



FIGURE. | *Humpback whale* (*Megaptera novaeangliae*). Photo: Pixabay.com

Marine mammals North Sea

U vindt een Nederlandse samenvatting aan het eind van de tekst.

KLAAS POST
NATURAL HISTORY MUSEUM
ROTTERDAM
WESTZEEDIJK 345
3015 AA ROTTERDAM
THE NETHERLANDS
KLAASPOST@FISHCON.NL

Over the last decades our knowledge of the origin and evolution of marine mammals has increased vastly. Most of the key mysteries, such as place and time of origin of seals (Pinnipedia) and whales (Cetacea), have been documented and solved. During the same period spectacular technical developments in molecular science have resulted in more reliable phylogenetic models and refined hereditary lines of most marine mammal lineages. Some of these recent discoveries and findings concerning key fossils have been published in eminent journals such as *Nature* and *Science*, which has caused the unravelling of these mysteries to attract an ever growing audience (for a summary see Berta (2017)). In recent years textbooks with more or less complete sequences of marine mammal evolution have started to appear (Thewissen, 2014; Marx *et al.*, 2016; Berta, 2017) - the first such sequences ever published.



Nonetheless, scientists still stumble in the dark regarding the faunas of a few specific geological eras, as fossils belonging to these periods are far out of reach in deep oceans and seas. The Late Pliocene to Early Pleistocene border (c. 2.6 Ma) and part of the Late Pleistocene (c. 100–20 Ka) are such fossil gaps (Tanaka & Fordyce, 2016). Both are particularly important eras because the ancestors of extant marine mammal faunas are thought to appear during the Late Pliocene and the Early Pleistocene, and extant taxa are expected to appear during the Late Pleistocene.

Thanks to the activities of the Dutch fishing fleet and the everlasting sand dredging operations commissioned by the Dutch government to create and maintain the beaches and dunes that protect the Low Countries from the high waters, the North Sea bottom is one of the best current sources of information on these mysterious faunas.

Late Pliocene/Early Pleistocene

Latest Pliocene/Early Pleistocene strata are present at the sea floor of at least two North Sea sites. One of them is known in detail, an area north of the Outer Gabbard (c. 52° 10'N – 2° 40'–50'E), while the other site combines several small spots in the Oosterschelde estuary off the Walcheren Coast (tidal channel 'Urk') (Fig. 1). Some geological and stratigraphically important information has been reported by Van der Feen (1968), Post & Bosselaers (2005) and Post & Kompanje (2010). Whether the marine mammals of these sites belong to one fauna or to several (timewise closely connected) faunas is not yet known.

Pinnipedia

The best-known marine mammal from the Late Pliocene/Early Pleistocene is the extinct walrus *Ontocetus emmonsii* Leidy, 1859. Fossils of this walrus are known from the Pliocene of East Coast USA, from the West Coast of North Africa, and from Belgium. The North Sea appears to be among its most recent habitats,

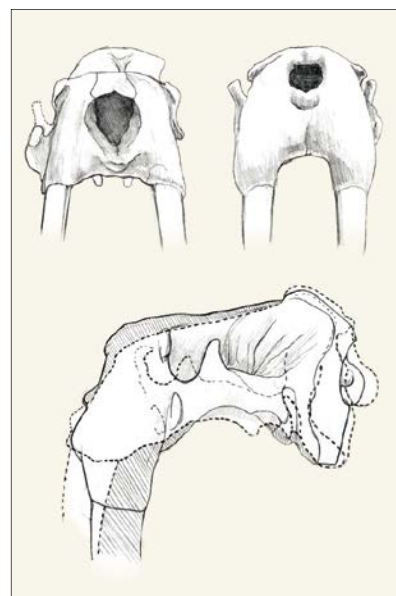


FIGURE 2. | Comparison of crania of *Odobenus rosmarus* (extant walrus) and *Ontocetus emmonsii*. (Kennis & Kennis)

and, with hundreds of cranial and postcranial fossils found, certainly the most productive (Bosscha Erdrink &

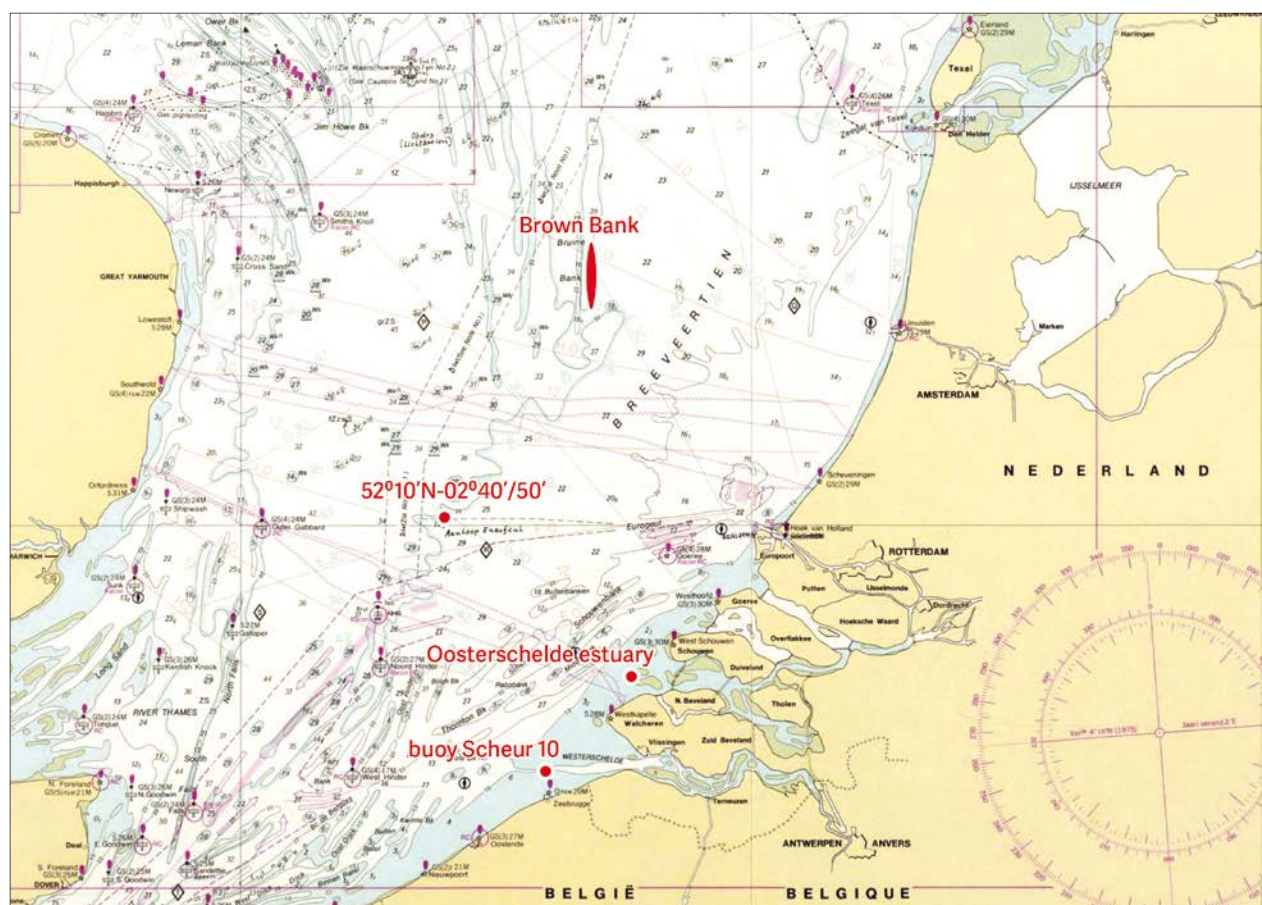


FIGURE 1. | Map of the southern North Sea with fossil sites: Brown Bank (1), 52°10'N-02°40'/50' (2), Oosterschelde estuary (3), buoy Scheur 10 (4).



Van Bree, 1990; Post, 2002b; Kohno & Ray, 2008). An almost complete cranium is curated in the Artis collection (in the historical ‘Groote Museum’). *Ontocetus* was more or less similar in size to the extant walrus, yet

morphologically strikingly different (Kohno & Ray, 2008) (Fig. 2). In addition to a more complicated dentition (possibly for a more piscivorous lifestyle), mandibular tusks, and a femur with a prominent third trochanter (implying more active movements of the hindlegs), this taxon shows extreme sexual dimorphism. Females are less than half the size of large (dominant) males, a feature as striking as in extant elephant seals.

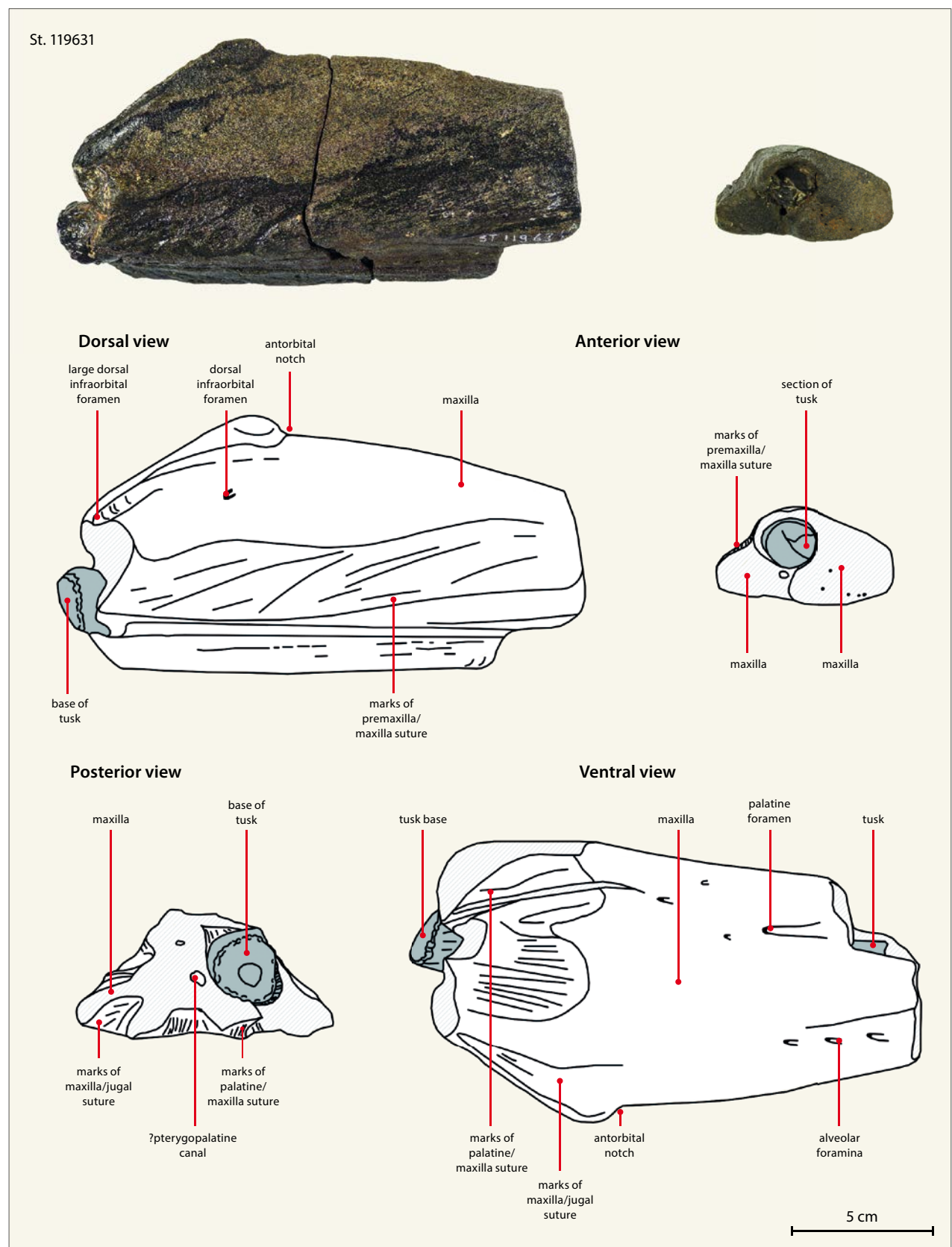


FIGURE 3. | Fragment of left maxilla with tusk of narwhal (*Monodon* sp.) (Naturalis Biodiversity Center, RGM 119631).



Fossils from seals are very rare and unfortunately taxonomically not specific. At least two different taxa may be recognised based on remains in the collection of the Natural History Museum Rotterdam; postcrania (humerus, femur) of one of them shows a resemblance to extant harp seal (*Phoca groenlandica* Erxleben, 1777).

Cetacea

Previous summaries of this fauna presumed that most genera were congeneric with extant genera (Post & Bosselaers, 2005). However recent finds of more completely preserved fossils indicate genera which are related to, but different from, extant genera.

Odontoceti

A rare and very large mandibular fragment identifies a very large beaked whale (Post & Bosselaers, 2017), while some postcrania suggest the presence of *Mesoplodon*-like sized beaked whales.

A narwhal similar to the extant narwhal (*Monodon monoceros* Linnaeus, 1758) is the only fossil proof of tusked monodontids known in the world (Post & Bosselaers, 2017) (Fig. 3). This fossil, together with some fossils in the British Museum (from the UK East Coast), is the object of ongoing studies. Several postcrania (humeri, radii, vertebrae – with distinctive atlas and axii) suggest that other monodontid beluga-like taxa may have been present.

One of the most spectacular dolphins is the aberrant pilot whale *Platalearostrum hoekmani* Post & Kompanje, 2010 (Fig. 4). Early finds of postcrania and some mandibular fragments had already indicated the presence of some pilot whale, until the discovery of a rostrum with alveoli of five teeth and an unusual morphology of the premaxilla allowed a detailed scientific description (Post & Kompanje, 2010). Distinctive mandible fragments and postcrania collected at shell piles in Yerseke (originally dredged from the North Sea for industrial purposes) belong to the extinct dolphin genus *Hemisyntrachelus* (Fig. 5), which is

related to the extant bottlenose dolphin *Tursiops truncatus* (Montagu, 1821) (Post & Bosselaers, 2005). Other postcrania (humeri and vertebrae) suggest the presence of a smaller dolphin cf. *Delphinus*, while some vertebrae show the typical *Lageorhynchus* morphology (high count of disk-like vertebrae).

Of special interest are fossils of a sperm whale and of a large orca-like killer whale. Both taxa are hotly debated among leading cetacean palaeontologists. Nothing is known about the predecessor of the large extant sperm whale (*Physeter macrocephalus* Linnaeus, 1758). The extant sperm whale is the single surviving genus of a lineage with an extremely taxon-rich Miocene past. Most were epipelagic raptors that suddenly vanished at the end of the Miocene/beginning of the Pliocene. Thereafter taxa and fossils are basically non-existent or very rare. The same holds true for the top predator of our oceans, the orca (*Orcinus orca* (Linnaeus, 1758)). When the largest mouth and teeth ever (the mighty sperm whale *Livyathan*) disappeared towards the end of the Miocene, a large dolphin



FIGURE 4. | Artist impression of *Platalearostrum hoekmani* (Remie Bakker).



must have taken the position at the top of the food chain. The question is which dolphin: an orca-like dolphin, the extant orca, or an as yet unidentified taxon? The Natural History Museum Rotterdam holds a large collection of fossils of these enigmatic 'missing links'. The most important

sperm whale fossil is a symphyseal part of a mandible (NMR999100000354). Although some alveoli are preserved, the fossil is taxonomically too limited to draw specific conclusions. The same holds true about the mysterious Pliocene/ Early Pleistocene orca. Over a hundred fossils are kept in Rotterdam, including several cranial parts, mandibular remnants, and important postcrania like humeri, radii and possibly ulnae. Although some fossils indicate a giant size (similar to or even larger than the maximum size of *O. orca*), alveoli indicate slender and longer teeth, and radii might indicate less rounded flippers, none of the known

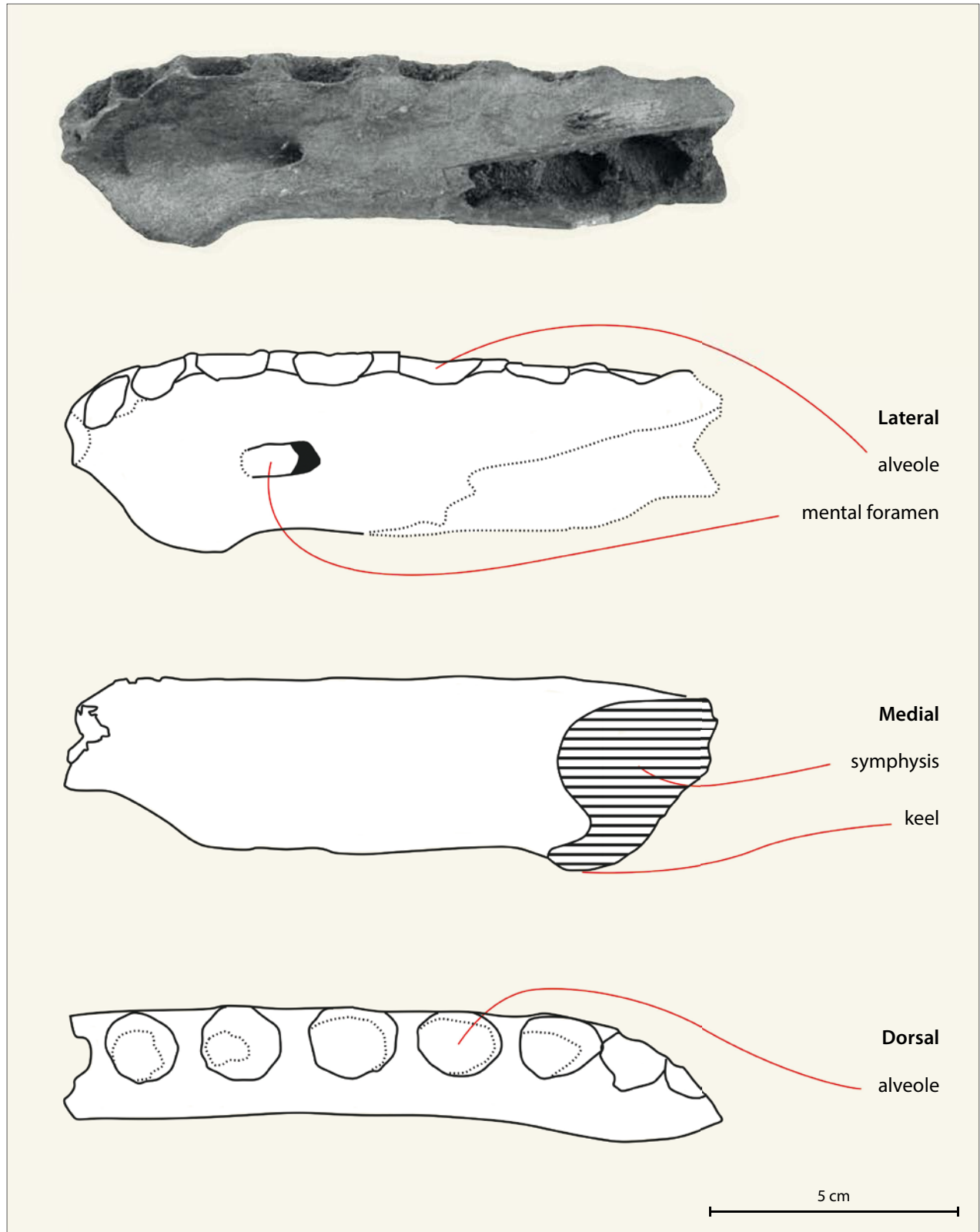


FIGURE 5. | Mandibular fossil of *Hemisyntrachelus* sp. (Natural History Museum Rotterdam, NMR999100001756).

fossils warrants a thorough scientific description and name. We will have to endure a tantalising wait until better preserved fossils are discovered.

Mysticeti

Lots of postcrania (especially vertebrae) and some partial crania (ear bones, vertex fragments) of mysticetes have been identified. However none of them can be considered to be of taxonomical value. At least one large whale taxon (cf. *Eubalaena*) is represented by several complete huge humeri, radii and ulnae. One or two taxa of large rorquals (cf. *Balaenoptera*) seem present as well.

Late Pleistocene

The North Sea has yielded thousands of fossils of a Late Pleistocene subarctic marine mammal fauna (Post, 2005) – and obligingly continues to do so. Remains of the fauna are found in scattered sites over vast areas of the Southern Bight of the North Sea west and south of the Bruine Bank (Brown Bank) (Fig. 1). The dating of this fauna is still disputed: ^{14}C data indicate 35–50 Ka (reaching to or even beyond the detection threshold, for a summary see Post & Brand (2016)). However the extremely low sea levels of these periods strongly contest these results. Recent research presumes a contamination of Carbon in some marine contexts and therefore casts are doubt on these ^{14}C datings. A Late Eemian to 70 Ka origin has now been proposed for these fossils (Hijma *et al.*, 2012; Busschers *et al.*, 2014).

Pinnipedia

Dutch collections of fossil walrus (*Odobenus rosmarus* (Linnaeus, 1758)) are the largest in the world and are the subject of numerous publications (Rutten, 1907; Van Deinse, 1943, 1944; Bosscha Erdbrink & Van Bree, 1986, 1990, 1999a,b,c; Post, 1994, 1999, 2005; Van Bree & Post, 1994; Post & Van Bree, 1996). More than a thousand postcrania and over one hundred cranial fossils (amongst them complete crania with dentition) are preserved in Dutch museums. Find sites are scattered throughout the southern North Sea and an extremely rich site called “Het Scheur” is located near the Belgian coast (Fig. 1). This southern-most site delivers fossils of all ontogenetic age groups (Post *et al.*, 2017), and might be related to a Late Eemian island location (De Clercq *et al.*, 2018).

Though harp seal is represented by thousands of postcrania, only approximately ten crania (with partial dentition) and a few mandibles have been reported (Post, 2000, 2005). It is obvious that the fragile crania of seals do not survive traditional collection methods (i.e. fishing or sand dredging activities) as well as the massive crania of walrus. Comparison of humeri and femora proves that the Late Pleistocene harp seal of the North Sea was significantly smaller than the extant species (Visser, 2004).

Fossils of bearded seal (*Erignatus barbatus* (Erxleben, 1777)) and ringed seal (*Phoca hispida* Schreber, 1775) are noted in small numbers and cranial remains are

extremely rare (Van Bree & Erdbrink, 1987; Post, 2000; Post & Brand, 2016).

Grey seal (*Halichoerus grypus* (Fabricius, 1791)) fossils have traditionally been dated to the Holocene (Post, 2005). Recent datings however have established some of these fossils to be (much) older (pers. com. Dick Mol). Whether this grey seal was part of the subarctic marine mammal fauna or might have been part of a more temperate period has not (yet) been resolved.

A recent spectacular find from one of the Dutch beaches is the partial mandible of a monk seal (*Monachus monachus* (Hermann, 1779)) which has been ^{14}C dated to c. 29 Ka (Mol & Langeveld, 2017) (Fig. 6). Obviously such a ‘warm’ seal does not fit well with the above-mentioned subarctic marine mammal fauna. Either there must have been a short warm interval just before the arctic conditions of the Last Glacial Maximum commenced, or this particular seal was a vagrant which lost its way into northern waters.

Cetacea

Odontoceti

A spectacular representative – and the only odontocete – of this fauna is the beluga (*Delphinapterus leucas* (Pallas, 1776)) (Post & Kompanje, 1995; Post, 2005). Hundreds of fossils allow reconstruction of more or less complete skeletons and faunal scenes (Fig. 7).

Mysticeti

The most abundant mysticete is the gray whale (*Eschrichtius robustus* (Lilljeborg, 1861)) which presently roams the North Pacific (Van Deinse & Junge, 1937) (Fig. 8). Studies based on the Atlantic gray whale fossils have established that several invasions from the Pacific Ocean to the Atlantic Ocean occurred during the Pleistocene via the northern passage (when this route was open). All Atlantic populations eventually died out due to limited genetic variety (Alter *et al.*, 2015). A number of rare fossils (some postcrania and a few cranial fragments) of bowhead whale (*Balaena mysticetus* Linnaeus, 1758), fin whale (*Balaenoptera physalus* (Linnaeus, 1758)) and blue whale (*Balaenoptera musculus* (Linnaeus, 1758)) have been noted, often identified by DNA, which is well preserved in most of the fossils of this fauna (Foote *et al.*, 2013a). A large



FIGURE 6. | Mandible of monk seal (*Monachus monachus*) (Nico Vermeer).



atlas which shows gnawing marks of hyena is the single fossil proof of blue whale (Post, 2005). These teeth marks corroborate the Late Pleistocene occurrence of this mighty whale.

Most of the members of this fauna (walrus, seals, beluga, gray whale, bowhead whale) indicate coastal shallow icy waters and/or shallow estuaries. However, fin whale and blue whale indicate that the North Sea was connected with open oceans which allowed large carcasses to beach.

Early Holocene

The start of the Holocene in the North Sea has been dominated by the submergence of the English Channel between the United Kingdom and France. This allowed taxa which had sheltered in more temperate southern waters during the Last Glacial Maximum to enter (or re-enter) the North Sea. Sites are scattered throughout the Southern Bight of the North Sea west and south of the Brown Bank (Fig. 1).

Pinnipedia

Staggering numbers of Early Holocene grey seal fossils have been found, especially postcrania (Post, 2005). But – surprisingly – not a single fossil of harbour seal (*Phoca vitulina* Linnaeus,

1758) has been reported – at least until modern times. In fact the harbour seal might have entered the Dutch fauna only fairly recently. The appearance in 16th and 17th century paintings and engravings of fish merchants showing their merchandise is its first ‘fossil’ sign of life in The Netherlands (‘t Hart, 2007).

Cetacea

Odontoceti

The most common fossil taxon is the bottlenose dolphin (*Tursiops truncatus*) of which numerous fossils have been found. ¹⁴C data indicate a return at the Dutch coastlines around 8000 BP (Kompanje & Post, 2017). Predation by white sharks has been noted (Schouten, 2017) and the evidence of a strange atlas suggests possible crossbreeding with other dolphins (Post, 2002a). Fossils of other odontocetes have been found but are not common. Amongst them are orca, common dolphin (*Delphinus delphis* Linnaeus, 1758), whiteside or white beaked dolphin (*Lageorhynchus* spp.), and the harbour porpoise (*Phocoena phocoena* (Linnaeus, 1758)) (Foote *et al.*, 2013b). Only few fossils have been dated and these are not older than c. 3000 BP.

Mysticeti

The gray whale was still present in the Early Holocene North Sea and this species is in fact the only cetacean which lived in the North Sea shortly before and after the Last Glacial Maximum. The youngest dated specimens from Dutch collections and sites are from (near) Roman times (Fig. 8). Rare fossils of other myticetes such as northern right whale, bowhead whale, and fin whale have been noted (Foote *et al.*, 2013a).

Samenvatting

Ondanks dat er de afgelopen twintig jaar wereldwijd door sensationele vondsten, voortschrijdende DNA-technieken en talloze publicaties steeds meer bekend is geworden over het ontstaan en de evolutie van zeezoogdieren, tasten wetenschappers nog steeds in het duister voor wat betreft de zeezoogdierfauna's van de Plio-Pleistoceen grens (ca. 2,6 miljoen jaar geleden) en uit het Weichselien (ca. 118.000–11.600 jaar geleden). Juist die fauna's kunnen ons iets vertellen over het hoe en waarom van de nu nog levende zeezoogdieren en juist die fauna's



FIGURE 7. | Reconstruction of Late Pleistocene coastal scene with beluga (*Delphinapterus leucas*) (Remie Bakker).





FIGURE 8. | *Atlas of gray whale (Eschrichtius robustus)*
(Natural History Museum Rotterdam, NMR99910003223).

liggen wereldwijd vaak verborgen onder tientallen meters zeewater. Maar er zijn uitzonderingen. Dankzij een op bodemvissoorten gespecialiseerde vissersvloot, de zich steeds repeterende zandsuppleties op onze stranden en vooral door talloze speurende strandzoekers, blijken juist in Nederland fossielen uit deze mysterieuze fauna's in groten getale te worden gevonden.

Van de grens van het Plio-Pleistoceen treffen we talrijke fossielen van een enorme uitgestorven walrus (*Ontocetus emmonsii*) aan die qua morfologie erg verschilt van de recente walrus. Dat beest kon bijvoorbeeld – en in tegenstelling tot de logge recente walrus – de achterpoten (vinnen) nog actief op land gebruiken. Heel spaarzaam treffen we ook fossielen van tenminste twee verschillende zeehonden aan, waarvan er een waarschijnlijk veel leek op de recente zadelrob (*Phoca groenlandica*). Helaas ontbreken schedels (of delen daarvan) die een determinatie op soort – of zelfs de beschrijving van een nog onbekende soort – rechtvaardigen. Datzelfde geldt voor de walvisachtigen uit deze fauna; hoewel we veel fossielen kennen van een grote echte walvis (die op de Groenlandse walvis moet hebben geleken) en van meerdere grote soorten vinvissen, dolfinen, spitsnuitdolfijnen en beloega's blijken deze soms enorme wervels, of delen van vinnen of schedelfragmenten bijna allemaal niet soort- of genusspecifiek. Ook de vele fossielen van de onbekende voorvaders van de potvis en de orka – fossiele soorten waar paleontologen van dromen en die veel kunnen betekenen voor het begrijpen van de evolutie van deze enigmatische beesten – kunnen door gebrek aan goede schedelfossielen nog niet beschreven worden. En zelfs het enige ter wereld bekende fossiel van een stukje schedel van een voorloper van de narwal met het deel van de stoottand er nog in, rust nog naamloos in een doosje in de collectie van Naturalis. Een uitzondering vormt het unieke fossiel van *Platalearostrum hoekmani*, een uitgestorven voorvader van de recente griend. De unieke kenmerken van dit fragment van de bovenkaak rechtvaardigden een naam en een reconstructie en bewijzen daarnaast dat soorten uit deze fauna, ondanks overeenkomsten, toch sterk verschillen van hun huidige verwanten.

Voor wat betreft fossielen uit het late Pleistoceen is Nederland een eldorado. De Nederlandse collecties behoren tot de meest uitgebreide ter wereld en worden regelmatig voor wetenschappelijk onderzoek gebruikt, vooral omdat veel van deze fossielen nog bruikbaar DNA bevatten. Voor wat betreft de datering is er wel discussie omdat er bij zeezoogdieren (in tegenstelling tot de fossielen van landzoogdieren) verontreiniging van koolstof blijkt op te treden die de ^{14}C -datering kan beïnvloeden. Doorgaans wordt 80.000–70.000 jaar als datering van deze

fauna aangenomen, met daarnaast mogelijk betrouwbare dateringen van enkele soorten rond 30.000–28.000 jaar. Nederlandse instituten herbergen duizenden fossielen van walrus (*Odobenus rosmarus*), baardrob (*Erignathus barbatus*), grijze zeehond (*Halichoerus grypus*), gewone zeehond (*Phoca vitulina*), ringelrob (*Phoca hispida*) en zadelrob. Daarnaast zijn er fossielen van blauwe vinvis (*Balaenoptera musculus* – een atlas die door hyena's afgekauwd werd), gewone vinvis (*Balaenoptera physalus*), grijze walvis (*Eschrichtius robustus*), Groenlandse walvis (*Balaena mysticetus*), orka (*Orcinus orca*), griend (*Globicephala melaena*) en meerdere kleinere dolfinen. De walrus heeft hier met enorme kolonies geleefd en we vinden fossielen van jonge en oude exemplaren. Ook de enorme aantallen fossielen van beloega's (*Delphinapterus leucas*) zijn het vermelden waard; kennelijk brachten die toen hun zomerreces in onze streken door.

Uitzonderlijk is de enigmatische strandvondst van een kaak van de monniksrob (*Monachus monachus*) met een ^{14}C -datering van 29.000 jaar. Dat is het enige pleistocene fossiel ter wereld van deze doorgaans warmere wateren prefererende zeehond.

Tot slot herbergde ons land een (vroeg-) holocene fauna (ca. 10.000 jaar oud tot nu) die met name gekenmerkt wordt door grote aantallen fossielen van grijze walvis en van tuimelaar (*Tursiops truncatus*). We weten door tientallen nauwkeurige ^{14}C -dateringen dat de grijze walvis nog tot na de Romeinse tijd regelmatig aan onze kusten voorkwam. De preferentie voor ondiep water (bijvoorbeeld de vondsten uit de Wieringermeer) impliceren dat deze walvis onze wateren op dezelfde manier waardeerde als de Californische baaien waar de nog levende Pacifische evenknie jaarlijks de jongen werpt. De tuimelaar komt massaal voor na de doorbraak van Het Kanaal (ca. 8000 v. Chr.), maar is heden ten dage in onze wateren niet meer algemeen. Fossielen van dolfinen als orka, griend, gewone dolfin (*Delphinus delphis*) en bruinvis (*Phocoena phocoena*) worden ook regelmatig gevonden. De vinvoetigen zijn daarentegen niet meer zo soortenrijk als in het late Pleistoceen en beperken zich tot de vertegenwoordigers die we nu nog kennen: de gewone zeehond en de grijze zeehond.

