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RESEARCH PAPER

Aktuo-paläontologie of the common cuttlefish, *Sepia officinalis*, an endocochleate cephalopod (mollusca) in the North Sea

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Abstract Following 3 days of gales in the North Sea off the Dutch coast, one part of the beach at Katwijk, Zuid-Holland, was littered with shells (cuttlebones) of the common cuttlefish, *Sepia officinalis* Linné. Over 100 specimens were collected. These *Sepia* may have died at the same time, with the storm as the probable cause of death (=life assemblage); alternately, did it just cause dead, floating cuttlebones to wash ashore as a monospecific death assemblage? The collected cuttlebones showed a great variation not only in their dimensions, but also in their preservation. All the cuttlebones were examined in detail. About one third of the shells were broken. Most of the cuttlebones have triangular holes and V-shaped scratches, which suggest that they were carried and attacked by birds; this kind of damage can only be made after the death of *Sepia*. One specimen preserved a bite mark of a fish. Some of the cuttlebones have algae or barnacles growing on them, suggesting they had a lengthy post-mortem residence floating in the North Sea. The diversity and common occurrence of evidence of interactions by other organisms with the cuttlebones, predatory, scavenging, and pseudoplanktonic, leads to a conclusion that these *Sepia* cuttlebones represent a death assemblage, possibly left over from the previous summer season and perhaps mixed with some older specimens.

Keywords Coleoidea Cuttlebones Preservation · Pseudoplankton · Ichnology

Kurzfassung Nach einem dreitägigen Sturm in der Nordsee vor der niederländischen Küste wurde ein Teil des Strandes von Katwijk in Südholland mit Schulpen des Gewöhnlichen Tintenfisches *Sepia officinalis* Linné übersät. Mehr als 100 Exemplare wurden aufgesammelt. Entweder sind diese Sepien gleichzeitig (mit dem Sturm als mögliche Todesursache) gestorben, oder aber im Wasser schwebende Schulpe wurden als monospezifische Grabgemeinschaft an den Strand gespült. Die aufgesammelten Tintenfischschulpe variieren nicht nur in ihren Abmessungen, sondern auch in ihrer Erhaltung. Alle Stücke wurden im Detail untersucht, wobei etwa ein Drittel der Schulpe zerbrochen war. Die meisten Tintenfischschulpe haben dreieckige Löcher und V-förmige Kratzspuren, die daraufhin deuten, daß diese den Sepien nach dem Tode von Vögeln beigebracht wurden. Bei einem Exemplar ist die Bissspur eines Fisches erhalten. Einige andere Tintenfischschulpe besitzen Algen- oder Seepockenbewuchs, welcher auf ein längeres Schweben dieser (post mortem) in der Nordsee hinweist. Aufgrund der Diversität und der Interaktionen mit anderen Organismen läßt sich insgesamt postulieren, daß die vorliegenden Sepiaschulpe eine Taphozönose darstellen, die eventuell vom vorherigen Sommer stammt, oder mit noch älteren Exemplaren durchmischt wurde.

Schlüsselwörter Coleoidea · Tintenfischschulpe · Erhaltung · Pseudoplankton · Ichnologie

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Introduction

Strong winds in the southern North Sea directly impacted the coastline of the Netherlands from Sunday to Tuesday, 29–31 March 2015. Around 8.00 a.m. on Wednesday, 1st

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April, the authors made a preliminary examination of part of the beach at Katwijk, Zuid-Holland, the Netherlands, as a preamble to a short project at the University of Leiden. Unexpectedly, part of the beach had an unusually rich accumulation of the mineralized internal shells (cuttlebones) of *Sepia officinalis* Linné (1758), the common cuttlefish (Coleoidea; Decabrachia). Over a hundred specimens were collected in under an hour in order to investigate the origins of this storm-generated accumulation. The results of this study are presented herein as a contribution to the burgeoning field of study of cephalopod (neo-) taphonomy or Aktuo-Paläontologie sensu Schäfer (1972). Our research question was whether the cuttlebone accumulation represents a life or death assemblage (sensu Ager 1963, p. 183 *et seq*.; Brenchley and Harper 1998, pp. 67–69). That is, did the cuttlefish die from the effects of the gale, or did the storm merely wash dead, floating shells onshore? The former option would require the dead animals to lose their cuttlebones following unusually rapid decomposition of its soft tissues in just a few days, whereas these typically disintegrate in weeks or months in cephalopods (Kear et al. 1995). This is a similar question to one that might be asked of an accumulation of fossil cephalopods, but which can rarely be explored in Recent material.

Locality

The specimens were collected from the strandline on the North Sea coast of the Netherlands at Katwijk, Zuid-Holland (52°12′38.9″N 4°23′52.6″E) (Fig. 1). All the cuttlebones were found within an area of c. 50 × 40 m^2 in under an hour of searching. The concentration of cuttlebones was especially high within the research area; outside of this part of the beach, few cuttlebones were apparent. The beach area that the authors studied mainly consisted of sand; pebbles and other rocks were scarce.

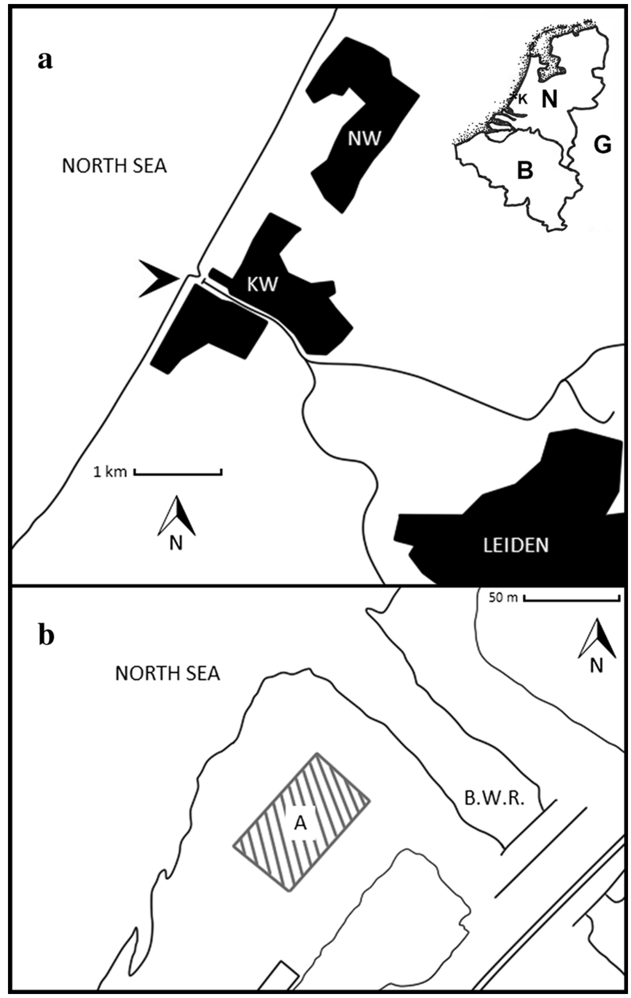


Fig. 1 **a** Outline map of the North Sea coast, showing the principal towns and cities in the proximity. The *black arrow* indicates the sampling area, *solid lines* are canals. Key: *NW* Noordwijk, *KW* Katwijk. The inset map (*top right*) shows the position of Katwijk (*K*) in northern Europe (*B* Belgium, *G* Germany, *N* Netherlands). **b** Large scale outline map of sampling area (*A*) at Katwijk. Key: *B.W.R.* Buitenwaterring (canal)

Materials and methods

The cuttlebones described herein were collected by the authors on the beach at Katwijk. The cuttlebones were collected in bulk in plastic bags and not separately packaged. During the search, the intention was to collect mainly complete specimens, but some broken ones were also brought back for comparison. All sizes were collected by hand, but this method may have biased our sample towards larger cuttlebones. The cuttlebones were carefully rinsed with tap water to remove sand, leaving any organisms attached to the shells intact. After rinsing, the cuttlebones were gently dried by natural heat, numbered, measured and described. The specimens are to be deposited in the collections of the Naturalis Biodiversity Center in Leiden (RMNH prefix), RMNH.MOL.338215-338222, 338223 (98 cuttlebones). The specimens were photographed using a Canon Powershot SX40HS digital camera.

Descriptions

One hundred and six cuttlebones of *Sepia* were collected. Thirty-four of the specimens were incomplete (broken when collected), so their total length was indeterminate. All the complete shells were measured, and the results are set out in size frequency histograms (Fig. 2); two size classes are apparent, but this may be an artefact of our collecting method (see above). Nearly all of the cuttlebones were damaged or had other “blemishes” as described

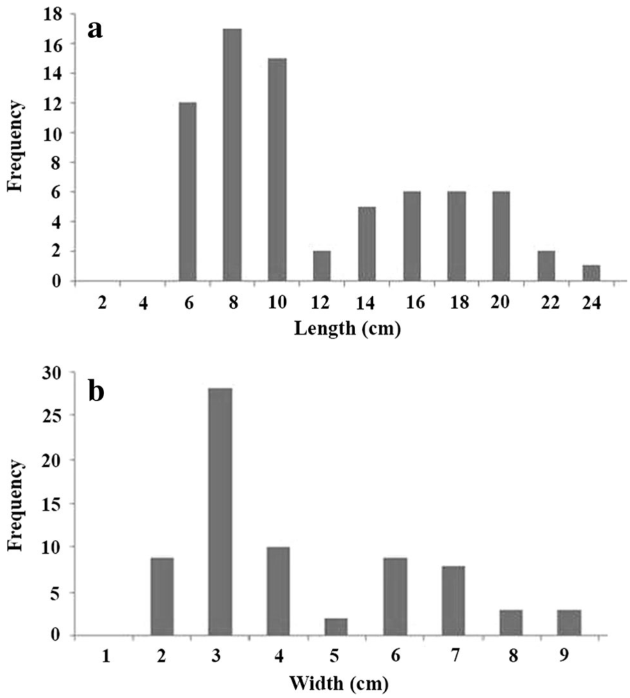


Fig. 2 The length (**a**) and width (**b**) of the cuttlebones displayed in histograms

below; every type of interaction, damage, or "blemish" is described and illustrated (Fig. 3).

Damaged cuttlebones

Triangular pits were found on 79 specimens (Fig. 3a, b). The pits are relatively deep and go through many calcareous layers of the cuttlebone. Triangular pits varied in size (Fig. 3a, b). The pits are mostly found on the ventral surface; only two specimens had similar marks on the dorsal side.

Scratch marks are also common (Fig. 3c). Seventy-two specimens had this kind of damage. The scratch marks vary from several layers deep to shallow markings penetrating only one or two shell layers. In our sample, scratches were only found on the ventral surface. The scratches and associated triangular marks commonly occur on the same specimens.

On specimen RMNH.MOL.338215, there was a unique crescent-shaped mark (Fig. 3d). Impressions of teeth were clearly visible on the shallow mark.

Ink marks

Seventeen specimens had black marks and spots in the calcareous layers of the cuttlebone (Fig. 3f). Nine of the spots were curved and parallel to the direction of growth, following the layers (chambers) of the cuttlebone (Clarkson 1998, fig. 8.21f, g). Other spots were roundish and stained several chambers of the shell.

Pseudoplankton

Several specimens had encrusting organisms attached as pseudoplankton (sensu Wignall and Simms 1990) to either one or both sides. Specimen RMNH.MOL.338218 had filaments of hair-like algae growing onto its shell (Fig. 3a). The algae were found on both dorsal and ventral surfaces of the cuttlebone.

Forty-one specimens were found with non-filamentous algae (Fig. 3i). These algae were apparent as green or brown, stain-like accumulations on the cuttlebone on both surfaces.

Balanid barnacles, tentatively identified as *Balanus* sp. cf. *B. improvisus* Darwin (1854), were found on 22 specimens (Fig. 3e; compare with Cadée 1997, fig. 3). Two size groups of barnacles (presumably representing separate spatfalls) were present on the cuttlebones, but the small size of both suggests neither was mature. Barnacles grew on both sides of the shells. The smallest barnacles were brown, whereas slightly larger, more mature individuals were grey in colour.

RMNH.MOL.338220 has a pattern of six little holes, oriented in a row. The holes are perfectly circular and are several layers deep (Fig. 3g).

Other blemishes

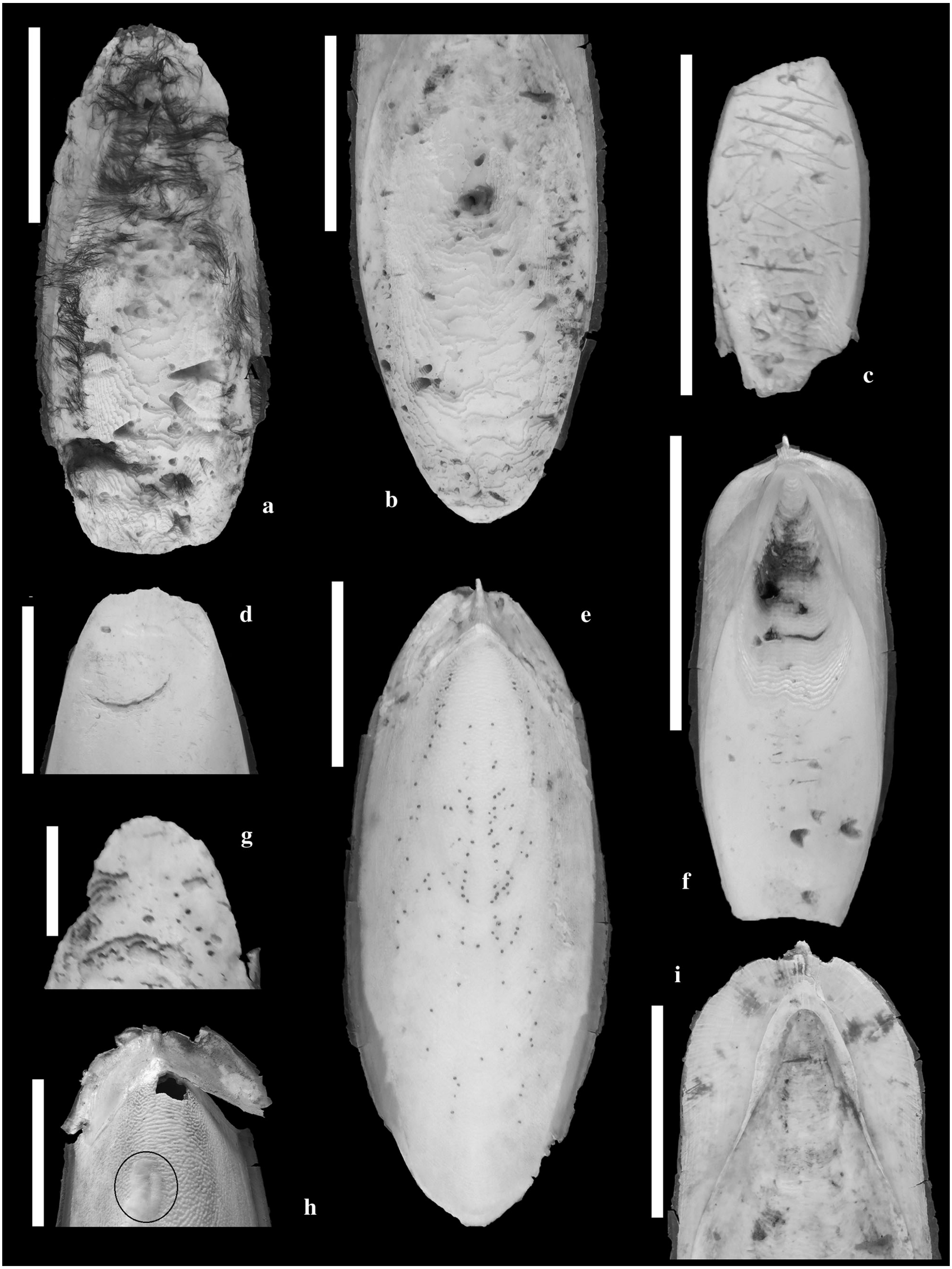
Apart from damage and/or pseudoplankton, some specimens show "lumps" with black spots on the dorsal side of the cuttlebone (Fig. 3h).

Discussion

Damaged cuttlebones

The shape of the triangular pits (Fig. 3a, b) indicates that they were caused by the beaks of birds. The holes were made after the *Sepia* died, when the cuttlebone separated from the mantle and floated to the surface under the influence of the gas-filled chamber. (For this reason, cuttlebones commonly wash ashore without any flesh attached. However, albeit rarely, a whole *Sepia* can wash up; Schäfer 1972, pp. 167–169.)

The birds made the triangular holes with their beaks to obtain calcium (carbonate) from the cuttlebones. The holes can be made either when the cuttlebones are afloat in the North Sea or after they washed up on the shore, although these two behaviours cannot be distinguished on the basis


a
b
c
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i

◀**Fig. 3** Examples of Recent *Sepia officinalis* Linné cuttlebones collected from the beach at Katwijk, the Netherlands, 1st April 2015. **a** RMNH.MOL.338218 showing several deep triangular pits and a dense accumulation of hair-like algae on the ventral surface. **b**, **i** RMNH.MOL.338219. **b** Showing a deep, rounded *hole* in the centre of the ventral surface (a damaged *triangular pit*?), associated with *small triangular pits*. **i** Showing some green "stains" of algae apparent as dark patches on the ventral surface. **c** RMNH. MOL.338222 showing several scratches on the ventral surface (commonly occurring in pairs, forming V-shapes). **d** RMNH. MOL.338215 showing several marks on the ventral surface, most obviously the crescent-shaped bite-mark. **e** RMNH.MOL.338217, dorsal surface encrusted by numerous immature *Balanus* sp. cf. *B. improvisus* (Darwin 1854), apparent as *dark dots* on either side of the mid-line. **f** RMNH.MOL.338221 showing a large black stain towards the top of the ventral surface, above a *black/brown line*. **g** RMNH.MOL.338220 showing six little holes, sloping towards the lower right, oriented in a row on the (posterior) ventral surface. *Scale bar* represents 10 mm. **h** RMNH.MOL.338216 showing a raised "lump" on the dorsal surface, inside the *dark circle*. Specimens uncoated. All *scale bars* represent 50 mm except **g**

of beak-marks alone. However, the triangular holes occur in a range of sizes, which suggests that they were made by a variety of bird species or, more speculatively, that the hole size is an ecological signal; it may be large holes are more easily generated when the cuttlebone rests on a substrate such as the beach. The beak marks occur only on the ventral side of the cuttlebones, most probably due to the hardness of the dorsal granulated shell layer, a secondary external layer (D. Fuchs, written comm.).

The scratch-marks (Fig. 3c) were also likely to have been made by birds (Cadée 2002); the possibility that they were made by fishes is considered small. As with the beak marks, the scratches could not be made when the *Sepia* were alive, because the ventral side of the cuttlebone was then protected by the mantle and other unmineralized tissues. There is no reason to assume that fishes attacked the separated cuttlebones when they were floating in the North Sea, because of their mouths are not commonly bird-beak-like and an absence of reports of them obtaining calcium from *Sepia* shells. It is more likely that the scratches were made by birds that picked up the cuttlebones with their beaks. This assumption is supported by most of the scratches occurring in pairs with a more or less tight V-shape.

Several bird species live along the Dutch coastline. The big and triangular holes were probably made by sea gulls, such as the lesser black-backed gull (*Larus fuscus* Linné), herring gull (*Larus argentus* Pontopiddan), and common gull (*Larus canus* Linné). The smaller triangular marks were most likely made by plovers (*Pluvialis* spp. and *Charadrius* spp.) or black-headed gulls (*Larus ridibundus* Linné). However, the scratches were made by birds with much longer beaks, presumably such as the Eurasian curlew (*Numenius arquata* (Linné)), Eurasian oystercatchers (*Haematopus ostralegus* (Linné)), and the typical waders (*Calidris* spp.). There were many birds scavenging on the beach on 1st April, including seagulls and other birds such as jackdaws (*Corvus monedula* (Linné)) (Arnhem et al. 1993). Cadée (2002) considered beak marks to be the spoor of fulmars.

The crescent-shaped mark (Fig. 3d) was most likely made by a predatory fish; other marks on this specimen can be interpreted as less successful bite-marks. The predator is most likely a type of small shark, like the nursehound (*Scyliorhinus stellaris* (Linné)) or the small-spotted catshark (*Scyliorhinus canicula* (Linné)). It is not certain whether the bites were the cause of death or were made post-mortem. The marks indicate that the teeth were small.

Ink marks

The ink marks (Fig. 3f) were probably a result of some sort of damage; when a cuttlefish is threatened, it emits a cloud of ink from the ink glands (Erhardt and Moosleitner 1998, p. 791). Ink is ejaculated out of the rectum, but only when the robust ink sac decomposes can it seep into the cuttlebone. Unstained cuttlebones are those that slipped out of the mantle before the ink sac disintegrated (D. Fuchs, written comm.). As a result, black spots can appear on the bone. The curved, line-shaped ink marks (=posterior margins of septa) are probably the result of ink, leaking into the chambered cuttlebone.

Pseudoplankton

The different types of marine algae must have encrusted the cuttlebones after the death of the *Sepia* and loss of the soft tissues. As noted by Schäfer (1972, p. 168), "… long beards of green algae are carried by cuttlebones and are good evidence of the length of the journey." The cuttlebones had to be floating on or close to the water surface, in order that the algae could flourish in the photic zone. There are at least three types of algae in the collected specimens: long hair-like algae (Fig. 3a), and brown and green stain-like algae (Fig. 3i). The algae do not use the calcium of the cuttlebone primarily as a source of minerals, but require the hard substrate for attachment (Wignall and Simms 1990).

The balanid barnacles (Fig. 3e) similarly require a hard substrate for successful growth. The occurrence of barnacles on both dorsal and ventral surfaces of cuttlebones indicates that the *Sepia* shells had been free of any soft tissues for a long time, that is, nekroplankton sensu Reyment (1986). The barnacles seen on the cuttlebones are most likely *B. improvisus*, a species which may colonise a range of substrates (Schäfer 1972, p. 117); certain other barnacle species avoid calcium-rich substrates.

The six little holes (Fig. 3g) are typical spoor of a boring clionoid sponge. These are well-known from the modern trace and trace fossil record as *Entobia* isp. (see, for example, Bromley 1970; Bromley and d'Alessandro 1984; Donovan and Lewis 2010, 2011).

Other blemishes

The lump (Fig. 3h) may the result of an injury to the living *Sepia*, which later healed. Alternately, it may be a reaction to a parasitic infestation as is known from, for example, decapod crustaceans (Klompmaker et al. 2014).

Variation in size

Commonly, individuals that wash onshore all have the same size because they die after spawning (Schäfer 1972, p. 169). However, the life cycle of *S. officinalis* is variable and the spawning period quite long. The specimens from Katwijk had a broad variation in size (Fig. 2). This is most likely the result of the storm, during which all floating cuttlebones, of differing ages and provenances, were washed onshore at the same time. This and other evidence already presented show that this accumulation represents a death assemblage (sensu Ager 1963; Brenchley and Harper 1998).

It is relevant to mention that *Sepia officinalis* is a seasonal migrant, only living in the North Sea from May to September (Schäfer 1972, p. 166). The reason the cuttlebones washed up when they did is probably because they represent a floating accumulation from the previous season(s). An undamaged sepia cuttlebone can float around for more than a year (Hewitt and Pedley 1978), but, once the shell breaks, it will sink in less than 8 days, because water encroaches into the chambers of the calcareous shell (Schäfer 1972, pp. 168–169). That about a third of the collected specimens were broken is presumably indicative of recent damage during the storm. Cuttlebones can travel for long distances, and dead shells have crossed the Atlantic Ocean, *Sepia* not being a denizen of the western Atlantic (Donovan et al. 2001).

Palaeontological significance

What is the relevance of our study in aktuo-paläontologie to the palaeontology of ancient cephalopods? Certainly, the data documented above might be widely analogous to that obtained from other recent endocochelate cephalopods (such as Donovan 1989). The accumulation at Katwijk was deemed worthy of study because the unusual profusion of *Sepia*; at other times of the year cuttlebones may be absent from the North Sea coast of the Netherlands. As such, it was treated as a proxy for a rich bedding plane assemblage of fossil cephalopods. Broadly comparable fossil assemblages have been interpreted as either life or death assemblages (see, for example, Kear et al. 1995), depending on available sources of evidence. Because the cuttlebone separates from its soft tissues after death (Schäfer 1972, p. 168), *Sepia* could be used as a taphonomic model, in a broad sense, for both endo- and ectocochleate cephalopods.

However, we do not choose to over-emphasise the relevance of these cuttlebones to cephalopod taphonomy. Fossil cephalopods are most commonly nautiloids and allied groups, ammonoids and belemnites, none of which is morphologically very close to *Sepia*. Sepiida do have a fossil record (see, for example, Hewitt and Pedley 1978; Košt'ák et al. 2013) and, in particular, those of the Eocene may be locally common (D. Fuchs written comm.). More relevant contributions to the neotaphonomy of ancient chambered cephalopods are possible by studying extant nautiloids, *Spirula* and argonauts. The true palaeontological contribution of the Katwijk cuttlebones is to a narrow area of palaeontology—the taphonomy of the sepiids—but also to a larger topic, that of pseudoplankton as a substrate for encrusters and traces.

Conclusions

Multiple lines of evidence indicate that the *Sepia* cuttlebone accumulation documented from Katwijk is a postmortem accumulation, a death assemblage in palaeontological terminology. Indeed, it is plausible that at least some of the specimens had been dead for two or more years. The assemblage was the result of a storm, but not as a catastrophic die-off event. Rather, they all died some months or even years before the storm blew them onshore at Katwijk as nekroplankton, so their occurrence is a sedimentological phenomenon. Variations in size of *Sepia*, and the variations in preservation and pseudoplanktonic associations, are conclusive evidence that they do not represent any sort of life assemblage.

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