The Pliocene locality Balgoy (province of Gelderland, The Netherlands) and a new record of the great white shark, *Carcharodon carcharias* (Linnaeus, 1758)

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The stratigraphy and geological context of the Balgoy locality (municipality of Wijchen, The Netherlands) is documented. In this subaqueous sandpit, fossiliferous Pliocene sands of the Oosterhout Formation are exposed, overlain by Quaternary sands and gravels. A tooth of the great white shark *Carcharodon carcharias* (Linnaeus, 1758) found in sediments extracted from the Balgoy site is described. It originates from the Oosterhout Formation (late Zanclean to early Piacenzian age, *c.* 3-4 Ma) and is the first record of fossil *C. carcharias* in stratigraphic context from the Netherlands. An overview of the fossil record of *C. carcharias* in the northeastern Atlantic is provided and the occurrence of great white sharks in the Pliocene of the southern North Sea Basin is discussed. Due to the warm temperate waters, the existence of a wide continental shelf with favourable water depths and the availability of prey, the Pliocene North Sea was apparently an attractive place to live for great white sharks.

Key words: *Carcharodon carcharias*, Pliocene, Oosterhout Formation, Balgoy, North Sea Basin

Introduction

The Balgoy locality is an artificial lake, formed as a result of subaqueous extraction of sands and gravels by suction dredging in the floodplain of the river Maas, locally called Loonse Uiterwaard, in the municipality of Wijchen in the southeastern part of the Netherlands (Figs 1, 3). The recent find of a tooth of the great white shark *Carcharodon carcharias* (Linnaeus, 1758) in sediments extracted from the Balgoy site was the reason to portray the stratigraphy and geological context of this little known Pliocene locality. There are few documented records of *in situ* occurrences of *C. carcharias* teeth in the North Sea Basin and the Balgoy specimen is the first record of fossil *C. carcharias* in stratigraphic context from the Netherlands. We provide an overview of the fossil record of *C. carcharias* in the North Sea Basin and northeastern Atlantic. The occurrence of *C. carcharias* in the Pliocene of the southern North Sea Basin is discussed and its presence can be explained by the same environmental factors that determine the present-day distribution of great white sharks.

Geological setting

The Balgoy locality (Fig. 1) is situated in the southeastern part of the Netherlands, on the southern fringe of the North Sea Basin, in the Roer Valley Rift System. Since the Oligocene, tectonic activity has increased in this region, both because of the Alpine orogeny and the accelerated widening of the northern Atlantic. The main tectonic structures in the study area (Figs 1, 2) are the Roer Valley Graben, an area of strong subsidence, and the Peel Block and the Venlo Block, which are areas of intermediate subsidence. The Peel Boundary Fault is the northeastern border of the Roer Valley Graben. The Venlo Block and Peel Block are seperated by the Tegelen Fault and the Venlo Block is slowly subsiding relative to the Peel Block. For details on the tectonic developments of the Roer Valley Rift System, we refer to *e.g.* Geluk *et al.* (1994), Houtgast & van Balen (2000), Michon *et al.* (2003) and van Balen *et al.* (2005).

Marine deposition predominated in the Netherlands during the Neogene. Tectonic activity resulted in differentiation in facies and sedimentation during parts of the Neogene and influenced the position of the coastline. During the early late Miocene (Tortonian), the assumed coastline was some 70 km to the SSE of Balgoy; during the early Pliocene (Zanclean), the coastline was probably situated about 20 km to the southeast (Zagwijn & Hager, 1987, fig. 2). General regression started during the late Pliocene and retreat of marine conditions coincided with progradation of fluvial systems. For details on the Quaternary evolution of this region, we refer to *e.g.* van Balen

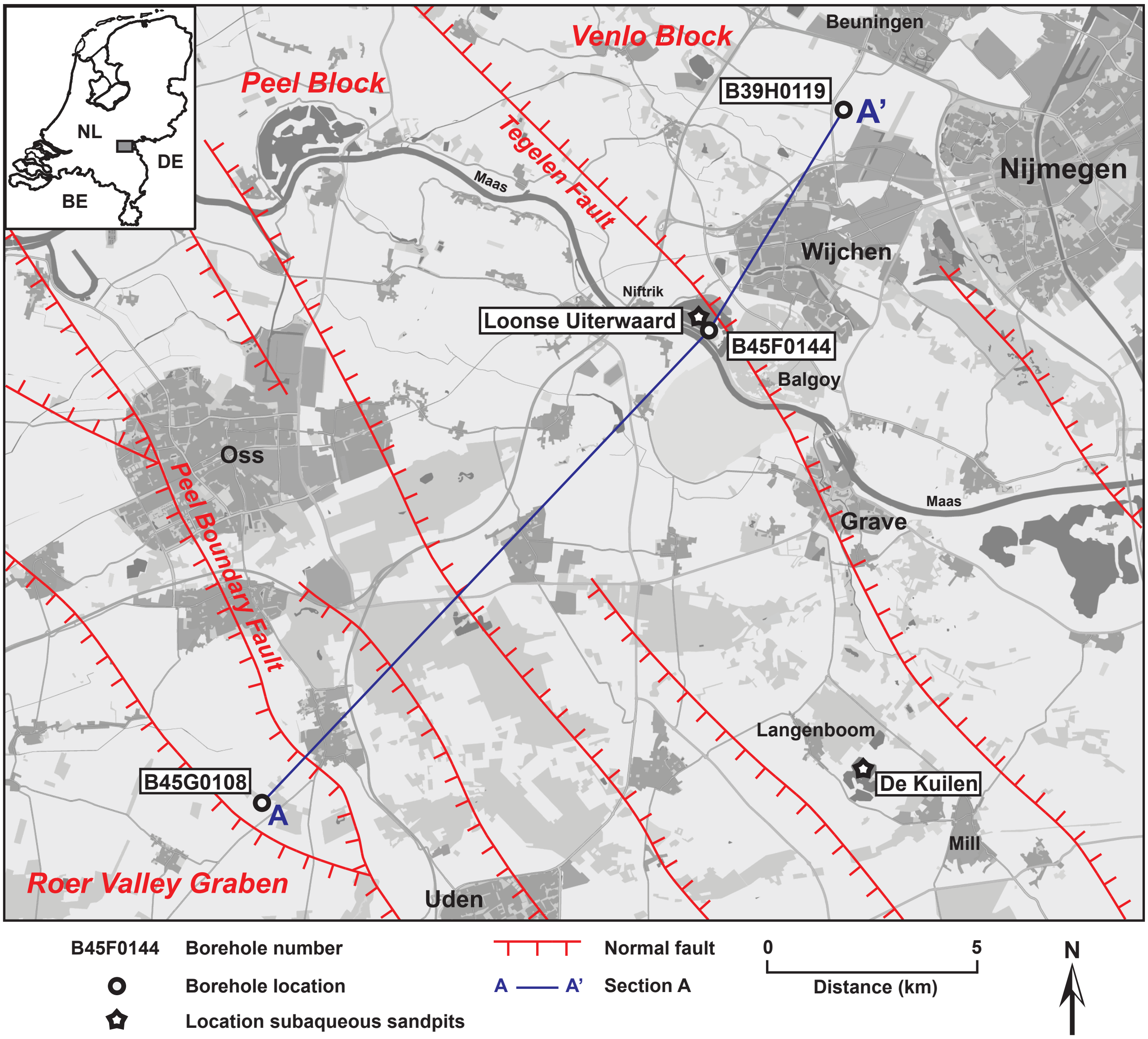

Figure 1. Map showing the location of the Balgoy site (Loonse Uiterwaard) in context with main regional tectonic structures. Indicated is cross-section A presented in Fig. 2, and the locations of the nearby Langenboom site (De Kuilen) and boreholes mentioned in the text. Map data: Google, customised with Google Styled Maps API. Location of tectonic structures after DGM v2.2 (Digital Geological Model, available at https://www.dinoloket.nl/ondergrondgegevens).

et al. (2000), Cohen *et al.* (2002), Berendsen (2005) and Busschers *et al.* (2007).

The Balgoy locality

The Balgoy site is an artificial lake in the floodplain of the river Maas, locally called Loonse Uiterwaard (Fig. 3), halfway between the villages of Balgoy (favoured local spelling; spelled Balgoij according to official government standards) and Niftrik in the municipality of Wijchen, The Netherlands (WGS84 coordinates 51.794426, 5.692118). The lake was formed between 1984 and 2008 due to subaqueous mining by suction dredging of sands and gravels for the construction industry by the Delgromij company. Dredging in the Loonse Uiterwaard reached depths of about 30 metres below water level (Peters & Wesselingh, 2009). After termination of the mining activities, the banks of the lake were restored and cultivated. Since 2000 the junior author has been regularly collecting fossils from the suction dredged sediments used to restore the banks of the lake, resulting in the finding of the *Carcharodon carcharias* tooth on the 24th of January 2015.
The Balgoy site is located on top of the Tegelen Fault, which runs in a NW-SE direction (orientation N135) through the Loonse Uiterwaard (Figs 1, 3). The southwestern and largest part of the locality is situated on an uplifted fault block that forms part of the Peel Block, whereas the northeastern part of the site is located on the relatively subsided Venlo Block. The Peel Boundary Fault is about 12.5 km to the southwest of the site.
Borehole B45F0144 (Fig. 3; WGS84 coordinates 51.79129,

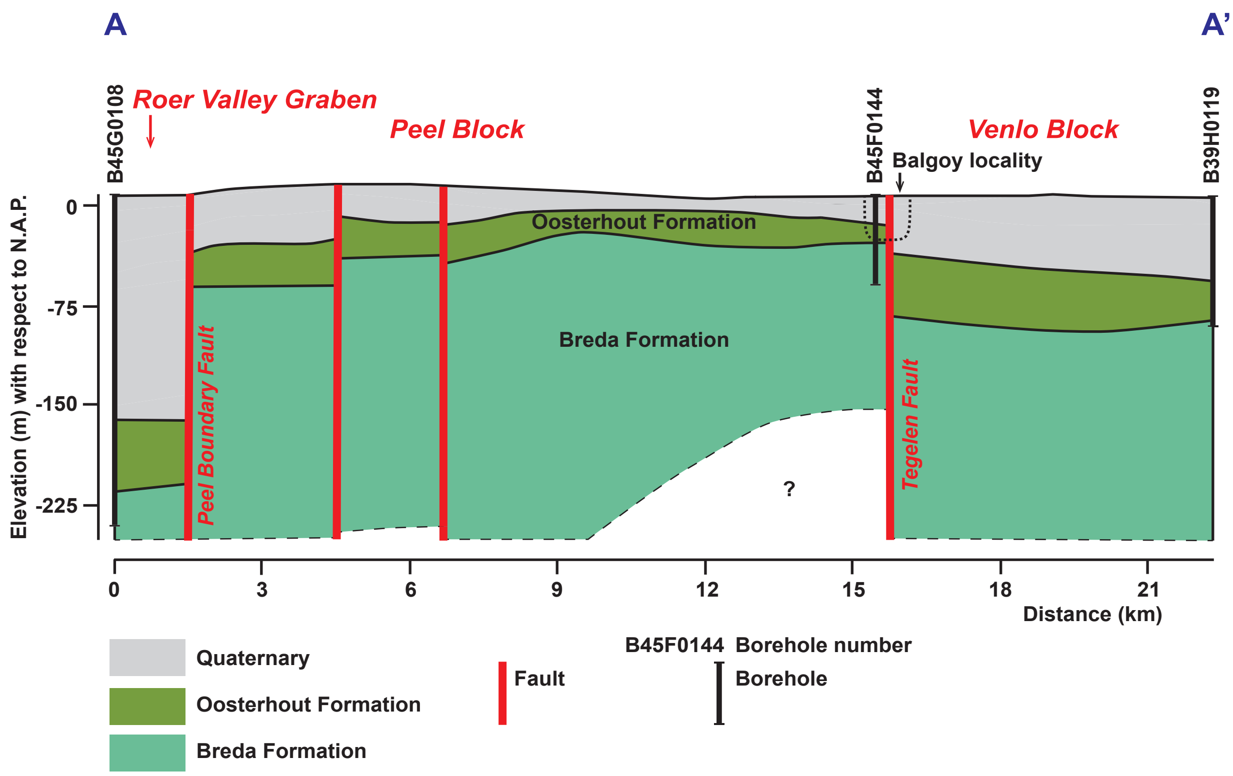

Figure 2. Schematic section A from southwest to northeast across the Balgoy locality, as indicated in Fig. 1. Source: DGM v2.2 (Digital Geological Model, available at https://www.dinoloket.nl/ondergrondgegevens).

5.69449; description see Appendix 1), is located approximately 220 m southwest from the Tegelen Fault and elucidates the stratigraphy on the Peel Block site of the locality (Fig. 4). From the surface to a depth of 21.6 m, light yellowish-grey silts, reddish-brown and light yellowish-grey medium and coarse grained sands and gravels are assigned to successively the Echteld, Kreftenheye, Beegden and Waalre formations (fluvial Holocene and Pleistocene deposits). From 21.6 to 35.0 m below surface, grey, predominantly moderately fine sands with mollusc shells, with a lag deposit of mollusc shells and bone fragments at the base, represent the Oosterhout Formation (marine Pliocene deposits). From 35.0 m below surface to the final depth of 70.0 m, moderately fine sands, dark green and strongly glauconitic in the upper part, grey with much mica in the lower part, are assigned to the Breda Formation (marine Miocene deposits). For stratigraphic details see Weerts & Busschers (2003; Echteld Fm.), Busschers & Weerts (2003; Kreftenheye Fm.), Westerhoff & Weerts (2003a; Beegden Fm.), Westerhoff & Weerts (2003b; Waalre Fm.), Ebbing & de Lang (2003; Oosterhout Fm.) and Westerhoff (2003; Breda Fm.).

Unfortunately there is no deep borehole available in the Loonse Uiterwaard just north of the Tegelen Fault. In borehole B39H0119 (Fig. 1; WGS84 coordinates 51.83830, 5.73918), about 6 km northeast of the Loonse Uiterwaard, the base of the Quaternary deposits is at 59 m below surface, underlain by the Oosterhout Formation from 59 to 100 m below surface, and the Breda Formation is present from 100 m below surface to the final depth of 250 m

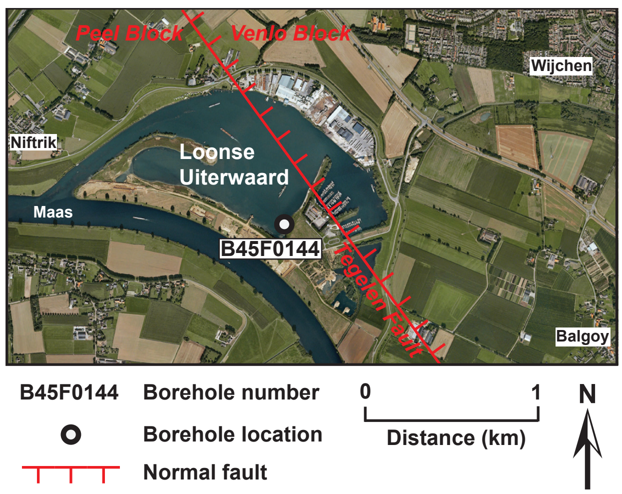

Figure 3. Aerial photo of the surroundings of the Balgoy locality. Indicated are the locations of the Loonse Uiterwaard, borehole B45F0144 (Appendix 1) and tectonic structures. Google Earth, image Aerodata International Surveys, imagery date 1/1/2005.

(Fig. 2). According to DGM v2.2 (Digital Geological Model of the Dutch subsurface, available at https://www.dinoloket.nl/ondergrondmodellen) is in the Loonse Uiterwaard at a given point 220 m northeast of the Tegelen Fault (WGS84 coordinates 51.79358, 5.70012), the base of the Quaternary deposits at a depth of *c.* 41 m and the

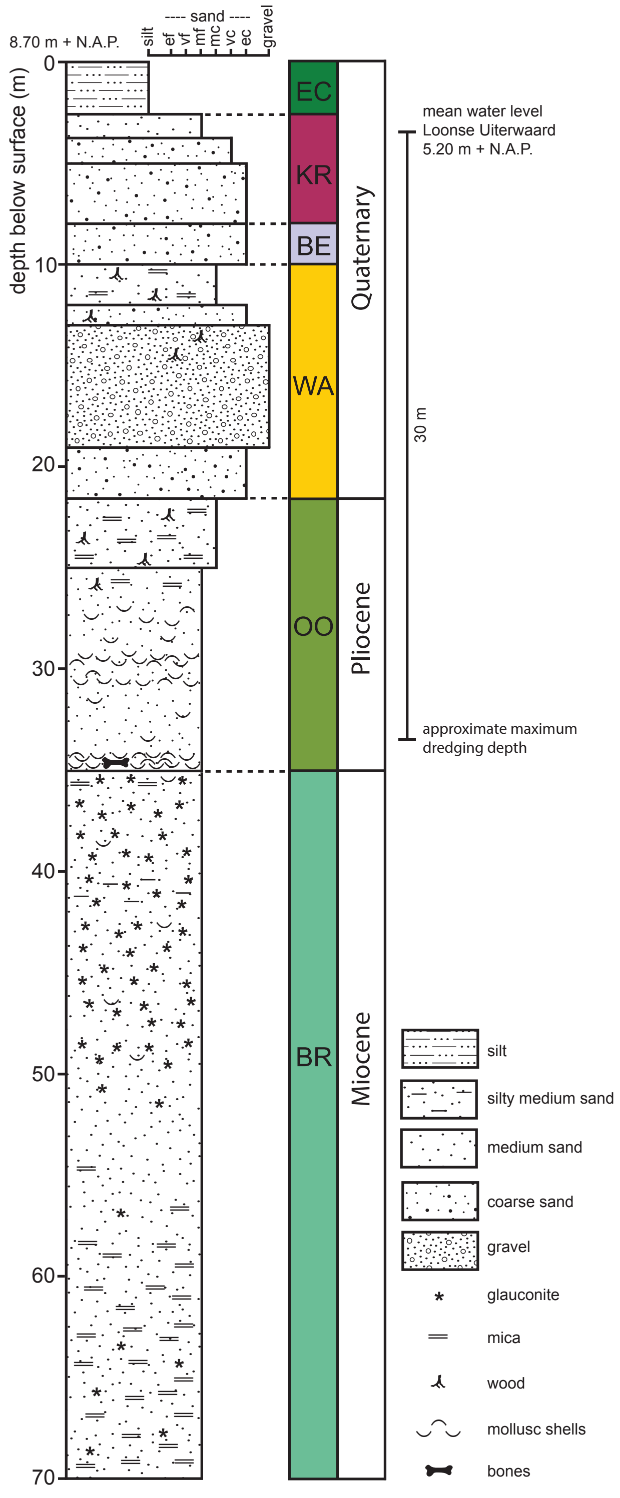

Figure 4. Lithology and stratigraphy of borehole B45F0144 (detailed description see Appendix 1). Source: Boorstaat TNO-Geological Survey of the Netherlands. Lithostratigraphical codes and colours according to DGM v2.2 (Digital Geological Model of the Dutch subsurface) standards, revised stratigraphic scheme since 2003: EC = Echteld Formation, KR = Kreftenheye Formation, BE = Beegden Formation, WA = Waalre Formation, OO = Oosterhout Formation, BR = Breda Formation. Abbreviations for the sand classes: ef = extremely fine; vf = very fine; mf = moderately fine; mc = moderately coarse; vc = very coarse; ec = extremely coarse.

base of the Oosterhout Formation at *c.* 87 m below surface. Hence in the Loonse Uiterwaard the Tegelen Fault's vertical throw for the base of the Quaternary is about 23 m and for the base of the Oosterhout Formation approximately 56 m, *i.e.* throw is increasing with depth which points to synsedimentary fault activity.

Dredging in the Loonse Uiterwaard reached depths of about 30 metres (Peters & Wesselingh, 2009). As the mean water level is approximately at 5.20 m + N.A.P. (reference water level Rijkswaterstaat for the Maas at Grave Beneden), the subaqueous extraction of gravels and sands presumably did not reach the base of the Oosterhout Formation (Fig. 4).

In a preliminary study, Peters & Wesselingh (2009) reported on a Pliocene mollusc fauna collected from the Balgoy site as float or from medium grained, reddish coloured sandstones. This mollusc fauna is dominated by a number of species and species-rich groups like *Varicorbula gibba* (Olivi, 1792) and several *Astarte*, *Ensis*, *Turritella*, *Hinia* and *Natica* species. Scaphopods are also rather common and presented by several species. Characteristic early Pliocene indicators in this mollusc fauna are *Palliolum gerardi* (Nyst, 1835), *Pygocardia rustica* (Sowerby, 1818) forma *solida* and forma *tumida*, *Astarte corbuloides corbuloides* de la Jonkaire, 1823 and *Euspira cirriformis gottschei* (Kautsky, 1925). Important is the absence of typical late Pliocene morphologies of *Pygocardia rustica* (Sowerby, 1818), forma *rustica* and forma *extensa*, and *Cerastoderma parkinsoni* (Wood, 1853). Combined with the presence of Pacific immigrant species like *Mya truncata* Linnaeus, 1758, *Mya arenaria* Linnaeus, 1758, *Mytilus antiquorum* Sowerby, 1821, *Macoma obliqua* (Sowerby, 1817) and *Neptunea angulata* Harmer, 1914 *s.s.*, this indicates a middle Zanclean to early Piacenzian age for this mollusc fauna. The faunal composition and articulated bivalves point to nearshore, rather shallow settings, between fair-weather (typically 5-15m) and storm wave-base (typically 15-40 m).

In addition to the above mentioned fauna, sediment blocks with a lithified yellowish grey sandstone matrix and a benthic macrofauna dominated by the lingulid brachiopod *Glottidia dumortieri* (Nyst, 1845) and the serpulid *Ditrupa arietina* (Müller, 1776) were collected at Balgoy and studied by Wesselingh *et al.* (2013). A common lithology is that of fossiliferous, well-sorted, fine-grained, yellowish grey, cemented quartzarenites. Mollusc taxa found in most blocks include the bivalves *Atrina fragilis* (Pennant, 1777) *s.l.* and *Varicorbula gibba* (Olivi, 1792), and the gastropod *Calyptraea chinensis* (Linnaeus, 1758). The presence of the gastropod *Nassarius spectabilis vandewouweri* (Glibert, 1959) coupled with the absence of the bivalve *Palliolum gerardi* (Nyst, 1835) suggests an early to middle Piacenzian age for these sediment blocks. Dinoflagellate cyst associations from these sediment blocks indicate a late Zanclean to (early) Piacenzian age. Wesselingh *et al.* (2013) conclude that these lingulid bearing calcareous quartzarenites must have been deposited under open marine, clear water conditions around storm wave-base (typically 15-40 m).

Over 330 fossil elasmobranch remains were collected

from the Balgoy site (collection W.J.M. Peters). Some specimens have cemented quartzarenite matrix containing dispersed shell fragments attached (typical for the Oosterhout Formation). The material is dominated by more then 200 bucklers of the thornback ray *Raja clavata* Linnaeus, 1758; the remainder of the material consists largely of lamnid (a.o. *Carcharodon* [= *Cosmopolitodus*] *hastalis* (Agassiz, 1838) and *Lamna nasus* (Bonnaterre, 1788)), odontaspidid (*Carcharias*) and hexanchid (*Hexanchus griseus* (Bonnaterre, 1788) and *Notorynchus cepedianus* (Péron, 1807)) teeth. The vast majority of this material shows dark colours, polished surfaces, blunt cutting edges, damaged roots and/or heavy mineralised dentine, which indicates reworking from older deposits. Only a few specimens are likely contemporaneous with deposition of the Oosterhout Formation. This includes a tooth of *Carcharodon carcharias*, which is subject of this study, and a few teeth belonging to *C. hastalis* and *H. griseus*.
Pliocene crabs from this locality were studied by Fraaije *et al.* (2007) and van Bakel *et al.* (2009). Yet other unpublished finds include remains of *e.g.* marine mammals, boney fishes and birds (collection W.J.M. Peters).
A lag deposit of mollusc shells and bone fragments is present at the base of the Oosterhout Formation in the Loonse Uiterwaard (borehole B45F0144, 34-35 m below surface, see Appenix 1). In several sediment blocks collected at Balgoy differential preservation of mollusc shells and some bone material are observed. These blocks may come from the basal or an intraformational lag, as lag deposits typically contain an admixture of both well preserved and abraded fossils. The Balgoy locality is situated only 11.4 km northwest of locality De Kuilen at Langenboom (Fig. 1; WGS84 coordinates 51.697218, 5.746803), also known as Mill. In this subaqueous sandpit, the Oosterhout Formation, overlain by Quaternary sands and gravels, and the top levels of the underlying Breda Formation were exposed (Wijnker *et al.*, 2008). Both localities are situated on the same uplifted fault block that forms part of the Peel Block and have comparable Neogene stratigraphic successions. In Langenboom, the basal lag of the Oosterhout Formation was dated early Zanclean based on dinoflagellate cyst associations (Wijnker *et al.*, 2008) and we assume that the basal lag of the Oosterhout Formation in the Balgoy locality has a similar age.

Systematic palaeontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Lamniformes Berg, 1958
Family Lamnidae Bonaparte, 1835
Genus *Carcharodon* Smith *in* Müller & Henle, 1838

Type species – *Squalus carcharias* Linnaeus, 1758, by subsequent monotypy through *Carcharias lamia* Rafinesque-Schmaltz, 1810 (International Commission on Zoological Nomenclature, 1965, Opinion 723).

***Carcharodon carcharias* (Linnaeus, 1758)**
Figure 5a-f

Selected references for Recent occurrences (Δ = teeth illustrated);

*1758	*Squalus carcharias* Linnaeus, p. 235.
1839	*Carcharodon Rondeletii* Müller & Henle, p. 70.
1947	*Carcharodon rondeletii* M. u. H. - Landolt, p. 336, fig. 22. (Δ)
1975	*Carcharodon carcharias* (Linnaeus, 1758) - Bass *et al.*, p. 22, figs 10-12, pl. 8. (Δ)
1996	*Carcharodon carcharias* - Hubbell, p. 9-18, figs 2-9. (Δ)
1996	*Carcharodon carcharias* (Linnaeus, 1758) - Applegate & Espinosa-Arrubarrena, p. 32, figs 3-4, 6. (Δ)
2005	*Carcharodon carcharias* (Linnaeus, 1758) - Martin *et al.*, p. 1126, 1131, fig. 2a-b. (Δ)
2012	*Carcharodon carcharias* - Cappetta, p. 214, fig. 200. (Δ)

References for Pliocene northeastern Atlantic occurrences:

1889	*Carcharodon rondeletii*, Müller & Henle - Woodward, p. 420.
1891	*Carcharodon Rondeleti* Müller & Henle - Newton, p. 104, pl. 9, figs 14-15.
1926	*Carcharodon Rondeleti*, Müller & Henle, 1841 - Leriche, p. 422, pl. 33, figs 9-12, pl. 34, figs 1-9.
1985	*Carcharodon carcharias* (Linné 1758) - in ‘t Hout, p. 137, fig. 20.
1986	*Carcharodon carcharias* (Linnaeus, 1758) - Nolf, p. 168, pl. 58, figs 1-4.
1987	*Carcharodon carcharias* - Ottema & in ‘t Hout, p. 84, 3 figs.
1988	*Carcharodon carcharias* (Linnaeus, 1758) - Nolf, p. 168, pl. 58, figs 1-4.
1995	*Carcharodon carcharias* - Vervoenen, p. 83, fig. 150, front cover.
2010	*Carcharodon carcharias* (Linné 1758) - Antunes & Balbino, p, 3, fig. 1.

Material examined – A singe left third upper anterior tooth (collection W.J.M. Peters, Balgoy, The Netherlands).

Locality – Balgoy, Loonse Uiterwaard, municipality of Wijchen, province of Gelderland, The Netherlands; Gravel beach at the lakeside of the embankment along the marina (WGS84 coordinates 51.793477, 5.696823) originating from suction dredged sediments.

Lithostratigraphy – Oosterhout Formation, based on the lithology of cemented quartzarenite matrix containing dispersed shell fragments that is attached to the root of the tooth. This type of sediment, according to data presented above and by Wesselingh *et al.* (2013, compare their fig. 2), most likely derived from levels between 28.0

Figure 5. Left 3rd upper anterior tooth of *Carcharodon carcharias* (Linnaeus, 1758). Balgoy, Loonse Uiterwaard, municipality of Wijchen, The Netherlands. Oosterhout Formation (Pliocene, late Zanclean to early Piacenzian). Collection W.J.M. Peters, Balgoy, The Netherlands. Scale bar equals 10 mm; a: lingual view, b: labial view, c: distal view, d: apical view, e: basal view, f: mesial view.

and 34.0 m below surface (Fig. 4; Appendix 1).

Age – Pliocene, late Zanclean to early Piacenzian, *c.* 3-4 Ma (Wesselingh *et al.*, 2013).

Measurements – Total height of the tooth (perpendicular to the crown base) 34.2 mm, crown height 26.8 mm, crown width 28.9+ mm, distal crown edge length 31.8 mm, mesial crown edge length 29.1+ mm and slant angle -6.0° (for methods see Hubbell, 1996, p. 10).

Description – The mesial-most part of the tooth is incomplete; a chip of 1-2 mm affecting both crown and root broke off. Apart from this, the tooth is well preserved. The crown is multicoloured, showing many shades of grey, brown and yellow, and has a triangular shape, a little wider than high, with a slightly mesially directed apex. Lateral cusplets are absent. As a whole, the tooth is rather flat and moderate in thickness. The lingual crown face is slightly convex with a medial flattening; the labial face is rather flat. Both surfaces are entirely smooth, but in oblique lighting some faint folds are visible in the basal parts. In labio-lingual view (Figs 5a-b), both cutting edges are slightly sigmoidal, concave in the lower half and convex in the upper half of the crown, converging towards the pointed apex. In profile, the distal cutting edge is nearly straight (Fig. 5c), in contrast to the mesial cutting edge which shows a clear labial curvature (Fig. 5f), creating a labially directed twist of the crown in apical view (Fig. 5d). Both cutting edges are serrated, with irregularly shaped and sized, blunt serrations separated by deep notches and directed at right angles to the crown edges. These serrations are more coarsely developed in the median part of the cutting edges; the number of serrations per millimetre is *c.* 0.8 in the median part and *c.* 1.4 in the basal and apical parts. There is small damage with loss of enamel matter on the mesial cutting edge near the apex, and both cutting edges show some damaged serrations. In labial and lingual views, the root-crown junction presents a concave outline. A distinct neck is lacking. The larger part of the root is hidden by matrix. The parts that are visible are dark brown coloured and not well-preserved. The surface layers of the root are abraded (probably due to bioerosion prior to fossilisation) and obscure its original outline. The root is moderate in height, the lobes are wide, not well individualised and do not extend beyond the crown extremities. The mesial root lobe is hardly visible, the distal root lobe is rounded and flattened.

Identification – Teeth of *Carcharodon carcharias* can easily be separated from those of *Otodus* [= *Carcharocles* or *Megaselachus*] *megalodon* (Agassiz, 1835) by the labio-lingually flattened crown, rather large and irregular serrations on the cutting edges, and the absence of a well marked chevron shaped neck (enameloid free band at the crown-root junction) on the lingual crown face. The serrations of *C. carcharias* and *O. megalodon* are very different, with *C. carcharias* exhibiting coarse and irregular serrations while those of *O. megalodon* are very fine and regular. However, occasionally *O. megalodon* teeth show a somewhat coarser serration that could be misleading (compare Ehret *et al.*, 2012, fig. 3).

Tooth position – Based on data presented by *e.g.* Hubbell (1996) and Applegate & Espinosa-Arrubarrena (1996) we consider the Balgoy tooth to represent a third upper anterior tooth [compare *e.g.* Bass *et al.* (1975, pl. 8), Hubbell (1996, fig. 2), Applegate & Espinosa-Arrubarrena (1996, fig. 6) and Martin *et al.* (2005, fig. 2b)]. Third upper anterior teeth of *Carcharodon* are often incorrectly named upper intermediate teeth by authors (Siverson, 1999).

Estimation of total body length – Figure 6 shows the relationship of crown height (CH) of the 3rd upper anterior tooth and total body length (TL) in 32 Recent great white shark specimens, spanning 1.25-5.94 m in TL, with data compiled from Hubbell (1996, table 1) and Shimada (2003, appendix 1). The equation of the regression line for this dataset was calculated in Microsoft Excel using XLSTAT: $y = 15.973x + 22.247$, where x is CH in mm and y is TL in cm ($R^2 = 0.927$). Using the CH of 26.8 mm for the Balgoy tooth in this equation, we can estimate that the tooth was shed by a great white shark with a TL of around 450 cm; Probably a young adult animal, as modern male great white sharks mature between 3.5 and 4.1 m TL and females between 4 and 5 m TL (Compagno, 2001).

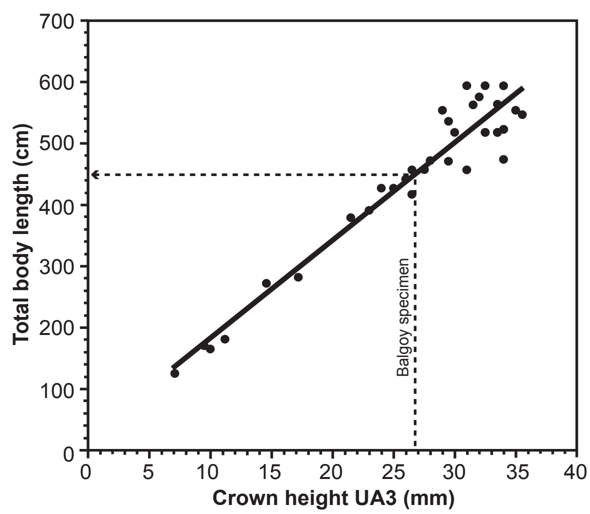

Figure 6. Relationship of the 3rd upper anterior tooth (UA3) crown height (CH) and total body length (TL) in 32 extant specimens of *Carcharodon carcharias*. Data compiled from Hubbell (1996: table 1) and Shimada (2003: appendix 1).

Stratigraphic range – The evolutionary origin of *Carcharodon carcharias* was revised and elucidated recently by Ehret *et al.* (2012). The species evolved during the latest Miocene (Messinian) in the Pacific Ocean, through *Carcharodon hubbelli* Ehret *et al.*, 2012, from *Carcharodon* [= *Cosmopolitodus*] *hastalis* (Agassiz, 1838). The dentition of the *Carcharodon* lineage shows a gradual and rapid morphological transition from the ancestral non-serrated *C. hastalis*, through the semi-serrated *C.*

hubbelli, to the fully serrated *C. carcharias*. The *Carcharodon hastalis-hubbelli-carcharias* transition is well documented from latest Miocene to earliest Pliocene deposits in *e.g.* Peru (Ehret *et al*., 2012) and California (Long *et al*., 2014). In Peru, recalibration of the absolute dates suggests that *C. hubbelli* is *c.* 6-8 Ma in age (Ehret *et al*., 2012). In California, the entire *C. hastalis* to *C. carcharias* evolutionary transition occurred within a 6.9-5.3 Ma time span (Long *et al*., 2014). *Carcharodon carcharias* is abundant only since the Pliocene and its geographic distribution becomes very wide. Miocene occurrences of *C. carcharias* are very doubtful and probably the result of erroneous labelling or misidentification (Cappetta, 2012). For example, a tooth with somewhat coarse serrations from the middle Miocene Calvert Formation in Maryland (USA), published by Gottfried & Fordyce (2001, p. 738, fig. 7) as an example that the fossil record of *C. carcharias* extends back to *c.* 16 Ma, is in fact a small *Otodus megalodon* tooth, based on the presence of a chevron shaped neck and the thickness of the crown (Ehret *et al*., 2012, p. 1143, fig. 3).

Fossil record of *Carcharodon carcharias* in the North Sea Basin and northeastern Atlantic

The Netherlands, Zeeland and Zuid-Holland provinces

Fossilised teeth of *Carcharodon carcharias* have incidentally been found on the beaches in the provinces of Zeeland and Zuid-Holland in the Netherlands, *e.g.* at Cadzand (Verschueren, 1998), De Kaloot (van Nieulande, 2001), Rockanje (Janse, 2005) and Maasvlakte 1 (Janse, 2004, 2005). These teeth reveal differential preservation and are washed ashore together with numerous molluscs of presumed Pliocene and/or Pleistocene age. Obviously a stratigraphic context is lacking for this material.

Kattenwinkel (2009) reported on a very well preserved, yellow brownish coloured *Carcharodon carcharias* tooth found between shell material of Holocene or Pleistocene age dredged from the Steenbanken, a North Sea shallow approximately 12 km northwest off the Walcheren coast. A comparably preserved tooth was found near Ouddorp, where sand from the Bollen van Goeree, another shallow *c.* 12 km northwest off the coast of Goeree, was used for beach nourishment. Because these very well preserved, yellow brownish coloured *C. carcharias* teeth are not at all associated with Pliocene shells and show a preservation that is very different from specimens of presumed Pliocene age, Kattenwinkel assumed a Pleistocene, possibly Eemian (*c.* 126-118 ka), age for these specimens.

The Netherlands, Noord-Brabant province

In the subaqueous sandpit De Kuilen at Langenboom (also known as Mill), the Oosterhout Formation and the uppermost part of the underlying Breda Formation were exposed (Wijnker *et al*., 2008). The stratigraphic succession at Langenboom is comparable to that in Balgoy and in spite of the fact that fossil collecting in Langenboom was far more intensive, it is surprising that *Carcharodon carcharias* is apparently absent in Langenboom (Peters, 2013).

Belgium, Antwerpen area

For the Pliocene succession of the Antwerpen area (Fig. 7) we follow Vandenberghe *et al.* (1998), Louwye *et al.* (2004), De Schepper (2006) and De Schepper *et al.* (2009).

Leriche (1926) illustrated 13 teeth of *Carcharodon carcharias* (as *C. rondeleti*) from the Antwerpen area, two from the 'Scaldisien' and the others unfortunately without any provenance data. Leriche reported the species from the 'Anversien' in Antwerpen and Burght, the 'Assise à *Isocardia cor*' of the 'Diestien' in Antwerpen and the 'Scaldisien' in the Amerikadok ('bassin America'), the Eerste, Tweede and Derde Havendok ('darses n^{os} 1, 2, 3'), and the Van Cauwelaertsluis ('écluse du Kruisschans') near Antwerpen. The deposits Leriche indicated with 'Anversien' are nowadays called the Berchem Formation, which is in the Antwerpen area subdivided in the Edegem, Kiel and Antwerpen members (Laga *et al*., 2006). However, extensive fossil collecting in the Berchem Formation in recent decades never revealed any *C. carcharias* teeth. The Berchem Formation is early to middle Miocene in age (Louwye *et al*., 2000), which predates the supposed origin of *C. carcharias* by roughly 10 Ma. Hence, Leriche's account on the presence of *C. carcharias* in the 'Anversien' is considered erroneous. The 'Diestien' as used by Leriche includes the Diest and Kattendijk formations, and the 'Assise à *Isocardia cor*' is now the Kattendijk Formation (Laga *et al*., 2006). The lithologic units Leriche indicated with 'Scaldisien' are now called the Lillo Formation, subdivided in the Luchtbal, Oorderen, Kruisschans and Merksem members (Laga *et al*., 2006). Nolf (1986, 1988) figured four *C. carcharias* teeth from the Pliocene in the Antwerpen area illustrated earlier by Leriche (1926), without any provenance data, and does not refer to additional material.

In 't Hout (1985) documented the quite rare *in situ* occurrence of large, well preserved blue *Carcharodon carcharias* teeth in the middle and upper parts of the Kattendijk Formation of the Vrasenedok ('4de Havendok') at Kallo. He explicitly mentioned that the species was not found in the basal gravels of the Kattendijk Formation at Kallo. Ottema & in 't Hout (1987, p. 79, 84) reported on the presence of *C. carcharias* in the Kattendijk Formation and Oorderen Member, and its absence in the post-Miocene basal gravel, in the Vrasenedok at Kallo. Two illustrated teeth were borrowed from in 't Hout (1985). Vervoenen (1995) illustrated a *C. carcharias* tooth from the Oorderen Sands, Vrasenedok, Kallo.

De Ceuster (private collection; pers. comm. 2015) collected a *Carcharodon carcharias* tooth from the upper part of the Kattendijk Formation in the Vrasenedok at Kallo. In De Schutter's private collection (pers. comm. 2015) a *C. carcharias* tooth is present from the Katten-

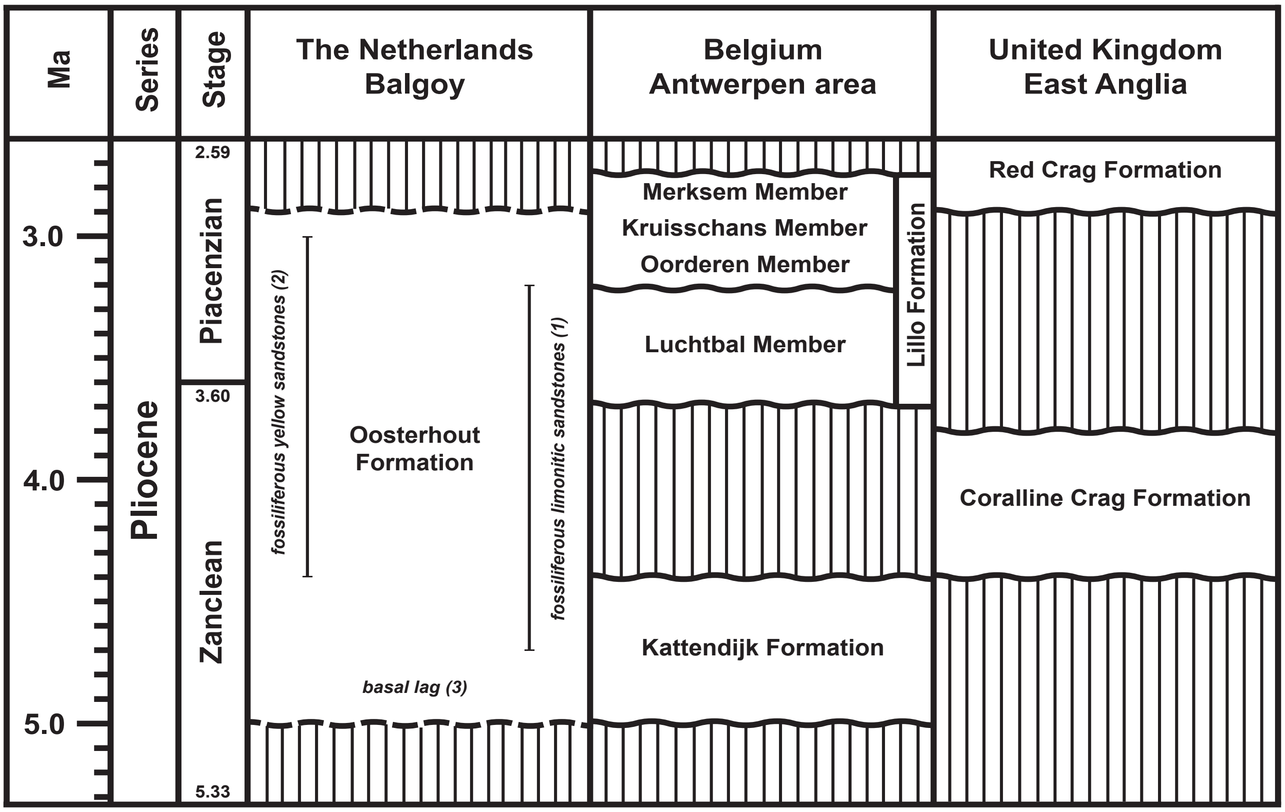

Figure 7. Stratigraphic framework for Pliocene successions in the southern North Sea Basin discussed herein. The Balgoy succession is based on (1) Peters & Wesselingh (2009) and (2) Wesselingh *et al.* (2013), the age of the basal lag (3) is extrapolated from the nearby locality De Kuilen at Langenboom (Wijnker *et al.*, 2008). The successions for Belgium and England are adapted from De Schepper *et al.* (2009). Hiatuses are indicated with vertical parallel lines.

dijk Formation in the Kallosluis-Beverentunnel at Kallo (Geological Survey Belgium section 27E204, -9.75 m DNG). De Schutter and Van Den Eeckhaut (pers. comm. 2015) collected 9 teeth of *C. carcharias* from the Oorderen Member during excavation of the Deurganckdok at Doel, the Verrebroekdok at Kallo and the Doeldok at Kieldrecht.

An excellently preserved specimen of *Carcharodon carcharias* was collected from reworked Pliocene Lillo Formation sediments overlying Miocene Antwerpen Sands in temporary exposure De Veldekens at Berchem (P.J. De Schutter collection). Four teeth were collected from reworked Pliocene deposits in a Pleistocene riverbed at Borgerhout (J. De Ceuster collection) and some specimens from reworked Pliocene deposits exposed in the Kruibeke and Tielrode quarries (*e.g.* G. Cleemput and D. Rosenbaum collections).

Frequently teeth of *Carcharodon carcharias* have been found *ex situ* in relocated and mixed Neogene sands extracted from the Antwerpen harbour area, often of uncertain provenance, *e.g.* at dumping sites near the town of Hoevenen, in the former Graandok and the 3M area near Zwijndrecht. Some tens of specimens are present in private collections (*e.g.* G. Cleemput, P.J. De Schutter, G. Marchand, D. Rosenbaum, J. Van Boeckel and G. Van Den Eeckhaut collections). Van Boeckel (pers. comm. 2015) collected two very well preserved *ex situ* teeth of *C. carcharias* at Grobbendonk, in relocated Pliocene sands (possibly Oorderen Member) from the construction of a waiting dock for barges in Wijnegem.

It is noteworthy that all *in situ* as well as *ex situ* and reworked specimens from the Kattendijk and Lillo formations were probably shed by (sub-)adult animals (TL > 3 m), judging from the CH/TL relationship for extant great white sharks in Hubbell (1996) and Shimada (2003).

Records of *C. carcharias* from pre-Pliocene deposits in the Antwerpen area must be refuted.

In the Pliocene, *Carcharodon carcharias* teeth occur rarely in the middle and upper part of the Kattendijk Formation and more frequently in the Oorderen Member of the Lillo Formation. Both the Kattendijk Formation and Oorderen Member represent warm temperate conditions, with the exception of a brief cooling event within the latter (De Schepper *et al.*, 2009). Deposition depths are estimated at 45-55 m and 35-45 m respectively, based on bivalves (Marquet, 2004). There are no reports of *C. carcharias* teeth from the Luchtbal, Kruisschans and Merksem members of the Lillo Formation, which represent cooler conditions (De Schepper *et al.*, 2009).

United Kingdom, East Anglia

Woodward (1889) documented that teeth of *Carcharodon* *carcharias* (as *C. rondeletii*) from the English Pliocene are housed in the British Museum (Natural History): a tooth with a scarcely abraded crown from the Coralline Crag of Orford, Suffolk, and 17 abraded teeth from the Suffolk Red Crag. Newton (1891), likely referring to the same specimens as Woodward (1889), reported on a well preserved tooth of *C. carcharias* (as *C. rondeleti*) from the Coralline Crag of Orford, Suffolk that is housed in the British Museum, but added that the Nodule Bed below the Suffolk Red Crag yielded by far the greater number of the specimens (two specimens from the Red Crag Nodule Bed at Boyton and Suffolk are illustrated by Newton). These specimens from the Nodule Bed, a basal lag of the Red Crag, are likely reworked from older deposits.

United Kingdom, Scotland

A fossilised *Carcharodon carcharias* tooth was found enmeshed in the rope of a creel hauled up from the seabed at a depth of 150 m in waters off Gairloch, on the west coast of Scotland (Underwood, 2012). The grey colour of the tooth suggests an age of hundreds to millions of years old. Based on the geological context, Underwood supposed that a Holocene age is most likely.

Portugal, Centro

Antunes & Balbino (2010) documented the occurrence of a single *Carcharodon carcharias* tooth from Pliocene sediments (dated latest Zanclean to early Piazencian on mollusc and calcareous nannoplankton evidence) at Matos, near Marinha Grande, Portugal. This is the only Pliocene record of *C. carcharias* from the Atlantic shores of southern Europe.

Discussion

The present-day western North Atlantic Ocean is a centre of relative abundance of great white sharks, where they range from the north coast of Newfoundland (51°N) to the British Virgin Islands (18°N). Curtis *et al.* (2014) analysed 649 confirmed records over the period 1800 to 2010 and concluded that sea surface temperature (SST) appears to exert a significant influence on the distribution of great white sharks, more important than prey availability. Great white sharks have a relatively narrow preferred SST of *c.* 14-23° C, which largely defines the boundaries of their latitudinal movements (Casey & Pratt Jr, 1985; Cliff *et al.*, 1989; Curtis *et al.*, 2014). The seasonal north-south migration of the great white shark population along the Atlantic coast of North America, allows them to remain within their preferred SST range. Great white sharks were predominantly encountered over continental shelf waters. The median reported occurrence depth was 30 m, 26 m for juvenile and 50 m for mature sharks.

On the contrary, in the present eastern North Atlantic Ocean *Carcharodon carcharias* is a rare species (Ferguson, 1996, and references therein). Either sizable or persistent populations are apparently absent. Most of the few available records are from oceanic islands, particularly the Azorean archipelago, but also from the Cape Verde, Madeira and Canary archipelagos, where these sharks are incidental visitors. There are only a few records from continental waters of the eastern North Atlantic: Senegal, Western Sahara, Morocco, Portugal and France. The present-day northernmost record of a great white shark in the eastern North Atlantic is from La Rochelle (46°N), Bay of Biscay, France (Quero *et al.*, 1995). There are no verified reports of great white sharks in waters off the United Kingdom or in the North Sea, where SSTs are most likely too low.

During the early Pliocene mean SSTs were up to *c.* 6° C higher in the eastern North Atlantic Ocean compared to present-day values (Lawrence *et al.*, 2009). From the beginning of the late Pliocene, North Atlantic mean SST declined gradually reaching temperatures comparable to present-day values at the major global glaciation event MIS M2 at *c.* 3.3 Ma (Lawrence *et al.*, 2009; Naafs *et al.*, 2010). Warmer climate conditions restored during the following so-called mid-Piacenzian Warm Period (previously named mid-Pliocene Warm Period, 3.29-2.97 Ma), when North Atlantic mean SSTs were *c.* 3 °C higher than at present (Lawrence *et al.*, 2009; Naafs *et al.*, 2010; De Schepper *et al.*, 2013). Towards the Pliocene-Pleistocene transition, sea-surface waters again gradually cooled further. Based on ostracods, Wood *et al.* (1993, figs 14, 15) estimated for the Coralline Crag Formation and Waltonian Crag Member of the Red Crag Formation in East Anglia summer sea temperatures *at depth* of 14-18 °C and winter sea temperatures *at depth* of 9-12 °C. Dinocyst assemblages from the Kattendijk and Lillo formations indicate that during the Pliocene the SST was generally higher in the southern North Sea Basin than it is at present (De Schepper, 2006, p. 261): Summer SST (August) was usually above 20.6 °C and occasionally lower; winter SST (February) was between 11.5 °C and 16.8 °C. This implies that the Pliocene SST of the southern North Sea was within the preferred SST range of *c.*14-23 °C of living great white sharks.

Present-day great white shark nursery regions have been identified along continents where larger areas of shelf habitat exist, *e.g.* between the coasts of New Jersey and Massachusetts (USA) in the western North Atlantic (Casey & Pratt, 1985; Curtis *et al.*, 2014), and the waters of southern California (USA) and Baja California (Mexico) in the eastern Pacific (Weng *et al.*, 2007; Domeier & Nasby-Lucas, 2013). In the Pliocene, the relatively warm and wide North Sea shelf might have been acting as a nursery region where young-of-the-year and juvenile great white sharks would have access to a wide variety of demersal and pelagic fishes for prey. However, teeth of juvenile great white sharks (TL < 3 m) are apparently lacking in collections from the Pliocene of the southern North Sea Basin. Perhaps this is collecting bias, but more likely is that juveniles were living in other shallower near-shore waters, as geographical size segregation is a characteristic of extant great white sharks (Casey & Pratt, 1985;

Klimley, 1985; Weng *et al*., 2007).
Larger great white sharks (TL > 3 m) tend to preferentially feed on marine mammals including pinnipeds, small cetaceans, and large whale carcasses (Tricas & McCosker, 1984; Cliff *et al*., 1989). In the Kattendijk and Lillo Formation deposits frequently remnants of marine mammals (whales, dolphins, porpoises and seals) have been found (Ottema & in 't Hout, 1987; Lambert & Gigase, 2007; Lambert, 2008). Marine mammal remains were also found at the Balgoy locality, some with cemented quartzarenite typical for the Oosterhout Formation, inclusive of skeletal elements of the walrus *Ontocetus emmonsi* Leidy, 1859 (collection W.J.M. Peters; identification K. Post). Hence, in the Pliocene southern North Sea was probably sufficient prey available.
Reconstructions of northwest European palaeogeography during the Pliocene proposed in literature generally do not postulate a direct southern connection between the North Sea Basin and the Atlantic Ocean (*e.g.* Zagwijn & Doppert, 1978; Torsvik *et al*., 2002; Meulenkamp & Sissingh, 2003). During the late Miocene and the first part of the early Pliocene the Dover Strait was closed, but there is stratigraphical and palaeontological evidence that it was flooded from *c.* 4.4 Ma until *c.* 1.8 Ma (late Zanclean, Piazencian and Gelasian) and then closed again until *c.* 160 ka (Meijer & Preece, 1995; Funnell, 1996; Vliet-Lanoë *et al*., 1998, 2002, 2010). A southern connection between the North Sea Basin and the North Atlantic could be used by great white sharks to migrate into the North Sea Basin. However, as this passage was relatively shallow and narrow (Vliet-Lanoë *et al*., 2002, fig. 3), it is more likely that *Carcharodon carcharias* arrived through the northern route in the North Sea. This is corroborated by the presence of *C. carcharias* in the southern North Sea Basin (Kattendijk Formation; *c*. 5.0-4.4 Ma) prior to the supposed opening of the Dover Strait at c. 4.4 Ma.
In summary, during deposition of the Kattendijk Formation and Oorderen Member in the Antwerpen area (Belgium), the Oosterhout Formation at Balgoy (The Netherlands) and the Coralline Crag in East Anglia (United Kingdom), circumstances in the North Sea Basin were favourable for great white sharks.

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References

Agassiz, L. 1835-1843. *Recherches sur les poissons fossiles. 3.* Neuchâtel (Petitpierre): 390 pp. [published in parts]

Antunes, M.T. & Balbino, A.C. 2010. The great white shark *Carcharodon carcharias* (Linné, 1758) in the Pliocene of Portugal and its early distribution in eastern Atlantic. *Revista Española de Paleontología* 25(1): 1-6.

Applegate, S. & Espinosa-Arrubarrena, L. 1996. A fossil history of *Carcharodon* and its possible ancestor, *Cretolamna*: A study in tooth identification. *In*: Klimley, A.P. & Ainley, D. (eds). *Great white sharks. The biology of Carcharodon carcharias.* San Diego (Academic Press): 19-47.

Bakel, B.W.M. van, Jagt, J.W.M., Artal, P. & Fraaije, R.H.B. 2009. *Harenacorystes johanjansseni*, a new Pliocene crab (Crustacea, Decapoda) from the Netherlands, and notes on Miocene-Pliocene corystoid crabs from the North Sea Basin. *Bulletin of the Mizunami Fossil Museum* 35: 79-85.

Balen, R.T. van, Houtgast, R.F., Wateren, F.M. van der, Vandenberghe, J. & Bogaart, P.W. 2000. Sediment budget and tectonic evolution of the Meuse catchment in the Ardennes and the Roer Valley Rift System. *Global and Planetary Change* 27: 113-129.

Balen, R.T. van, Houtgast, R.F. & Cloetingh, S.A.P.L. 2005. Neotectonics of the Netherlands: a review. *Quaternary Science Reviews* 24: 439-454.

Bass, A.J., D'Aubrey, J.D. & Kistnasamy, N. 1975. Sharks of the east coast of southern Africa, 4. The families Odontaspididae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. *Investigational Report Oceanographic Research Institute* 39: 102 pp.

Berendsen, H.J.A. 2005. *The Rhine-Meuse delta at a glance.* Utrecht (Faculty of Geosciences, Department of Physical Geography, Utrecht University): 54 pp.

Berg, L.S. 1958. *System der rezenten und fossilen Fischartigen und Fische.* Berlin (Deutscher Verlag der Wissenschaften): 310 pp.

Bonaparte, C.L. 1835. Prodromus systematis ichthyologiae. *Nuovi Annali delle Scienze naturali Bologna* (1), 2(4): 181-196, 272-277. [journal dates to 1840, but distributed in 1835 as a separate *Prodromus systematis ichthyologiae*: 21 pp.]

Bonaparte, C.L. 1838. Selachorum tabula analytica. *Nuovi annali delle scienze naturali e rendiconto dei lavori dell'Accademia della Scienze dell'Instituto di Bologna con appendice agraria* 2: 195-214.

Bonnaterre, J.P. 1788. *Tableau encyclopédique et méthodique des trois règnes de la nature. Ichthyologie.* Paris (Panckoucke): 215 pp.

Busschers, F.S., Kasse, C., Balen, R.T. van, Vandenberghe, J., Cohen, K.M., Weerts, H.J.T., Wallinga, J., Johns, C., Cleveringa, P. & Bunnik, F.P.M. 2007. Late Pleistocene evolution of the Rhine-Meuse system in the southern North Sea Basin: imprints of climate change, sea-level oscillation and glacio-isostacy. *Quaternary Science Reviews* 26: 3216-3248.

Busschers, F.S. & Weerts, H.J.T. 2003. Formatie van Kreftenheye. *In*: TNO. *Lithostratigrafische nomenclator van de ondiepe ondergrond, versie 2013*. Retrieved March 2015 from https://www.dinoloket.nl/formatie-van-kreftenheye.

Cappetta, H. 2012. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. *In*: Schultze, H.P. (ed.). *Handbook of Paleoichthyology, 3E*. München (Friedrich Pfeil): 1-512.

Casey, J.G. & Pratt Jr, H.L. 1985. Distribution of the white shark, *Carcharodon carcharias*, in the western North Atlantic. *Memoirs of the Southern California Academy of Sciences* 9: 2-14.

Cliff, G., Dudley, S.F.J. & Davis, B. 1989. Sharks caught in the protective gillnets off Natal, South Africa, 2. The great white shark *Carcharodon carcharias* (Linnaeus). *South African Journal of Marine Science* 8: 131-144.

Cohen, K.M., Stouthamer, E. & Berendsen, H.J.A. 2002. Fluvial deposits as a record for late Quaternary neotectonic activity in the Rhine-Meuse delta, The Netherlands. *Netherlands Journal of Geosciences* 81(3-4): 389-405.

Compagno, L.J.V. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date, 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). *FAO Species Catalogue for Fishery Purposes* 1(2): 269 pp.

Curtis, T.H., McCandless, C.T., Carlson, J.K., Skomal, G.B., Kohler, N.E., Natanson, L.J., Burgess, G.H., Hoey, J.J. & Pratt Jr, H.L. 2014. Seasonal distribution and historic trends in abundance of white sharks, *Carcharodon carcharias*, in the western North Atlantic Ocean. *PLoS ONE* 9(6), e99240: 1-12.

De Schepper, S. 2006. Plio-Pleistocene dinoflagellate cyst biostratigraphy and palaeoecology of the eastern North Atlantic and southern North Sea Basin. PhD thesis, University of Cambridge, Cambridge, U.K.: 327 pp. (unpublished)

De Schepper, S., Groeneveld, J., Naafs, B.D.A., Van Renterghem, C., Hennissen, J., Head, M.J., Louwye, S. & Fabian, K. 2013. Northern hemisphere glaciation during the globally warm early late Pliocene. *PLoS ONE* 8(12), e81508: 1-15.

De Schepper, S., Head, M.J. & Louwye, S. 2009. Pliocene dinoflagellate cyst stratigraphy, palaeoecology and sequence stratigraphy of the Tunnel-Canal Dock, Belgium. *Geological Magazine* 146(1): 92-112.

Domeier, M.L. & Nasby-Lucas, N. 2013. Two-year migration of adult female white sharks (*Carcharodon carcharias*) reveals widely separated nursery areas and conservation concerns. *Animal Biotelemetry* 1(2): 1-9.

Ebbing, J.H.J. & Lang, F.D. de 2003. Formatie van Oosterhout. *In*: TNO. *Lithostratigrafische nomenclator van de ondiepe ondergrond, versie 2013*. Retrieved March 2015 from https://www.dinoloket.nl/formatie-van-oosterhout.

Ehret, D.J., MacFadden, B.J., Jones, D.S., Devries, T.J., Foster, D.A. & Salas-Gismondi, R. 2012. Origin of the white shark *Carcharodon* (Lamniformes: Lamnidae) based on recalibration of the upper Neogene Pisco Formation of Peru. *Palaeontology* 55(6): 1139-1153.

Fergusson, I.K. 1996. Distribution and autecology of the white shark in the eastern North Atlantic Ocean and the Mediterranean Sea. *In*: Klimley, A.P. & Ainley, D. (eds). *Great white sharks. The biology of Carcharodon carcharias*. San Diego (Academic Press): 321-345.

Fraaije, R.H.B., Bakel, B.W.M. van & Jagt, J.W.M. 2007. A new species of Goniocypoda and the first record of *Glyphithyreus wetherelli* (Bell, 1858) (Decapoda, Brachyura) from the Eocene of Nieuwvliet-Bad, The Netherlands. *Memorie della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano* 35: 37-42.

Funnell, B.M. 1996. Plio-pleistocene palaeogeography southern North Sea Basin (3.75-0.60 Ma). *Quaternary Science Reviews* 15(5-6): 391-405.

Geluk, M.C., Duin, E.J., Dusar, M., Rijkers, R., Berg, M.W. van den & Rooijen, P. van 1994. Stratigraphy and tectonics of the Roer Valley Graben. *Geologie en Mijnbouw* 73: 129-141.

Glibert, M. 1959. Gastropodes du Diestien, du Scaldisien et du Merxémien de la Belgique, 3. *Bulletin de l'lnstitut royal des Sciences naturelles de Belgique* 35: 1-36.

Gottfried, M.D. & Fordyce, E. 2001. An associated specimen of *Carcharodon angustidens* (Chondrichthyes, Lamnidae) from the Late Oligocene of New Zealand, with comments on *Carcharodon* interrelationships. *Journal of Vertebrate Paleontology* 21(4): 730-739.

Harmer, W.F. 1914. The Pliocene Mollusca of Great Britain, being supplementary to S.V. Wood's Monograph of the Crag Mollusca, 1. *Monograph Palaeontographical Society* 67: 1-200.

Hout, W. in 't 1985. Haaietanden en andere Tertiaire visresten uit Kallo (België). *Gea* 18: 125-144.

Houtgast, R.F. & Balen, R.T. van 2000. Neotectonics of the Roer Valley Rift System, The Netherlands. *Global and Planetary Change* 27: 131-146.

Hubbell, G. 1996. Using tooth structure to determine the evolutionary history of the white shark. *In*: Klimley, A.P. & Ainley, D. (eds). *Great white sharks. The biology of* Carcharodon carcharias. San Diego (Academic Press): 9-18.

Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 43: 649-661.

International Commission on Zoological Nomenclature. 1965. Opinion 723. Repeal of the ruling given in Opinion 47 together with the stabilisation of the generic names *Carcharhinus* Blainville, 1816, *Carcharodon* Smith, 1838, and *Odontaspis* Agassiz, 1838, in their accustomed sense (Pisces). *Bulletin of Zoological Nomenclature* 22: 32-36.

Janse, A.C. 2004. Opmerkelijke vondsten: *Carcharodon* van de Maasvlakte. *Afzettingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 25(3): 48-49.

Janse, A.C. 2005. Opmerkelijke vondsten: *Carcharodon* - 2. *Afzettingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 26(3): 44-45.

Jonkaire, M. de la. 1823. Note sur le genre *Astarte*, Sowerby (Crassine, Lamarck). *Mémoires de la Société d'Histoire naturelle de Paris* 1: 127-131.

Kattenwinkel, L. 2009. Goudbruine tand van een witte haai. *Voluta* 2009(2): 4-6.

Kautsky, F. 1925. Das Miocän von Hemmoor und Basbeck-Osten. *Abhandlungen der Preußischen Geologischen Landesanstalt,* Neue Folge 97: 1-255.

Klimley, A.P. 1985. The areal distribution and autoecology of the white shark, *Carcharodon carcharias*, off the west coast of North America. *Memoirs of the Southern California Academy of Sciences* 9: 15-40.

Laga, P., Louwye, S. & Mostaert, F. 2006. Disused Neogene and Quaternary regional stages from Belgium: Bolderian, Houthalenian, Antwerpian, Diestian, Deurnian, Kasterlian, Kattendijkian, Scaldisian, Poederlian, Merksemian and Flandrian. *Geologica Belgica* 9(1-2): 215-224.

Lambert, O. 2008. A new porpoise (Cetacea, Odontoceti, Phocoenidae) from the Pliocene of the North Sea. *Journal of Vertebrate Paleontology* 28(3): 863-872.

Lambert, O. & Gigase, P. 2007. A monodontid cetacean from the early Pliocene of the North Sea. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 77: 197-210.

Landolt, H.H. 1947. Ueber den Zahnwechsel bei Selachiern. *Revue Suisse de Zoologie* 54(19): 305-367.

Lawrence, K.T., Herbert, T.D., Brown, C.M., Raymo, M.E. & Haywood, A.M. 2009. High-amplitude variations in North Atlantic sea surface temperature during the early Pliocene warm period. *Paleoceanography* 24(2), PA2218: 1-15.

Leidy, J. 1859. Remarks on *Dromatherium sylvestre* and other fossils from Chatham Co., N.C. *Proceeding of the Academy of Natural sciences of Philadelphia* 11: 162.

Leriche, M. 1926. Les poissons néogènes de la Belgique. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique* 32: 367-472.

Linnaeus, C. 1758. *Systema Naturae - per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis,*. 10(1) Holmiae (Laurentii Salvii): ii + 824 pp.

Long, D.J., Boessenecker, R.W. & Ehret, D.J. 2014. Timing of evolution in the *Carcharodon* lineage: rapid morphological change creates a major shift in a predator's trophic niche. *In:* Programm and Abstracts of Shark International, Durban, South Africa 2014: 123.

Louwye, S., De Coninck, J. & Verniers, J. 2000. Shallow marine lower and middle Miocene deposits at the southern margin of the North Sea Basin (northern Belgium): dinoflagellate cyst biostratigraphy and depositional history. *Geological Magazine* 137(4): 381-394.

Louwye, S., Head, M.J. & De Schepper, S. 2004. Dinoflagellate cyst stratigraphy and palaeoecology of the Pliocene in northern Belgium, southern North Sea Basin. *Geological Magazine* 141(3): 353-378.

Marquet, R. 2004. Ecology and evolution of Pliocene bivalves from the Antwerp Basin. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la terre* 74 supplement: 205-212.

Martin, R.A., Hammerschlag, N., Collier, R.S. & Fallows, C. 2005. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal of the Marine Biological Association of the United Kingdom* 85: 1121-1135.

Meijer, T. & Preece, R.C. 1995. Malacological evidence relating to the insularity of the British Isles during the Quaternary. *Geological Society Special Publication* 96: 89−110.

Meulenkamp, J.E. & Sissingh, W. 2003. Tertiary palaeogeography and tectonostratigraphic evolution of the northern and southern Peri-Tethys platforms and the intermediate domains of the African-Eurasian convergent plate boundary zone. *Palaeogeography, Palaeoclimatology, Palaeoecology* 196: 209-228.

Michon, L., Balen, R.T. van, Merle, O. & Pagnier, H. 2003. The Cenozoic evolution of the Roer Valley Rift System integrated at a European scale. *Tectonophysics* 367: 101-126.

Müller, J. & Henle, F.G.J. 1838. On the generic characters of cartilaginous fishes, with descriptions of new genera. *Magazine of Natural History*, n.s. 2: 33-37, 88-91.

Müller, J. & Henle, F.G.J. 1838-1841. Systematische Beschreibung der Plagiostomen. Berlin (Von Veit & Comp.): xxii + 200 pp. [pp. 1-28 published in 1838, reset pp. 27-28, 29-102 in 1839, i-xxii + 103-200 in 1841]

Müller, O.F. 1776. *Zoologiae Danicae Prodromus, seu animalium Daniae et Norvegiae indigenarum. Characteres, nominam, et synonyma imprimis popularum.* Havniae (Typis Hallageriis): 274 pp.

Naafs, B.D.A., Stein, R., Hefter, J., Khélifi, N., De Schepper, S. & Haug, G.H., 2010. Late Pliocene changes in the North Atlantic Current. *Earth and Planetary Science Letters* 298: 434-442.

Newton, E.T. 1891. The vertebrata of the Pliocene deposits of Britain. *Memoirs of the Geological Survey of the United Kingdom* (1891): xi + 137 pp.

Nieulande, F.A.D. van 2001. Mensenhaai ('Jaws') aangespoeld op het Kalootstrand! *Afzettingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 22(1): 14-15.

Nolf, D. 1986. *Haaie- en roggentanden uit het Tertiair van België*. Brussels (Institut royal des Sciences naturelles de Belgique): 172 pp.

Nolf, D. 1988. *Haaie- en roggentanden uit het Tertiair van België* (2nd ed.). Brussels (Institut royal des Sciences naturelles de Belgique): 180 pp.

Nyst, H. 1835. *Recherches sur les coquilles fossiles de la province d'Anvers*. Bruxelles (Perichon): 36 pp.

Nyst, P.-H. 1845. Description des coquilles et des polypiers fossiles des terrains tertiaires de la Belgique. *Mémoires couronnés et mémoires des savants étrangers, publiés par l'Académie Royale des Sciences et belles-lettres de Bruxelles* 17: 1-697. [imprinted 1843]

Olivi, G. 1792. *Zoologia Adriatica ossia catalogo ragionata degli animali del Golfo e delle Laguna di Venezia; preceduto da una dissertazione sulla storia fiscia e naturale del Golfo; e accompagnato da memorie, ed osservazioni di fisica storia naturale ed economia*. Bassano: xxiii +334 pp.

Ottema, J. & Hout, W. in 't 1987. *Fossielen uit het 4e Havendok by Kallo, België*. Amsterdam (Geologisch Museum Universiteit van Amsterdam): 111 pp.

Pennant, T. 1777. *British Zoology,* 4. *Crustacea. Mollusca. Testacea*. London (Benjamin White): 154 pp.

Péron F. 1807. *Voyage de découvertes aux Terres Australes, exécuté par ordre de sa majesté l'Empereur et Roi, sur les corvettes le Géographe, le Naturaliste et la goulette le Casuarina, pendant les années 1800, 1801, 1803 et 1804*, 1. Paris: 496 pp.

Peters, N. 2013. *Van reuzenhaai tot* Chalicotherium. *Fossielen uit Mill-Langenboom*. Boxtel (Oertijdmuseum De Groene Poort): 158 pp.

Peters, W.J.M. & Wesselingh, F.P. 2009. Balgoy: Een nieuwe Plioceen vindplaats voor Nederland met implicaties voor de pliocene mollusken zonering van het Noordzeebekken. *Afzettingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 30(1): 12-18.

Quero, J.C., Decamps, P., Emonnet, R. & Vayne, J.J. 1995. Requins de l'ordre des Lamniformes observés dans Le Golfe de Gascogne. *In*: Cendrero, O. & Olaso, I. (eds). *Actas del IV Coloquio Internacional sobre Oceanografía del Golfo de Vizcaya. Santander*: 313-325.

Rafinesque-Schmaltz, C.S. 1810. *Indice d'ittiologia siciliana; ossia, catalogo metodico dei nomi latini, italiani, e siciliani dei pesci, che si rinvengono in Sicilia disposti secondo un metodo naturale eseguito da un appendice che contiene la descrizione de alcuni nuovi pesci siciliani.* Messina (Giovanni del Nobolo): 70 pp.

Shimada, K. 2003: The relationship between the tooth size and total body length in the white shark, *Carcharodon carcharias* (Lamniformes:Lamnidae). *Journal of Fossil Research* 35(2): 28-33.

Siverson, M. 1999. A new large lamniform shark from the uppermost Gearle Siltsone (Cenomanian, Late Cretaceous) of Western Australia. *Transactions of the Royal Society of Edinburgh Earth Sciences* 90(1): 49-66.

Sowerby, J. 1815-1818. *The mineral conchology of Great Britain; or, coloured figures and descriptions of those remains of testaceous animals or shells which have been preserved at various times and depths in the earth,* 2. London (Arding and Merrett): 235 pp. [published in parts]

Sowerby, J. 1818-1821. *The mineral conchology of Great Britain; or, coloured figures and descriptions of those remains of testaceous animals or shells which have been preserved at various times and depths in the earth, 3.* London (Arding): 184 pp. [published in parts]

Torsvik, T.H., Carlos, D., Mosar, J., Cocks, L.R.M. & Malme, T.N. 2002. Global reconstructions and North Atlantic paleogeography 400 Ma to Recent. *In*: Eide, E.A. (ed.). *BATLAS - Mid Norway plate reconstructions atlas with global and Atlantic perspectives.* Trondheim (Geological Survey of Norway): 18-39.

Tricas, T.C. & McCosker, J.E. 1984 Predatory behavior of the white shark (*Carcharodon carcharias*), with notes on its biology. *Proceedings of the California Academy of Sciences* 43(14): 221-238.

Underwood, C. 2012. White Sharks in UK Waters. *Shark Focus*, 45: 6-7.

Van Vliet-Lanoë, B., Gosselin, G., Mansy, J.-L., Bourdillon, C., Meurisse-Fort, M., Henriet, J.-P., Le Roy, P. & Trentesaux, A. 2010. A renewed Cenozoic story of the Strait of Dover. *Annales de la Société géologique du Nord* (2)17: 59-80.

Van Vliet-Lanoë, B., Mansy, J.L., Margerel, J.P., Vidier, J.P., Lamarche, J. & Everaerts, M. 1998. Le Pas de Calais un détroit cénozoïque à ouverture multiple. *Comptes Rendus de l'Académie des Sciences* IIA*, Earth and Planetary Science* 326(10): 729-736.

Van Vliet-Lanoë, B., Vandenberghe, N., Laurent, M., Laignel, B., Lauriat-Rage, A., Louwye, S., Mansy, J.-L., Mercier, D., Hallégouët, B., Laga, P., Lacquement, F., Meilliez, F., Michel, Y., Moguedet, G. & Vidier, J.-P. 2002. Palaeogeographic evolution of northwestern Europe during the Upper Cenozoic. *Geodiversitas* 24(3): 511-541.

Vandenberghe, N., Laga, P., Steurbaut, E., Hardenbol, J. & Vail, P.R. 1998. Tertiary sequence stratigraphy at the southern border of the North Sea Basin in Belgium. *SEPM Special Publication* 60: 119-154.

Verschueren, S. 1998. Fossiele haaien, roggen en draakvissen van het strand van Cadzand en Nieuwvliet-Bad. *In*: Lindemann, T. (ed.). Gids voor strandfossielen van Cadzand en Nieuwvliet-Bad. Haaien- en roggentanden, schelpen, krabben, slangsterren, zoogdierresten. *Geode* 1998(2): 29-67.

Vervoenen, M. 1995. Taphonomy of some Cenozoic seabeds from the Flemish region, Belgium. *Geological Survey of Belgium Professional Paper* 272: 122 pp.

Weerts, H.J.T. & Busschers, F.S. 2003. Formatie van Echteld. *In*: TNO. *Lithostratigrafische nomenclator van de ondiepe ondergrond, versie 2013.* Retrieved March 2015 from https://www.dinoloket.nl/formatie-van-echteld.

Weng, K.C., O'Sullivan, J.B., Lowe, C.G., Winkler, C.E., Dewar, H. & Block, B.A. 2007. Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Marine Ecology Progress Series* 338: 211-224.

Wesselingh, F.P., Peters, W.J.M. & Munsterman, D.K. 2013. A brachiopod-dominated sea-floor assemblage from the late Pliocene of the eastern Netherlands. *Netherlands Journal of Geosciences* 92(2-3): 171-176.

Westerhoff, W.E. 2003. Formatie van Breda. *In*: TNO. *Lithostratigrafische nomenclator van de ondiepe ondergrond, versie 2013.* Retrieved March 2015 from https://www.dinoloket.nl/formatie-van-breda.

Westerhoff, W.E. & Weerts, H.J.T. 2003a. Formatie van Beegden. *In*: TNO. *Lithostratigrafische nomenclator van de ondiepe ondergrond, versie 2013.* Retrieved March 2015 from https://www.dinoloket.nl/formatie-van-beegden.

Westerhoff, W.E. & Weerts, H.J.T. 2003b. Formatie van Waalre. *In*: TNO. *Lithostratigrafische nomenclator van de ondiepe ondergrond, versie 2013.* Retrieved March 2015 from https://www.dinoloket.nl/formatie-van-waalre.

Wijnker, E., Bor, T.J., Wesselingh, F.P., Munsterman, D.K., Brinkhuis, H., Burger, A.W., Vonhof, H.B., Post, K., Hoedemakers, C., Janse., A.C. & Taverne, N. 2008. Neogene stratigraphy of the Langenboom locality (Noord-Brabant, the Netherlands). *Netherlands Journal of Geosciences* 87(2): 165-180.

Wood, A.M., Whatley, R.C., Cronin, T.M. & Holtz, T. 1993. Pliocene palaeotemperature reconstruction of the southern North Sea based on Ostracoda. *Quaternary Science Reviews* 12: 747-767.

Wood, S.V. 1851-1861. *A monograph of the Crag Mollusca; with description of shells from the upper Tertiaries of the British Isles,* 2. *Bivalves.* London (Palaeontographical Society): 341 pp. [published in parts]

Woodward, A.S. 1889. *Catalogue of the fossil fishes in the British Museum (Natural History)* 1 *containing the Elasmobranchii.* London (British Museum (Natural History)): 474 pp.

Zagwijn, W.H. & Doppert, J.W.C. 1978. Upper Cenozoic of the southern North Sea Basin: palaeoclimatic and palaeogeographic evolution. *Geologie en Mijnbouw* 57(4): 577-588.

Zagwijn, W.H. & Hager, H. 1987. Correlation of continental and marine Neogene deposits in the southeastern Netherlands and the Lower Rhine district. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie* 24(1-2): 59-78.

Appendix 1. Lithological description of borehole B45F0144 - Loonse Uiterwaard, municipality of Wijchen; WGS84 coordinates 51.79129, 5.69449. Height of surface c. 8.70 m + N.A.P. Borehole made by RGD in October 1973. Stihl drill rig with bailer sampling to final depth at 70 m below surface. Description by A. Steegs & P. van de Ven (RGD), lithostratigraphical interpretation 12-06-2001 by W. Dobma (TNO-NITG). Source: Boorstaat TNO-Geological Survey of the Netherlands

Depth below surface (m)	Description	Stratigraphic interpretation
0.00 -0.80	Light yellowish grey, stiff silt	Echteld Formation
0.80 -2.60	Light yellowish grey, stiff silt, laminated with moderately fine sand	
2.60 -3.70	Light yellowish grey, moderately fine sand	Kreftenheye Formation
3.70 -5.00	Light yellowish grey, very coarse sand, few coarse gravel, rusty stains	
5.00 -6.00	Reddish brown, extremely coarse sand, 5% fine gravel	
6.00 -7.00	Reddish brown, extremely coarse sand, 5% fine gravel	
7.00 -8.00	Reddish brown, extremely coarse sand, 30% fine gravel	
8.00 -9.00	Grey, extremely coarse sand, 15% fine gravel, traces of silt	Beegden Formation
9.00-10.00	Light yellowish grey, extremely coarse sand, 15% fine gravel, large pebbles	
10.00-11.00	Light yellowish grey, moderately coarse sand, 10% fine gravel, traces of mica, traces of wood	Waalre Formation
11.00-12.00	Light yellowish grey, moderately coarse sand, few fine gravel, mica, traces of wood	
12.00-13.00	Light yellowish grey, extremely coarse sand, few fine gravel, traces of wood	
13.00-14.00	Fine and coarse gravel (40%) with extremely coarse, beige sand, traces of wood	
14.00-15.00	Fine and coarse gravel (40%) with extremely coarse, beige sand, traces of wood	
15.00-16.00	Fine and coarse gravel (75%) with large pebbles and extremely coarse, light yellowish grey sand	
16.00-17.00	Fine and coarse gravel (60%) with extremely coarse, beige sand	
17.00-18.00	Fine and coarse gravel (50%) with extremely coarse, beige sand	
18.00-19.00	Fine and coarse gravel (50%) with extremely coarse, beige sand	
19.00-20.00	Beige, extremely coarse sand, 15% very fine and fine gravel	
20.00-21.60	Beige, extremely coarse sand, 20% very fine and fine gravel	
21.60-23.00	Grey, silty, moderately coarse sand, some fine gravel, mica, traces of wood, some streaks of dark, organic-rich silt	Oosterhout Formation
23.00-24.00	Grey, moderately coarse sand, mica, traces of wood, some organic-rich streaks	
24.00-25.00	Grey, silty, moderately coarse sand, mica, some clay, pebbles traces of wood	
25.00-26.50	Grey, silty, moderately fine sand, mica, some clay pebbles, traces of wood	
26.50-28.00	Grey, silty, moderately fine sand, 10% mollusc shells, a large clay pebble, a single streak of weak silt	
28.00-29.00	Grey, moderately fine sand, 5% mollusc shells	
29.00-30.00	Grey, moderately fine sand, 35% mollusc shells, a single streak of weak silt	
30.00-31.00	Grey, moderately fine sand, 20% mollusc shells	
31.00-33.00	Grey, moderately fine sand, few mollusc shells	
33.00-34.00	Grey, moderately fine sand, few mollusc shells	
34.00-35.00	Grey, moderately fine sand, 85% mollusc shells, bone fragments	
35.00-36.00	Dark greyish green, moderately fine sand, mica, much glauconite, few mollusc shells	Breda Formation
36.00-40.00	Dark greyish green, moderately fine sand, much glauconite, traces of mollusc shells	
40.00-42.00	Dark greyish green, silty, moderately fine sand, much glauconite	
42.00-46.00	Dark greyish green, moderately fine sand, much glauconite, traces of mollusc shells	
46.00-48.00	Dark greyish green, moderately fine sand, much glauconite, traces of mollusc shells	
48.00-50.00	Dark greyish green, moderately fine sand, much glauconite, a single silt pebble, traces of mollusc shells	
50.00-52.00	Greyish green, moderately fine sand, streak of very sandy weak silt, glauconite	
52.00-54.00	Greyish green, moderately fine sand, a single silt pebble	
54.00-56.00	Greyish green, moderately fine sand, a single silt pebble, traces of mica	
56.00-58.00	Dark grey, moderately fine sand, traces of mica, few glauconite	
58.00-60.00	Dark grey, moderately fine sand, much mica, a single streak of silt	
60.00-62.00	Dark grey, moderately fine sand, much mica, a single streak of silt	
62.00-70.00	Dark grey, moderately fine sand, few glauconite, much mica, thin streak of grey weak silt	