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# Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea

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#### Abstract

The Wadden Sea is the world's largest intertidal ecosystem and one of the most productive coastal areas worldwide. People have fished and hunted marine resources in the Wadden Sea since its origin ~7500 years ago, but have since depleted the majority of formerly important species and their supporting habitats. Most of these changes have been lost from memory. Here, I reconstructed the history of fishing and marine resource use in the Wadden Sea using a multi-disciplinary approach that combines archaeological, historical, fisheries, and ecological records.

Early farmers and settlers used a great variety of coastal mammals, birds, fish, and shellfish from  $\sim$ 5000–500 years ago. During the Middle Ages (500–1500 AD) fish gained in importance over birds, mammals, and shellfish, and fishing gradually replaced hunting and gathering along the coast. About 1000 years ago, freshwater and migrating fish stocks in European inland lakes and rivers declined because of overfishing and habitat degradation. This induced an expansion and commercialization of marine fisheries along the coast, first for herring and oysters in the 12th and 13th centuries, later for haddock and cod in the 16th century. Exploitation of birds and whales was also commercialized and some species started to decline with increasing exploitation pressure. During Modern Times (1500–1800 AD), commercial fisheries further developed for rays, flatfish, lobster, and shrimp along the coast and for sturgeon and salmon in the estuaries. Intensification of exploitation in the 19th century led to strong depletion of many coastal resources and several fisheries collapsed in the early 1900s. As a result, new fisheries were developed for formerly less valued species but many declined or collapsed before the end of the 20th century. Today, the only remaining commercial fisheries target shrimp, blue mussels, and cockles. On the other side, conservation efforts have recovered some formerly exploited species, especially birds and seals. Meanwhile, fishing has been gradually replaced by tourism and nature conservation along the coast.

The history of the Wadden Sea may serve as an example for a coastal region that sustained people for millennia, was heavily exploited and transformed over time, but still shows some potential for recovery where protection and restoration efforts are integrated into coastal management plans.

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## 1. Introduction

The present Wadden Sea is considered one of the most important coastal wetlands and the largest intertidal ecosystem worldwide (Wolff, 1983; Meltofte et al., 1994; Reise, 2005). With its 10–12 million migratory waterbirds visiting each year, its recovering populations of harbour and grey seals, and its traditional shrimp fishery the Wadden Sea attracts millions of tourists each year and is ecologically as well as economically important. Conservation efforts have been intensified since the 1980s with the declaration of three National Parks (De Jong et

0165-7836/\$ – see front matter © 2007 Elsevier B.V. All rights reserved. doi:10.1016/j.fishres.2006.12.009 al., 1999) and the region is under consideration as a UNESCO Natural World Heritage site.

Despite its great natural value, however, the Wadden Sea is also a heavily transformed ecosystem due to a long history of human influences and interventions (Lotze et al., 2005). Since its origin through retreating glaciers and rising sea level  $\sim$ 7500 years ago, people lived in the Wadden Sea region and used its rich and diverse coastal and marine resources, transformed habitats, discharged waste water, and introduced non-indigenous species (Lotze et al., 2005). Today, the Wadden Sea is among the most degraded estuarine and coastal ecosystems worldwide together with the Baltic and Adriatic Seas (Lotze et al., 2006).

The ecological history of human-induced changes in the Wadden Sea has been recently reviewed in a series of articles (Lotze and Reise, 2005) documenting the history of human settlement

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and cultural change (Knottnerus, 2005), habitat transformation (Reise, 2005), exploitation (Hoffmann, 2005; Holm, 2005, Wolff, 2005), eutrophication (van Beusekom, 2005), as well as the archaeological (Prummel and Heinrich, 2005) and ecological (Lotze, 2005; Lotze et al., 2005) records of change. The Wadden Sea is also one of 12 estuarine and coastal ecosystems worldwide in which ecological changes have been traced from the onset of human settlement until today (Lotze et al., 2006).

In this paper, I combined the above and additional sources of archaeological, historical, fisheries, and species records to analyze the history of fishing and marine resource use in the Wadden Sea. My main goal was to reconstruct when different fisheries and marine resource uses in the Wadden Sea region started, how they developed over time, and when and why they came to an end. To achieve this, I used (i) archaeological data to trace consumption patterns and changes in resource use of coastal people, (ii) historical records to reconstruct the beginning, expansion, and decline of important fisheries and resource uses, (iii) fisheries data to quantify the development of commercial fisheries over time, and (iv) species records to assess changes in resource availability and ecological abundance.

#### 2. Methods

## 2.1. Study site

The Wadden Sea is the coastal stretch of the southern North Sea bordering the Netherlands, Germany, and Denmark (Fig. 1). Defined as the Trilateral Wadden Sea Cooperation area, it reaches from Den Helder in the Netherlands to Blåvandshuk, Skallingen in Denmark including the estuaries and coastal waters inside and outside the barrier islands (De Jong et al., 1999). For this study, the island of Helgoland (Fig. 1) was also included since several important fisheries developed around this rocky outlet in the southern North Sea.

#### 2.2. Archaeological records

Archaeological data were extracted from a database of excavated bone and shell remains of terrestrial and marine mammals, birds, fish, and molluscs from the Wadden Sea region (Prummel and Heinrich, 2005) and additional sources (Brinkhuizen, 1979; Zeiler, 1997; Dirk Heinrich, personal com-



Fig. 1. Map of the Wadden Sea showing important localities that are mentioned in text.

munication). Remains were excavated at 44 former human occupation sites along the coasts of Denmark, Germany, and the Netherlands (Table 1). Most of the sites were located at or near the coast with seven sites near major rivers and five sites on islands. Dated material belonged to seven cultural periods: the Late Neolithic (~2700–2300 BC), Bronze Age (~2100-800 BC), Iron Age (~800 BC-100 AD), Roman Period  $(\sim 200 \text{ BC}-400 \text{ AD})$ , Migration Period  $(\sim 300-600 \text{ AD})$ , Middle Ages ( $\sim$ 500–1500 AD), and Modern Times ( $\sim$ 1500–1800 AD), and five sites were occupied over more than one period. Because of the small amount of data, I combined the Bronze Age with the Iron Age, and the Migration Period with the Middle Ages. Also, I combined sites that were occupied from the Iron Age to Roman Period or Middle Ages into the Roman Period. At a few sites, remains were reported as present (+) or absent (-) only, which I transformed to 1 (present) or zero (absent) to include the qualitative information.

Table 1

Overview on the number of archaeological sites in each cultural period and separated by country (Dk, Denmark; G, Germany; NL, Netherlands), method of excavation (si, sieved; hc, hand collected; ?, unknown), species group represented

Period	Time	Sites	Country			Method			Species groups present				
			Dk	G	NL	si	hc	?	Terrestrial mammals	Marine mammals	Birds	Fish	Molluscs
Late neolithic	2700-2300 вс	2		1	1	1	1		2	1	1	1	1
(Bronze) Iron age	(2100–) 800 BC–100 AD	11		3	8		11		5	4	2	3	4
Roman period	200 BC-400 AD	11		6	5	1	10		5	5	4	4	5
(Migration) Middle ages	(300-) 500-1500 AD	17	2	4	11	5	11	1	6	11	3	9	7
Modern times	1500–1800 ad	3			3	3			3	0	1	3	1
Total		44	2	14	28	10	33	1	21	21	11	20	18

Archaeological data have inherent limitations and biases that need to be considered in the interpretation of former species occurrence: (1) former people selected certain species for different uses including food, furs, tools, ornaments, and domestication; (2) only species with persistent body parts such as bones, antlers, teeth, fish scales, and mollusc shells can be preserved overtime; (3) preservation of remains over time depends on soil characteristics; (4) the excavators' taxonomic or cultural focus as well as the recovery method applied (e.g. hand collected or sieved) will influence the collection of remains (see Prummel and Heinrich, 2005 for discussion). Sieving allows better recovery of smaller remains of fish and birds compared to hand collection (Prummel and Heinrich, 2005).

Given the low sample size I aggregated the data (individual species into species groups, single sites into cultural periods) in order to derive some general results about changes in species composition in the archaeological record over time. I calculated the number of remains and number of species identified per site, cultural period, and species group. I then calculated the percent of remains belonging to species groups and subgroups as follows: mammal subgroups included terrestrial mammals, large whales, small whales, and seals; bird subgroups included waterfowl and waders, seabirds, shorebirds, raptors, and some terrestrial birds; fish subgroups included marine, freshwater and migrating species; and mollusc subgroups included marine, freshwater, and terrestrial species (see Prummel and Heinrich, 2005 for detailed species lists).

#### 2.3. Historical records

Historical data consisting of narrative information on fishing and marine resource use were extracted from Hoffmann (2005), Holm (2005), Wolff (2005), Lotze (2005), Lotze et al. (2006) and sources cited therein. From this information, I derived the timelines from the beginning to end of fisheries and marine resource uses in the Middle Ages (500–1500 AD) throughout Europe, and in the last 1000 years in the Wadden Sea area. For the latter, I focused on commercial or large-scale exploitation rather than artisan exploitation, which likely occurred at all times for many of the species described.

## 2.4. Fisheries records

Fisheries records consisting of landings and effort data were compiled for the Danish (Holm, 2005), Dutch (Wolff, 2005), and German Wadden Sea (Lotze, 2005; Lozan, 1990, 1994; CWSS, 2002). Some records reached back 500 or 300 years ago, others only covered the last decades of the 20th century. In the Danish haddock and plaice fishery that lasted from 1562–1930 and ranged from 500 to 3000 t (Holm, 2005), I replaced qualitative records of 'low' with 10 t and 'some' with 50 t to continue the time series. I report available trends as landings by weight or number or as effort by number of fishermen or boats. Reported fisheries data rarely covered the entire period of a fishery taking place, and often only the later periods are described. However, the initiation of a fishery could often be derived from the historical records (see above).

#### 2.5. Species records

Records on relative abundance of resources over time were extracted from a comprehensive database on historical changes in 12 estuaries and coastal ecosystems worldwide (Lotze et al., 2006). The database contains some of the archaeological, historical, and fisheries records described above plus ecological information on species abundance, distribution, size, and threats over time (see Lotze et al., 2006 for detail). For the Wadden Sea, trends in relative abundance were available for 77 species which were considered economically or ecologically (functionally, structurally) important throughout history. Data included 6 species of marine mammals (large whales, small whales, pinnipeds), 37 coastal birds (seabirds, shorebirds, waterfowl and waders, raptors), 19 fish (groundfish, pelagic fish, migrating fish), 12 invertebrates (crustaceans, gastropods, bivalves, echinoderms, polychaetes, hydrozoans), and three types of vegetation (seagrass, macroalgae, wetlands) (for detailed species list see Lotze et al., 2006). Qualitative and quantitative records of abundance were integrated into relative abundance estimates defined as pristine (100%), abundant (90%), depleted (50%), rare (10%), and extinct (0%). Recovery was defined as an increase from 0 or <10% to >10% (partial recovery) or >50% (substantial recovery) of original abundance (see Lotze et al., 2006 for detailed methods). I calculated the average trends in relative abundance for the 5 species groups (marine mammals, birds, fish, invertebrates, vegetation) over the last 5000 years and the rate of depletions, collapses, extinctions, and recoveries among all 77 species. I further analyzed trends in 26 commercial fish and invertebrate species and calculated the percent of fisheries resources depleted, collapsed or extinct over time.

# 3. Results

#### 3.1. Trends in the archaeological record

Remains of marine and coastal animals were found at 44 sites along the Wadden Sea coast spanning the Late Neolithic until Modern Times (Table 1). There were only two Late Neolithic sites (and for one site only one species was reported) and three Modern Times sites, but for both periods >2000 remains from different species groups were reported. Not all species groups were represented at each site or in each cultural period (Table 1). On average, however, each species group was represented at 18 sites (range 11–21) and in all five cultural periods except for marine mammals missing from Modern Times sites (Table 1).

The total number of remains excavated was highest for the Middle Ages and lowest for the Iron Age (Fig. 2A, black bars), likely because the number of excavated sites was greater in the Middle Ages and sieving was applied at 5 sites compared to none in the Iron Age (Table 1). However, for the remaining three cultural periods similar amounts of remains were excavated despite differences in the number of excavated sites and recovery method applied (Table 1). Importantly, despite the smaller number of remains, the total number of identified species was highest in the Roman period followed by Middle Ages (Fig. 2A, white bars). Even in the Iron Age, with the smallest amount



Fig. 2. Summary of archaeological remains from 44 sites along the Wadden Sea coast. (A) Total number of archaeological remains (black bars) and number of species (white bars) identified in each cultural period. (B) Percent of remains belonging to each species group (mammals, birds, fish, molluscs) and subgroup as depicted in the legend. Note that fish and molluscs are likely underrepresented in the Late Neolithic period because of missing quantitative information. Cultural periods are identified by name and time, for detail on sites refer to Table 1 (data adapted from Prummel and Heinrich, 2005 with additional information from Brinkhuizen, 1979; Zeiler, 1997).

of remains recovered, 32 species were identified while only 26 species were identified for Modern Times (Fig. 2A).

With the limitations of the data in mind (see Methods), changes in species composition in the archaeological record over time have to be viewed with caution. However, the general picture derived from the data (Fig. 2B) can be corroborated with historical accounts from the same region (see below) as well as with archaeological accounts from the North Sea (Enghoff, 2000) and around Great Britain (Barrett et al., 2004). Thus, general changes in marine resource use over time may be interpreted as follows.

During the Late Neolithic, remains of waterfowl were abundant in the archaeological record followed by terrestrial and marine mammals (Figs. 2B and 3A). Waterfowl were mostly represented by ducks (*Anas* spp., *Mareca* spp.) and terrestrial mammals by wild boars and pigs (*Sus scrofa*, *S. domesticus*), rodents, red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), Western polecat (*Mustela putorius*), European beaver (*Castor fiber*), otter (*Lutra lutra*), and voles (*Microtus* spp.), among other species (see Prummel and Heinrich, 2005). Marine mammals included the grey seal (*Halichoerus grypus*), harbour porpoise (*Phocoena phocoena*) and Cetacea. Fish remains were only identified as species present including cod (*Gadus morhua*), sturgeon (*Acipenser sturio*), thin-lipped grey mullet (*Mugil capito*), and some flatfish (Brinkhuizen, 1979). Similarly, mollusc remains were identified as species present only with an indication of the blue mussel (*Mytilus edulis*) being most common. Thus, fish and mollusc remains are likely underrepresented in Fig. 2B. Although essentially coming from only one archaeological site at Kolhorn, Netherlands (the second Late Neolithic site only reported the presence of aurochs, *Bos primigenius*), this set of remains gives insight into the great variety of species present and resources used (55 species identified, Fig. 2A) by coastal people 4000–5000 years ago (see also Bantelmann, 2003; Lotze, 2005).

During the Bronze-Iron Age and Roman Period, remains covered a great variety of resources from all species groups (Figs. 2B and 3A). Among terrestrial mammals, red and roe deer, elk (Alces alces), aurochs, red fox (Vulpes vulpes), beaver, wild boar, wild cat (Felis silvestris), and northern vole (Microtus oeconomus) were important. Marine mammal remains came from harbour seal (Phoca vitulina), grey seal, harbour porpoise, bottlenose dolphin (Tursiops truncates), killer whale (Orcinus orca), and some larger Cetaceans. Bird remains mainly represented waterfowl (ducks, waders), but in Roman Times a variety of seabirds (northern gannet, Morus bassanus, cormorant, Phalacrocorax carbo, gulls, Larus spp.), shorebirds (plovers, Calidris spp., Limosa spp.), raptors (white-tailed eagle, Haliaeetus albicilla, marsh harrier, Circus aeruginosus) and land birds (crows and ravens, Corvus spp.) was also found. Among fish, marine (cod, haddock, Melanogrammus aeglefinus, flatfishes) and migrating species (sturgeon, salmon, Salmo salar)



Fig. 3. Timelines of fishing and marine resource use from: (A) archaeological records in the Wadden Sea from 3000 BC to 1800 AD, (B) historical records for the Middle Ages (500–1500 AD) in Europe, and (C) historical and fisheries records for commercial fisheries and resource uses for the Wadden Sea since 900 AD. Note that timelines are minimum estimates based on available data and that gaps in timelines (e.g. for plaice and rays 1700–1890) may indicate lack of data on or absence of a fishery. Species groups are color-coded as in Fig. 2, "HG" identifies. fisheries from the island of Helgoland (data adapted from Prummel and Heinrich, 2005; Hoffmann, 2005; Holm, 2005; Wolff, 2005; Lotze et al., 2005, and references therein).

were important, but no freshwater fish were identified. Mollusc remains were dominated by blue mussels, cockles (*Cerasto-derma* spp.), and *Macoma balthica* (see Prummel and Heinrich, 2005 for detail).

During the Migration Period and Middle Ages, remains also covered a great variety of resources with all subgroups present except freshwater molluscs (Figs. 2B and 3A). However, fish and especially marine fish remains (cod, haddock, flatfishes, but also thornback ray, *Raja clavata*, and grey mullets, *Chelon labrosus, Liza ramada*) dominate the record over mammals, birds, and molluscs. This trend continued in Modern Times with fish now representing 95% of total remains, 76% of which being marine fish (cod, haddock, flatfishes). However, migrating (sturgeon, salmon, eel, *Anguilla anguilla*) and freshwater fish (roach, *Rutilus rutilus*, pike, *Esox lucius*, perch, *Perca fluviatilis*, carp, Cyprinidae) were also present in both periods. There were no remains reported for marine mammals at Modern Times sites, and terrestrial mammals, birds and molluscs had little importance (Figs. 2B and 3A). The increased use of marine fish in the Middle Ages is also well documented from archaeological records around England, where a strong shift from freshwater and migrating fish towards marine fish, especially herring, cod, and other groundfish, occurred in the 11th and 12th century AD (Barrett et al., 2004), and from Ribe in Denmark, where increased abundance of cod and haddock becomes apparent in the 9th century AD (Enghoff, 2006a).

#### 3.2. Historical trends in the Middle Ages in Europe

Historical information on fish use and consumption patterns in the Middle Ages across inland regions of Europe indicate that until about the 12th century people preferred freshwater and migrating fish such as pike, salmon, and sturgeon, which were locally available and hence could be sold fresh (Fig. 3B, Hoffmann, 2005). However, during the 12th and 13th centuries these preferred species declined as a result of overexploitation, habitat deterioration, and water quality degradation in rivers and lakes (Hoffmann, 2005). For migratory species, depletion started in the highest river tributaries and over time gradually moved towards the estuaries and coasts, where fisheries for sturgeon and salmon peaked and declined during the late 19th century (see below). During medieval times, rising human populations and demand but also the formation of more complex economic and political institutions throughout Europe initiated great changes in many fisheries. Along the coasts, increasing demand for fish was met by an economic reorientation from subsistence and artisan to full commercial development of estuarine and marine fisheries. In the North Sea and Baltic Sea, fisheries for pelagic herring were intensified during the 12th and 13th centuries (Fig. 3B), which were packed in barrels, salted, and shipped to inland markets. On the other hand, inland regions started to develop aquaculture for carp sometime in the 11 and 12th centuries to enhance local production of fresh fish. By 1300, inland regions were producing carp on a large scale (Fig. 3B, Hoffmann, 2005). By the end of the Middle Ages, former subsistence fisheries for cod and haddock along the North Sea coast became subject to commercial exploitation (Fig. 3B), and an expansion of fisheries to resource frontiers became well established throughout Europe (Hoffmann, 2005).

#### 3.3. Historical trends in the Wadden Sea

Strong shifts and fluctuations in commercial fisheries and marine resources uses can also be recognized along the Wadden Sea coasts over the past 1000 years (Fig. 3C). Whaling and sealing were reported in the southern North Sea throughout the Middle Ages. While large whales (gray whale, Eschrichtius gibbosus, right whale, Eubalaena glacialis) became scarce, commercial whaling for large Cetaceans moved towards Spitsbergen, Greenland, and Newfoundland in the 16th century (Bryant, 1995). However, porpoises (harbour porpoise, Phocoenaphocoena) and dolphins (bottlenose dolphin, Tursiops truncatus) were hunted for their oil and flesh until the early 20th century, and seals (harbour seal, Phoca vitulina) until the 1960s (Fig. 3C). Coastal birds were exploited for food, feathers, eggs and down along the coast since prehistoric times. However, in the Middle Ages exploitation of bird products became commercialized (Fig. 3C), and colonially breeding birds in particular suffered from high exploitation pressure (Lotze, 2005). Hunting of bird populations continued throughout the following centuries, and many species declined or disappeared during the 19th and 20th century before protection efforts increased (Lotze, 2005). Another resource use that became commercially important during the Middle Ages was the harvesting of plants (Fig. 3C), especially seagrass (*Zostera marina*) for dike building (Wolff, 2005) and peat exploitation for salt production (Behre, 2002). Seagrass harvest was still practiced in the early 20th century before the wasting disease largely destroyed seagrass meadows (Wolff, 2005). Thus, the use of marine mammals, coastal birds, and plants which were important resources over the past centuries and millennia (Fig. 3A and C), came to an end in the 20th century except for some recreational hunting of a few species of birds (e.g. Wolff, 2005).

As with other resources, fishes were used by coastal people throughout history (Figs. 2B and 3A), but commercialization only started in the Middle Ages with herring (Clupea harengus) and oyster (Ostrea edulis) being the first commercial fisheries in the 12th and 13th century (Fig. 3C). Because of the depletion of inland freshwater and migrating fish (see above), coastal resources became important in supplying markets further inland (Barrett et al., 2004; Hoffmann, 2005). In the 16th century, commercialization expanded to groundfish, with haddock, cod, ray (especially thornback ray), and plaice (*Pleuronectes platessa*) becoming important targets in the fisheries (Fig. 3C, Holm, 2005; Lotze, 2005). Migrating fish were important resources along the coast (Fig. 3A, Barrett et al., 2004, Prummel and Heinrich, 2005) and inland (Fig. 3B, Hoffmann, 2005) throughout history, but commercialization of migratory fisheries in the estuaries became important only in the 19th century (Fig. 3C, Lotze, 2005). Lobster (Homarus gammarus) and shrimp (Crangon crangon) were important fisheries since the 17th century, but other invertebrates and shellfish, with the exception of oyster, became important only in the 20th century (Fig. 3C).

This historical timeline indicates strong shifts in the importance of different resources and fisheries over time, with a general trend of large, valuable, and easily accessible resources commercialized first, and - often as these resources became depleted - sequential expansion to smaller, less valuable, and less accessible resources later on (Pauly et al., 1998; Lotze, 2004). Today, there is no direct, full-time fishery for finfish in the Wadden Sea left. Flatfish, mainly plaice and sole (Solea solea), are caught as bycatch in the shrimp fishery and small-scale recreational or part-time fyke and gill net fishery exists in all Wadden Sea regions targeting herring, eel, mullets, and salmonids (Dahl et al., 1994). The only commercial fisheries are targeting shrimp, blue mussels, and cockles (Cerastoderma edule). Also, there is some lugworm digging (Arenicola marina, Nereis diversicolor) as bait for sport fishermen (Wolff, 2005) and some exploratory fisheries for other shellfish such as Spisula subtruncata and the introduced American razor clam Ensis directus (CWSS, 2002; Wolff, 2005).

# 3.4. Trends in commercial fisheries

Available catch and effort data are presented in Fig. 4. The earliest evidence comes from surviving tax accounts from the early 1500s. These indicate that about 1500 fishermen were catching herring around the island of Helgoland in 1513, and 2400 fishermen in 1520, but the fishery declined towards the end of the 16th century (Fig. 4A, Holm, 2005). The herring fishery around Helgoland had also been important from the



Fig. 4. Records of landings and effort for fisheries in the Danish (DK), German (G), and Dutch (NL) Wadden Sea since 1500, separated by species groups: (A) pelagic fish, (B) groundfish, (C) migrating fish, (D) invertebrates, and (E) shellfish. Species, units of catch (t, kg, #) and effort (# fishermen, # dinghies), and regions or rivers are identified in the legend. Note the log-scale on *y*-axis and break on *x*-axis (data adapted from Holm, 2005; Wolff, 2005; Lotze, 2005 and references therein).

12th to 14th century (Fig. 3B and C, Hoffmann, 2005; Lotze, 2005), but wasn't mentioned after the 16th century. Herring and other pelagic species, however, have supported important fisheries in the former Zuiderzee with >12,000 t annually before its damming in 1932 (now Iisselmeer, Fig. 1), and along the coast until the 1970s (Fig. 4A, Lozan, 1994).

The next available records come from the coastal Danish groundfishery which flourished in the 16th century (Fig. 4B).

In 1562, about 1200 t haddock and 1800 t plaice were landed, and the fishery employed about 1200 fishermen on 150 vessels (Holm, 2005). The combined catch of the two species dropped to 1500 t in the early 1600s and declined further towards the end of the century. The fishery probably stayed at low levels throughout the 18th and 19th century and had a slight comeback in the 1890s before finally coming to an end in the early 20th century (Fig. 4B). Similarly, an important haddock fishery

around Helgoland that landed >2,000,000 fish in the late 18th century declined during the 19th and came to an end in the early 20th century (Lozan, 1990). Another important center for the coastal groundfishery was the island of Norderney, where about 900 t of haddock and cod were landed in the late 19th century, but landings declined towards 1900 and the fishery ceased in the early 20th century (Lozan, 1994). To replace former haddock and cod resources, fisheries for other groundfish were developed in the late 19th and early 20th century such as for dab (*Limanda limanda*) in Denmark and thornback ray and lesser-spotted dog-fish (*Scyliorhinus caniculus*) in the Netherlands (Fig. 4B, see also Fig. 3C). However, the fishery for dab only lasted until 1950 and that for ray and dogfish until the 1970s. Today, the only groundfish species caught in the Wadden Sea are plaice and sole as bycatch in the shrimp fishery (Dahl et al., 1994).

Fisheries for migrating and estuarine species became commercially important in the 19th century, and many of them peaked in the late 1890s such as the sturgeon and salmon fisheries in the Elbe and Ems rivers, and the shad (*Alosa alosa*) fishery in the Netherlands (Fig. 4C). However, overfishing, destruction and pollution of their river habitats led to the collapse and extinction of these species in most of their former habitat (Lozan, 1990). As a consequence, estuarine fisheries moved towards less valuable species such as flounder (*Platichthys flesus*), eel, and lampreys, but none of them lasted until the 1990s (Fig. 4C).

Among invertebrate fisheries, early records of a lobster fishery around Helgoland indicate a catch of 20,000 kg in 1615 (Fig. 4D). The fishery apparently fluctuated between 10,000 and 45,000 kg over the centuries until dropping <10,000 kg in the 1950s, <1000 kg in the 1970s, and <100 kg in the 1990s. The fishery for shrimp was important since the 17th century (Fig. 3C), but the catch level is not known. Towards the end of the 20th century, it was one of the last fisheries left in the Wadden Sea with annual catches between 9000 and 27,500 t (Fig. 4D). In the 20th century, fisheries also existed for seamoss (*Sertularia cupressina*), marketed as decorative items, and starfish (*Asterias rubens*), used for fertilizer production, but ceased because of declining markets (Fig. 4D, Lozan, 1994).

Among shellfish resources, the fishery for the European oyster (Ostrea edulis) was the earliest and most important one (Figs. 3C and 4E). The East Frisian oyster fishery produced between 46,000 and 306,800 oysters per year in the 18th century, but dropped to 20,000 in 1802, and declined further and finally ceased in the mid 19th century (Fig. 4E). The North Frisian oyster fishery produced 3,000,000 oysters in 1725, 4,600,000 in 1860, and peaked at 5,292,000 in 1869 (Fig. 4E). Then, the fishery fluctuated for a number of years between 100,000 and 1,000,000 but collapsed after 1925 as result of destructive fishing practices (Lotze, 2005). There was also an important oyster fishery in the Dutch Wadden Sea since about 1700 that shared a similar fate and came to an end by the early 20th century (Wolff, 2005). To replace native oyster resource, cultivation of the introduced Pacific oyster (Crassostrea gigas) started in the 1960–1970s and reached a production of >15,000,000 oysters annually by 1995 (Lotze, 2005). Other shellfish fisheries were developed in the late 19th century for the blue mussel, and the 20th century for whelks (Buccinum undatum), soft-



Fig. 5. Ecological consequences of human impacts in the Wadden Sea through time. (A) Decline of relative abundance in marine mammals, coastal birds, fish, invertebrates, and vegetation, and (B) percent of fisheries that became depleted, collapsed, or extinct (data extracted from a database described in Lotze et al., 2006).

shelled clam (*Mya arenaria*), cockles (Fig. 4E), as well as razor clams, *Spisula*, and periwinkles (Fig. 3C). Only the blue mussel and cockle fishery still existed at the end of the 20th century.

#### 3.5. Trends in resource abundance

Reconstruction of relative abundance trends in 77 species over the past 5000 years revealed strong declines in marine mammals, coastal birds, fish, invertebrates, and vegetation (Fig. 5A). In general, declines in birds started 2000 years ago and continued until 1900 or 1950, after which several species began to recover (Fig. 5A). For mammals, declines started about 1000 years ago and continued until today. Although marked recovery occurred among seal populations (Lotze, 2005), strong declines in small whales are masking this trend for the group of mammals. Declines in fish and invertebrates mainly occurred from 1800 until today, while vegetation experienced an early decline in 1000-1500, mainly driven by reclamation of wetlands, and another strong decline in 1900-1950. This second decline (Fig. 5A) was driven to some extend by large embankments and to another extent by the loss of eelgrass beds due to the wasting disease (Labyrinthula zosterae) in the 1930s from which the intertidal but not the subtidal beds recovered (De Jong et al., 1999). By the year 2000, none of the taxonomic groups and only 11.7% of the 77 species were still considered abundant, while 88.3% were depleted, of which 58.4% were rare and 20.8% extinct. On the positive side, conservation efforts enabled 18.2% of species to recover partially (to >10% of former abundance) and 3.9% substantially (to >50%).

Trends for 26 commercial fisheries resources in the database were available for 9 species of groundfish, 7 migrating fish, 3 pelagic fish, 3 crustaceans, and 4 shellfish species. Until 1500, no record indicated depletion (>50% decline from former abundance) of any of the resources considered (Fig. 5B). However by 1800, at least 12% or 3 of the resources were depleted, namely haddock, sturgeon, and oysters. By 1900, the ratio of depleted fisheries increased to 31% with 15% being collapsed, and by 1950, 65% of fisheries were depleted with 27% collapsed and 23% extinct (Fig. 5B). The extinct species included European sturgeon, Atlantic salmon, shad, sea trout (*Salmo trutta*), houting (*Coregonus oxyrhynchus*), and the European oyster. By 2000, 88% of the fisheries were depleted with 58% collapsed, and the only resources still considered abundant were shrimp, crabs, and smelt (*Osmerus eperlanus*).

# 4. Discussion

Since its origin  $\sim$ 7500 years, the Wadden Sea experienced a great rise and fall of fishing and marine resource use that almost ceased at the turn of the 21st century. Already 5000 years ago, Neolithic people were in transition from a subsistence huntergatherer way of life to permanent settlement, farming and fishing (Bantelmann, 2003; Knottnerus, 2005; Lotze et al., 2005). The archaeological record indicates an increasing importance of fish, especially marine fish (see also Enghoff, 2000, 2006a; Barrett et al., 2004), and a decreasing importance of wild marine and land mammals, coastal birds, and molluscs for coastal people until Modern Times (Figs. 2B and 3A, Prummel and Heinrich, 2005; Enghoff, 2006b). Thus, fishing appears to have gradually replaced hunting and gathering as a way to supplement food derived from agriculture. During the Middle Ages, another shift occurred when former subsistence or artisan fisheries were expanded and commercialized driven by the demand from people in the European inland where local freshwater and migrating fish stocks were depleted (Hoffmann, 2005). In Modern Times, commercial exploitation was intensified and coastal societies became integrated into the modern world economy (Lotze et al., 2005). During the 19th century increasing exploitation pressure and industrialization first led to peaks but then to declines in many coastal fisheries and resources. The 20th century witnessed many collapses and several extinctions of formerly important resources, and a shift towards formerly less-valued and smaller species (Pauly et al., 1998; Lotze, 2004). The use of marine mammals, coastal birds, and plants, which were important resources over centuries and millennia, came to an end in the 20th century except for some recreational bird hunting (Wolff, 2005). At the turn of the 21st century, there is no direct, full-time fishery for finfish left in the Wadden Sea (Dahl et al., 1994), but the fisheries for shrimp, blue mussels, and cockles are still viable. This could partly be due by a release from predation (Worm and Myers, 2003).

The reconstructed timelines for the Wadden Sea may illustrate the trajectories of fisheries and marine resource use worldwide. Throughout Europe, fisheries and marine resource uses were expanded and commercialized during the Middle Ages (Barrett et al., 2004; Hoffmann, 2005). In the Mediterranean Sea this had started during Roman Times 2500 years ago (Lotze et al., 2006), likely declined after the collapse of the Roman Empire and increased again in the Middle Ages. By the end of the Middle Ages, coastal ecosystems around Europe were highly exploited and commercial fisheries expanded to offshore regions in the North Sea and Iceland (Hoffmann, 2005) and commercial whaling to Spitsbergen, Greenland, and Newfoundland (Bryant, 1995). When Europeans colonized North America and Australia, similar timelines and trends of humaninduced changes occurred in just a few centuries (Lotze et al., 2006; Sáenz-Arroyo et al., 2006).

Whenever a valuable resource declined, people adopted similar management strategies (Lotze, 2004). They either expanded the fishery or resource use spatially (expanding the frontier), switched to a less valuable species often smaller and lower in the food chain (fishing down the food web), increased effort and efficiency (technological progress masking declines), or enhanced local food production through cultivation (aquaculture) (Lotze, 2004). From the Wadden Sea perspective, the sequential depletion of fisheries started in the European inland in the last 1000 years (Hoffmann, 2005), in the Wadden Sea in the last 500 years (this paper), in the North Sea (Jennings and Blanchard, 2004) and North Atlantic (Christensen et al., 2003) in the last 100 years, in the open ocean in the last 50 years (Myers and Worm, 2003; Worm et al., 2005), and finally reached the deep sea in the last 15 years (Pauly et al., 2003; Devine et al., 2006). With its history of species extinctions, fisheries collapses, and ecosystem degradation, the Wadden Sea may forecast what will happen to other regions of the ocean if we don't change the way we manage our fisheries and their supporting ecosystems. On the other hand, with its recoveries, the Wadden Sea may also serve as an example for how to turn the trends of depletion and degradation around.

While the rise of fisheries and marine resource uses throughout history was driven by cultural changes (consumption patterns, life style), economic changes (demand, market), or resource depletion, the fall of fisheries was mostly driven by population declines and in a few cases by ceasing markets. By the end of the 20th century, 88% of formerly common and important species were depleted with 58% being collapsed and 21% extinct (Fig. 5). The main drivers that caused or contributed to species extinctions in the Wadden Sea were habitat loss (70.2% of extinctions) and exploitation (54.4%) followed by pollution (8.8%), climate change (1.8%), and disease (1.8%) (Lotze et al., 2005). In comparison, a worldwide analysis identified exploitation as the main driver for species extinctions (96%) followed by habitat loss (42%) and pollution (9%) (Lotze et al., 2006). This discrepancy is likely the result of the focus on economically important species in the worldwide comparison and may highlight the great importance of habitat loss for the decline of non-commercial species. Moreover, in many cases more than one human impact was involved in recent extinctions. Similarly,

recovery was often achieved by reducing multiple sources of mortality (Lotze et al., 2006). These cumulative impacts of multiple human activities play a significant role in population and ecosystem changes and need to be addressed in management and conservation strategies.

#### 5. Conclusions

The rise and fall of fishing and marine resource use in the Wadden Sea indicates that this productive ecosystem sustained people for millennia but that high exploitation pressure, habitat destruction, and pollution greatly reduced its potential to provide diverse and productive resources for human use. However, the Wadden Sea ecosystem has not lost its potential for recovery as indicated by the increasing populations of many birds and seals. What can be learned from the reconstruction of the history of the Wadden Sea history is that (1) there is a finite endpoint in the sequential exploitation of marine resources, (2) negative trends can be turned around if protection and restoration are integrated into ecosystem-based management plans, and (3) the cumulative impacts of multiple human activities need to be managed together to prevent further declines and extinctions, but also to enhance the rate of recoveries.

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