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Barnacles (Cirripedia, Balanomorpha) in Belgian waters, an overview of the species and recent evolutions, with emphasis on exotic species

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Abstract

In the present article an overview is given of all the recent Cirripedia Balanomorpha mentioned for Belgian waters with an appraisal of their present status and possible new evolutions. Historical data are reviewed, and completed with data from recent research and additional fieldwork.

A recent and remarkable increase of the number of species belonging to the Belgian fauna was noted. The causes for this augmentation are discussed.

Although some other species were mentioned, it appears that only 3 species were common in Belgium until World War II: *Semibalanus balanoides*, *Balanus crenatus* and *B. improvisus*. The former 2 are boreo-arctic species and can be considered as indigenous to the region. The latter is probably an early immigrant into European waters. During World War II, the New Zealand barnacle *Elminius modestus* reached Europe as fouling on ships of the Allied Powers. Nowadays, this species is the most common barnacle in Belgian waters. In 1996, *B. amphitrite* was discovered at several places along the Belgian coast. This cosmopolitan warm water species is now common in suitable habitats. During a recent study from buoys off the Belgian coast, 6 additional species were found: *B. reticulatus, B. variegatus, B. trigonus, Megabalanus coccopoma* and *M. tintinnabulum*, which are mainly cosmopolitan species living in tropical or warm temperate waters, and *B. perforatus*, a Lusitanean species apparently spreading to the south. For the time being these species are still rare and their occurrence is restricted to the specific habitat of the offshore buoys.

Introduction

The most recent checklist of the Belgian cirriped fauna (VAN FRAUSUM 1989) enumerates only five Balanomorpha: *Elminius modestus* (DARWIN, 1854), *Semibalanus balanoides* (LINNAEUS, 1767), *Balanus crenatus* BRUGUIÈRE, 1789, *B. improvisus* DARWIN, 1854, and *B. balanus* (LINNEAUS, 1758). In a recent study of the barnacle fauna occurring on buoys off the Belgian coast, KERCKHOF & CATTRIJSSE (2002) found not less than 11 species, several new to the Belgian fauna, some even new to the North Sea. Of this 11 species, only 2 are definitely native to the Belgian fauna.

All over the world's seas many barnacle species are extending their geographical range, spreading to regions where they did not occur before (ZULLO 1992). The main cause of this phenomenon is shipping. With the increase of transcontinental shipping activities, the dispersion probability of species augmented. As a result, many exotic species reached European waters, as fouling, in ballast or bilge water, or in association with aquaculture activities. Especially barnacles, well-known fouling species, took advantage of the opportunity to reach new regions which they successfully colonised (BISHOP 1951, SOUTHWARD 1975). As NEWMAN & ROSS (1976) stated: "we are living in the age of barnacles".

But the augmentation of the species number has also to do with recent climatic changes favouring the establishment of warm water species, the investigation of special habitats like buoys and harbours and a better taxonomic insight.

Given the recent evolutions within the Balanomorpha and their world-wide expansion, more changes in the Belgian balanomorph barnacle fauna could be expected.

Historical overview

Who ever wants to study barnacles cannot disregard "A monograph on the subclass Cirripedia" by DARWIN (1854). In this monumental work, DARWIN presents detailed descriptions of all species known to him at that time, including many new ones. Until this milestone publication, reliable records of even common species were scarce. Due to the difficult accessibility of this publication, it lasted until 1895 before the 3 most common species occurring in Belgian waters were properly recognised.

From the distribution given by DARWIN (1854) for several species, it is possible to conclude that some of them are likely to occur in the North Sea, thus also along the Belgian coast. For one species, the newly described *Balanus improvisus* (DARWIN, 1854), he mentions, though with a question mark, the presence in Belgium. However, VAN BENEDEN (1861), who was the first to give a list of the Belgian crustacean fauna, only mentions one balanomorph species namely *Balanus ovularis*. As he had no access to the work of Darwin, he clearly mixed up under this name at least *S. balanoides* and *B. crenatus*. Subsequently, PELSENEER (1881a & b, 1882) added two more species namely *B. perforatus* BRUGUIÈRE, 1789 and *Megabalanus tintinnabulum* (LINNEAUS, 1758). As he

too did not have the publication of DARWIN at his disposal, he stated that he was not able to distinguish between the white intertidal species, although he noticed the occurrence of several species.

Next, LAMEERE (1895) listed four species. He was the first to make the difference between *S. balanoides* (LINNEAUS 1758), *B. crenatus* BRUGUIÈRE, 1789 and *B. improvisus*, being the 3 common intertidal species occurring at that time. In addition, he also included *B. balanus*. In his checklist of the Dutch and Belgian fauna, MAITLAND (1897) made some sort of synthesis, including all the species being known to him at that time from the coasts of Belgium and the Netherlands. For this compilation, he heavily relayed on work done by HOEK (1876) for the Dutch barnacle fauna. Considering the Belgian fauna, he simply listed all the species mentioned in former publications. Thus, he enumerated seven species for the southern North Sea. Besides the species already mentioned above, he added *Chirona (Balanus) hameri* (ASCANIUS, 1767). MAITLAND noted however that *B. perforatus* was only known from Belgium and that *M. tintinnabulum* and *C. hameri* were only occasional records.

In the first half of the 20th century, the Belgian barnacle fauna received little or no attention. During World War II, there was the introduction of the New Zealand barnacle *Elminius modestus* (DARWIN, 1854) in Europe (BISHOP 1947, CRISP 1958). This species rapidly spread along the European coasts in the next decades. LELOUP & LEFEVERE (1952) confirmed its presence in Belgian waters. Next, VAN FRAUSUM (1989), who produced the most recent checklist of the Belgian cirriped fauna, listed only five balanomorph species: *E. modestus*, *S. balanoides*, *B. crenatus*, *B. improvisus,* and *B. balanus*. She based her checklist on samples collected during a survey along the Belgian coast in 1985 and on the collections of the Royal Belgian Institute of Natural Sciences. After the publication of the checklist by VAN FRAUSUM (1989), KERCKHOF (1997) discovered yet another exotic species: *Balanus amphitrite* DARWIN, 1854. Finally, in their recent study of the barnacle fauna occurring on buoys off the Belgian coast, carried out between November 1997 and November 1999, KERCKHOF & CATTRIJSSE (2002) found 11 species.

In addition to the more usual hard substrates like harbours, groins, buoys, etc., one very specific habitat has to be mentioned: floating objects. They form a very suitable habitat for barnacles and provide a way for their spreading. Many such objects can be found on Belgian beaches originating from the region itself or coming from farther away. Some of the species mentioned above are common on these floating objects. Apparently, no exotic species have been encountered on them, but during the last decades there were several findings of *Solidobalanus fallax* (BROCH, 1927) (KERCKHOF 1997a & b).

This raises the maximum number of barnacle species effectively found or mentioned as possibly occurring in Belgian waters to 14. It is clear that not all of them belong to the Belgian fauna. In the following, the current status of the Balanomorpha in Belgian waters is reviewed. The boundaries of the Belgian waters used here coincide with these of the Belgian Continental Shelf as defined under the 1982 Law of the Sea Convention (MAES *et al.* 2000). They slightly differ from the ones often used in earlier publications on the Belgian marine fauna, e.g. BACKELJAU (1986). On the other hand, a certain species is considered as effectively belonging to the Belgian fauna, if it occurs within the 12 nautical mile limit zone (approximately 22 km), *i.e.* the Belgian territorial sea.

Chirona hameri (ASCANIUS, 1767)

C. hameri is a North Atlantic deepwater species (NEWMAN & ROSS 1976, Zullo 1979). NILSSON-CANTELL (1978), who gives more detailed spreading charts for the North Sea, indicates its occurrence in the southern North Sea namely the Pas de Calais near Belgian waters and off the Dutch Wadden Islands.

Although not explicitly stated by MAITLAND (1897), *C. hameri* was at that time only known from two records of specimens washed ashore on the northern Dutch coast (HOEK 1876). Apart from this early record, there were some findings on northern Dutch beaches during the 20th century, particularly in the 1970's, almost all from the Wadden Islands. As HUWAE (1985) stated, *C. hameri* clearly belongs to the so called trawler-fauna, being species which are occasionally brought in by fishermen. Since NILSSON-CANTELL (1978) probably only used those published records of specimens washed ashore and presumably originating from trawlers, the indication of this species as occurring in the southern North Sea is incorrect.

To my knowledge, there are no observations of this species neither on Belgian beaches nor in Belgian waters. Moreover, during the last century, Belgian fishermen presumably brought in *C. hameri* only rarely. Although it is present in collections of naturalia related to the fisheries (e.g. former collection Paster Pype, collection van Outryve, Oostende), I have never seen any in the last decades.

This species clearly doesn't belong to the Belgian fauna and apparently will not be found in Belgian waters.

Balanus balanus (LINNAEUS, 1788)

This is mainly an arctic boreal deepwater species, although it can occur into the lower third of the intertidal zone. Its distribution encloses the North Atlantic and North Pacific (NEWMAN & ROSS 1976, Zullo 1979). According to the charts given by NILSSON-CANTELL (1978), the distribution of this species is mainly restricted to the central and northern parts of the North Sea and the east coasts of Great Britain. Although absent from the southern North Sea, NILSSON-CANTELL (1978) gives an, apparently verified, record from the Pas de Calais. However, GLAÇON (1971) does not mention this species neither in the fauna of the Boulonnais coast and the eastern Channel, nor in the subsequent additions.

B. balanus is first mentioned by LAMEERE (1895): "on

shells, uncommon''. This species was also collected farther offshore by GILSON during his sampling campaigns ''Explorations de la Mer'' in the early 19 hundreds. The collection of the Royal Belgian Institute of Natural Sciences contains only a few specimens from GILSON's campaigns dating from the beginning of the 19th century. It is not clear yet if these samples are really originating from Belgian waters but VAN FRAUSUM (1989) added this species to her list.

There is a possibility that this species might be present farther offshore on big shells or stones, for example on the boulders or pebbles of the Hinder Banks area, but this needs to be further investigated.

Wall plates of this species are present in many of the sediment samples taken off the Belgian coast (own obs.). This is probably transported or reworked (fossil?) material.

LAMEERE (1895) listed the species probably because at that time fishermen brought it to the Belgian coast. In the early 19 hundreds, fishermen often cleaned their nets on the beaches. It was often present in older collections of naturalia related to the fisheries, mainly on large shells such as *Pecten maximus* or *Neptunea antiqua*. However, to my knowledge, it has never been found washed ashore, certainly not in the past decades. Nowadays trawlers, before interring into port, clean their nets and decks farther offshore, reducing the chance to find specimens of *B. balanus* on the Belgian beaches. HUWAE (1985) also states that this species belongs to the so-called trawler-fauna.

However, there is one autochthonous Dutch record of *B. balanus* (FAASSE 1990). He found a large specimen at very low tide on a basalt stone of a large groin in Vlissingen, near the entrance to the Western Scheldt estuary.

The species has never been found on floating objects reaching the Belgian coast neither was it present on the buoys. So far it has not been found on wrecks off the Belgian coast.

Since this species apparently does not live within the 12 nautical mile zone, *B. balanus* does not belong to the Belgian fauna.

Balanus crenatus BRUGUIÈRE, 1789

This is a boreal species distributed in the North Pacific and the North Atlantic (NEWMAN & ROSS 1976). It has a similar distribution as *B. balanus,* a species it is often associated with.

B. crenatus prefers fully marine conditions and can not withstand long periods of emersion.

Although one of the common species along the Belgian coast and in the North Sea, *B. crenatus* is only first mentioned by LAMEERE (1895): ''on crabs, shells and stones at a certain depth, common''. However it was recognised already earlier from the Dutch coast, e.g. HOEK (1876).

In Belgian waters it is usually found low in the intertidal zone and in submersed conditions, in waters with high salinity. Along the Belgian coast, *B. crenatus* is very common on the various, mainly artificial hard substrata, forming a specific zone and replacing *Semibalanus balanoides*. Further, *B. crenatus* is probably the only common subtidal barnacle in Belgian waters. It is a member of the offshore pebble and boulder community, but it also lives on a variety of other suitable subtidal hard substrata such as wrecks, shells, crustacean carapaces and even Bryozoa such as *Flustra foliacea* and *Alcyonidium* sp. It is common on buoys off the Belgian coast (KERCKHOF & CATTRIJSSE 2002), on which it often grows bigger than on the subtidal substrata. It is also a common member of the fouling community in the Belgian ports and on ships' hulls. Finally it can also be found on floating objects stranding on the Belgian beaches.

This species is native to the North Sea and belongs to the Belgian fauna.

Balanus improvisus DARWIN, 1854

This species is very widespread around the Atlantic and has been dispersed by shipping to many parts of the world, for example into the Indo Pacific and Australasia. As a result, it has now a world-wide distribution in tropical and temperate seas (RAINBOW 1984, LEPPÄKOSKI 1999).

B. improvisus occurs low on the shore and in the sublitoral zone. It is a very euryhaline species able to live, at least as an adult, in fully marine as well as in nearly freshwater conditions. It prefers permanently submersed locations but is apparently restricted to shallow coastal areas or, when occurring farther offshore, to floating structures.

Early reliable records of this species for northwest Europe are scarce, in the first place because DARWIN only properly recognised and described the species in 1845. Moreover, it was difficult for former scientists to distinguish it from other common white barnacle species occurring along the northwest European coasts. But surprisingly, as already stated above, precisely this species is probably the first barnacle ever mentioned for the Belgian coast (DARWIN 1854). In the Netherlands, *B. improvisus* has been recognised by HOEK (1876). As he pointed out, the species was already recorded from Holland as early as in the year 1827. Subsequently, LAMEERE (1895) was the first to mention it for the Belgian fauna.

In Belgian waters, this species is common in harbour environments where it is, especially on the hulls of yachts and other permanently moored vessels and pontoons, often the most common barnacle. However, *B. improvisus* suffers now from some competition with (other) alien species such as the recently introduced *B. amphitrite* and *Elminius*. In more estuarine conditions, where it is the only barnacle, it can also be found typically on submersed structures like reed-stems. In the fully marine littoral region, for example on the groins and dikes, records of *B. improvisus* are very rare, probably due to competition with *B. crenatus*. Only occasionally, some specimens were found in the lower regions of groins, nearby har-

bours (VOLCKAERT, pers. com.). Rather surprisingly, the species was often very abundant on several of the studied buoys, where it occurs together with *Elminius*, and/or *B. crenatus* and *S. balanoides*. The species is sometimes present on floating objects mostly originating from nearby estuaries and harbours.

Considering the question if *B. improvisus* should be regarded as a native species or as introduced to northwest Europe, and in particular to the North Sea, some problems remain to be solved.

For a long time *B. improvisus* has been regarded as native to the European fauna by several Dutch, French and English workers like BASSINDALE (1964) and HUWAE (1985). It is not mentioned by ENO *et al.* (1997). But recently this species is regarded as introduced, mainly in Scandinavian and Baltic publications. In those articles, *B. improvisus* is considered as an introduction from warmer seas (BROCH 1924, NILSSON-CANTELL 1978) or from (North) America (GISLÉN 1950, REISE *et al.* 1999, LEPPÄKOSKI 1999). Several other authors, mainly in compilation works on introduced species, seem to have adopted this view. SOUTHWARD (1958) gives an indication of *B. improvisus* being a species possibly originating from warmer waters and which has adapted to more temperate conditions.

However, as older cases are not always well documented, it is often unclear whether a certain species is really introduced or not. Moreover, it is often difficult to establish the true origin and the moment of introduction. The problem is that before, and even decades after the publication of the work by DARWIN, the species was not properly recognised, as it was difficult to distinguish between *B. improvisus, B. crenatus* and *Semibalanus balanoides*. These are all white, intertidal barnacles of a similar size (VAN BENEDEN 1861, HOEK 1876, PELSENEER 1882). In particular, *B. improvisus* is similar in appearance to smooth specimens of *B. crenatus*.

I recently found *B. improvisus* to be present in archaeological material, amongst food rests, from Antwerpen, Belgium, dating back from the 17th century. This is earlier than the data given by Scandinavian authors like LEPPÄKOSKI (1999) for the introduction of this species. On the other hand I could not ascertain the occurrence of *B. improvisus* in an excavation in Oostende dating from the 9th century. However this does not necessarily mean that the species was not living at that time in Belgian waters or in the broader region of the southern North Sea.

According to DAVADIE (1963) and NEWMAN & ROSS (1976) there were no reliable fossil records of *B. improvisus*. However, MENESINI & CASELLA (1988) found it to be present in the Pliocene of the Almeria Province, Southern Spain. There are apparently no records of the Pliocene around Antwerpen although the barnacles of these layers, rich in fossils, have not been studied thoroughly.

Considering the fact that *B. improvisus* belongs to the *B. amphitrite* group, a group of closely related species (HENRY & MCLAUGHLIN 1975) and well-known foulers with a marked preference for ships' hulls (DARWIN 1854, BROCH 1924, BISHOP 1951, UTINOMI 1960), that are rapidly spreading all over the world, *B. improvisus* may indeed be an introduced species into European waters. If really so, it must have been an early one, probably comparable to *Mya arenaria* LINNEAUS, 1758. This species invaded the European coast probably between the 13th and the 17th century for the second time after its disappearance during the Pleistocene glaciation (STRASSER 1999). One has thus to consider that, as in the case of *M. arenaria*, *B. improvisus* could also be a reintroduced species. Maybe GISLÉN (1950) is right in supposing that *B. improvisus* reached Europe with trading vessels from America.

After its initial and probably early (re)introduction in European waters, the species may have been introduced in the 19th century into the Baltic, where it was spreading during the past decades (GISLÉN 1950, NILSSON-CANTELL 1978, LEPPÄKOSKI 1999). But again, the fact that it may have been overlooked or not recognised has to be kept in mind.

This species can now be considered as belonging to the Belgian Fauna.

Balanus amphitrite DARWIN, 1854

B. amphitrite is a cosmopolitan tropical and subtropical species (NEWMAN & ROSS 1976) that normally occurs intertidally, often in brackish waters (HENRY & MCLAUGHLIN 1975). It is a typical fouling and harbour species, able to withstand low salinity levels (SOUTHWARD 1975, UTINOMI 1960). It is often abundant in habitats exposed to physical stress and pollution (LIPKIN & SAFRIEL 1971, SHKEDY *et al.* 1995, own observations). It is even able to withstand oil covering. In the tropical and subtropical areas, *B. amphitrite* occurs abundantly in the intertidal zone of sheltered coasts, usually below the mean seawater level. In the more northern temperate areas, such as the Japanese and Californian coasts, the species is generally restricted to quiet enclosed bays or harbours (UTINOMI 1960).

The first autochthonous record of this species for Belgium was made in 1995 when it was found on a groin in Koksijde (KERCKHOF 1996). One year later, KERCKHOF (1997c) observed it in the harbours of Oostende and Nieuwpoort.

Today, this species is very common in the harbour of Oostende. It lives on the masonry of the docks and on other harbour constructions. In Oostende this species is competing with the other barnacle species occurring in the docks. It is also present on the hulls of yachts in the docks of the Mercator marina. Especially on the hulls of ships, it competes with *B. improvisus*. In the open marina of Nieuwpoort, the species is present only on the hulls of yachts. Until now, it has not been found in the harbour of Zeebrugge.

Specimens are also regularly present on buoys in Belgians waters, although not in high numbers. It is most common on the buoys close to the coast.

During former years, there were also records of single specimens washed ashore on the beach (own obs., VAN

HAELEN, pers. comm.). Finally, the species is present on floating objects.

Although there are fossil European records of this species, *B. amphitrite* presumably disappeared after the Messinian salinity crisis. Thus, also in the case of *B. amphitrite*, it is unclear where and when it was reintroduced – probably first in the Mediterranean – in Europe (CARRIOL, in prep.). DARWIN (1845) already mentioned the species from the Mediterranean and the Portuguese coast. The first record for the Channel area however dates from the early 19 hundreds (PRENANT 1929).

B. amphitrite was recorded for the first time in the Southern Bight of the North Sea in 1962 (BORGHOUTS-BIERSTEKER 1969). Later, it was found on several other places in the Netherlands (HUWAE 1985). In 1983, the species was observed for the first time in the harbour of Dunkerque (DAVOULT *et al.* 1993) where it is now very abundant in the whole harbour (own obs.). In the eastern Channel, BISHOP (1950) found it in Shoreham in 1937, the most northern observation at that time (CRISP & MOLESWORTH 1951). All of these records were made in harbour environments where the water temperature was artificially raised.

The first French and Belgian records were probably made far too late to deduce the true appearance date of *B. amphitrite* in the eastern part of the Channel and the southern North Sea. Indeed, material from the Royal Belgian Institute of Natural Sciences showed that in 1952 LELOUP collected some specimens near an oyster farm in the harbour of Oostende. These have later been misidentified as *Megabalanus tintinnabulum* and the record remained unpublished.

Along the western European coasts, *B. amphitrite* was considered as a species mainly living in harbours and, in the eastern Channel and the southern North Sea, in environments where the temperature was artificially raised (BISHOP 1950, SOUTHWARD & CRISP 1963, HAYWARD & RYLAND 1999). In contrast herewith, *B. amphitrite* lives in Belgian waters in conditions where the temperature is not artificially raised and even outside harbours, in fully marine conditions. The occurrence on a groin may have been an exceptional event. Here, the competition with the better adapted *Semibalanus balanoides* and especially *Elminius* is too harsh so that it may be difficult for this species to establish viable populations. But the presence of two-year-old and/or gravid individuals on the buoys (KERCKHOF & CATTRIJSSE 2002) indicates that the species is able to reproduce outside harbour areas.

Balanus reticulatus UTINOMI, 1967

UTINOMI (1967) described *Balanus reticulatus* originally from Japan, where it occurred in fully marine conditions (UTINOMI 1967 & 1970). He remarked that it probably had a world-wide distribution due to transportation by ships, but stated that the species was often not recognised due to the resemblance with especially *B. amphitrite*.

It is a well-known circumtropical fouling form (SOUTHWARD 1975, HENRY & MCLAUGHLIN 1975). YAMAGUCHI (1977) noted that in Japanese waters, where *B. reticulatus* and *B. amphitrite* are often occurring together, the former was mainly found on floating objects and sometimes in the lower intertidal region. *B. amphitrite* was more abundant in bays with little oceanic influence, while *B. reticulatus* was dominant in bays facing the open ocean. It is highly probable that *B. amphitrite* was a newcomer in historical age and now is competing with *B. reticulatus*. However, SOUTHWARD (1975) noted that in Caribbean waters, it was less a fouling species than *B. amphitrite* and was mostly restricted to sublitoral conditions, with normal or moderate salinity.

This species was not recorded in the North Sea before the study of the buoys off the Belgian coast. During that survey, 5 living specimens were found on the Kwintebank buoy (KERCKHOF & CATTRIJSSE 2002).

SOUTHWARD & CRISP (1963) already remarked that this species (figured as *B. amphitrite* variety) was a likely candidate for introduction in European waters, due to its occurrence on ships throughout the tropics. In the Mediterranean, it was sampled at the Toulon harbour in 1977, in the fouling community of a ship arriving from the Indian Ocean (ZIBROWIUS 1991). ZEVINA & POLTARUKHA (1999) also recorded it in the Black Sea with the same origin and in analogous conditions. During the summer of 2000, I found many living specimens on the hull of a Belgian Navy vessel one month after its return from the East-Indian archipelago.

Because *B. reticulatus* belongs to the *B. amphitrite* group, it may indeed spread to new regions and even replace other species. However, there are indications that although being a common fouler, it is apparently difficult for this species to establish new populations. Illustrative of this is that it failed to establish in northern Tasmanian and Australian waters (CRANFIELD *et al.* 1998, COUTTS 1999), although it was by far the most common exotic cirriped encountered by COUTTS (1999) in his investigation of the fouling of merchant vessels entering these waters. These observations make a possible establishment of *B. reticulatus*, in analogy with those of *B. improvisus* and *B. amphitrite* in Belgian waters, unlikely.

As yet, I do not regard this species as belonging to the Belgian fauna.

Balanus variegatus DARWIN, 1854

B. variegatus was recorded twice by KERCKHOF & CATTRIJSSE (2002) from 2 buoys off the Belgian coast, respectively in 1997 and 1999. The species had not been observed before in the North Sea.

This Indo-Pacific species, native to the Indo-Malayan region and Australia, is also typically found on man-made structures in rather sheltered bay waters (UTINOMI 1968, FOSTER 1978). Like *B. amphitrite,* it is mainly a harbour species, being able to withstand varying salinities and pollution (HENRY & MCLAUGHLIN 1975).

Similar to the observations of *Balanus amphitrite,* KERCKHOF & CATTRIJSSE (2002) found gravid and two-year-old individuals indicating a potential to maintain

self-sustaining and self-regulating populations within the area.

As yet I do not regard this species as belonging to the Belgian fauna.

Balanus perforatus BRUGUIÈRE, 1789

This species is an eastern Atlantic warm water species, occurring commonly in the Mediterranean (RELINI 1980, KOUKOURAS & MATSA 1998). Its range extends southward to the north-western coast of Africa. Along the English Channel, it occurs up to the Isle of Wight (STUBBINGS 1967).

B. perforatus is a shallow water species, common on wave-exposed shores. It is usually found near the low water mark and does not extend far into the subtidal zone. Near the northern limit of its distribution, it tends to be confined to the sublittoral zone and to embayed locations (BASSINDALE 1964).

PELSENEER (1882) gives autochthonous records from the Belgian coast. He reports finding this characteristic barnacle, although not abundant, in 1882 on the piers of Blankenberge and Oostende. Amongst the common white species of intertidal barnacles, different to *B. perforatus,* the presence of this species was conspicuous. MAITLAND (1897) includes this species in his checklist, defining that *B. perforatus* was only known from Belgium. However, LAMEERE (1895) does not mention the species and it is also omitted in the checklist by VAN FRAUSUM (1989).

In 1982, its presence was noted in the harbour of Boulogne (DAVOULT *et al.* 1993). However, despite intense searching during the past years in the lower intertidal on the artificial substrata along the Belgian coast, I could not find any *B. perforatus*. There are also no Dutch intertidal records.

In the southern North Sea, the species is regularly found on floating objects washed ashore (PELSENEER 1881, HUWAE 1985, own observations). In 1978, it was recorded from buoys off the Dutch coast (BUIZER 1978 & 1980). KERCKHOF & CATTRIJSSE (2002) observed the species twice on buoys in Belgian waters. During occasional investigations of the offshore buoys during the last three years, I have found the species again on one occasion in 2002.

However, it seems improbable that this species will be able to establish important populations along the Belgian coast, e.g. on the groins. In the lower shore regions of the Southern Bight, it could be in severe competition with *B. crenatus* where the latter is the dominant species. The hatching period of nauplii of *B. crenatus* starts earlier and lasts longer than that of *B. perforatus*. The period of settling of the cyprids is also later and shorter in *B. perforatus* (BASSINDALE 1964). This might cause difficulties for *B. perforatus* to establish itself on the groins or other artificial intertidal substrata along the Belgian coast. Furthermore, the groins are not wave beaten enough to let it form stable populations and probably the load of suspended material in the coastal waters of the Southern Bight is also too heavy. But apparently, the offshore buoys can provide a suitable habitat for *B. perforatus*.

It could be that *B. perforatus* spread temporally to the north-east in the last century, that its range declined again short afterwards, and that the species is now once more extending its distribution north-eastwards due to more favourable climate conditions. Therefore, this species should be regarded as a vagrant.

As *B. perforatus* was observed several times in Belgian coastal waters even with gravid specimens, I consider this species as belonging to the Belgian fauna.

Balanus trigonus DARWIN, 1854

This species is a cosmopolitan inhabitant of tropical and warm temperate seas. The species is common in the Mediterranean (RELINI 1980, KOUKOURAS & MATSA 1998). In the eastern Atlantic, the northern limit of its distribution is believed to lie somewhere along the Atlantic coast of the Iberian Peninsula (ZULLO 1992).

B. trigonus is sometimes recorded from intertidal zones but is more common in the sublittoral. It has been found growing on a variety of substrates: on the external skeletons of living invertebrates, inside sponges and sometimes completely covering all sorts of floating objects. It is a euryhaline species but is relatively intolerant to both high and low temperatures (WERNER 1967). In the Mediterranean and on the Atlantic coast of Africa, it often occurs together with *B. perforatus* (ZULLO 1992).

According to ZULLO (1992), the species seems to expand its geographical range northwards in the Atlantic. He suggests that the species was introduced into the South Atlantic in the late 1860's by ships from the Pacific and Indian Ocean and assumes that it was brought to the Central and North Atlantic by whaling ships. DARWIN (1854) did not mention *B. trigonus* from the Mediterranean, where the species was not recorded until the 1920's. It was unknown to the Atlantic and Gulf coasts of the U.S. until the 1950's.

During their survey, KERCKHOF & CATTRIJSSE (2002) found only one empty specimen on an offshore buoy. For the southern North Sea no autochthonous records are available. Only one record of a specimen on a drifting object was made for the Netherlands (ADEMA 1990). As a common biofouler, the species was recorded several times in Great Britain on ships returning from warmer areas and on drifting objects (BISHOP 1947, BASSINDALE 1964).

I do not regard this species as belonging to the Belgian fauna.

Elminius modestus DARWIN, 1954

E. modestus is native to Australia, Tasmania and New Zealand, where it is a common coastal barnacle, avoiding extreme wave beaten conditions. It is often a dominant barnacle in harbour fouling communities (FOSTER 1978). This species reached Europe between 1940 and 1943 (BISHOP 1947, CRISP 1958). In the next decades, it rapidly

spread all over the European coasts and even to other places in the world like South Africa and Japan, but the species is not yet recorded from the Mediterranean (KOUKOURAS & MATSA 1998). The introduction of *E. modestus* in Europe is well-documented.

This species is mentioned for the first time in relation to the Belgian fauna by LELOUP & LEFEVERE (1952). It was observed in 1950, attached to a ship's hull, but it may have been present already earlier.

Elminius is now by far the most common barnacle of the Belgian fauna, occurring in a variety of habitats and competing with all the other species. Also on most of the offshore buoys, *Elminius* is the most abundant species (KERCKHOF & CATTRIJSSE 2002). Only subtidal offshore substrata are not colonised by this species and remain the exclusive habitat of *B. crenatus*. But on the groins, *Elminius* is present in almost the entire intertidal range, excepted the lowest littoral zone. In damp places, *Elminius* even occurs above *S. balanoides*. In contrary to the latter, *Elminius* can be found epizoic on the shells of living *Littorina littorea* in the intertidal zone.

This species thanks part of it success to its great fecundity. Furthermore, the release and settlement of its larvae, although starting later in the season, lasts much longer. Thus, *Elminius* is able to occupy every open space left or arisen for some reason later in the season. This is clearly an advantage on such artificial habitats as ports and groins where space is limited, but where on the other hand the substrate surface is subject to frequent abrading for example by mooring vessels, or, as on the groins, by destruction of the earlier settled specimens due to crowding, smothering or other events.

E. modestus is now a well-established member of the Belgian fauna.

Megabalanus tintinnabulum (LINNEAUS, 1758)

This is a cosmopolitan species in warm seas. According to NEWMAN & ROSS (1978), its distribution is mainly natural.

M. tintinnabulum is one of the best known sessile barnacles and like *Balanus amphitrite* it is a well-known fouling species. For three or four hundred years, it has constantly been brought into almost every port in the world. There are many records from the 18th and 19th century, whereby most specimens originate from fouling on ship's hulls. As such, it is well represented in many museum collections like that of the Royal Belgian Institute of Natural Sciences.

It was thus not a surprise that this cosmopolitan species has been recorded several times washed ashore on the Dutch and Belgian coasts (PELSENEER 1881a & b, HOLTHUIS & HEEREBOUT 1972). Besides obviously looking old, maybe even fossil, specimens – the species is present with beautiful and well preserved specimens in the Pliocene of Antwerpen – several fresh looking specimens have been reported during the past decades, washed ashore on the Belgian coast (own obs.).

Between 1997 and 1999, *M. tintinnabulum* was present on three different buoys off the Belgian coast (KERCKHOF & CATTRIJSSE 2002). Surprisingly, these records were the first autochthonous records for the Belgian coast and also for the southern North Sea, because BUIZER's records of *M. tintinnabulum* (BUIZER 1980) for the Dutch coast were, as KERCKHOF & CATTRIJSSE (2002) pointed out, in fact *M. coccopoma.* Additionally, during 2001, living specimens of *M. tintinnabulum* have been found again on 3 occasions on offshore buoys.

In view of the several findings of this species in Belgian waters, *M. tintinnabulum* can now be regarded as belonging to the Belgian fauna. Interesting is the fact that this species was present on several very near shore buoys making a possible occurrence on the groins likely.

Megabalanus coccopoma (DARWIN, 1854)

M. coccopoma originates from the tropical eastern Pacific coasts of Central and South America. SOUTHWARD & NEWMAN (1977) state that the species has an uncertain distribution, but that it was once possibly endemic to the tropical eastern Pacific. The species has been "successfully" introduced in Southern Brazil (LACOMBE & MONTEIRO 1974). It is a common littoral barnacle found in shallow marine waters (NEWMAN & MCCONNAUGHEY 1987).

KERCKHOF & CATTRIJSSE (2002) found this species on quite a number of buoys and on one occasion in relatively high numbers. These should have been the first records of this species for the North Sea but during the seventies of the past century, *M. coccopoma* occurred already on buoys off the Dutch coast. However BUIZER (1978 & 1980), who reported this findings, failed to make a correct determination. As KERCKHOF & CATTRIJSSE (2002) pointed out, the specimens firstly named by BUIZER (1978) as *Balanus perforatus* and in a later revision of the same material as *M. tintinnabulum* (BUIZER 1980), in fact proved to be *M. coccopoma.*

According to NEWMAN & MCCONNAUGHEY (1987), *M. coccopoma* is a typical fouling species preferring clean man-made structures to settle. It shares this feature with other members of the *Megabalanus tintinnabulum* group. But there are little published records of this species as a hull fouler perhaps due to its restricted distribution or to confusion with other species. NEWMAN & MCCONNAUGHEY (1987) state further that *M. coccopoma* is an unlikely candidate for transport with ballast water.

The first European record of this species was made in 1851 in Le Havre, probably originating from a ship's hull (NILSSON-CANTELL 1932).

Given its restricted distribution, one could argue that the occurrence of this species in the coastal waters is due to the settlement of larvae released by individuals occurring within the area. Indeed, KERCKHOF & CATTRIJSSE (2002) found two-year-old and gravid individuals, a reason to believe that this species has the potential of forming a self-sustaining population within the southern North Sea.

Thus, although *M. coccopoma* was initially a species with a limited distribution, it seems to have a considerable spreading potential as is illustrated with its occurrence in the North Sea.

In view of the several findings of this species in Belgian waters and in the Southern Bight of the North Sea, *M. coccopoma* can now be regarded as belonging to the Belgian fauna.

Semibalanus balanoides (LINNEAUS, 1767)

S. balanoides lives in the intertidal zones of the boreoartic regions of the Atlantic and Pacific oceans (NEWMAN & ROSS 1976, ZULLO 1979).

Along the Belgian coast, *S. balanoides* is very common in the intertidal zone, forming a characteristic belt on hard substrata in the upper shore regions. It occurs also to some extend in harbours, but not in closed docks, where the salinity might be too variable and the pollution too high. In the lower intertidal zone, the species is replaced by *B. crenatus*. Now, *S. balanoides* suffers from severe competition of the alien species *Elminius modestus*. The latter is now forming a broad belt between *S. balanoides* and *B. crenatus*. On the groins, *S. balanoides* can only survive because the one and only settlement of its larvae occurs in early spring, in March, *i.e.* much earlier than the settlement of *Elminius'* larvae. Afterwards *Elminius'* larvae will settle and occupy all free places.

Apart from competition with *Elminius*, *S. balanoides* might also suffer form the changing climate as higher temperatures will affect the level of reproductive output, settlement and recruitment of this species (SOUTHWARD *et al.* 1995).

The species is never present on subtidal structures such as wrecks, stones etc. Records from such habitats are thus erroneous and mainly due to the fact that one of the 2 described forms of *S. balanoides* (DARWIN 1854, STUBBINGS 1975) very much resembles *B. crenatus*. Especially if one disposes only of removed specimens *i.e.* without the calcareous base typical for *B. crenatus*, and without prior noting the presence of such a structure.

On the other hand, *S. balanoides* is sometimes present on floating objects. And rather surprisingly the species was frequently present on the buoys off the Belgian coast, even on those far away (KERCKHOF & CATTRIJSSE 2002). There, the specimens apparently grew much larger than in its usual and well-known intertidal habitat. When looking at the moment of depositing of those buoys on which *S. balanoides* was abundant, they always were laid out early in the year. Also here, the early settlement of this species proves to be an advantage in the competition with the other species.

This species can be regarded as native to the Belgian fauna.

Solidobalanus fallax (BROCH, 1927)

This species is native to the African west coast. SOUTHWARD (1998) discovered it for the first time in European waters in the eastern Channel where it occurred on the shells of *Chlamys opercularis* (SOUTHWARD 1995).

Living specimens of this species are sometimes present on various floating objects originating from the Channel and stranding on Belgian beaches when there is an influx of such material (own obs.).

Although this species may have been overlooked or confused with other barnacle species like *B. crenatus, B. venustus* or *B. perforatus* (SOUTHWARD 1995, KERCKHOF 1997b) it is rather surprising that it was not recorded earlier from other European coasts. Recent investigations made clear that this species is very common along the coasts of Spain, Portugal and the French Atlantic (KERCKHOF, in prep.). Besides on *Chlamys opercularis* and other shells, this species often lives on lobster or crab pots, octopus pots or floating objects. This explains the repeated records of this species during the last decade on floating objects washed ashore on the Belgian beaches.

Discussion

In former days, the Belgian barnacle fauna received little or no attention, at least not the Balanomorpha. Even renowned scientists as VAN BENEDEN and PELSENEER were not able to provide a complete list of the common species occurring along the Belgian coast, leaving the balanomorph barnacles often unnamed, e.g. VAN BENEDEN (1883). This is rather surprising since they were able to provide species records for some Lepadomorpha or Rhizocephala. Obviously, this had nothing to do with a lack of interest, but rather with difficulties encountered while trying to identify correctly the species. The publication by DARWIN (1854) made such identification possible but then, one has to have access to this publication. It lasted until 1895 till the 3 most common species occurring in Belgian waters were properly listed (LAMEERE 1895). HOEK, who made a detailed study of the Dutch barnacle fauna – much resembling the Belgian situation – in the contrary already provided a complete species list for the Dutch fauna in 1875. He clearly had DARWIN's work at his disposal.

Looking at the evolution of the Belgian balanomorph barnacle fauna and abstraction made of those species not really belonging to the Belgian fauna, a rather drastical augmentation of the number of species is noted. Until WW II, only 3 species were common along the Belgian coast, namely *Semibalanus balanoides*, *Balanus crenatus* and *B. improvisus*. During the following half century, 2 additional species (*Elminius modestus* and *B. amphitrite*) managed to establish healthy and self-sustaining populations, while 3 others (*B. perforatus*, *Megabalanus coccopoma* and *M. tintinnabulum*), although much more scarce and apparently restricted to the specific habitat of offshore buoys, can also be regarded as belonging to the Belgian fauna. This makes that the overall number of species belonging to the Belgian fauna increased to 8. Additionally, the specific habitat of offshore buoys yielded autochthonous records of 3 other, not yet estab-

lished, species. There are a number of reasons for this augmentation.

As demonstrated above, the majority of these species are not native. The intertidal and subtidal habitats occurring in Belgian waters originally consist mainly of deposits of soft sediments such as sandbanks and sandy beaches. Therefore, one could argue that, since barnacles are typical foulers on hard substrata in the intertidal zone, in fact all barnacle species occurring along the Belgian coast and the southern North Sea are not native. This statement is not really true. In fact there always existed some natural hard substrata occurring off the Belgian coast, consisting of pebbles and boulders in tide swept areas and sometimes peat. And for some Balanomorpha other living organisms such as crabs can very well act as a substratum for their settlement as it is the case for example for *B. crenatus*. Also in the littoral zone and even without human interference, there were natural hard structures present, e.g. wood trunks, mussel beds, peat. JOCQUÉ & VAN DAMME (1971) found on the now disappeared intertidal peat beds on the beach of Raversijde abundant numbers of *E. modestus* and *B. crenatus*, but no *S. balanoides*. In earlier excavations along the Belgian coastal plain dating around the 9th century, the remains of *S. balanoides* and *B. crenatus* were present (own obs.).

Thus, of the 11 species encountered, only *S. balanoides* and *B. crenatus* are native to the Belgian fauna. Later, due to the construction of many coastal defence works such as groins, dikes and harbours, they became gradually more abundant. Moreover, all these man made constructions, together with others such as buoys and wrecks, provide suitable substrates for several new and exotic species.

This augmentation of the number of balanomorph species due to the occurrence of exotic species is clearly related to shipping. Traditionally, shipping has been considered a major introduction pathway (CARLTON 1998). The amount of transoceanic shipping increased enormously and modern vessels tend to move faster. Cirripedia can be transported as fouling on the hulls of the ships or as larvae in ballast water. The southern North Sea has a dense ship traffic. Off the Belgian coast, there is also an anchorage area where ships await piloting to the harbours of Zeebrugge, Vlissingen or Antwerpen. Larvae may originate from gravid individuals present on the hulls of the waiting ships. Even if treated with antifouling, most vessels are carrying a – sometimes important – fouling community including barnacles. Moreover there are particular regions on ships' hulls like, among others, sea chests, that are very susceptible for fouling (COUTTS 1999).

In the same context, the increasing number of pleasure crafts and yachts form an important spreading pathway. The repeatedly introduction and spreading of *B. amphitrite* is probably due to the movements of pleasure crafts between the various European marinas. I could in many cases observe the presence of this species on the hulls of yachts, some of them coming from the France Atlantic coast and even from the Mediterranean.

But barnacle larvae also may originate from ballast water (e.g. CARLTON 1985, CARLTON & GELLER 1993, LAVOIE *et al.* 1999). In most cases, ships start emptying their ballast water already before entering the coastal zone. Indeed, many of the exotic species are littoral or harbour species that are susceptible to be transported in ballast water. One might question whether, after the long stay in the ballast tanks, the larvae are still viable and able to settle in the new environment. NEWMAN & MCCONNAUGHEY (1987) for instance strongly doubt that *M. coccopoma* is capable of surviving in ballast water.

Over the past decades, the importance of hull fouling as a major vector for the transfer of marine organisms has been overshadowed by the importance of ballast water. But I believe that in the case of barnacles, hull fouling is the most frequently used pathway for introduction.

Besides travelling with ships and favourable physical factors, recent climate changes favour the establishment and survival of subtropical and tropical species in the coastal waters of Europe. There is the phenomenon of global warming (e.g. DELWORTH & KNUTSON 2000). For example, the past decade was the warmest of the century for the North Sea and the mean sea temperatures during the first half of the year have been higher than during the previous three decades (O'BRIEN *et al.* 2000). Consequently, warm water species may survive or reproduce and the larval stage has a better chance of survival and settlement. Small increases in temperature may already cause improved reproduction conditions for some of the species under consideration (PLATEL & CRISP 1960). Yearly and decadal cycles in temperature fluctuations have an effect on the abundance and the occurrence of barnacles (SOUTHWARD 1991, SOUTHWARD *et al.* 1995).

The augmentation of the number of species has also to do with the study of specific habitats. Recent investigations of the fouling in the Belgian harbours revealed the common occurrence of *B. amphitrite* and the study of the offshore buoys (KERCKHOF & CATTRIJSSE 2002, BUIZER 1978) revealed, beside the 5 common coastal species, the presence of 6 additional species, although much more scarce and apparently restricted to this specific habitat. Two of these species, *M. tintinnabulum* and *M. coccopoma*, belonging to the "titinnabulum" group have now been found regularly with mature and gravid individuals. Two other species, *B. reticulatus* and *B. variegatus*, have been found only occasionally, but also with mature and gravid individuals. Considering the expansive behaviour of some other members of the "amphitrite" group to which they belong, one can imagine that they could become more common in the future. Finally, one of the species present on the buoys in the area is a vagrant expanding its range and finding in the buoys a suitable substrate to live. In general, the buoys provide an ideal habitat for barnacles: all species tend to grow faster and become larger.

Another remark that can be made is that, although there is definitely competition due to the increasing number of species – in fact in some harbours alien species are competing with each other – apparently no species are outcompeted yet. Some of the recorded species occur

predominantly in man-made and heavily disturbed habitats. Such substrates are in general very suitable for invasive species (DEN HARTOG & VAN DER VELDE 1987). Due to competition, some species are pressed to more unfavourable habitats like harbours. There, some species are even becoming abundant, like species of the *B. amphitrite* group, although this is obviously not their most favourable habitat. In harbour environments with many man-made constructions, only those species can survive that are able to withstand harsh conditions or very specific condition like low salinities. The often made statement as if they should prefer man-made constructions is not correct. Another relevant fact is that the Atlantic, being the youngest ocean, has had the least time to develop a broad selection of endemic species. Species are still spreading, filling in new unoccupied niches. Man is just fastening this process. More exotic species may thus take advantage of the favourable habitat characteristics of the buoys and the recent climate changes.

Regarding the evolution in the barnacle group and the rapid spreading of several species, all over the world, maybe we can expect that one day or another, other species will be encountered in Belgian waters which could even be able to establish viable populations. There are of course many candidates but especially species from the "tintinnabulum" group such as *M. tulipiformis* (ELLIS, 1758) or from the "amphitrite" group such as *B. eburneus* GOULD, 1841 are possible candidates. We found *M. tulipiformis* along the coast of Portugal and it is known from the Bay of Biscay (KISH 1958). *B. eburneus* has been recorded in the Netherlands (STOCK 1995). This American subtropical species was probably introduced in Europe during the last century. It is now locally common in harbours in Spain and the French Atlantic coast (BISHOP *et al.* 1957, SOUTHWARD & CRISP 1963). The species was also present in 1997 on the hull of a yacht in the harbour of Nieuwpoort that returned from the Caribbean.

A rising of the temperature will lead to latitudinal shifts in the species distribution (SOUTHWARD *et al.* 1995). Apparently this is already demonstrated by the cases of *B. perforatus* and *Solidobalanus fallax*. But this could also be the case for other southern European species, like for example members of the "chthamalus" group. These warm water species reach their north eastern limit somewhere in the entry of the eastern Channel.

New records of species also raise the question as to whether they have been introduced or whether they represent natural extensions in range or have always been present but undetected. Thus it will also be necessary to examine not only fossil, but also archaeological material in order to detect the moment of introduction of some balanomorph species. Fortunately we are dealing with organisms that leave fossil traces easy to study.

Finally, what became also clear is that if we want to be able to detect changes in the distribution of species, it is very important firstly that the autochthonous fauna is well-known and secondly that new introductions are readily and correctly recorded, thus emphasizing the necessity of correct identifications and reliable records. Otherwise such possible underlying processes as climatic changes could not adequately be revealed.

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