Nonetheless, an ecotope map can give a simple first–order estimate of the potential spatial distribution of species and communities, which can be used in research and management. More sophisticated multivariate species distribution techniques such as evaluated by Folmer et al. (2017) are recommended, although these also suffer from limitations of missing variables and absence of biological interactions. Applications of ecotope maps in ecological studies can be found in freshwater as well as in marine environments. Schipper et al. (2011) mapped river ecotopes to derive landscape patches and related these to the presence-absence of corncrake (*Crex crex*) using logistic regression. Piet et al. (2000) analysed beam-trawl frequency in relation to marine ecotopes defined by grain size and depth in the Dutch sector of the North Sea. Van Loon et al. (2015) applied a simple ecotope classification based on salinity and depth in transitional and coastal water bodies to assess the status and trend of benthic invertebrates for the Water Framework Directive. Baptist (2017) applied the simplified ZES.1 ecotope typology in the Ems-Dollard estuary in a prospecting study for the year 2050. He used results from Delft3D model computations applied to different hydromorphological measures in the estuary to spatially predict changes in ecotope distribution and associated benthos and bird suitability. Resulting maps were used to assess the ecological perspective of the estuary in 2050 under conditions of sea level rise and human interventions.

Another application of ecotope maps is to compare the historical ecotope composition of subsequent years or multi-annual periods to denote environmental changes. In doing so it is of utmost importance to

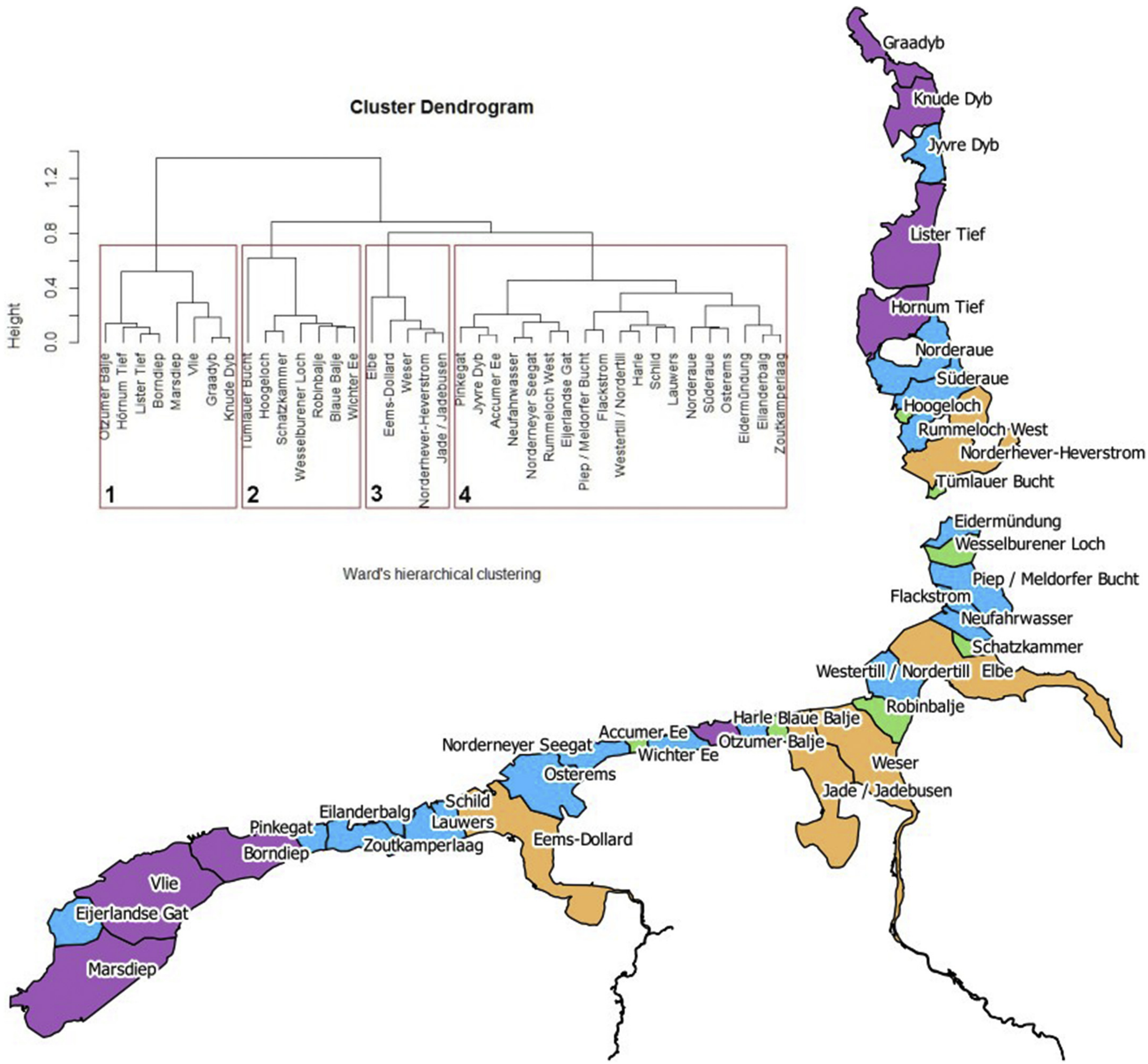

Fig. 4. Cluster dendrogram for tidal basins in the trilateral Wadden Sea. Cluster 1 basins (purple) have a large proportion of low-dynamic low-littoral ecotopes in combination with low-dynamic sublittoral ecotopes, cluster 2 basins (green) have a large proportion of low-dynamic mid-littoral ecotopes, cluster 3 basins (brown) have a large proportion of high-dynamic sublittoral ecotopes and cluster 4 basins (blue) have a large proportion of low-dynamic low-littoral and low-dynamic mid-littoral ecotopes in equal distribution.

apply a uniform and consistent typology. A comparison between two ecotope maps of the Dutch Wadden Sea both applying the ZES.1 typology, one from 2009 and one from 2000, failed because of the use of different (2D vs. 3D) numerical models for generating hydrodynamic input (Baptist et al., 2016). For future use of ecotope maps, it is therefore very important to pay attention to clear and consistent applications of base maps, ecotope typology and model input.

Our trilateral ecotope map provides the most recent and full-coverage information on the ecotope distribution in the entire Wadden Sea. The clustering in four major tidal basin types gives clear guidance for comparative ecological and morphological studies between tidal basins. Van Beusekom et al. (2012) show that the river basin approach of the EU Water Framework Directive is not appropriate to explain the eutrophication status of the Wadden Sea, but instead recommend a tidal basin approach. Wang et al. (2018) show that sediment budgets and morphological developments of the Wadden Sea are highly dependent on tidal basin properties. Last but not least Kraft et al. (2011) made a first data inventory of the tidal basins in the trilateral Wadden Sea and show first applications to ecological studies. They conclude that comparative research at the level of tidal basins is promising and feasible for various kinds of policy and research topics. They also stated that the development of a tidal basin atlas is an important contribution to the field. Our ecotope map thus can be used for environmental research, policy and conservation purposes of the trilateral Wadden Sea in an integrated manner.

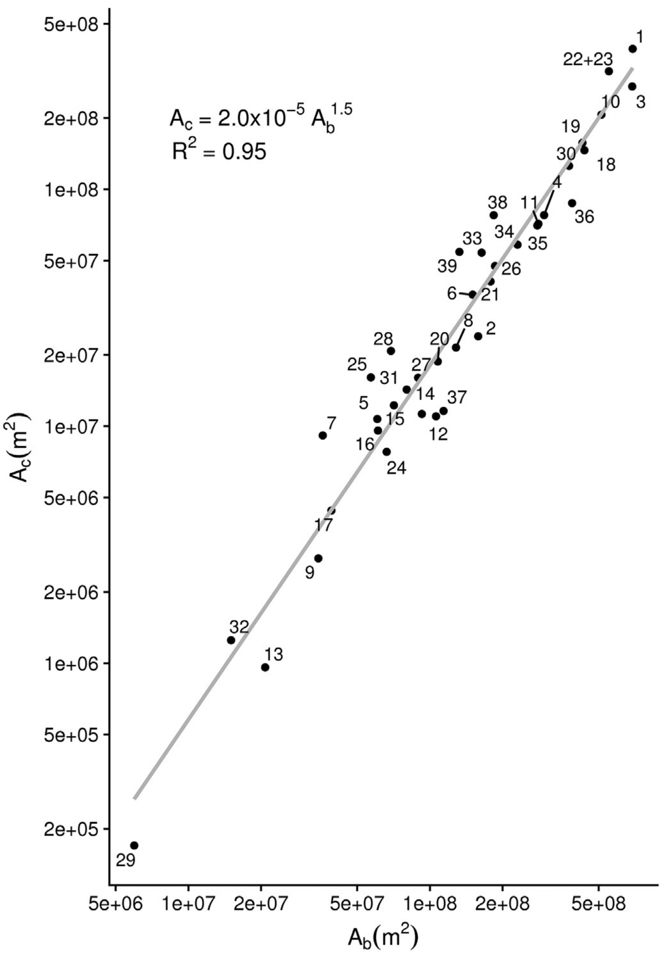

Fig. 5. Relationship for the channel area (m^2) as function of the basin area (m^2) in the entire trilateral Wadden Sea, $A_c = 2.0 \cdot 10^{-5} \cdot A_b^{1.5}$ with an $R^2 = 0.951$.

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