Trans-Atlantic rafting by the brooding reef coral *Favia fragum* on man-made flotsam

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ABSTRACT: Specimens of the brooding reef coral *Favia fragum* were found on man-made flotsam stranded on the North Sea shore of the Netherlands. Based on the associated epifauna originating from the southeast USA, we estimate that the corals must have crossed the Atlantic Ocean, transported by the Gulf Stream and the North Atlantic Drift. The size of the corals suggests that they might have had enough time to cross the Atlantic alive and that they already reached the age of possible self-fertilization before they entered waters that were too cold to survive. The temperature requirements and the presently known geographic range of *F. fragum* are compared with Atlantic summer and winter isotherms and oceanic currents in order to project a hypothetical northernmost range boundary. With increasing pollution, man-made flotsam may become a progressively more common substrate for reef corals that depend on rafting for long-distance dispersal. Eventually, with warming seawater, floating debris may cause tropical marine species to expand their distribution ranges towards higher latitudes.

KEY WORDS: Distribution range · Epifauna · Life history · Long-distance dispersal · Ocean currents · Temperature tolerance

INTRODUCTION

Many species of shallow-water marine benthic invertebrates use rafting for long-distance dispersal. Buoyant plant material, such as macroalgae thalli, seagrass leaves, and driftwood, is commonly known as a biotic carrier for epifaunal communities despite exposure to air, strong temperature fluctuations, and harmful UV-radiation at the sea surface (Cheng 1975, Thiel & Gutow 2005a,b, Fraser et al. 2011). The success of dispersal depends on the size, buoyancy, and permanence of the floating substrate (particularly if organic), the longevity of the sessile phase in their life cycle, and the course and velocity of the carrying currents and winds. Eventually the floating objects may become cast up onshore, which is evi-

dent on beaches around the world (Harrold & Lisin 1989, Thiel & Gutow 2005a).

Anthropogenic flotsam and jetsam consisting of non-biodegradable debris have a long durability and increasingly are becoming more common on beaches than natural floating substrata (Thiel & Gutow 2005a). The litter usually originates from land via river mouths and drainage outlets and rarely as a result of storms and tsunamis. Shipping activities (merchant vessels), offshore industry, fisheries, and garbage dumping by coastal communities may also play a role in the production of marine debris, although only part of it is floating (Jones 1995, Hess et al. 1999, Donohue et al. 2001, Thiel & Gutow 2005a, Richards & Beger 2011), and predominantly consists of fisheries gear and packaging materials
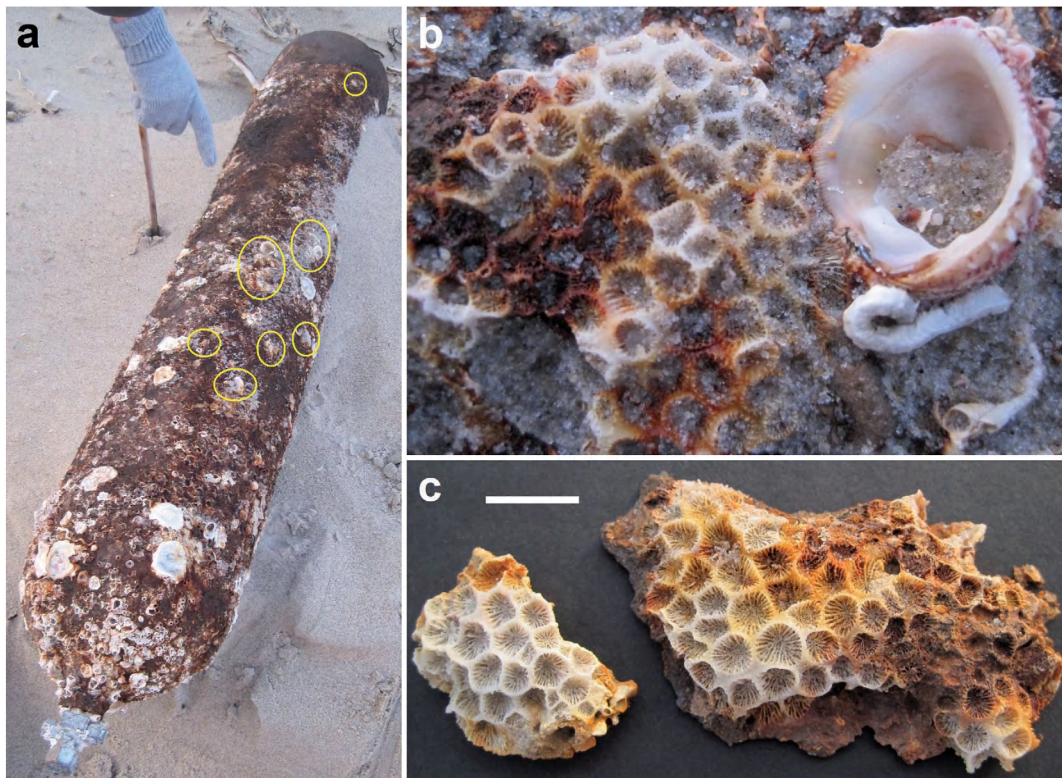
Fig. 1. *Favia fragum*. Gas cylinder (1.5 m long) with remnants of tropical epifauna washed ashore on the North Sea beach of Texel, The Netherlands. (a) The cylinder probably 3 yr after its stranding (positions of corals encircled). (b) Dead encrusting coral on cylinder together with an empty tube of a serpulid polychaete and a shell of the bivalve *Chama congregata*. (c) Specimens removed from their rusty substrate (RMNH Coel. 39909; scale bar: 1 cm)

(Uneputty & Evans 1997, Willoughby et al. 1997, Derraik 2002, Thiel et al. 2003, Taffs & Cullen 2005, Gregory 2009, Ryan et al. 2009).

The growth in man-made flotsam also causes an increase of buoyant substrate for benthic organisms, which has become most evident in areas where it used to be rare (Barnes 2002, Aliani & Molcard 2003). Fouling organisms are able to reach remote coastlines as long as their growing weight does not negatively affect the buoyancy of their substrate. Eventually, long-lasting flotsam can become responsible for the introduction of exotic species (Winston 1982, Winston et al. 1997, Barnes & Fraser 2003, Barnes & Milner 2005). When these exotic species appear to colonize new areas and become harmful to allochtonous species, it is important to know their origin and natural environment for their control.

Recently, several specimens of the brooding amphi-Atlantic reef coral *Favia fragum* (Esper, 1793), together with other fouling animals, were discovered on a gas cylinder that was beached on Texel, the Netherlands, (Fig. 1). Although the corals were dead, they were large enough to tell that they must have sur-

vived for a long time. So far, it has only been hypothesised that the wide distribution range of brooding organisms, and *F. fragum* in particular, may be caused by long-distance dispersal through rafting (Highsmith 1985, Goodbody-Gringley et al. 2010). Based on the species composition of the epifauna of the cylinder, the course of oceanic currents, the size and growth form of the corals, and information on the biogeography and life history of *F. fragum,* we reconstruct a scenario in order to explain how these reef corals were able to reach the temperate coastline of the Netherlands.

MATERIALS AND METHODS

A 1.5 m long, rusty metal gas cylinder covered by abraded encrusting tropical epifaunal remains (Fig. 1a) was examined (29 November 2009) on the North Sea beach of Texel, the westernmost of the Frisian Islands. A report in the local newspaper resulted in comments from readers testifying that the cylinder must have been lying there for at least 3 yr. The epi-

fauna consisted of several specimens of the Atlantic coral *Favia fragum*, barnacles, bryozoans, serpulids, and bivalves. The encrusting corals were removed from the metal cylinder with a knife to enable their identification using a binocular dissecting microscope. They were compared with an illustration of the type specimen of *F. fragum* (Esper, 1793) and with specimens from various localities in the coelenterate reference collection of Netherlands Centre for Biodiversity Naturalis, Leiden Naturalis (catalogued as RMNH Coel. and ZMA Coel.) in order to verify their identity. They were also compared with the types of *F. gravida* (Verrill, 1868), which also has an amphi-Atlantic distribution range (Laborel 1974, Hoeksema 2012). These specimens (YPM 1465a, 1465b, 4549) were sent on loan from the Yale Peabody Museum of Harvard University at New Haven, Connecticut, USA.

After the analysis, 2 beached specimens (Fig. 1c) were deposited in the collection of NCB Naturalis as reference material (RMNH Coel. 39909). We com-pared the distribution range of *Favia fragum* with the course of North Atlantic currents in order to retrace the cylinder's journey. Furthermore we reviewed the life history and habitat requirements of the species and compared these with summer and winter surface seawater isotherms in order to estimate the age of the corals and how far they could have travelled when still alive.

RESULTS

Identity of the beached corals

The beached corals were small ($\varnothing$ < 5.5 cm) and encrusting (Fig. 1). Despite their abraded condition, they could be identified as *Favia fragum* based on skeletal characters when compared to undamaged specimens (Fig. 2). *F. fragum* shows much variation in skeleton morphology (Roos 1971). The corals are usually small ($\varnothing$ < 10 cm), encrusting or massive and
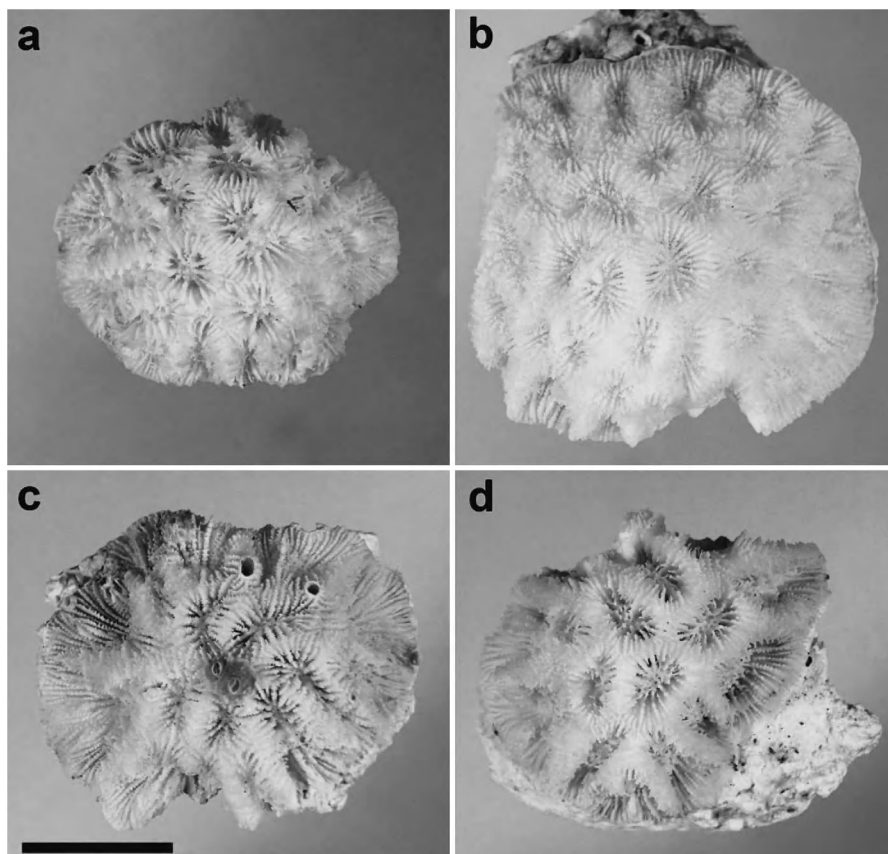

Fig. 2. *Favia fragum*. Morphological similarity of encrusting coral from the West and East Atlantic. Specimens from (a,b) Curaçao, formerly part of the Netherlands Antilles (Piscadera Bay, collected on 18 March 1974; ZMA Coel. 7568) and (c,d) the Cape Verde islands (SW coast of Sao Vicente, San Pedro Bay, collected on 21 June 1982; RMNH Coel. 16978). Scale bar: 1 cm (applies to all panels)
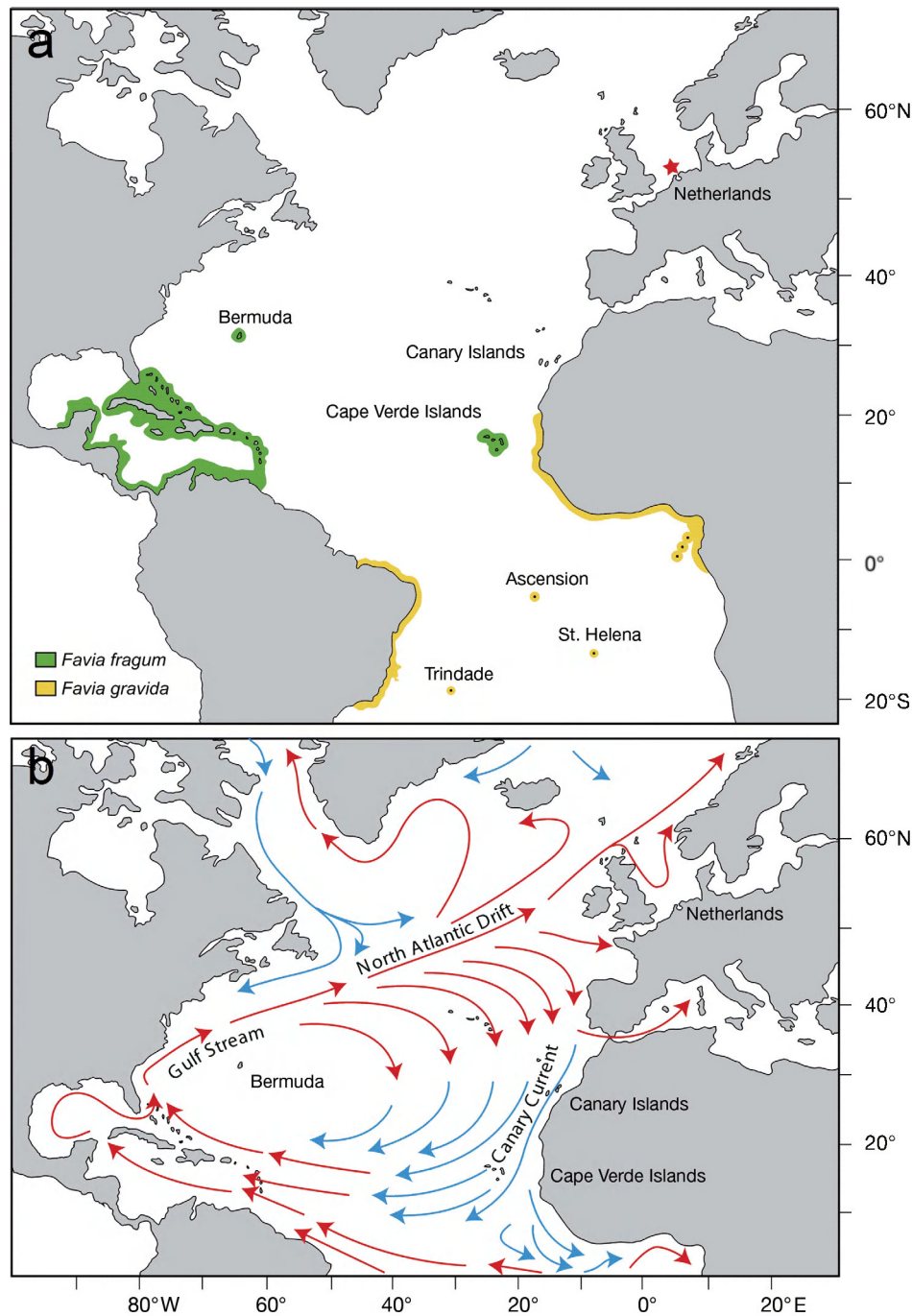
Fig. 3. *Favia fragum* and *F. gravid.* (a) Distribution ranges (after Laborel 1974, Aronson et al. 2008). The location of the dead beached specimens is indicated by a red star. (b) Course of the Gulf Stream and North Atlantic Drift from the Caribbean to western Europe (red = warm water current, blue = cool water current; http://www.noc.soton.ac.uk/rapid/sis/popups/ gulf_stream.php; used with permission from National Oceanography Centre, Southampton; see also USASF 1943)

spherical, with small corallites ($\varnothing < 0.5$ cm), and an irregular septal ornamentation (Roos 1971, Fig. 2). The type of *F. fragum* from 'the southern American seas' (translated from Esper 1795) is missing (Scheer 1990), but Esper's (1793) illustrations are clear enough to confirm the identity of our specimens.

The distribution of *Favia fragum* ranges from the Caribbean and Bermuda (northernmost locality) to the Cape Verde Islands (Laborel 1974, Boekschoten & Borel Best 1988, Fig. 3a). The skeleton morphology does not show clear intraspecific variation between the west and east Atlantic (Fig. 2) and can therefore

not help to indicate the origin of the beached specimens.

The species resembles its congener *Favia gravida*, a predominantly littoral species with longer calices. Both species have amphi-Atlantic distributions but they are genetically distant species (Nunes et al. 2008, 2011) and show no range overlap (Laborel 1974, Hoeksema in press, Fig. 3a).

Origin of the marine fauna on the stranded gas cylinder

The remains of the other epifauna helped to reconstruct its west Atlantic origin (Cadée & Cadée-Coenen 2010). A small bivalve hidden in one of the barnacles belongs to the gray pygmy venus shell *Timoclea grus* (Holmes, 1858), which has a distribution range from Louisiana and the west coast of Florida to the Atlantic coast of Florida and North Carolina, southeast USA (Tucker Abott 1954, Warmke & Tucker Abott 1961, Turgeon et al. 2009). Representatives of 2 other bivalves belong to species with a subtropical amphi-Atlantic distribution: the crested oyster *Ostrea equestris* (Say, 1834) and the corrugate jewelbox *Chama congregata* (Conrad, 1833). Shells of bivalves with an even wider, more northward Atlantic distribution range were also present, i.e. *Hiatella arctica* (Linnaeus, 1767) and *Gastrochaena dubia* (Pennant, 1777). The barnacles covering large parts of the cylinder belong to *Balanus trigonus* Darwin, 1854, originally a Pacific species but now dispersed worldwide in the subtropical seas as fouling on ships (Cadée 2011). The subtropical species represented on the gas cylinder, in particular *Favia fragum* and *T. grus*, have overlapping distribution ranges in southern Florida.

DISCUSSION

The Gulfstream track

Within the geographical range of *Favia fragum*, the Cape Verde Islands are the closest locality to the Netherlands (Fig. 3a). However, it is doubtful that the Texel specimens came from there because there are no oceanic currents that confirm such a track (Fig. 3b). Based on the course of the Gulf Stream and the North Atlantic Drift and the range overlap of the associated fauna on the cylinder, the most likely origin would be southern Florida. The corals could also have settled in the Caribbean, after which the cylinder became inhabited by the bivalve *Timoclea grus* at the southeastern coastline of the USA along the Gulf Stream track (Fig. 3b). Various estimates have been made regarding the expected time interval for passive eastward long-range dispersal from the southeastern USA to western Europe, ranging at least 14 to 18 mo (Guppy 1917, Cadée 2008, Bonhommeau et al. 2009), but if the cylinder would have entered the Columbus gyre, the expected travel time could have lasted 3 yr extra or more (Ebbesmeyer & Scigliano 2009). The corals themselves were not overgrown by other organisms (like barnacles), which indicates that they may have been dead for a short time when the cylinder washed ashore.

Settlement and age of rafting corals: a life history

In order to be a successful rafter a species needs a life-history strategy that facilitates settlement on floating substrates, and it has to live long enough to reach a suitable destination. The brooding coral *Favia fragum* is a simultaneous hermaphrodite with high rates of self-fertilization during lunar cycles of gametogenesis and planulation (Szmant-Froelich et al. 1985, Brazeau et al. 1998, Gleason et al. 2001, Carlon 2002, Goodbody-Gringley 2010). Planulation is monthly throughout the year in the Caribbean (Szmant 1986, Soong 1991) or seasonal at higher latitude (Bermuda), usually taking place before the water temperature reaches its maximum (Goodbody-Gringley & de Putron 2009). Therefore the corals on the cylinder must have settled when the cylinder was in close proximity to a reef where planulation took place, most likely year-round.

Favia fragum larvae survive only a few days after release. They are initially phototaxic but become rapidly negatively buoyant and settle on dark surfaces in clusters close to their parents (Lewis 1974a,b, Carlon & Olson 1993, Carlon 2002, Petersen et al. 2007, Norström & Sandström 2010). They prefer horizontal, flat, uneven surfaces for settlement (Petersen et al. 2005a,b, 2007). Because the cylinder was floating (reaching not deeper than 1.5 m), the larvae probably settled on it when they were still phototaxic. The cylinder may already have been rusty at that time (Fig. 1), providing the larvae with a rough surface for attachment. In shallow water, the cylinder may have been touching the reef bottom but during its journey in open water, it could have been deeply submerged and perhaps in vertical position considering its heavy weight.

The corals on the cylinder were relatively large (5.5 cm). In their first 2 to 4 yr *Favia fragum* corals grow rapidly, after which they grow more slowly (Vaughan 1916). They have been estimated to grow 16 mm in diameter per year in a growth range from 11 to 27 mm (Van Moorsel 1988). They have a fast generation turnover and can become fertile within 1 yr, implying that they reach maturity when they are still very small with even marginal polyps able to produce gonads (Soong & Lang 1992, Petersen et al. 2007). The maximum corallum size in *F. fragum* is smaller (<10 cm) in comparison with many other Atlantic coral species and appears to be related to its reproductive strategy as a brooder (Vaughan 1916, Soong 1993). They start to die when they reach a size at which other species are considered juveniles (Edmunds 2000). The corals on the cylinder may have been about 3 yr old when they died, which would have given them more than enough time to survive up to 14 to 18 mo and cross over the Atlantic. If they had reached a suitable habitat, they may also have been able to reproduce soon after due to early maturity and self-fertilization.

Rafting opportunities: substratum and depth preferences

In order to use rafting as a means for long-range dispersal, *Favia fragum* must be able to live on floating substrates. *Favia fragum* is able to grow on many kinds of shallow water substrates (<15 m, predominantly <3 m depth), including inland waters (Roos 1971, Bak 1975, Carlon 2002). They generally grow on solid substrate remote from sand, which may even consist of erect branches of alcyonarians (Kissling 1965). *F. fragum* has been found growing on mangrove prop roots but with no mention of potential buoyancy and dispersal (Roos 1964, 1971, Rogers 2009). Their larvae can settle on thalli of the calcareous green alga *Halimeda opuntia*, although it is not expected that recruits will reach adult size due to the short life span of the thallus segments (Nugues & Szmant 2006). Because the species occurs at both sides of the Atlantic, it may use firm floating substrates for long-distance dispersal, which is supported by the present observation.

Adult *Favia fragum* corals may resist exposure to air and high temperatures, enabling them to survive in shallow water heated by the sun (Vaughan 1916, Mayer 1917). On the other hand, their larvae cannot endure long exposure to elevated seawater temperature (31°C) (Randall & Szmant 2009). If they settle on the shaded side of a floating substrate, recruits risk exposure to air and sunlight if the drifting substrate rolls over. Nevertheless, corals of this shallow-water species are well able to resist heat exposure and show much intraspecific morphological variation, which enables them to survive in various environments (Roos 1971, Carlon & Budd 2002).

Eventually, rafting corals die when they reach cold water and they are not successful colonizers unless their offspring reach a suitable substrate first. Edinger & Risk (1994) considered *Favia fragum* cold-tolerant compared to other Caribbean corals. Adult *F. fragum* are also able to endure cold water (14°C) for short periods but not without damage (Mayer 1914), which agrees with the general pattern that Atlantic reef corals are sensitive to temperatures below 16°C (Burns 1985). This implies that the range limits for *F. fragum* depend on seasonal temperature fluctuations (Fig. 4). They may survive travel longer in the summer than in winter, but eventually they are limited by minimum winter temperatures. In their present range, Bermuda in the West Atlantic appears to be the coldest area where they persevere, with a minimum temperature of 20°C (Figs. 3 & 4), whereas surface water in the more southward Cape Verde Islands in the East Atlantic is about 22°C.

Natural substrates of rafting corals

Jackson (1986) argued that the wide distribution ranges of brooding Atlantic reef corals (including *Favia fragum*) can only be explained by rafting. Some reef corals are known to become floatable after exposure to air without a floating substrate (Kornicker & Squires 1962). Although, driftwood in the form of trees is used by many rafting organisms (Thiel & Haye 2006), this has not yet been observed for corals. A likely natural substrate for rafting reef corals is volcanic drift pumice (Jokiel 1984, 1989, 1990a,b, Jokiel & Cox 2003), which has indeed been reported from the North Atlantic (Binns 1972) and may stay afloat long enough to enable dispersal by rafting (Whitham & Sparks 1986, Bravo et al. 2011). Dead unattached corals may become buoyant due to gas production and become rafting substrates themselves (DeVantier 1992).

Rafting corals on man-made substrates

There is little information on rafting by corals on anthropogenic substrates. All available records concern dead specimens. Boekschoten & Borel Best
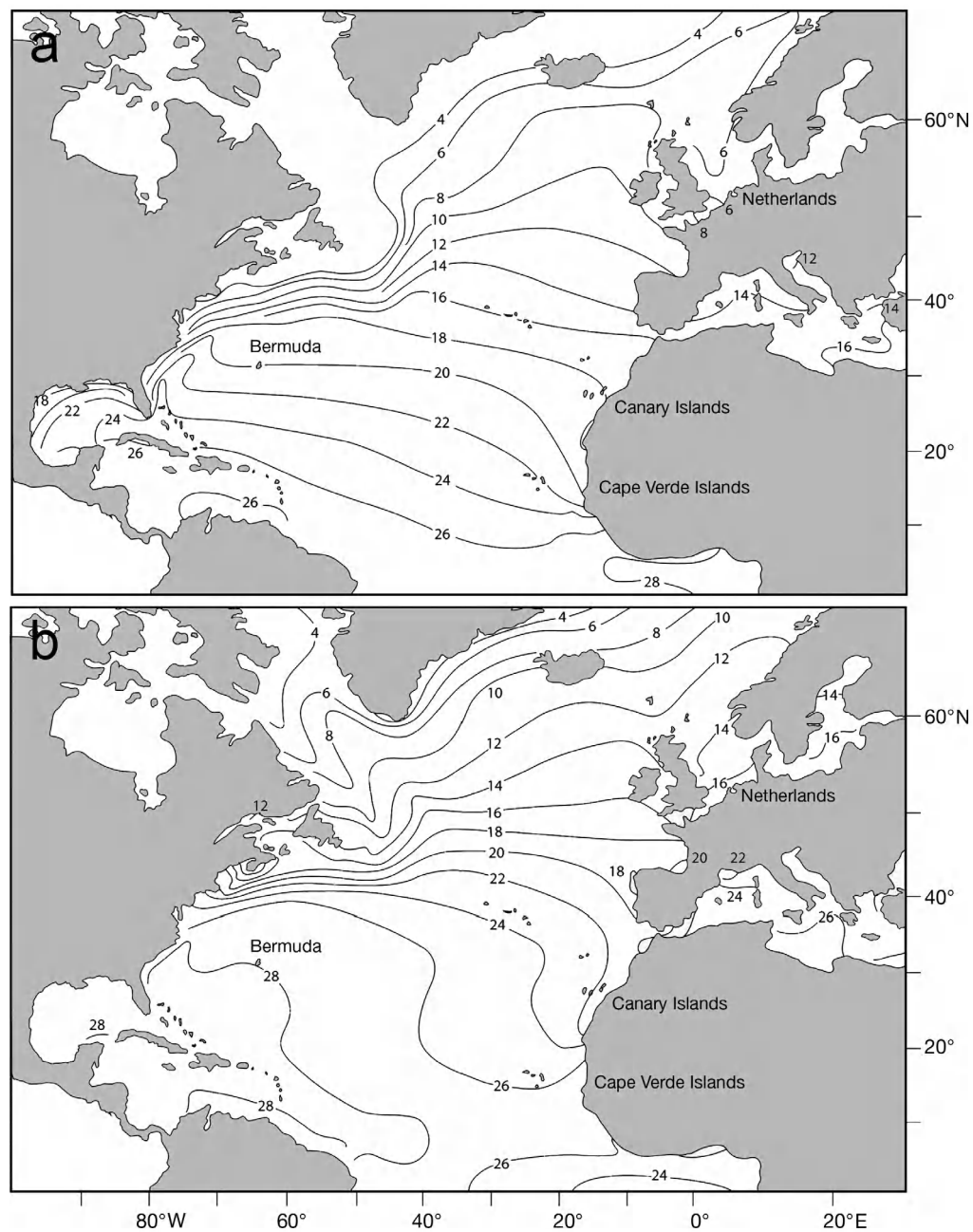
Fig. 4. (a) Winter (February) and (b) summer (August) isotherms of surface water in the northern Atlantic (source Cambridge et al. 1987)

(1988) argue that the presence of dead *Favia* corals on Brazilian cobbles along Cape Verdian coastlines can be explained by their use as ballast in salt vessels from Brazil. They resemble *F. gravida* corals from the coast of West Africa and Brazilian waters (Laborel 1974, Amaral & Ramos 2007).

The present case of *Favia fragum* corals reaching the Netherlands is the first record of a tropical zooxanthellate coral species for the North Sea. Previous records of scleractinians in the Netherlands (e.g.

Adema 1987, 1995) concern dead specimens of Northeast Atlantic species (Zibrowius 1980), like azooxanthellate Devonshire cup corals, *Caryophyllia smithii* Stokes & Broderip, 1828, on various plastic objects and a piece of bitumen, and specimens of *Thalamophyllia gasti* (Döderlein, 1913) on a glass fish net buoy. These records suggest that man-made objects may serve well as substrates for corals, which may enlarge their chances for long-distance dispersal.

Rafting corals and sea water warming

Rising seawater temperatures will cause summer and winter sea water surface isotherms to shift towards higher latitudes, which may facilitate the settlement of zooxanthellate corals in areas where they previously did not occur. Recent examples of range shifts among reef corals concern species occurring along continuous coastlines (Florida, West Australia, Japan), possibly through larval dispersal (Precht & Aronson 2004, Greenstein & Pandolfi 2008, Yamano et al. 2011). Examples of non-indigenous corals that showed range expansion after settlement are Indo-Pacific azooxanthellate *Tubastraea* species entering the West Atlantic, most likely as fouling on ships or oil rigs (Fenner & Banks 2004, Hoeksema et al. 2011, Mantelatto et al. 2011). An example of a zooxanthellate coral invading European waters is *Oculina patagonica* De Angelis, 1908, which is presumed to be of temperate Atlantic-South American origin. It has been recorded in the Mediterranean since 1966, where it probably arrived by a ship because it was first found in and around harbours (Fine et al. 2001, Sartoretto et al. 2008). An example of a tropical zooxanthellate coral settling in subtropical water is the hydrocoral *Millepora* in the Canary Islands, where the seawater is reported to range between 18 and 25°C (Clemente et al. 2010), whereas earlier sources mention 18 to 22°C (Cambridge et al. 1987, Earle, 2000). *Millepora* corals are known to use pumice as rafting substrate (Jokiel 1989), which may also have been the case in the Canary Islands. A winter temperature of 18°C is warmer than the tolerance limit of 16°C for Caribbean corals (Burns 1985) and certainly for *Favia fragum*, which is considered more cold-tolerant than many other reef coral species (Edinger & Risk 1994). With rising seawater temperatures the Canary Islands would indeed be a likely candidate for the settlement of reef corals drifting across the Atlantic (Fig. 4).

CONCLUSIONS

The present case indicates (1) that brooding reef corals can survive for periods that are long enough to enable long-distance dispersal through rafting, (2) that the availability of man-made flotsam may contribute to this, and (3) that seawater warming may help brooding reef corals to expand their ranges towards regions that at present are still considered subtropical.

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