

FIRST REPORT OF *QUINQUELOCULINA CARINATASTRIATA* (WIESNER, 1923) (FORAMINIFERA) ALONG THE FRENCH ATLANTIC COAST (MARENNES-OLÉRON BAY AND ILE DE RÉ)

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ABSTRACT

Large populations of the living benthic foraminifera *Quinqueloculina carinatastriata* (Wiesner, 1923) are reported for the first time from intertidal mudflats of the French Atlantic coast (Marennes-Oléron Bay and Ile de Ré). Maximum abundance of living specimens was recorded in early autumn. The species was previously described from the Adriatic and Tyrrhenian Seas (central Mediterranean Sea) and reported from the Eastern Mediterranean and Red Seas, as well as tropical and subtropical regions. A survey of available literature to trace records of the species in muddy shallow habitats along the western coasts of Europe and Africa reveals that the species is unrecorded from the Western Mediterranean Sea and is unknown in the eastern Atlantic Ocean from the Ivory Coast to Denmark, including the British Isles. This supports the hypothesis that the species has been accidentally introduced outside its natural range as a probable result of mariculture trade and/or shipping activities. This is the first report of a successful introduction of a non-indigenous benthic foraminifera to the Atlantic coast of Europe.

INTRODUCTION

The foraminifera *Quinqueloculina carinatastriata* (Wiesner, 1923) was first reported in the Adriatic Sea (Wiesner, 1923) and later in the Mediterranean Sea from the Eastern Mediterranean to the Tyrrhenian and Adriatic Seas (e.g., Daniels, 1970; Cimerman and Langer, 1991; Avşar and others, 2001; Debenay and others, 2005; Bernasconi and others, 2006). The species has also been reported in tropical and subtropical areas, such as Xisha Island, China (Zheng, 1979); the Indian River, Florida (Buzas and Severin, 1982); and the Papuan Lagoon, New Guinea (Haig, 1988). Belonging to the difficult group of striate miliolids, the species might have been included in other striate or costate miliolids by some authors, and confusion with similar-looking *Q. tasmanica* Albani, 1978 is possible. Nevertheless, none of the striate species previously reported from the European Atlantic coast has characteristics similar enough to these species to lead to an incorrect identification (e.g., Le Campion, 1968; Rosset-Moulinier, 1972; Redois and Debenay, 1996; Debenay and others, 2001; Cearreta and others, 2002a; Cearreta and others, 2002b; Arminot du Chatelet and others, 2005; Ruiz and others, 2005; Morvan and others, 2006).

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The objectives of the present study were twofold: (1) to elucidate the taxonomic status of *Quinqueloculina* populations recently sampled on intertidal mudflats of the Marennes-Oléron Bay and Ile de Ré (French Atlantic coast), and (2) to evaluate the hypothesis that the species has been accidentally introduced into these sheltered bays outside its native range. The latter was evaluated through a literature synopsis to trace records of the species in similar muddy habitats along the Mediterranean, Western African and Western European coasts. This biogeographic approach was combined with a review of introduction pathways, particularly those that are known to be involved in the successful transportation of non-indigenous species into the Marennes-Oléron Bay.

ENVIRONMENTAL SETTING

The Marennes-Oléron Bay and Ile de Ré are located on the French Atlantic coast north of the Gironde estuary (Fig. 1). The Marennes-Oléron Bay is a semi-enclosed bay with large intertidal areas dominated by muddy sediments (Sauriau and others, 1989) and devoted to the cultivation of the Pacific oyster *Crassostrea gigas* (Thunberg) (Goulletquer and Héral, 1997). The bay is Europe's largest production area for the Pacific oyster, which was introduced during the 1970's, after the Portuguese oyster, *C. angulata* (Lamarck), was decimated by a viral disease (Grizel, 1989). Oyster culture was extended to the northern parts of Ile de Ré, mainly in sheltered habitats characterized by muddy and muddy-sand sediments (Faure, 1969).

The nearest major seaport handling international cargo is the Port de La Rochelle-Pallice, which is located north of the Marennes-Oléron Bay and east of the Ile de Ré (Fig. 1). From 1993 to 1995, Masson (2003) classified the ballast of cargo vessels arriving in the port based on the last port of call (i.e., probable source of ballast waters and/or sediments). Although most of the vessels originated from the northeast Atlantic coasts, a few were from other areas: 7% originated from the Mediterranean and Black Seas and 2% were from subtropical and tropical regions, including the Atlantic and Indian Oceans and the Red Sea (Masson, 2003; Masson, communication, 2006). Nowadays, the Port de La Rochelle-Pallice is the largest in Europe for the importation of tropical wood from northwest Africa, South America, the Caribbean, Ile de La Réunion and Indonesia. Fertilizers are also imported and come mainly from the Arabian Peninsula (Subdivision Port Hydrographie et Dragage, 2006).

MATERIALS AND METHODS

The foraminiferal samples of this study were collected as part of a benthic survey performed to describe changes in

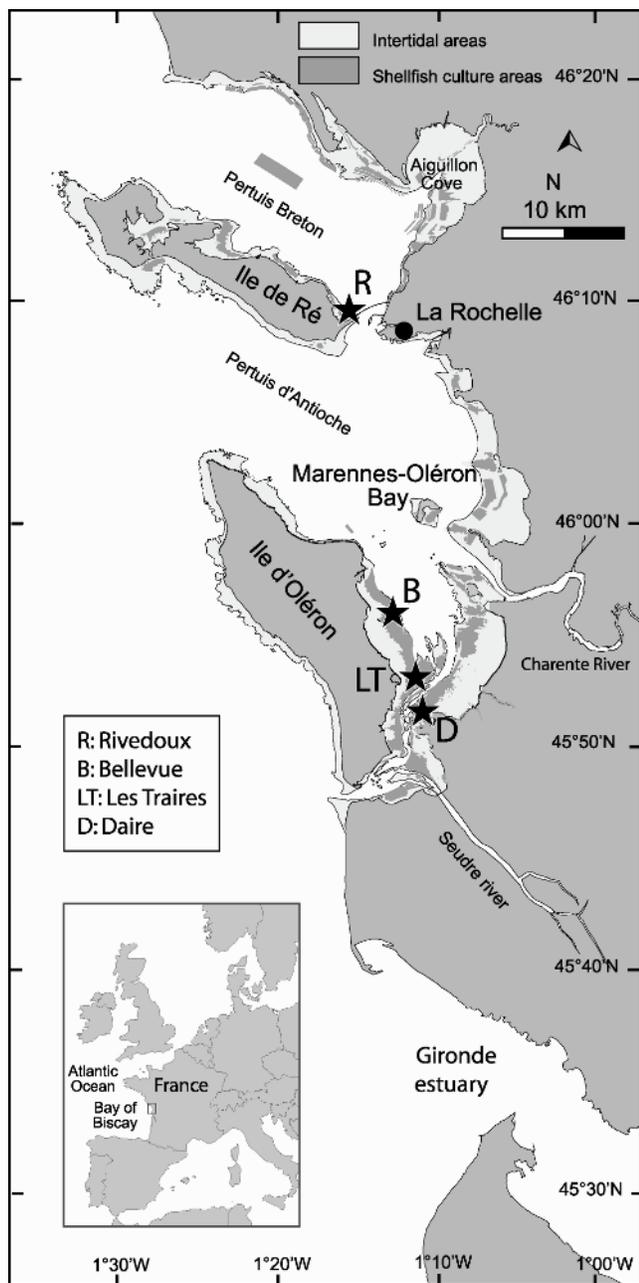


FIGURE 1. Map of the Marennes-Oléron Bay and Ile de Ré with location of the sampling sites at Bellevue (B), Les Traires (LT), Daire (D) and Rivedoux (R).

benthic foraminiferal assemblages under the influence of oyster cultures. Thirty-two samples were collected at four intertidal sites in March, June, September and December 2004. Sampling sites were located at Bellevue (B), Les Traires (LT) and Daire (D) from the Marennes-Oléron Bay and Rivedoux (R) from Ile de Ré (Fig. 1). At each sampling site, samples were taken from both oyster parks (off- and on-bottom culture) and oyster-free areas (control).

At the time of sampling, water salinity was measured at each station. In order to determine grain size distribution at each sampling site, sediment samples were collected in March 2004. Using a pseudo-replication method (Hurlbert, 1984), the uppermost layer of the sediment (5 mm) was

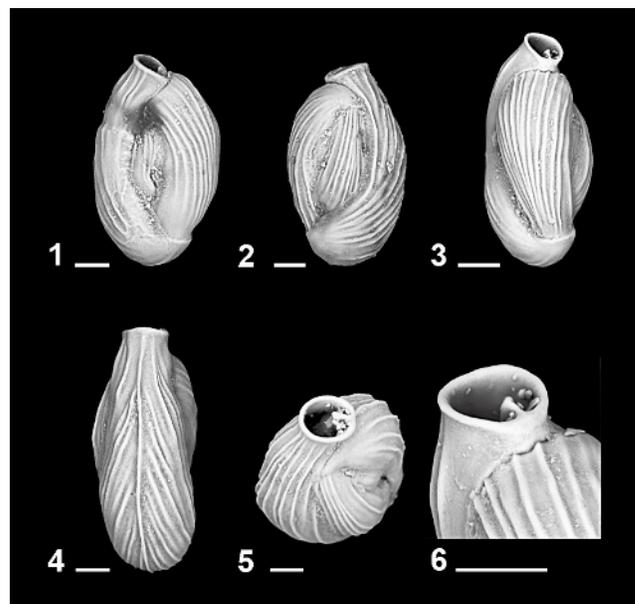


PLATE 1

SEM microphotographs of *Quinqueloculina carinatastriata* from Les Traires, France, September 2004 (scale bar: 50 μ m): 1 Ventral view; 2 Dorsal view showing chambers arranged in a quinqueloculine pattern; 3 Left view showing costae running obliquely on the chambers; 4 Carinal view; 5, 6 Apertural view showing a small peristomial lip and a small tooth, slightly bifid at the tip.

scraped off and kept in 70% alcohol mixed with seawater for foraminiferal study.

Sediment analyses were conducted using a laser granulometer (Malvern Instruments; grain size from 0–800 μ m). The weight values of each size were expressed as percentages. The sediments were classified according to their sand-mud (mud = silt + clay) ratio (Folk, 1954).

In the laboratory, “living” foraminifera were identified following rose Bengal staining (Walton, 1952). After drying of the sediment, foraminifera were concentrated by flotation in carbon tetrachloride. More than 150 dead foraminifera and 150 living (stained) foraminifera were collected and identified in each sample and the abundance of each species (number of stained foraminifera in 50 cm^3 of sediment) was determined.

Specimens of *Quinqueloculina carinatastriata* were collected for detailed taxonomic studies. Scanning electron microphotography was performed on living (stained) specimens of *Q. carinatastriata* with a FEI Quanta 200F scanning electron microscope after samples had been coated with gold.

SYSTEMATIC POSITION

The classification follows that of Loeblich and Tappan (1987).

- Order FORAMINIFERIDA Eichwald, 1830
- Suborder MILIOLINA Delage and Hérouard, 1896
- Family HAUERINIDAE Schwager, 1876
- Genus *Quinqueloculina* d'Orbigny 1826
- Quinqueloculina carinatastriata* (Wiesner, 1923)

Adelosina milletti Wiesner var. *carinata-striata* Wiesner in Wiesner, p. 76–77, Pl. 14, figs. 190, 191.
Quinqueloculina carinatastriata (Wiesner) in Buzas and Severin, Pl. 2, figs. 11–13.

TABLE 1. Morphological characteristics of *Quinqueloculina carinatastriata* (Wiesner, 1923) and *Q. tasmanica* Albani, 1978 as reported in previous studies (vertical descriptions on the right margin are common characters of both species).

***Quinqueloculina carinatastriata* (Wiesner, 1923)**

Wiesner, H., 1923; Pl. 14, figs. 190–191

The type description of Wiesner for *Adelosina milletti* var. *carinata-striata* mentions oblique costae and a carina. It does not describe the aperture, but illustrates a rounded aperture with a rim in figure 191. The tooth is not discernible. In figure 1b of the type species *A. milletti*, the tooth is small and simple.

Zheng, S., 1979; Pl. 5, figs. 4a–c.

Aperture with a rim and a long, simple tooth at the inner margin and a short, simple tooth at the outer margin.

Buzas, M. A., and Severin, K.P., 1982; Pl. 2, figs. 11–13.

Aperture with a rim and a small, simple tooth.

Haig, D. W., 1988; Pl. 5, figs. 6–8.

Tests laterally somewhat compressed, with a long neck, aperture with a small rim. Seems to be close to *Q. tasmanica*.

Haig, D. W., 1988; Pl. 5, figs. 9–10.

Larger tests inflated, aperture with a rim, simple tooth.

Cimerman, F., and Langer, M. R., 1991; Pl. 20, figs. 1–4.

Inflated chambers, periphery carinate in juveniles and truncate in adult specimens; aperture rounded. The figures show a simple tooth, inflated at its tip rather than a real T-shaped tooth as mentioned by the authors.

***Quinqueloculina tasmanica* Albani, 1978 (= *Quinqueloculina poeyana carinata* Albani, 1974)**

Albani, A. D., 1974; Pl. 1, figs. 4–6.

The type description of Albani mentions an elongated test, chambers with a rounded periphery, the apertural end slightly extended, with a small lip and a small bifid tooth. The ornamentation consists of a series of longitudinal costae.

However, according to Haig (written communication, 2007), the holotype of *Q. tasmanica* has a laterally compressed test, an elongate neck, an oval-shaped aperture with a small simple tooth.

Baccaert, J., 1987; Pl. 47, figs. 4a, 4b.

Larger tests inflated, aperture with a rim, weak carina, simple tooth that seems slightly inflated at its end.

Baccaert, J., 1987; Pl. 47, figs. 5a–c.

Smaller tests compressed, elongate neck, aperture with a rim, strong carina, simple tooth that seems slightly inflated at its end.

Hottinger, L., Halicz, E., and Reiss, Z., 1993; Pl. 32, figs. 1–9.

Ornamentation ranging from fine longitudinal striations to strong costae, aperture with a rim and a simple tooth slightly inflated at its end.

Yassini, I., and Jones, B. G., 1995; fig. 217.

Aperture with a small rim and a simple tooth.

Aperture terminal, rounded or oval-shaped, produced on a neck
longitudinal costae meeting at the periphery, forming a carina.

Quinqueloculina poeyana carinata Albani in Baccaert, Pl. 47, figs. 4a, 4b.

Quinqueloculina carinatastriata (Wiesner) in Haig, Pl. 5, figs. 9–10.

Adelosina carinata-striata Wiesner in Cimerman and Langer, Pl. 20, figs. 1–4.

Cycloforina (?) *carinata* (Albani) in Hottinger, Halicz and Reiss, Pl. 32, figs. 1–9.

Adelosina carinata striata Wiesner in Debenay, Millet and Angelidis, Pl. 1, fig. 15.

Description. Specimens collected from both the Marennes-Oléron Bay and Ile de Ré have chambers arranged in indistinctly quinqueloculine patterns with 3–5 chambers visible from the exterior (Pl. 1). About 12 costae run obliquely along the chambers and may unite peripherally. A carina may run longitudinally on the last chamber from the neck to the aboral end of the test. The aperture is terminal, generally at the end of a short neck, bordered by a small peristomal rim, with a small tooth, somewhat inflated, slightly bifid at the tip. Great variability occurs in ornamentation and the size of the rim and carina.

Remarks. Our specimens show some similarities with the Atlantic striate species *Quinqueloculina poeyana* d'Orbigny, 1839. However, the neotype of this species, illustrated by le Calvez (1977), has parallel costae without a carina and an aperture that is almost flush with the surface and provided with a bifid tooth. Thus, our specimens cannot be placed into *Q. poeyana*. They closely resemble two species that are somewhat confused in the literature: *Q. carinatastriata* (Wiesner, 1923) and *Q. tasmanica* Albani, 1978 (Table 1).

The two species have common characteristics, mainly longitudinal costae meeting at the periphery where they form a carina and an aperture produced on a neck, generally with a simple tooth that is

sometimes somewhat inflated at its tip. Their main differences are the lateral compression and the longer neck of *Quinqueloculina tasmanica*. However, Haig (written communication, 2007) considers that variations in the neck length may be intraspecific. The same author (Haig, 1988) placed morphotypes similar to *Q. tasmanica* into *Q. carinatastriata* (Pl. 5, figs. 6–8), even when they have the long neck typical of *Q. tasmanica* (Haig, written communication, 2007). The specimens from Marennes-Oléron Bay and Ile de Ré closely resemble the specimens from the Great Barrier Reef assigned to *Q. poeyana carinata* (now renamed *Q. tasmanica* Albani, 1978) by Baccaert (1987, Pl. 47, figs. 4a, b) and the specimens from the Red Sea figured by Hottinger and others (1993, Pl. 32, figs. 1–9) as *Cycloforina* (?) *carinata* (Albani). They are also similar to the specimens from the Papuan Lagoon, New Guinea, assigned to *Q. carinatastriata* by Haig (1988, Pl. 5, figs. 9, 10), to *Adelosina carinatastriata* figured by Cimerman and Langer (1991, Pl. 20, figs. 1–4) from the Adriatic Sea, and to *A. carinata striata* figured by Debenay and others (2005, Pl. 1, fig. 15) from the Aegean Sea. Owing to their inflated chambers and relatively short neck, we chose to attribute our specimens to *Quinqueloculina carinatastriata* (Wiesner, 1923).

RESULTS

Salinity and grain size distribution are reported in Table 2. Salinity ranged from 30.2 psu at Daire to 32.5 psu at Rivedoux, and sediments from the study site were composed of more than 80% mud (<63 µm).

TABLE 2. Water salinity and grain size distribution of surface sediments at Bellevue, Les Traires, Daire and Rivedoux during the sampling period.

Study site	Bellevue		Les Traires		Daire		Rivedoux	
	Off-bottom	Control	On-bottom	Control	Off-bottom	Control	Off-bottom (site 1)	Off-bottom (site 2)
SALINITY								
Range	31.2–32.2		31.1–32.1		30.6–32.4		31–32.5	
GRAIN SIZE DISTRIBUTION								
Sand	0.6%	15.4%	9.3%	11.5%	1.8%	17.4%	4.2%	7.3%
Mud	96.1%	81.4%	85.8%	85.9%	95%	77.6%	92%	89.6%
Silt								
Clay	3.3%	3.2%	4.9%	2.6%	3.2%	5%	3.8%	3.1%
Textural group	Mud	Sandy mud	Mud	Sandy mud	Mud	Sandy mud	Mud	Mud

Quinqueloculina carinatastriata was found in fourteen of thirty-two samples from the Marennes-Oléron Bay and Ile de Ré (Fig. 1). Living individuals were collected only in September and December in all the sampling sites (Fig. 2). The highest abundance of about 2500 living individuals of *Q. carinatastriata* in 50 cm³ of sediment was recorded in September in the oyster-free zone of Les Traires and constituted up to 54% of the living foraminiferal assemblage at this site. Individuals were free living in the sediment.

The main living foraminiferal species associated with *Quinqueloculina carinatastriata*, ordered by decreasing abundance, were as follows: *Ammonia tepida* (Cushman), *Criboelphidium excavatum* (Terquem), *Haynesina germanica* (Ehrenberg), *Brizalina striatula* (Cushman), *Hopkinsina pacifica* Cushman and *Q. seminula* (Linné) at all sites, *Criboelphidium gunteri* (Cole) at all sites but Daire, *Stainforthia fusiformis* (Williamson) at all sites but Bellevue, *Textularia earlandi* Parker at Les Traires and Rivedoux,

Cornuspira involvens (Reuss) at Les Traires, and *Eggerelloides scabrus* (Williamson) at Rivedoux.

DISCUSSION

Along the northeast Atlantic coast, the only striate or costate species with a morphology related to *Quinqueloculina carinatastriata* is *Q. jugosa* Cushman, 1944 (e.g., Redois and Debenay, 1996; Cearreta and others, 2002a; Cearreta and others, 2002b; Ruiz and others, 2004; Ruiz and others, 2005; Debenay and others, 2006; Morvan and others, 2006). Nevertheless, the two species can be easily distinguished based on the almost parallel costae and the absence of a carina that characterize *Q. jugosa* but not *Q. carinatastriata*. Among the species that have some morphological similarity with *Q. carinatastriata*, Le Campion (1970) reported one specimen of *Q. costata* Terquem, 1878 (renamed *Q. tenagos* Parker, 1962) in the Bassin d'Arca-chon, south of the study area, but he did not provide an

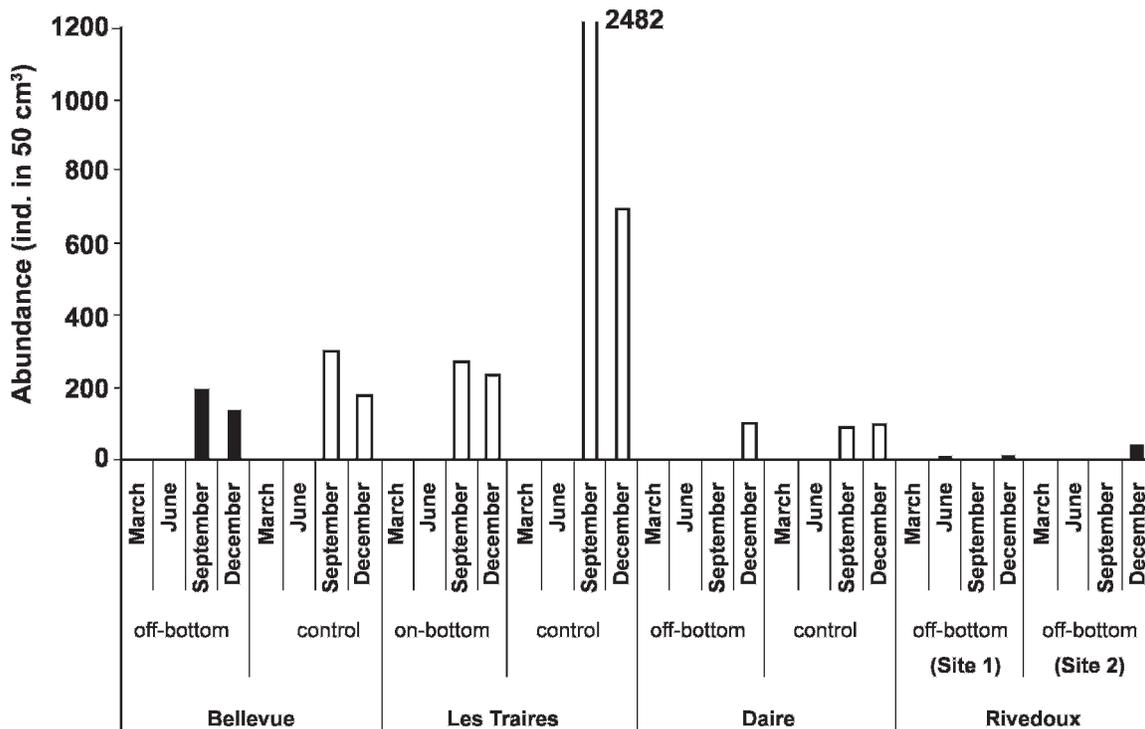


FIGURE 2. Abundance of living (stained) *Quinqueloculina carinatastriata* (number of stained individuals in 50 cm³ of sediment) at Bellevue, Les Traires, Daire and Rivedoux on March, June, December and September 2004 (black: oyster park; white: control).

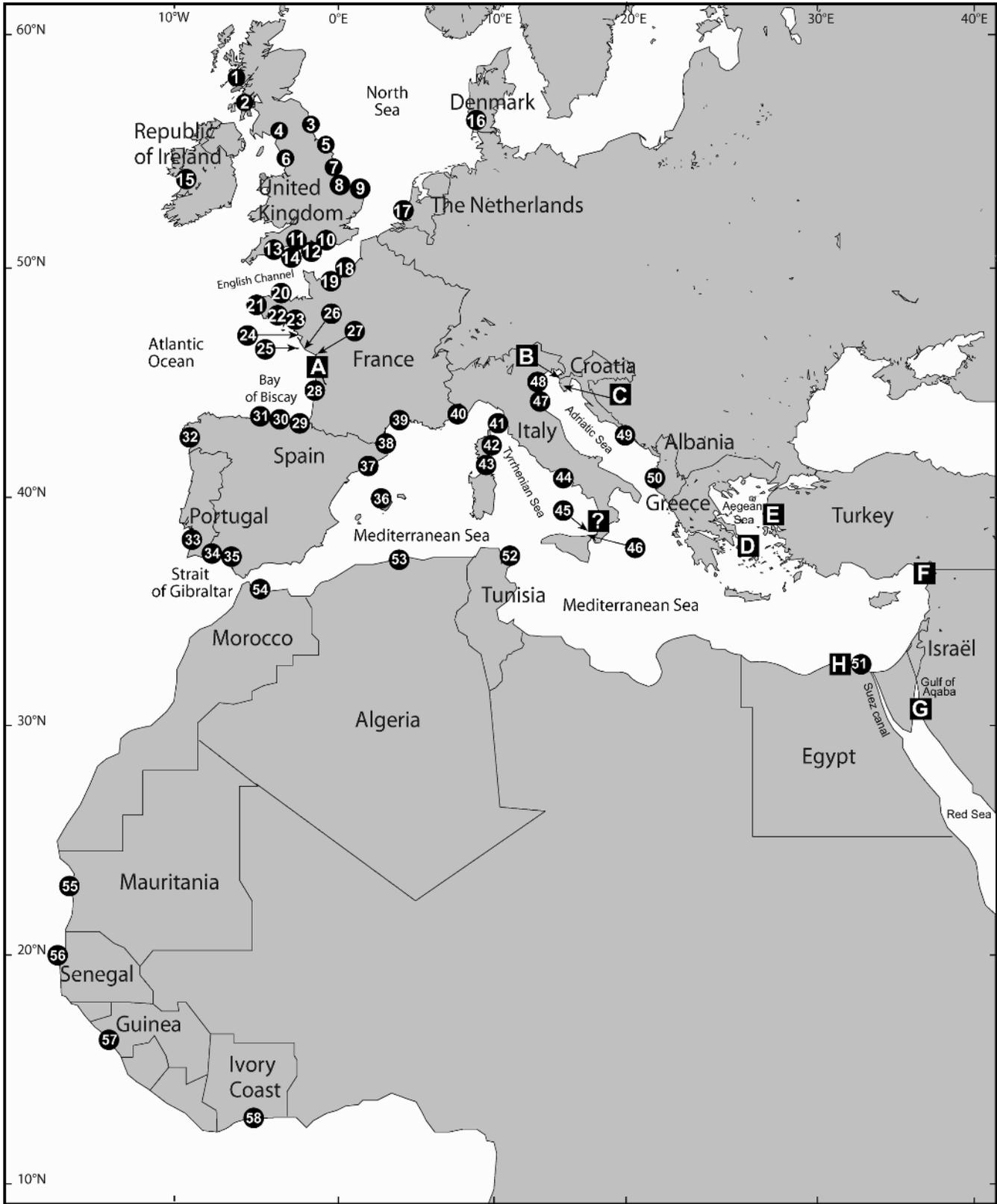


FIGURE 3. Location of previous studies on foraminiferal faunas in similar habitats where *Quinqueloculina carinatastriata* was mentioned (filled square) or not mentioned (filled circle). **MENTIONED:** A present study; B Bay of Piran (Cimernan and Langer, 1991); C Istrian Peninsula (Wiesner, 1923; Daniels, 1970); D Naxos Island (Langer, written communication, 2007); E Gulf of Kalloni (Debenay and others, 2005); F Iskenderum Bay (Avşar and others, 2001); G Gulf of Aqaba (Hottinger and others, 1993); H Alexandria Harbour (Bernasconi and others, 2006). **MENTIONED BUT NOT ILLUSTRATED:** ? Gulf of Policastro (Sgarella and others, 1983). **NOT MENTIONED:** 1 Kentra Bay, 2 Training Bay, 3 Alnmouth Marsh, 4 Nith estuary,

illustration of this single specimen, which might belong to *Q. jugosa*. One of the specimens illustrated by Terquem (1878, Pl. 6, fig. 3) is closely related to *Q. poeyana*, but the other ones are quite different, hence the concept of this species is rather confused (Le Calvez and Le Calvez, 1958).

According to previous studies (Fig. 3), *Quinqueloculina carinatastriata* has been reported from the Red Sea (Hottinger and others, 1993), the Eastern Mediterranean Sea along the Egyptian and Turkish coastlines (Avşar and others, 2001; Bernasconi and others, 2006), the Aegean Sea (Debenay and others, 2005) and in several localities within the Adriatic and Tyrrhenian Seas (Wiesner, 1923; Daniels, 1970; Cimerman and Langer, 1991). However, our literature survey failed to detect any record of the species in coastal lagoons of the Western Mediterranean Sea or in intertidal or shallow subtidal habitats of the Atlantic coasts of Western Africa and northwestern Europe (Fig. 3). The current, disjunct, geographical distribution of *Q. carinatastriata* with only one Atlantic record of a well-established population, which is located far from the natural pathway between the Atlantic Ocean and the Mediterranean Sea (Strait of Gibraltar), supports the conclusion that the species is not native to the Atlantic coast and has been introduced into the Marennes-Oléron Bay and Ile de Ré.

Gouletquer and others (2002) stated that the Marennes-Oléron Bay and coastal areas in the vicinity of La Rochelle are particularly exposed to the introduction of non-indigenous species (NIS): at least 40 NIS have been reported in Marennes-Oléron Bay and adjacent areas from a total of 104 NIS recorded along the English Channel and French Atlantic coast since the beginning of the 19th century. However, the list provided by Gouletquer and others (2002) does not include any non-indigenous foraminiferal species and neither do the synopses of Leppäkoski and others (2002), nor Streftaris and others (2005), for NIS across European waters. Similarly, the current 1032 records of the database, Delivering Alien Invasive Species Inventories for Europe (DAISIE; Gollasch, 2006), do not include any non-indigenous foraminiferal species (Gollasch and Gouletquer, written communication, 2006). Worldwide, few non-indigenous foraminiferal species with naturalized populations in recipient regions have been reported to date (e.g., McGann and others, 2000), and just one non-indigenous foraminiferal species is currently known from

the North Sea (Hayward and others, 2004). As these North Sea specimens came from populations suspected of having been introduced by transoceanic ships (McGann, written communication, 2006), this would constitute the first case of a successful introduction of a non-indigenous foraminifer into European waters. Consequently, the present results on *Quinqueloculina carinatastriata* would constitute the second described case of a successful introduction of non-indigenous foraminifera into European waters and the first described case on the European Atlantic coast.

Apart from species deliberately introduced for aquaculture purposes, the main vectors of NIS introductions are ballast waters and/or ballast sediments, ship hull fouling and accidental releases linked to shellfish activities (Carlton, 1992; Gollasch, 2002; Leppäkoski and others, 2002; Gollasch, 2006). For instance, among the documented NIS introductions into the Marennes-Oléron Bay and adjacent areas, 14 species have been introduced via ballast waters and/or ship hull fouling and 16 as accidental releases linked to mariculture (Gouletquer and others, 2002). Ballast waters discharged from ships are recognized as a primary vector for global transport of non-indigenous aquatic species (Smith and others, 1999; Gollasch, 2002). Among transported invertebrate taxa in ballast waters, foraminiferal species are not rare (Gollasch and others, 2002) and have been recorded on numerous occasions all over the world (McGann and others, 2000; see the review of Drake and others, 2001). Similarly, Gollasch (2002) reported at least nine examples, including five NIS, of benthic foraminifera transported in ballast tank sediments of ships visiting German ports. Because *Quinqueloculina carinatastriata* is reported from tropical and subtropical areas, it could not be definitively excluded that living specimens of *Q. carinatastriata* might have been transported by transoceanic ships. Shellfish industries have also led to numerous human-mediated dispersal of NIS (Carlton, 1992; Gouletquer and others, 2002). Easy transportation of sediments and associated living organisms along with molluscs for aquaculture has been reviewed by Wolff and Reise (2002). Transfers of commercial molluscs, such as the European flat oyster *Ostrea edulis* Linné, the Pacific oyster *Crassostrea gigas* and the Manila clam *Ruditapes philippinarum* (Adams and Reeve), have been plentiful between Mediterranean and Atlantic shellfish areas (Sauriau, 1991; Gou-

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5 Cowpen Marsh, 6 Roudsea Marsh, 7 Welwick Marsh, 8 Brancaster Marsh, and 9 Thornham Marsh (Horton and Edwards, 2006); 10 Hamble estuary (Alve and Murray, 2001); 11 Keyhaven Marsh, 12 Bury Farm, 13 Arne Peninsula, 14 Newton Bay, and 15 Rusheen Bay (Horton and Edwards, 2006); 16 Ho Bugt (Gehrels and Newman, 2004); 17 Dutch tidal flats and salt marshes (Hofker, 1977); 18 Authie estuary (Debenay, communication, 2007); 19 Bay of Seine (Moulinier, 1967); 20 Northern Brittany, and 21 Western Brittany (Rosset-Moulinier, 1972); 22 Southern Brittany (Redois and Debenay, 1996); 23 Gulf of Morbihan (Duchemin and others, 2005); 24 Bay of Bourgneuf (Morvan and others, 2006); 25 Ile d'Yeu (Debenay and others, 2001); 26 Vie estuary (Debenay and others, 2006); 27 Aiguillon cove (Armynot du Chatelet and others, 2005); 28 Arcachon Bay (Le Campion, 1968); 29 Bilbao estuary (Cearreta and others, 2000); 30 Plentzia estuary (Cearreta and others, 2002b); 31 Santoña estuary (Cearreta, 1988); 32 Ria de Vigo (Diz and others, 2006); 33 Santo André lagoon (Cearreta and others, 2002a); 34 Odiel estuary (Ruiz and others, 2004); 35 Huelva coast (Ruiz and others, 2005); 36 Balearic Islands, and 37 Cataluna coasts (Mateu, 1970); 38 Bay of Banyuls (Véneç-Peyré, 1984); 39 Prévost Lagoon (Favry and others, 1998); 40 Bay of Villefranche (Le Calvez and Le Calvez, 1958); 41 Elba Island (Langer and Schmidt-Sinns, 2006); 42 Diana and d'Urbino lagoons (Guelorget and others, 1999); 43 Lavezzi Islands (Langer and others, 1998); 44 Gulf of Naples (Sgarella and Moncharmont Zei, 1993); 45 Vulcano (Langer, 1988); 46 Milazzo (Langer, written communication, 2007); 47 Goro Lagoon (Coccioni, 2000); 48 Gulf of Venice (Albani and others, 1998); 49 Mljet Lakes (Vanicek and others, 2000); 50 Karavasta, Narta and Butrinti (Guelorget and others, 2000b); 51 Manzalah and Edku lagoons (Samir, 2000); 52 Tunisia coasts (Langer, written communication, 2007); 53 Bou Ismail Bay (Moufli-El-Houari and others, 1999); 54 Nador lagoon (Guelorget and others, 2000a); 55 Cap Timiris, 56 Senegalian estuaries and lagoon, 57 Kaloum peninsula, and 58 Ebrie lagoon (Debenay and others, 1987).

letquer and Héral, 1997). Particular attention should be drawn to the development of the Manila clam industry in Adriatic lagoons since the mid 1980's, because Italy has become the leading European producer of clams in the last decade (Flassch and Leborgne, 1992; Breber, 2002). As a number of accompanying NIS have been attributed to the Manila clam trade (Gofas and Zenetos, 2003), a convincing argument has been recently given by Simon-Bouhet and others (2006) using mitochondrial gene sequences from the gastropod *Cyclope neritea* Linné, one of the NIS species reported from the Marennes-Oléron Bay and Ile de Ré by Gouletquer and others (2002). This species has extended its range northward along the French Atlantic coast since the 1980's (Sauriau, 1991), and mitochondrial analyses have revealed that it was the result of multiple introductions from its Mediterranean native range, particularly from the Eastern Adriatic Sea. All sampled populations of *C. neritea* from Marennes-Oléron, Ile de Ré and Brittany appeared to have been mixed with haplotypes recorded from Eastern Adriatic lagoon populations (Simon-Bouhet and others, 2006) as the result of Manila clam exchanges. Since *Q. carinatastriata* populations of this study have been sampled from intertidal areas where *C. neritea* has been previously recorded (see details in Sauriau, 1991; Bouchet and Sauriau, unpublished data), it is likely to have been introduced in sediments associated with shellfish imported from the Adriatic Sea.

Our specimens have been found in mud facies, as reported by Wiesner (1923) and Haig (1988) in their studies in the Istrian Peninsula and in the Papuan Lagoon, respectively. The large population of *Quinqueloculina carinatastriata* (2500 living individuals in 50 cm³ of sediment) shows that this species has found favorable conditions for its growth and reproduction along the French Atlantic coast. Maximum abundance of living individuals in September suggests a massive reproduction event during the summer, when water and superficial sediments at low tide were the warmest, reflecting the origin of the species from warmer climates, which seems to corroborate Mediterranean and/or tropical-subtropical origin. The same timing of reproduction has been reported for other macrofaunal NIS originating from warmer regions and introduced into the Marennes-Oléron Bay and Ile de Ré in similar intertidal habitats, such as the Mediterranean gastropod *Cyclope neritea* (Sauriau, 1991; Simon-Bouhet and others, 2006). Newly introduced populations of *C. neritea* have also benefited from the warming of coastal waters within the Marennes-Oléron Bay during the last two decades (Sauriau, 1991; Soletchnik and others, 1998). Finally, the process of acclimatization and naturalization of NIS from warmer regions into temperate recipient regions with active shellfish activities and shipping ports is likely to continue in the present era of climate warming.

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