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The littorinid fauna of the Belgian coast (Mollusca, Gastropoda)

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Summary

During an intensive survey of the littorinid fauna of the Belgian coast, five species were recorded alive, viz. *Littorina littorea, L. saxatilis, L. obtusata, L. mariae* and *L. neglecta*. The latter two of these are new to the Belgian fauna, but they occur only in very restricted populations. *L. obtusata* shows a local distribution, whereas *L. littorea* and *L. saxatilis* are both very common. For each species occurring in Belgium, detailed information on distribution, habitat and polymorphism is provided. Finally, some topics for further research are outlined.
Key-words : *Littorina*, faunistics, polymorphism, systematics.

Résumé

Durant une étude intensive de la faune littorinide belge, cinq espèces furent rencontrées vivantes : *Littorina littorea, L. saxatilis, L. obtusata, L. mariae* et *L. neglecta*. Les deux dernières sont nouvelles pour la faune belge, mais elles ne se trouvent que dans des populations très limitées. *L. obtusata* montre une distribution locale, tandis que *L. saxatilis* et *L. littorea* sont communes sur toute la côte. Pour chaque espèce belge, des informations détaillées concernant la distribution, l'habitat et le polymorphisme sont fournis. Finalement, quelques sujets pour la recherche future sont discutés.
Mots-clefs : *Littorina*, faunistique, polymorphisme, systématique.

Introduction

According to a recent revision of the classification of the prosobranch family Littorinidae (REID, in press a), the genus *Littorina* FERUSSAC, 1822 occurs only in the northern hemisphere, in both the Atlantic and Pacific Oceans. It comprises about 20 species, which live mainly in the intertidal zone of rocky coasts, but may also be found in estuaries and mangroves. The systematics and taxonomy of this genus of winkles have undergone important changes after the discovery that some classical species are in fact complexes of sibling forms. Two such cases have been described in Europe, viz. the *L. saxatilis* group and the *L. obtusata* group.

L. saxatilis (OLIVI, 1792) was several times split into different species. HELLER (1975) distinguished four species : *L. nigrolineata* GRAY, 1839, *L. neglecta* BEAN, 1844, *L. patula* THORPE, 1844 and *L. rudis* (MATON, 1797). The former species had already been recognised by DEYGLUN (1955) and SACCHI (1974, 1975). All species are rock-dwelling, "rough" winkles. *L. nigrolineata* (oviparous) and *L. neglecta* (ovoviviparous) are now generally accepted (SACCHI, 1975; CAUGANT, 1979: FISH & SHARP, 1985).

L. rudis, however, proved to be a junior synonym of *L. saxatilis* (RAFFAELLI, 1982; S. SMITH, 1982; JANSON, 1985), while *L. patula* seems to be a mixture of *L. saxatilis* and a newly described species, *L. arcana* HANNAFORD-ELLIS, 1978 (RAFFAELLI, 1979a; HANNAFORD-ELLIS, 1978, 1979). The main difference between these two species is that *L. saxatilis* is ovoviviparous, while *L. arcana* is oviparous. The latter is considered a good species by most (e.g. JANSON, 1985), but not all (e.g. CAUGANT & BERGERARD, 1980), littorinologists. Differences between the two species are discussed by WARD & WARWICK (1980), ATKINSON & WARWICK (1983), HANNAFORD-ELLIS (1983, 1985) and WARD & JANSON (1985). Finally, *L. tenebrosa* (MONTAGU, 1803), considered by several authors (e.g. S. SMITH, 1982) as a distinct species, was conclusively shown to be a brackish water form of *L. saxatilis* by JANSON & WARD (1985).

In older publications, the Scandinavian *L. obtusata* (LINNAEUS, 1758) and the British *L. littoralis* (LINNAEUS, 1758) were considered to be distinct species; this is not the case, as shown by COLMAN (1932). As there is considerable doubt about the true identity of *L. littoralis*, this name should be discarded (S. SMITH, 1982). *L. palliata* (SAY, 1821) has also regularly been considered to be a distinct species (e.g. THORSON, 1941). However, COLMAN (1932) and KNUDSEN (1949) proved that this "species" is very near to *L. obtusata* (*s.l.*). Recently, SEELEY (1986) demonstrated that *L. palliata* is just a form of *L. obtusata* (*s.s.*) which has not been subjected to selection by crab predators for a thick and flat shell.

L. obtusata was shown by SACCHI & RASTELLI (1966) to consist of two distinct species : *L. obtusata s.s.* and *L. mariae* SACCHI & RASTELLI, 1966. Both species are oviparous, live on large brown weeds, mainly *Fucus* and *Ascophyllum*, and are now generally accepted as good species (GOODWIN & FISH, 1977). However, REIMCHEN (1981) described two forms of *L. mariae*, which could eventually reflect the occurrence of sibling species within the taxon. Nomenclaturally there also remains a problem, since S. SMITH (1982) stated that *L. mariae* should be regarded as a junior synonym of *L. fabalis* (TURTON, 1825).

Besides *L. obtusata s.l.* and *L. saxatilis s.l.* one other *Littorina* species occurs in NW-Europe : *L. littorea* (LINNAEUS, 1758). Another European intertidal littorinid, *L. neritoides* (LINNAEUS, 1758), is now placed in the genus *Melarhaphe* MENKE, 1828 (REID, in press a). *L. littorea* and *M. neritoides* have planktonic eggs and larvae and are unanimously regarded as good species.

Thus, while 25 years ago only four *Littorina* species were known in Europe, at this time, eight species are recognised in two genera. Consequently, older accounts of European winkles should be reconsidered, while in the context of the European Invertebrate Survey, the distribution of the newly described species should be established. This applies particularly to the Belgian coast, which has been somewhat neglected by malacologists during the past fifty years.

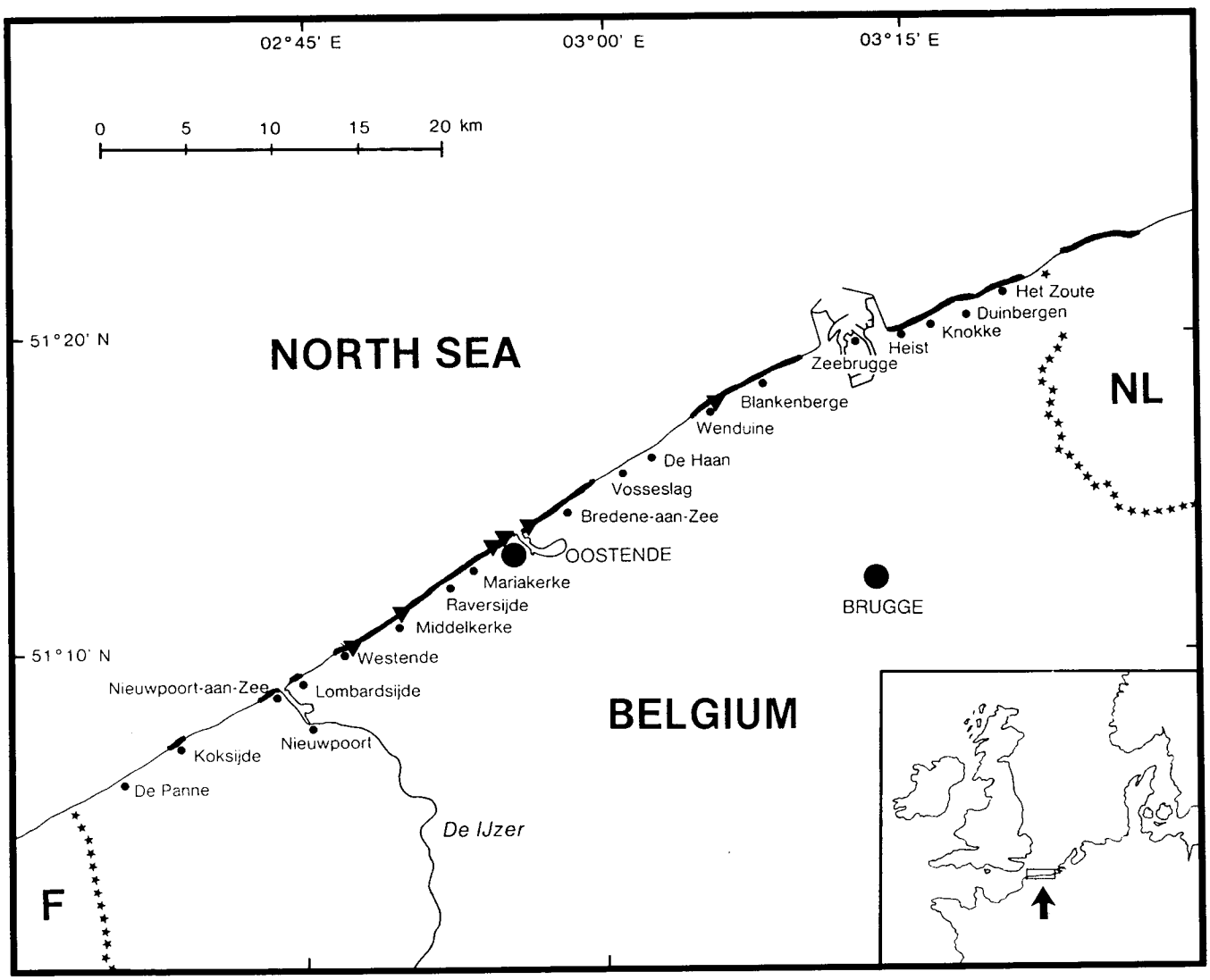
Recently, however, the foundation of the "Strandwerkgroep" (a society for the study of NW-European marine life) and the publication of an annotated checklist of the Belgian marine molluscs (BACKELJAU, 1986) have resulted in a renewed interest in our marine malacofauna.

In his list, BACKELJAU (1986) mentioned three *Littorina* species as being recorded alive on the Belgian coast : *L. littorea, L. saxatilis s.s.* and *L. obtusata s.s.* The occurrence of other species was not excluded, but their presence could only be determined accurately after a detailed revision of the Belgian Littorinidae. Such an investigation was conducted by one of us (T.W.) and part of the results are presented in this paper.

Material and methods

Live winkles were sampled all along the coastline in 1986, 1987 and 1988. This was done by exploring suitable substrates and picking up the winkles that were found. Brackish waters were not surveyed during this study. Samples were stored in a freezer (– 18° C) for later electrophoretic analysis, or in 70 % ethanol. The latter samples are deposited in the collections of the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels (KBIN).

Fig. 1. – *Map of the Belgian coast showing the localities visited during this study. Bold line : parts of the coast where breakwaters were constructed; triangles : places where the dike is in contact with the sea at high water.*



The existing collections of the KBIN were also examined. The material studied is listed in the appendix.
A number of specimens of *L. obtusata s.l.* and *L. saxatilis s.l.* from each sample were dissected in order to distinguish the different species. Identifications were based on SACCHI & RASTELLI (1966), HELLER (1975), SACCHI (1975), GOODWIN & FISH (1977), HANNAFORD-ELLIS (1979, 1980), FRETTER & GRAHAM (1980) and FISH & SHARP (1985).
Reference material from Wales (Great-Britain) was kindly provided by Dr. CELIA J. HANNAFORD-ELLIS (Institute of Oceanographic Sciences, Surrey, GB), while material from France, The Netherlands, Denmark, Norway, Scotland and Ireland was also at the authors' disposal for comparison.

Description of the Belgian coast

The Belgian coast (fig. 1) borders the Channel (southern North Sea), is about 65 km long and forms a rather straight line between 51°05'N - 02°32'E and 51°22'N - 03°22'E. Its natural profile is that of a large sandy beach stretching from Calais in France up to North Holland and even further northward in Germany and Denmark. The inland side is bordered by a range of dunes. This coastal profile is of course not very suitable for winkles or other rocky shore organisms.
However, man has provided a series of suitable substrates for such organisms; these can be divided roughly into three categories :

1. Dikes are constructed parallel to the coastline. The first stone dike, the Spinola dike in Oostende, was built in 1602. At present, stony dikes stretch over some 40 km of the coastline, but due to a general spouting up of the shore with sand, only a few parts of the dike are still in contact with the sea at high water : Westende (Rotonde), Middelkerke (Casino), Mariakerke, Oostende (Hippodroom, Zeeheldenplein-Kursaal, Halve Maan) and Wenduine (Wielerbaan; fig. 2 A). The materials recently used for the construction of these dikes are concrete, bricks, basalt blocks or asphalt.
2. The infrastructure related to harbours consists of dikes, docks, sluices, jetties, moles and fences or railings (fig. 2 C-D). Four harbours are situated on the Belgian coast : Nieuwpoort (51°09'N - 02°44'E; built around 1900), Oostende (51°14'N - 02°56'E; 1443), Blankenberge (51°19'N - 03°05'E; 1861) and Zeebrugge (51°21'N - 03°12'E; 1908). Zeebrugge has become the most important port and is the only one with a (large) outer habour, protected by two moles of about four km length. In this outer harbour, we can find several unused places and the old western mole (Leopold-II-dam; 2487 m). In Blankenberge a pier was built in 1893, purely as a touristic attraction. It was rebuilt with concrete gaugers in 1931-33.
3. A whole series of stone breakwaters (fig. 2 E) was built in order to break the force of the waves and thus to stabilize and protect the beaches. They are built, just like piers and moles, perpendicular to the coastline. Their length is about 400 m and a large part is situated in the intertidal zone. The distance between succeeding breakwaters varies between 200 and 500 m. Most are built with basalt stones, regularly placed and joined with asphalt on the upper part, but irregularly dumped on the lower part. Some breakwaters consist mainly of concrete (e.g. in Raversijde). According to BECUWE (1971), the first breakwaters were built on the Belgian coast between 1815 and 1830. The oldest still in place are situated in Zeebrugge (W) and Blankenberge; they were built around 1880. At present, 136 normal and 40 small breakwaters have been constructed on the following parts of the coast : Koksijde (ca. 1 km), Nieuwpoort (1 km), Lombardzijde - Bredene (20 km), Wenduine - Zeebrugge (7 km) and Knokke-Heist (9 km). In addition, sandbags were placed on the shore at De Haan (fig. 2 B) and Lombardzijde, while in several places (e.g. in Duinbergen and Knokke) rows of wooden piles on the beach act as breakwaters (fig. 2 F). Breakwaters represent a very rigorous habitat since they are highly exposed to waves and to the desiccating effect of wind and drifting sand.

The western- and easternmost parts of the Belgian coast remained natural and so without suitable substrate for winkles. In the west, the closest populations of *Littorina* live in the harbour of Dunkerque (France), about 18 km from the breakwaters of Koksijde, where the westernmost Belgian populations live. In the east, only 2 km separate the breakwaters of Knokke-Het Zoute from the small harbour of Cadzand in The Netherlands. Large populations of *L. saxatilis, L. obtusata* and *L. littorea* also occur in Breskens at the mouth of the river Schelde, about 16 km from Knokke-Het Zoute.
The sublittoral habitat outside the shore is a shallow sandy bottom; 10 m of depth is reached between 3 and 10 km off the coast. A coastal current in the Channel flows parallel to the shore from west to east, while tidal currents may flow either in the same direction or opposite to it. The currents may reach a speed of 5.5 km/h. The tidal range in Zeebrugge is 4.70 m (HW) and 0.40 m (LW) above MLLWS at spring tide and 3.82 m (HW) and 1.05 m (LW) above MLLWS at neap tide. At mean tide these figures are 4.35 m and 0.70 m.

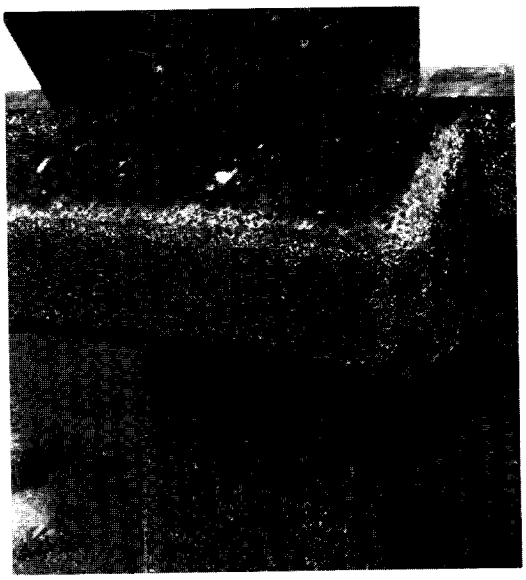
Account of the species

Five out of the seven European *Littorina* species were found living along the Belgian coast. These are *L. littorea, L. saxatilis, L. neglecta, L. obtusata* and *L. mariae*. The other species, *L. nigrolineata, L. arcana* and *M. neritoides* were not found alive, nor in the collections of the KBIN. We will now present an account of the different species. For descriptions, as well as for general information, we refer to SACCHI & RASTELLI (1966), SACCHI (1966, 1974, 1975), JAMES (1968), HELLER (1975), D. SMITH (1976), GOODWIN & FISH (1977), RAFFAELLI (1979a, 1979b, 1982), HANNAFORD-ELLIS (1979, 1980, 1983, 1984), FRETTER (1980), FRETTER & GRAHAM (1962, 1980), J. SMITH (1981), S. SMITH (1982) and FISH & SHARP (1985).

A

B

C



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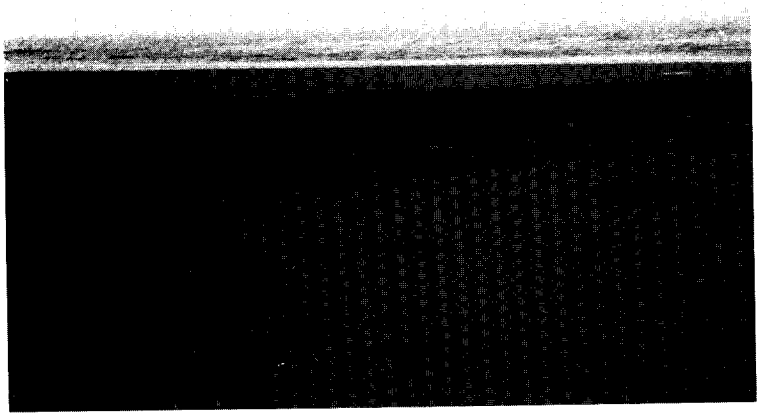

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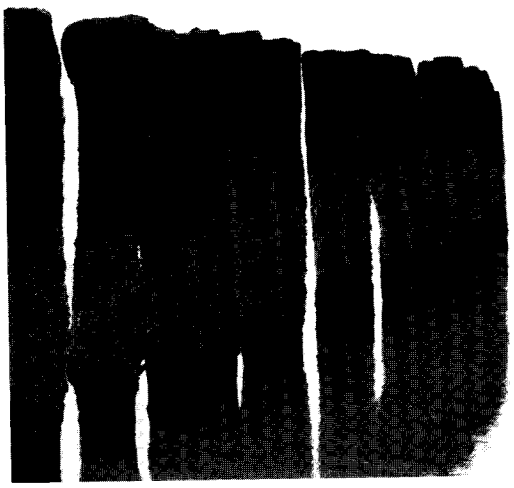


F

1. *Littorina littorea*

GEOGRAPHICAL DISTRIBUTION

In Europe from W-Spain to the White sea; Greenland; Spitsbergen; in the Baltic Sea as far as Bornholm; imported on the east coast of northern America and occurring there from Labrador to New Jersey; absent from the Mediterranean, Iceland and rare on the Scilly Islands (BEQUAERT, 1943; FRETTER & GRAHAM, 1980).

OCCURRENCE IN BELGIUM

The species was found alive by the authors in Koksijde, Nieuwpoort, Westende, Middelkerke, Raversijde, Mariakerke, Oostende, Bredene, Vosseslag, De Haan, Wenduine, Blankenberge, Zeebrugge, Heist, Duinbergen, Knokke and Het Zoute.
The KBIN-collections contained wet material from Nieuwpoort (1930-36), Westende (1936), Raversijde (1974), Oostende (since 1900), Wenduine (1935, 1937), Blankenberge (1934-37, 1974), Zeebrugge (since 1911), Heist (since 1928), Duinbergen (1936), Knokke (1949) and Het Zoute (1937, 1972). Moreover, the species is repeatedly reported in the literature, the oldest records known to the authors being from Blankenberge, Oostende and Nieuwpoort (DE MALZINE, 1867).
As *L. littorea* was found alive on nearly all hard substrates examined, the species is very common along the Belgian coast. It was only missing on the dike in De Panne and Sint-Idesbald, on a breakwater in Westende, on the short breakwaters in Lombardzijde and in some (probably too polluted) places in the harbours of Blankenberge and Zeebrugge.
L. littorea is often found resting freely on the substrate. On breakwaters and other well-exposed sites, the animals concentrate in the crevices and cracks in and between the basalt blocks. Maximal density and shell height are reached on the lower part of the breakwaters, well below the barnacle zone.
However, the species also lives in the barnacle zone, together with *L. saxatilis*. Juvenile specimens can occur in large numbers in this zone and are sometimes difficult to distinguish from *L. saxatilis*. This was very striking on the western wooden railing of Nieuwpoort.

DESCRIPTION OF THE MATERIAL

The majority of the shells are yellowish, orange, greenish, greyish, chestnut of dark brown coloured, with dark brown or black spiral bands of varying width and numbers. Completely dark coloured shells originate by the fusion of many broad spiral bands. They are not rare.
Light yellowish shells without or with few (1-4) faint spiral bands can be found in small numbers in most populations, especially amongst the juvenile specimens. Unbanded greenish, purple and red shells are very rare and local. The latter are more common among juveniles.
Specimens living on breakwaters and other exposed substrates are rather small; most mature specimens have a shell height of 10-20 mm. Yet, in sheltered localities, *L. littorea* reaches considerable sizes. At the "Toegangsgeul" in Zeebrugge, for example, specimens are very large, many of them being larger than 25 mm, some even larger than 30 mm. In this population, the surface of the largest shells was considerably eroded and ash-grey. About half of the collected specimens were partly overgrown by the barnacle *Semibalanus balanoides*.

2. *Littorina saxatilis* and *L. arcana*

GEOGRAPHICAL DISTRIBUTION

L. saxatilis can be found from SW-Spain to the Arctic seas (Nova Zembla); Greenland; Iceland; Faroës; Spitsbergen; in the Baltic sea up to Rügen; in the western Atlantic from Ontario to New Jersey (BEQUAERT, 1943; FRETTER & GRAHAM, 1980). Isolated populations occur in the Strait of Gibraltar (GOFAS, 1975), the northern Adriatic, the Gulf of Gabès (Tunisia; SACCHI & TORELLI, 1973), southern Morocco (FISCHER-PIETTE *et al.*, 1970), the Canary Islands (R. MOOLENBEEK, pers. comm.), the Azores (REID, in press b) and South Africa (HUGHES, 1979). BEQUAERT (1943) also mentions the species from the NE Pacific, the Black Sea and Japan, but these records are unreliable. *L. arcana* was already reported from the British Isles (HANNAFORD-Ellis, 1979), northern Brittany (CAUGANT & BERGERARD, 1980; pers. obs.), northern France (Boulogne, KRAAK, 1984; Wimereux, pers. obs.), The Netherlands (STOKER, 1986) and Norway (Trondheimfjord and Oslofjord; SNELI & VAN MARION, 1979). Searching for *L. arcana* in Denmark was unsuccesful (NIELSEN, 1980).

OCCURRENCE IN BELGIUM

L. arcana was not found in the material examined anatomically (394 FF, 188 MM, 59 juv.). *L. saxatilis*, however, was found alive by the authors in Koksijde, Nieuwpoort, Lombardsijde, Westende, Middelkerke, Raversijde, Mariakerke, Oostende, Bredene, Vosseslag, De Haan, Wenduine, Blankenberge, Zeebrugge, Heist, Duinbergen, Knokke and Het Zoute.
L. saxatilis in the wet collections of the KBIN comes from Nieuwpoort (1955), Raversijde (1974), Oostende (1900, 1935-38), Wenduine (1935), Blankenberge (1934), Zeebrugge (1934-38, 1947), Heist (1946-47, 1973-74), Duinbergen (1936), Knokke (1949) and Het Zoute (1972). DE

◁ Fig. 2. – *Habitats of Littorinidae along the Belgian coast. — A : The dike in Wenduine — B : Sandbags in De Haan — C : General view of the eastern railing in Oostende — D : Close-up of a gauger where* L. neglecta *and* L. saxatilis *live in crevices and holes in and above the barnacle belt — E : A breakwater in Oostende — F : Wooden piles in Duinbergen.*

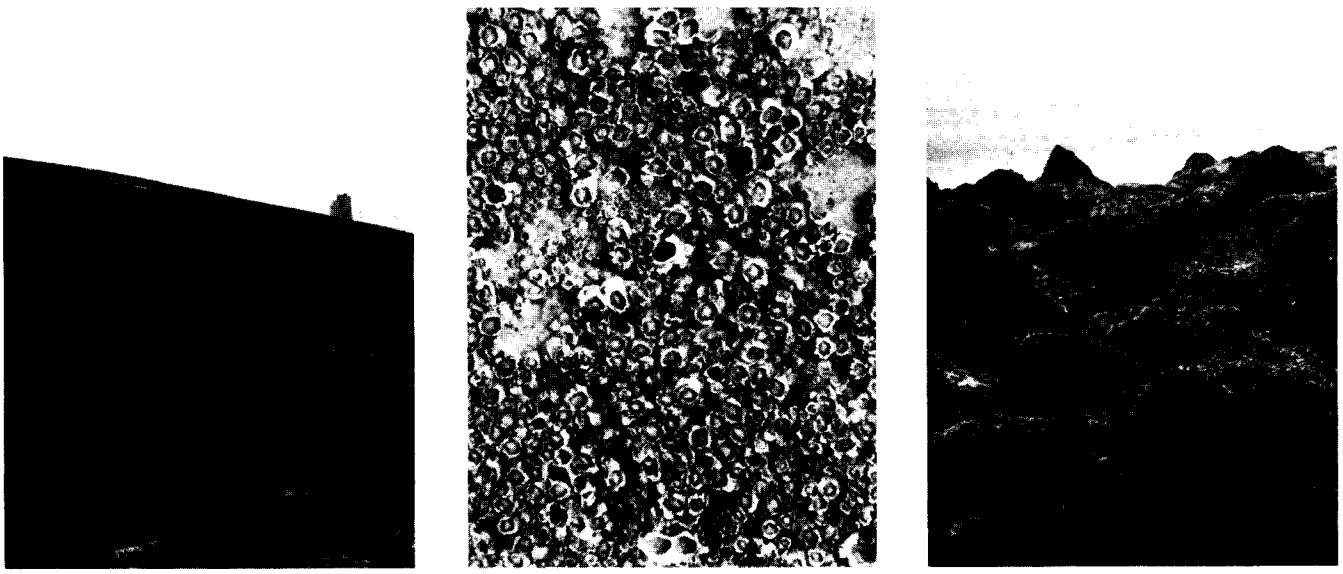


Fig. 3. – *Habitats of Littorinidae along the Belgian coast. — A : General view of the dike at the "Halve Maan" in Oostende, where* L. neglecta *lives on the concrete block in the centre of the photograph — B : Close-up of the surface of the concrete block in fig. 3 A, showing* L. neglecta *sheltering within and between barnacles — C : The* Fucus *belt on the westside of the western mole in Zeebrugge, where both* L. mariae *and* L. obtusata *occur.*

MALZINE (1867) found *L. saxatilis* in Blankenberge, Oostende and Nieuwpoort.

Thus, *L. saxatilis* was found alive on most hard substrates examined and the species is common on the Belgian coast. However, the populations living on the breakwaters show remarkable low densities. We measured density roughly as the number of specimens found after one hour of intensive search and this figure varied between 32/h and 192/h on "normal" breakwaters, but on a breakwater with wooden piles it was as high as 372/h. However, on natural rocky coasts a comparable picking rate yields more than thousand specimens per hour (pers. obs.; Boulogne).

Factors apparently influencing the density of *L. saxatilis* are density and depth of cracks and joints, density of barnacles, height on the shore and distance from the nearest high density population. The first two factors are obviously correlated with each other and with the age and construction of the breakwater. Moreover, vertical substrates, like piles and gaugers, seem to show higher densities than horizontal ones, like breakwaters.

L. saxatilis was not found on the dike in De Panne and Sint-Idesbald, on the recent breakwaters no. 4, 5 and 6 in Westende, on the dike and breakwater no. 3 in Middelkerke (despite intensive search), on the western mole of Zeebrugge (in Heist) and on several places in the harbours of Zeebrugge and Blankenberge.

On breakwaters, wooden piles and sandbags, *L. saxatilis* is more or less restricted to the barnacle belt, where it hides between the barnacles *Semibalanus balanoides*, in dead animals of that species or in cracks in the substrate. Free resting specimens are rarely found. Generally, on dikes, piers and moles (mostly with deeper cracks), the species tends to occur higher up on the shore; in addition, specimens are on the average larger, densities are higher and in sheltered sites, like the Leopold-II-dam in Zeebrugge, free resting specimens are quite numerous.

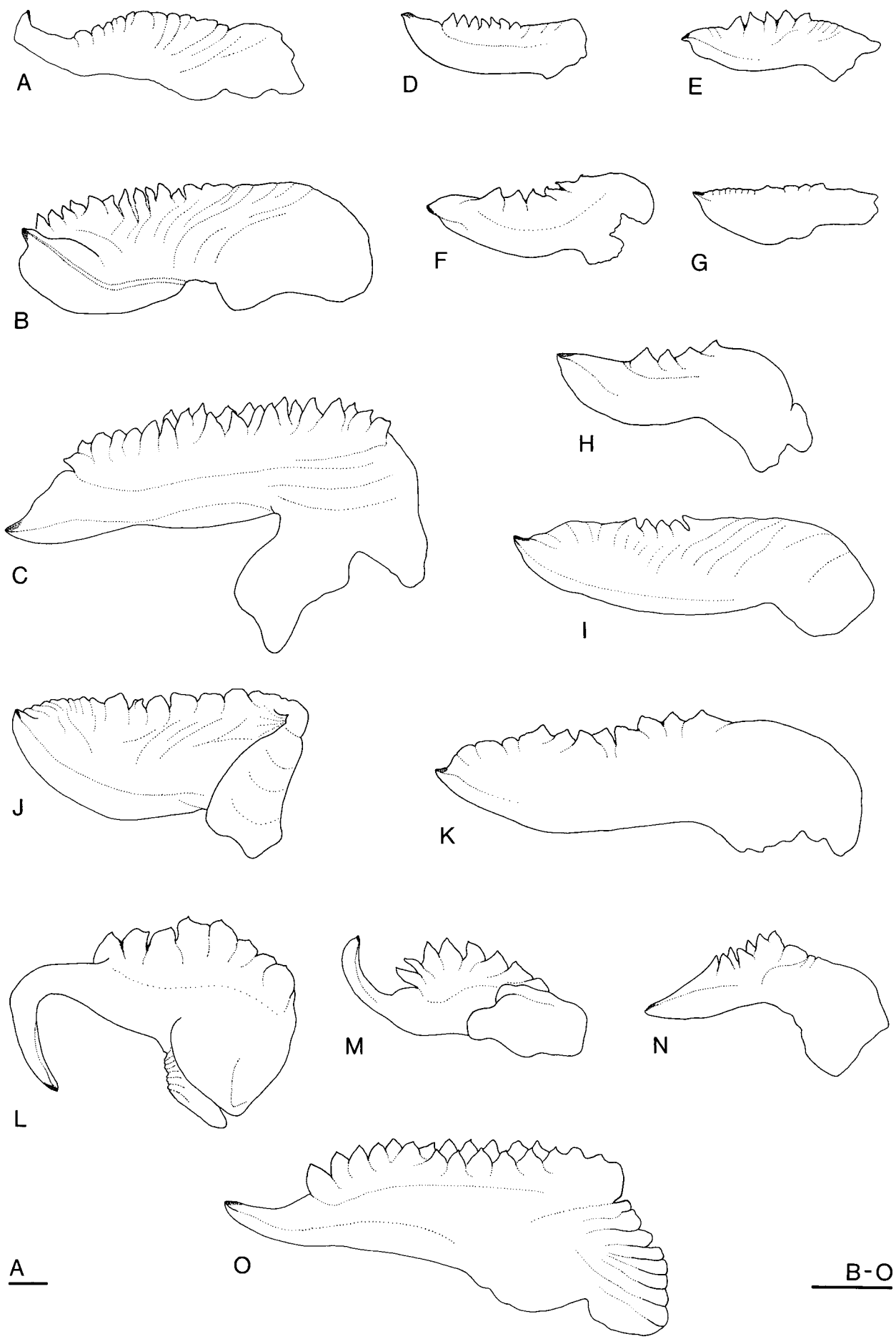
DESCRIPTION OF THE MATERIAL

The striking colour polymorphism of this species, as it has been described from British and French material, is remarkably reduced in the Belgian populations.

The overwhelming majority of the shells show some shade of brown, grey or green, varying from dark grey or brown — nearly black — to pale brown or green, beige or light limestone grey. In many cases, the colour changes gradually over the last whorl, i.e. from grey to brown or beige, from green to yellowish of from greenbrown to darkbrown. A lot of shells have a pale tesselation pattern combined with one of the above groundcolours.

Other colour morphs are rare and local : uniform orange and red shells can be found in a few populations. Other patterns than the pale tesselation are dark tesselation, irregular white spots on dark background (this pattern is often

Fig. 4. – *Penes of* Littorina *species. Scale lines indicate 1 mm. — A :* L. littorea *("Toegangsgeul", Zeebrugge) — B :* L. saxatilis *(Wimereux, France) — C :* L. *cf.* arcana *(Roscoff, France) — D - G :* L. neglecta *("Halve Maan", Oostende) — H :* L. saxatilis *(Raversijde) — I - K :* L. saxatilis *("Halve Maan", Oostende) — L :* L. mariae *(western mole, Zeebrugge) — M :* L. mariae *(Beg Meil, Britanny, France) — N :* L. obtusata, *immature specimen (Portchannel, Blankenberge) — O :* L. obtusata, *adult (Heist).* ▷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restricted to the spire whorls), dark and light spiral bands; but all these patterns were seen only on a very small number of shells.
Differences between populations can be important, despite the restricted overall polymorphism. The populations of Koksijde present relatively more banded shells; orange shells were not rare in the Sluice-Dock of Oostende, while tesselated shells seem to be absent there.
While the populations of breakwaters and wooden piles were of the *saxatilis* morph, the dikes and moles with deep cracks and the sheltered sites like the Leopold-II-dam in Zeebrugge typically housed populations of the *rudis* morph.
The penis (see fig. 4) usually shows a mucronate tip and the number of glands is low, in a large majority of the specimens not more than 10.

3. *Littorina neglecta*

GEOGRAPHICAL DISTRIBUTION

L. neglecta has been reported from the western British coasts, Massachussets (FRETTER & GRAHAM, 1980), Nova Scotia (ROBERTSON & MANN, 1982), Norway (Trondheimfjord and Oslofjord; SNELI & VAN MARION, 1979), Brittany (France; pers. obs.) and Iceland (JANSON, *in litt.*). The species was not found in Denmark (NIELSEN, 1980).

OCCURRENCE IN BELGIUM

The distribution of *L. neglecta* along the Belgian coast is restricted to the "Halve Maan" in Oostende. Here, *L. neglecta* lives sympatrically with *L. saxatilis* on a concrete block of about 2 m^3, which is completely overgrown by the barnacle *Semibalanus balanoides* (Fig. 3 A-B). At some 20 metres from this site, another (less typical) population inhabits the barnacle belt and the small cracks and holes above this belt, in the concrete gaugers (fig. 2 D).
The species possibly also occurred in Zeebrugge (KBIN collections, 1947) and Heist (1946, 1974), but seems now extinct in this area. Pollution or physical destruction (by harbour expansion) of the sites where the species lived may have caused this extinction. However, the harbour of Zeebrugge could still house one or more populations.

DESCRIPTION OF THE MATERIAL

It was difficult to assign small rough winkles from the "Halve Maan" in Oostende to either *L. saxatilis* or *L. neglecta,* though typical specimens of both species were found. The identification of these specimens as *L. neglecta* was provisionally confirmed by Dr. C.J. HANNAFORD-ELLIS, Dr. D.G. REID [British Museum (Natural History), London] and by Mr. R. MOOLENBEEK (Zoölogisch Museum, Amsterdam, The Netherlands).
Typical *L. neglecta* (fig. 5 A-B) shows a small, relatively (but not totally) smooth shell, with one or two brown spiral lines running on the lower half of the body whorl. Shell coloration consists of a pattern of dark lines and stripes on pale background or of pale tesselations on dark background. Some shells show more pronounced ridges. In some specimens the typical subopercular pattern is visible, but in most it is too faint or absent. The aperture is more or less rounded, with a thin edge. The profile of the body whorl at the junction with the outer lip is convex in all small (< 3 mm) rough winkles examined, though somewhat less than in figure 10.2. A of FISH & SHARP (1985).
All kinds of intermediate forms between the typical *L. neglecta* described above and the typical *L. saxatilis* (with well pronounced, sharp ridges, different aperture shape, thicker outer lip and a different colour pattern) can be found in the Belgian material.
Study of the anatomy is of little help, since Belgian *L. saxatilis* mature very early; mature individuals of 3 mm height are not exceptional in most populations of this species. Nevertheless, the typical *L. neglecta* shells contained either females with full brood pouches or males with a typical *neglecta*-like penis (tapering tip and one row of 3-7 penial glands; fig. 4 D-G). However, some contained immature specimens (at a shell height of 2-3 mm), while some atypical specimens were males with a *neglecta*-like penis.

4. *Littorina nigrolineata*

GEOGRAPHICAL DISTRIBUTION

L. nigrolineata has been collected only in Brittany and Normandy (France; CAUGANT & BERGERARD, 1980; REID, in press b), the British Isles (FRETTER & GRAHAM, 1980) and The Netherlands (one locality; STOKER, 1986). The species was not found in Denmark and Norway (SNELI & VAN MARION, 1979; NIELSEN; 1980).

OCCURRENCE IN BELGIUM

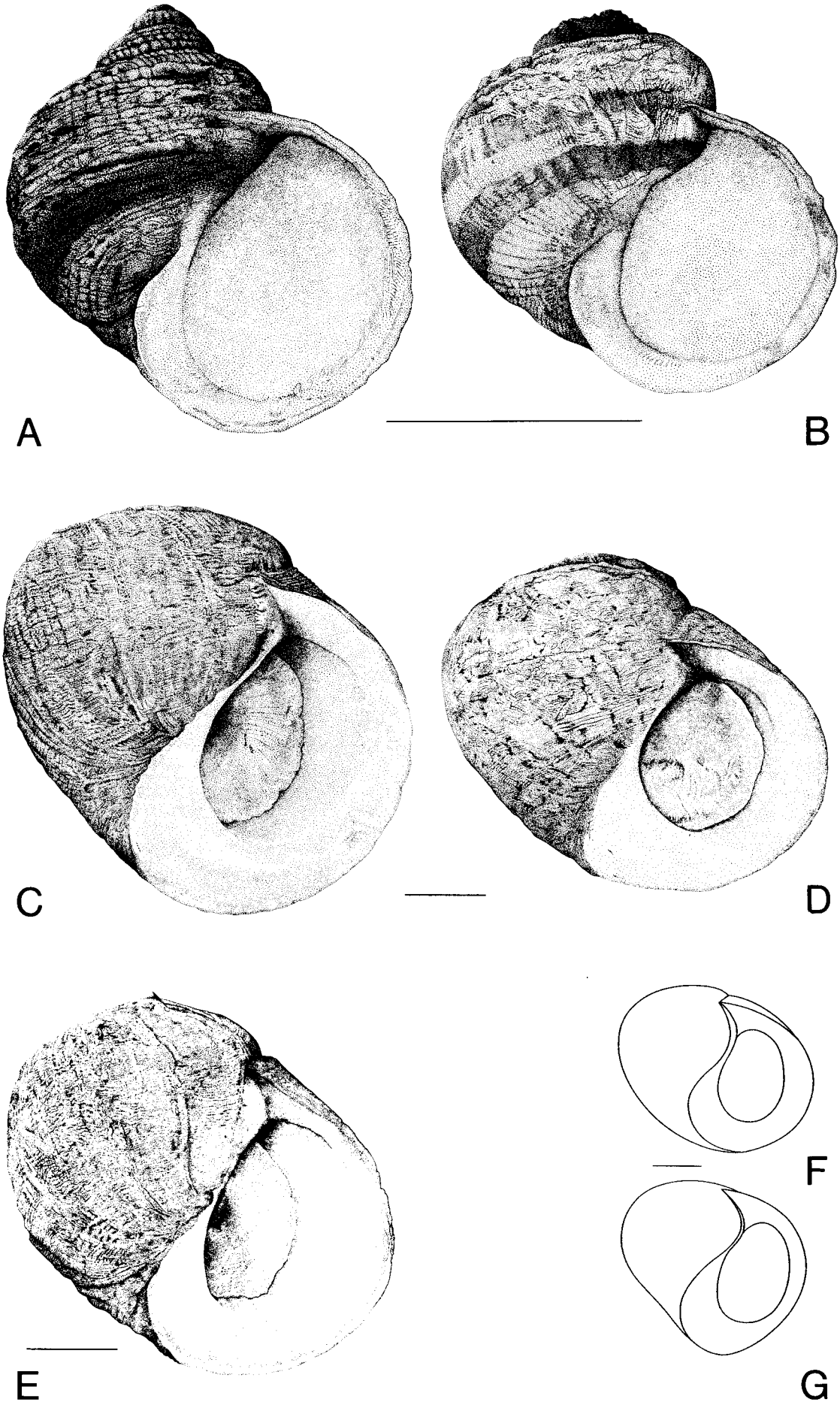
We did not find *L. nigrolineata* on the Belgian coast nor in the collections of the KBIN.

5. *Littorina obtusata*

GEOGRAPHICAL DISTRIBUTION

From Portugal to the White Sea (USSR); Greenland; Iceland; Spitsbergen; Faroës; Jan Mayen Island; Lofoten Islands; in the Baltic as far as the Lübecker Bucht; in the eastern Atlantic from Newfoundland to New Jersey

Fig. 5. – *Shells of* L. neglecta *and* L. obtusata *s.l. Scale lines indicate 2 mm.* — *A :* L. neglecta *("Halve Maan", Oostende)* — *B :* L. neglecta *(Wimereux, France)* — *C :* L. mariae *(western mole, Zeebrugge)* — *D :* L. mariae *(Roscoff, Brittany, France)* — *E :* L. obtusata *("Toegangsgeul", Zeebrugge)* — *F :* L. mariae, *(western mole, Zeebrugge)* — *G :* L. obtusata, *juvenile ("Toegangsgeul", Zeebrugge).* ▷


A
B
C
D
E
F
G

(BEQUAERT, 1934; BARKMAN, 1955; FRETTER & GRAHAM, 1980; REID, in press b). Several authors doubt the records from the West-Mediterranean (Malaga and Corsica) and the Azores (BEQUAERT, 1943; BARKMAN, 1955).

OCCURRENCE IN BELGIUM

L. obtusata lives at present on *Fucus vesiculosus* and/or *F. spiralis* in Blankenberge (portchannel), on the outside of the western mole and in the outer harbour of Zeebrugge (several populations). The populations of Heist (outside eastern mole, Zeebrugge) and Zeebrugge ("Toegangsgeul") are presently extinct; the former probably because of silting up with sand, the latter because of infrastructural works (complete destruction of the habitat).
The population of Blankenberge shows a very low density. On the eastside of the portchannel only three specimens were found after an intensive search of 30 minutes. Although density is higher in the other populations, it is never as high as the densities we observed in Brittany (France).
L. obtusata is absent in Nieuwpoort and some parts of the harbour of Zeebrugge, despite the occurrence of (quite large) areas overgrown by *Fucus vesiculosus* in these localities.
In the KBIN-collections, we found two specimens captured in a plankton net in the Sluice-Dock of Oostende in 1938 and one specimen collected in 1938 on a breakwater in Zeebrugge. The specimens of Oostende were probably carried by the water coming into the basin (LELOUP & MILLER, 1940).
DE MALZINE (1867) reports the species from Oostende and Nieuwpoort, but his records are probably based on shell material. COLBEAU (1868) accepts the occurrence of the species in Belgium, as reported by older authors, but he did not find the species alive himself. According to LELOUP & MILLER (1940), *L. obtusata* can (commonly ?) be found on breakwaters overgrown by *Fucus*.

DESCRIPTION OF THE MATERIAL

Only two colour morphs were found. *Olivacea* made up the total of the (few) collected specimens in Blankenberge. *Citrina* accounted for respectively 3, 7 and 1 (juv.) out of the 46, 143 and 35 collected specimens in the populations of Zeebrugge ("Leopold-II-dam" and "Toegangsgeul") and Heist. Thus, *critina* makes up only about 4.5 % of the collected specimens, despite the fact that this morph is easier to find on the green-brown *Fucus* background than the *olivacea* morph. It is remarkable too that the *reticulata* morph was not found at all.
The *olivacea* morph occurs in different shades of green, from very dark green to light grass green; fairly brownish specimens can also be found.
The outer lip and throat of the aperture of the *olivacea* shells is always coloured purple; this purple is very dark in juvenile specimens (which often have a yellow growing edge) and seems to become more pale as shells grow older. The body of most animals is heavily dark coloured, but some, which have light green shells, have a pale body. *Citrina* specimens have a pale outer lip, inner aperture and body.
Shell morphology (fig. 5 E, G) and penes (fig. 4 N-O) appeared similar to the reference material from France and Great-Britain.
45 (almost 36 %) out of the 126 shells collected in the "Toegangsgeul" (Zeebrugge) were partly overgrown by the barnacle *Semibalanus balanoides*. But in the population of the "Leopold-II-dam" (Zeebrugge), none was. In all populations, green algae grow on the surface of most shells.

6. *Littorina mariae*

GEOGRAPHICAL DISTRIBUTION

There are records from NW-Spain (Galicia; SACCHI, 1969), northern and southern Britanny (France; SACCHI, 1969; pers. obs.), N-France (Wimereux; pers. obs.), Zeeland (S-Netherlands; FORTUIN, 1979), the British Isles (GOODWIN & FISH, 1977), Helgoland (GALLARDO & GÖTTING, 1985), Denmark (NIELSEN, 1980) and Norway (SNELI & VAN MARION, 1979). Thus, it seems that *L. mariae* has a geographical distribution similar to that of *L. obtusata*.

OCCURRENCE IN BELGIUM

The only known Belgian population lives with *L. obtusata* on the outside of the western mole of Zeebrugge (fig. 3 C). The species is restricted to the lower part of the *Fucus* belt and lives exclusively on *F. vesiculosus*. *L. mariae* could not be found on *F. spiralis*, which grows higher on the shore. No specimen was found in the collections of the KBIN.

DESCRIPTION OF THE MATERIAL

All the collected specimens belong to the morph *citrina*, with yellow shell, pale outer lip and body. Conchyliologically Belgian *L. mariae* (fig. 5 C) is not very typical; there is some difference with the specimens collected by us in Brittany (fig. 5 D).
Height and breadth were taken from a number of specimens. The average size (in mm) of 8 males was 74.5 x 77.3 (range : 65.0-82.5 x 68.5-90.5), that of 5 females 88.7 x 92.1 (range : 75.5-98.5 x 86.5-98.0).
All males examined had a fully developed penis with 9 or 10 glands and a markedly prolonged tip (fig. 4 L). All but one female showed a (slightly) pigmented ovipositor; this is in contrast with the results of GOODWIN & FISH (1977) and the description of FRETTER & GRAHAM (1980).

7. *Melarhaphe neritoides*

GEOGRAPHICAL DISTRIBUTION

M. neritoides is a southern species, occurring in the Black Sea, the Mediterranean and along the coasts of West-Europe up to the Isle of Wight (British side of the Channel)

and Normandy (France); it is common on the British Isles (CRISP & SOUTHWARD, 1958; FRETTER & GRAHAM, 1980). Isolated and unstable populations can be found up to Calais (northern France; VADER, 1965, 1976; pers. obs.), in The Netherlands (STOCK, 1950, 1975; VADER, 1976). NW-Denmark (NIELSEN, 1980), W-Sweden (LEWIS & TAMBS-LYCHE, 1962; JOHANNESON, K. and SAUR, M., pers. comm.). SW-Norway (Bergen; LEWIS & TAMBS-LYCHE, 1962; SNELI & VAN MARION, 1979) and Helgoland (KUNZE, 1952; but see also JANKE, 1986).

OCCURRENCE IN BELGIUM

Only one shell of *M. neritoides* was found several decades ago in Nieuwpoort, but no further details are available concerning this find.

Discussion

1. *Faunistic aspects*

Our survey has demonstrated that five of the seven NW-European *Littorina* species are living on the Belgian coast. These are : *L. littorea, L. saxatilis, L. obtusata, L. mariae* and *L. neglecta,* the latter two being new to the Belgian fauna. Hence, the occurrence of these species in Belgian coastal waters should no longer be questioned as was done by BACKELJAU (1986). *L. arcana, L. nigrolineata* and *M. neritoides,* on the other hand, may be deleted from the species list since, even after intensive search, they could not be found and no reliable Belgian records of these species exist.

L. obtusata, L. saxatilis and *L. littorea* are repeatedly reported from the Belgian coast in the literature (DE MALZINE, 1867; COLBEAU, 1868; PELSENEER, 1882; LAMEERE, 1896, 1913; MAITLAND, 1897; VONCK, 1933; LELOUP & MILLER, 1940; LELOUP, 1950; VERSTRAELEN, 1966; DARO, 1969). However, some authors, like VERSTRAELEN (1966) and DARO (1969), seem to mix up the latter two species, so that care should be taken in literature surveys. Moreover, it is not always clear if the records are based on live or on shell material.

We can assume that *L. saxatilis* and *L. littorea* were quite common on the Belgian coast at the end of the last century, although their distribution must have been more local at that time, because there were fewer suitable sites. *L. obtusata* seems to have occured on breakwaters overgrown with *Fucus,* but it is unclear how numerous such breakwaters were in the past. Presently, they have nearly disappeared. DE MALZINE (1867), COLBEAU (1868) and MAITLAND (1897) mention also *L. palliata* from the Belgian coast. This is probably based on a misidentification, since *L. palliata* is an arctic morph of *L. obtusata,* living in northern Norway, the USSR, Iceland, Greenland and Canada. On the other hand, it cannot be excluded that shells of *L. palliata* have been transported accidentally by fishermen returning from Iceland.

The occurrence of *L. tenebrosa* (*L. saxatilis f. tenebrosa*) in Belgium has been reported by COLBEAU (1868). E. DUMOULIN (*in litt.*) was not able to find this brackish water morph in Belgium, despite intensive search, but found it in Terneuzen, just over the Dutch border (DUMOULIN, 1983). On the other hand, STOKER (1986) dit not succeed in finding live specimens in The Netherlands, and as strated before, brackish waters were not included in this survey.

M. neritoides too has been reported from the Belgian coast (DE MALZINE, 1867; COLBEAU, 1868; PELSENEER, 1882; VONCK. 1933; VERSTRAELEN, 1966). During the last fifteen years, however, the species has never been found alive, despite regular searches by STOCK (1975), members of the "Strandwerkgroep" and the authors. Moreover, the species is absent in the wet collections of the KBIN.

Thus, older Belgian records of *M. neritoides* may refer to misidentifications or may be based upon transported shells. The latter possibility can certainly not be excluded since *M. neritoides* lives both in NW-France and The Netherlands (STOCK, 1950, 1975; VADER, 1965, 1976; GLACON, 1977). Therefore, it is not unlikely that empty shells of the species are (rarely) transported by sea currents to the Belgian coast; such sea currents may indeed also be responsible for other rare findings of allochthonous species on the Belgian coast [e.g. *Patina pellucida* (L.)]. It seems rather unlikely that subfossil specimens of *M. neritoides* have been washed ashore, since the species is absent from the Belgian-Dutch Neogene (VAN REGTEREN ALTENA *et al.,* 1965).

Another possibility that cannot be totally excluded, however, is that some specimens of *M. neritoides* were found after mild winters. Indeed, VADER (1976) and LEWIS & TAMBS-LYCHE (1962) report large numbers of *M. neritoides* in, respectively, The Netherlands and Scandinavia after such winters.

In contrast to *M. neritoides,* there are no literature records of *L. arcana* and *L. nigrolineata* from the Belgian coast. Both species were, however, recently reported from The Netherlands by STOKER (1986). She found *L. arcana* in a number of localities in the province of Zeeland. The species was, for example, collected in Breskens and Cadzand. Therefore, it would seem unlikely that *L. arcana* does not live in Belgium.

However, an examination of the material collected by STOKER revealed that a large number of immature female *L. saxatilis* were wrongly identified as *L. arcana* according to the description and illustrations of HANNAFORD-ELLIS (1979). We do not rely on the ciliated field but on the features of the oviduct for the separation of both species, since the ciliated field is hardly discernible in preserved specimens and, according to HANNAFORD-ELLIS (1980), this feature may not apply for non-British material. Although we have seen a few "doubtful" specimens (*L. saxatilis* females with quite large oviduct, but no shelled embryos), we seriously doubt on the occurrence of *L. arcana* in The Netherlands. No specimen was comparable to *L. arcana* from Brittany or Wales. Moreover, the records of *L. arcana* from Norway (SNELI & VAN MARION, 1979) seem also not reliable (K. JOHANNESON, pers. comm.).

Therefore, the northern limit of the distribution of *L. arcana* on the continental side of the Channel is probably

situated somewhere in the "Pas de Calais"; the most northern finding locality of the species in France, known to the authors, is Wimereux (50°56'N; 01°51'E), some 100 km from Koksijde.
L. nigrolineata, on the other hand, occurs only very locally in The Netherlands, namely in the Oosterschelde. Only six specimens were found by STOKER (1986), so that we can assume that the species was imported in the area with French oysters and that no stable population is established yet.
In France, *L. nigrolineata* was found in Trébeurden (northern Brittany; pers. obs.) and in Barfleur (some 25 km east of Cherbourg, Normandy; REID, in press b), but not in the "Boulonnais" (northern France; GLACON, 1977; KRAAK, 1984; MOOLENBEEK, pers. comm.; pers. obs,).
Finally, according to STOKER (1986), *L. neglecta* is absent in The Netherlands. Yet, the population of *L. saxatilis* living on the pier of Scheveningen (prov. Zuid-Holland) shows a confusing resemblance to the *L. neglecta* population of Oostende (pers. obs.).

2. *Dispersal mechanisms*

For *M. neritoides,* a species with planktonic eggs and larvae, larval transport from the northern French populations has been invoked to explain the occurrence and subsistence of the species on some very exposed sites in The Netherlands (VADER, 1976). Yet, we wonder why there is apparently no successful larval transport from the populations in the north of France to the Belgian coast. The concrete gaugers of the eastern railing of Oostende and the large western mole of Zeebrugge seem to provide suitable substrates for this species, but no specimen was found. Unfortunately, we have not been able to explore the latter site completely, because a large part of it is not accessible.
L. littorea and *L. saxatilis* are so common that their spreading probably occurred naturally. In the case of *L. littorea* larval transport is obviously the mechanism involved. This cannot be the case for *L. saxatilis,* which is ovoviviparous. The fact that *L. saxatilis* was found on nearly all breakwaters examined, even on those of Koksijde which are quite isolated (18 km from Dunkerque and 5.5 km from Nieuwpoort), could indicate that the mobility of this species is not as low as usually thought (e.g. JANSON, 1987) and that colonisation of new suitable sites is fast, at least if possible stock populations are not too distant and in the special conditions of a shallow sandy shore.
The mechanism for this colonising ability is still unclear; transport by birds (waders, ducks, gulls; see e.g. REES, 1965) could be important, while ships could carry winkles from one harbour to another. Transport by tidal and sea currents can also occur, as can be concluded from the finding by E. DUMOULIN (*in litt.*) of some live juvenile *L. saxatilis* on a tide line in Heist (June 1984) and by one of us (T.W.) of two specimens on a large basalt block on the beach (April 1988). JANSON (1987) suggests also a role for drifting sea-weed or ice.
As in the past some 40 km of dike has been in contact with the sea, and thus was populated by winkles, new breakwaters might have been colonized by the dike populations; at present, however, this is no longer possible since only small parts of the dike are suitable for *Littorina.*
It is likely that several factors are responsible for the transport of winkles and that their relative importance is different in various regions; for example, transport mechanisms between the small skerries and islands of the Koster archipelago on the Swedish west coast (described in JANSON, 1987) are probably totally different from those between the breakwaters of the Belgian coast, since the former area is almost atidal and coastal waters are very deep, in contrast with the Belgian situation.
The distribution of *L. obtusata* and *L. mariae* depends on the occurrence of large brown weeds, which are necessary for the feeding and reproduction of the species. As these weeds are not common on the Belgian coast, the flat winkles show a very local distribution.
The main spreading mechanism for these species is probably the drifting of weed. The fact that *L. obtusata* was not found in Nieuwpoort and some parts of the harbour of Zeebrugge suggests that the spreading of the species is limited by some factor(s), such as the accessability of the site to drifting weed; sheltered sites in harbours may be difficult to colonise, while exposed sites, such as the mole of Zeebrugge, are reached easily.

3. L. obtusata *in Blankenberge*

Some observations show that the *L. obtusata* populations of Blankenberge undergo important changes in density over the years. The species was found in large numbers in June 1976 (VAN GOMPEL & RABAUT, 1976) and was still present in September 1976, but apparently in smaller numbers (RAPPÉ, 1977); it was not found in February 1978 (RAPPÉ, 1978), while in April 1979, it was found again (VERBOVEN, 1979). The authors found the species in very low densities on both sides of the portchannel in February 1986 (E-side), in December 1986 (W-side) and in April 1988 (W-side).
It seems unlikely that seasonal changes in reproduction are responsible for these observations, since according to GOODWIN (1978) there is little evidence of a well-defined cyclical system of reproduction and there is a stable adult component for most of the year.

4. *Polymorphisms*

In comparison with other regions (see e.g. FISCHER-PIETTE & GAILLARD, 1971; D. SMITH, 1976; RAFFAELLI, 1979b; SACCHI, 1984), Belgian *L. saxatilis, L. obtusata* and, to a lesser extent, *L. littorea,* show a strongly reduced colour polymorphism. Many factors may be responsible for this phenomenon.
The fact that white and red shells are much more common in small (< 10 mm) than in large *L. littorea* might suggest a role for visual selection. Several authors (e.g. ATKINSON & WARWICK, 1983) state that this phenomenon is important in the regulation of the colour polymorphism of *L. saxatilis* (*s.l.*).

Most breakwaters and dikes have a dark grey background colour, except for the variegated pattern of the barnacle belt. Hence, white and red shells of *L. littorea* are less cryptic than brown, grey or black ones. They may be selected against, but larval input could maintain a low percentage of (young) specimens with such shells.

Purple Sandpipers (*Calidris maritima*) and Turnstones (*Arenaria interpres*) are known to consume large quantities of small winkles (mainly *L. saxatilis* and juvenile *L. littorea*; FEARE, 1966; PRATER, 1972; PETTITT, 1975). Both species of waders are common on Belgian breakwaters between September and May. Maximum numbers are 330 Purple Sandpipers and 800 Turnstones from Koksijde to Breskens (NL) between January and April (BÉCUWE, 1971, 1973; BÉCUWE *et al.*, 1983), which makes a mean of about six birds per breakwater! Moreover, the distribution is not equal all along the coast. The two species can thus be assumed to exert an important pressure on the littorinid populations of the breakwaters.

The shore crab, *Carcinus maenas,* which is also an important predator of *Littorina* (e.g. B. JOHANNESON, 1986), is common on the Belgian breakwaters in summer, but in winter the species lives in deeper water.

While both crabs and birds undoubtedly consume significant quantities of winkles, their exact role in the process of visual selection is still unknown. Only REIMCHEN (1979) has demonstrated clearly the importance of visual selection in *L. mariae,* through predation by the intertidal fish *Lipophrys pholis.*

It is also possible that the reduced shell colour polymorphism observed in the Belgian populations of *Littorina* is the result of founder events or population bottlenecks. Indeed, the breakwaters are relatively recent constructions (most of them were built after 1950) and there is a certain physical barrier (the sandy beach) between the different populations, even though it is not yet clear how effective this barrier is. Moreover, many breakwaters were rebuilt several times and, as this is a very drastic intervention, the populations of these breakwaters must have faced severe bottlenecks.

An electrophoretic study is in progress to assess whether the reduced shell polymorphism in Belgian *L. saxatilis* is accompanied by a reduced genetic polymorphism (K. JOHANNESON & WARMOES, in press). However, in our experience, Belgian *L. saxatilis* is very cryptic in its environment and this seems to point to a preponderant role for visual selection.

The reduction of the colour polymorphism is dramatic in *L. obtusata.* The *olivacea* morph makes up more than 95 % of the collected specimens and the *reticulata* morph was not found at all, while this latter morph makes up 33 % of British specimens (D. SMITH, 1976). FORTUIN (1979) was not able to find *reticulata* in The Netherlands either. However, according to DUMOULIN (1983), the polymorphism is important in Zeeuws-Vlaanderen (SW-Netherlands). Several morphs were found there : *olivacea, fusca, critina* and *retusa.*

SACCHI (1974) states that populations missing one of the three main colour morphs (*olivacea, reticulata* and *critina*) are exceptional, but D. SMITH (1976) found that *critina* is often missing in Scotland and NE-England. Geographical differences in colour morph frequencies seem important. According to D. SMITH (1976), "low diversity probably implies specialisation rather than lack of success as several of the populations involved were of high density" and "low (colour) diversity is associated with marginal habitats, particularly low salinity and pollution".

Belgian coastal waters are indeed polluted (D'HONDT, 1988), especially inside the harbours, and salinity is somewhat reduced (25.5 - 30 g/l in Knokke (DARO, 1969), instead of the normal 33 g/l), but whether these factors are strong enough to cause a significant reduction in polymorphism remains questionable.

Visual selection could play a role too (see REIMCHEN, 1979), while the absence of *reticulata* in Belgium may perhaps be related to its particular association with the weeds *Ascophyllum nodosum* and *Fucus serratus* (D. SMITH, 1976), which are very rare or absent on the Belgian coast (DE VOS, 1978). D. SMITH (1976) also associates low colour diversity with poor weed cover and the absence of some weed species, both situations found in Belgium.

Interesting is the observation of SACCHI (1974), who notes that *olivacea* is more frequent in harbours, estuaries and bays (in general, in sheltered habitats). This finding is in agreement both with the associations of D. SMITH (1976) and with our data. Finally, SACCHI (1974) states that geographical isolation seems to enforce the concentration of certain phenotypes.

Concluding, several factors may be responsible for the remarkable dominance of *olivacea* on the Belgian coast : reduced salinity, pollution, visual selection, poor weed cover, absence of *F. serratus* and *A. nodosum,* sheltered sites and geographical isolation. In this case too, an electrophoretic study would be interesting to assess the degree of genetic polymorphism.

It should be stressed, however, that important changes in morph frequencies in populations can occur rather rapidly (SACCHI, 1974), so that our observations may just reflect a temporal situation.

5. L. neglecta

The taxonomic status of *L. neglecta* appears doubtful to us, since identification of the species was highly difficult and intermediates with *L. saxatilis* made up the majority of the population. Presently, there seem to be no clearcut characters by which the species can be separated from *L. saxatilis.* A similar situation was found by K. JOHANNESON (*in litt.*) in Iceland and by KRAAK (1984) in NW-France, while in The Netherlands, a population of *neglecta*-like *L. saxatilis* occurs in Scheveningen. On the other hand, the problem seems not to exist in Brittany (France; pers. obs.) nor in the British Isles (HANNAFORD-ELLIS, 1984; FISH & SHARP, 1985; REID, *in litt.*).

FISH & SHARP (1985) report that *L. neglecta* and juvenile *L. saxatilis* are very similar in anatomy, i.e. in radula morphology, extent of the ciliated field near the anus and infection by the trematode *Parvatrema homoeotecnum*

JAMES. They suggest that *L. neglecta* arose as a neotenous form of *L. saxatilis* through "selection for early maturation, which enabled the species to exploit the security of the barnacle belt throughout life". In Belgium, we can see that *L. saxatilis* shows early maturation too, as pregnant females of 3.0 - 3.5 mm shell height are not uncommon.
Finally, recent studies reveal that there are nearly no, if any, differences in allele frequencies and shell morphology between *L. neglecta* and *L. saxatilis* (K. JOHANNESON & B. JOHANNESON, in press; B. JOHANNESON & K. JOHANNESON, in press).

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Appendix

List of the material collected during this study (years 1986-1988) and from the wet collections of the KBIN (before 1975). The localities are listed from West (Koksijde) to East (Het Zoute).

Abbreviations

F : female(s), dissected
M : male(s), dissected
j : juvenile(s)
E : East(ern)
W : West(ern)
(W) : West from city center or portchannel
(E) : East from city center or portchannel
(C) : in front of city center
im : immature(s)
ad : adult(s), not dissected
sp : specimen(s)
Es : Eastside
Ws : Westside

Remarks on the columns

— Substrate : if not built with basalt stones, but with bricks or concrete the material used is indicated.
— Date : collecting date.
— No Sp : the first numbers refer to the specimens examined (F, M, j, im and ad), the number followed by "sp" indicates the number of remaining specimens in the sample.
— KBIN-IG-No : IG-registration number in the KBIN-collections.

1. *L. littorea*

Municipality	Locality	Substrate	Date	No Sp	KBIN-IG-No
KOKSIJDE	Koksijde (W)	breakwater no. 9	12.05.87	1j, 11sp	
	Koksijde (C)	breakwater no. 6	12.05.87	1j	
	Koksijde (E)	breakwater no. 4	12.05.87	5j	
NIEUWPOORT	Nieuwpoort	?	14.08.30	2sp	9389
	id.	breakwater	10.07.36	>10sp	10820
	Nieuwpoort-Bad	?	07.07.34	>10sp	10199
	id.	?	13.07.35	>10sp	10543
	Nieuwpoort (W)	breakwater no. 3	12.05.87	2j, 11sp	
	id.	jetty	02.02.86	5M, 7F, 4sp	
	id.	wooden railing	02.02.86	6M, 7F, 13sp	
	id.	id.	10.12.86	30sp	
MIDDELKERKE	Westende	breakwater	28.08.36	34sp	10820
	id.	breakwater no. 5	05.04.88	>50sp	
	Casino	dike	10.12.86	35sp	
	id.	dike + breakwater no. 3	12.05.86	>100sp	
	Middelkerke (E)	breakwater no. 2	12.05.86	1F	
OOSTENDE	Raversijde	breakwater	25.06.74	>150j	24988
	id.	breakwater	19.06.74	1j	24907
	Raversijde (C)	breakwater no. 15	02.02.86	6M, 8F	
	id.	id. (concrete)	10.12.86	1j	
	Mariakerke	breakwater no. 12	11.05.87	71sp	
	Oostende	breakwater	20.02.46	6sp	
	id.	breakwaters	02.10.47	>10sp	
	id.	breakwaters	09.09.73	>50sp	24749
	Oostende (W)	breakwaters	1900	>10sp	8132
	id.	breakwater no. 7	05.04.88	2j	
	id.	breakwater no. 6	05.04.88	2j	
	id.	breakwater	07.08.38	50sp	11452
	Zeeheldenplein	dike	11.05.87	3sp	
	Ws portchannel	wooden railing	30.01.46	4sp	
	id.	pier	09.01.46	2sp	
	id.	id.	19.07.46	>10sp	
	Channel	?	16.03.37	11sp	11126
	Sluice-Dock	dike (brick)	02.02.86	2M	
	Halve Maan	dike	01.02.86	3M, 2F, 3sp	
	Oostende (E)	breakwater	02.05.38	99sp	11452
BREDENE	Bredene-aan-Zee	breakwater no. 2	11.05.87	12sp	

DE HAAN	Vosseslag	sandbags	11.05.87	6sp	
	De Haan (W)	sandbags	11.05.87	3j	
	Wenduine	breakwater	28.04.35	>10	10543
	id.	breakwater	23.07.37	14sp	11126
	id.	?	24.08.37	3sp	11126
	Wenduine (W)	dike	11.12.86	1j	
BLANKENBERGE	Blankenberge	?	?	3sp	3527
	id.	?	17.07.36	4sp	10820
	id.	breakwater	29.07.37	>10sp	11126
	id.	breakwater	12.09.74	>100sp	24907
	Ws portchannel	dike	11.12.86	4sp	
	id.	concrete gaugers	11.12.86	2j	
	Es portchannel	jetty	01.02.86	5sp	
	Blankenberge (C)	breakwater?	02.07.34	>100sp	10199
	id.	breakwater no. 20-22?	03.07.34	>100sp	10199
	id.	breakwater no. 14	06.04.88	5j	
	id.	breakwater no. 21	06.04.88	6j	
	id.	breakwater no. 22	06.04.88	2j	
	Blankenberge (C)	pier (concrete)	11.12.86	1j	
BRUGGE (ZEEBRUGGE)	Zeebrugge	?	?	1sp	9224
	id.	?	17.03.11	>10sp	8132
	id.	?	04.06.37	1j	11126
	id.	?	18.06.37	5sp	11126
	Zeebrugge (W?)	breakwater	22.04.38	12sp	11452
	id.	stones on beach	18.03.47	>10sp	
	id.	beach	01.12.48	4sp	
	id.	beach	03.07.36	6sp	10820
	id.	?	30.07.37	16sp	11126
	Zeebrugge (W)	mole + breakwater	26.08.47	>10sp	
	Leopold-II-dam	mole	05.07.34	>10sp	10199
	id.	mole	13.09.45	9sp	
	id.	stones near mole	17.09.47	>10sp	
	id.	?	01.07.37	>100sp	11126
	id.	mole (concrete)	12.12.86	5sp	
	Zeegeulstraat	dike	12.12.86	55sp	
	Toegangsgeul (E)	dike + large blocks	15.08.86	46sp, 2j	
	Channels mouth (W)	concrete surface	15.08.86	33sp	
	Channels mouth (E)	dike + large blocks	12.12.86	6sp	
	Brittania Dock	large blocks	12.12.86	1j	
KNOKKE-HEIST	Es E mole Zeebrugge	large blocks	02.02.86	6M,7F, 7sp	
	Heist	breakwater	1928	1sp	9110
	id.	?	10.08.32	6sp	9772
	id.	?	13.09.45	>10sp	
	Heist (W)	wooden piles	28.01.74	1ad, 6j	24907
	id.	breakwater no. 49?	28.01.74	>400j	24907
	id.	breakwater no. 2	28.01.73	>200sp	24749
	id.	id.	28.01.74	>100sp	24907
	Duinbergen	breakwater	13.07.36	18sp	10820
	Duinbergen (C)	wooden piles	02.08.87	1ad	
	Albertstrand	wooden piles	15.09.87	3sp	
	Knokke	?	22.04.49	?	16437
	Het Zoute	beach	23.07.37	18sp	11126
	id.	breakwater no. 10	20.08.72	19sp	24576
	id.	breakwater no. 12	07.04.88	4j	
	id.	breakwater no. 14	11.09.87	5sp	
	id.	breakwater no. 15	11.09.87	8sp	
	id.	breakwater no. 17	11.09.87	5sp	
	id.	breakwater no. 19	11.09.87	10sp	

2. *L. saxatilis*

Municipality	Locality	Substrate	Date	No Sp	KBIN-IG-No
KOKSIJDE	Koksijde (W)	breakwater no. 9	12.05.87	30M, 24F, 1j, 2sp	
	Koksijde (C)	breakwater no. 6	12.05.87	1M, 2F, 13sp	
	Koksijde (E)	breakwater no. 4	12.05.87	3F, 12sp	
NIEUWPOORT	Nieuwpoort	?	16.02.55	1M, 1F, 2sp	20077
	Nieuwpoort (W)	breakwater no. 7	12.05.87	1M, 2sp	
	id.	breakwater no. 3	12.05.87	2M, 10F, 5j, 2sp	
	id.	wooden railing	02.02.86	15M, 32F, 6j, 14sp	
	id.	id.	10.12.86	2M, 3F, 45sp	
	Lombardzijde	breakwater no. 1	12.05.87	12M, 39F, 4j, 54sp	
MIDDELKERKE	Westende (E)	dike (brick)	12.05.87	1M, 1F, 1sp	
	Middelkerke (W)	breakwater no. 5/6	12.05.87	3F, 2sp	
	Middelkerke (E)	breakwater no. 2	12.05.87	20M, 24F, 16sp	
OOSTENDE	Raversijde	breakwater	19.06.74	8M, 3F, 2j	24907
	id.	?	25.06.74	2sp	24988
	Raversijde (C)	breakwater no. 15	02.02.86	5M, 5F, 1j	
	id.	id. (concrete)	10.12.86	2sp	
	Mariakerke	breakwater no. 12	11.05.87	1M, 2F, 11sp	
	Oostende (?)	?	11.06.35	2F, 1j, 4sp	10543
	Oostende (W)	breakwater	1900	>10sp	8132
	id.	breakwater no. 9	11.05.87	1M, 2F, 4j, 28sp	
	id.	breakwater no. 8	11.05.87	1M, 2F, 50sp	
	id.	breakwater no. 7	05.04.88	2sp	
	id.	breakwater no. 6	05.04.88	5M, 7F, 32sp	
	id.	breakwater no. 5	26.08.38	8j	11452
	id.	breakwater no. 4	11.05.87	4M, 6F, 100sp	
	Zeeheldenplein	dike + breakwater no. 1	11.05.87	7M, 38F, >100sp	
	Halve Maan	concrete gaugers	11.12.86	2F, 64sp	
	id.	dike	02.02.86	1M, 20F, 4j	
	id.	id.	11.12.86	2F, >80sp	
	Oostende (E)	?	?	>50sp	8306
	id.	?	23.03.37	3j	11126
	id.	breakwater	11.03.38	7M, 8F, 3im, 23sp	11452
	Sluice-Dock	dike (brick)	02.02.86	7M, 13F, 65sp	
BREDENE	Bredene-aan-Zee	breakwater no. 2	11.05.87	3F, 11sp	
	id.	breakwater no. 4	11.05.87	1M	
DE HAAN	Vosseslag	sandbags	11.05.87	6M, 10F, 8j	
	De Haan (W)	sandbags	11.05.87	1imF	
	Wenduine	breakwater	28.04.35	4F, 10sp	10543
	Wenduine (W)	dike	11.12.86	1M, 4F, >65sp	
BLANKENBERGE	Ws portchannel	concrete gaugers	11.12.86	3F, 1im, >65sp	
	Es portchannel	wooden railing	01.02.86	3M, 7F, 5im	
	id.	id.	06.04.88	1M, 4F, 5sp	
	Blankenberge (C)	?	03.07.34	>50sp	10199
	id.	breakwater no. 14	06.04.88	21sp	
	id.	breakwater no. 15	06.04.88	37sp	
	id.	breakwater no. 16	06.04.88	42sp	
	id.	breakwater no. 21	06.04.88	50sp	
	id.	breakwater no. 22	06.04.88	37sp	
	id.	pier (concrete)	11.12.86	5F, >150sp	
BRUGGE (ZEEBRUGGE)	Zeebrugge (W?)	breakwater	22.04.38	2M, 2F, 10sp	11452
	id.	beach	1947	1M, 4F, 2j	15391
	id.	breakwater & mole	26.08.47	>10sp	
	Ws W mole	large blocks	11.05.87	8M, 24F, 3sp	
	Leopold-II-laan	mole (concrete)	05.07.34	>10sp	10199
	id.	id.	12.12.86	13F, 3imF, >40sp	
	Channels Mouth (E)	boulder shore	04.06.37	13sp	11126
	id.	?	18.07.37	3M, 7F, 20sp	11126
	id.	boulder shore	12.12.87	3M, 2F, >90sp	

KNOKKE-HEIST	Heist (W)	large blocks	17.09.47	6M, 5F, >100sp	15391
	id.	id.	15.10.46	2M, 7F, 29sp	14901
	id.	wooden piles	28.01.74	8F, >100sp	24907
	id.	breakwater no. 49?	28.01.74	2F, 2sp	24907
	id.	breakwater no. 2	28.01.73	1F	24749
	Duinbergen	breakwater	13.07.36	1F, 1sp	10820
	id.	wooden piles	02.08.87	1M	
	Albertstrand	wooden piles	15.09.87	1M, 1im	
	Knokke	dike?	22.04.49	>10sp	16437
	Het Zoute	breakwater no. 10	20.08.72	2sp	24576
	id.	breakwater no. 12	07.04.88	12M, 14F, 36sp	
	id.	basalt blocks	07.04.88	1sp	
	id.	breakwater no. 13	07.04.88	5F, 55sp	
	id.	breakwater no. 14	11.09.87	1F, 2im, 8sp	
	id.	breakwater no. 15	11.09.87	1sp	
	id.	breakwater no. 17	11.09.87	9sp	
	id.	breakwater no. 19	11.09.87	7sp	

3. *L. neglecta*

Municipality	Locality	Substrate	Date	No Sp	KBIN-IG-No
OOSTENDE	Halve Maan	dike	02.02.86	7M, 3F	
	id.	id.	11.12.86	3M, 2F, 1j	
BRUGGE	Zeebrugge (W)	beach	1947	4F	15391
	id.	id.	15.10.46	2M, 7F, 29sp	14901
KNOKKE-HEIST	Heist (W)	large blocks	15.10.46	1M	14901
	id.	piles	28.01.74	2F, ?sp	24907

4. *L. obtusata*

Municipality	Locality	Substrate	Date	No Sp	KBIN-IG-No
OOSTENDE	Sluice-Dock	walls of sluice	29.04.38	1M, 1j	11452
BLANKENBERGE	Ws portchannel	dike	11.12.86	1sp	
	Es portchannel	jetty	01.02.86	2M, 1F, 2j	
	id.	id.	06.04.88	3sp	
BRUGGE	Zeebrugge (W)	breakwater	22.04.38	1F	11452
(ZEEBRUGGE)	Ws W mole	large blocks	11.05.87	1F, 3j	
	Leopold-II-dam	mole (concrete)	12.12.86	2M, 3F, 41sp	
	Toegangsgeul (E)	dike + large blocks	15.08.86	3M, 14F, 126sp	
KNOKKE-HEIST	Es E mole	large blocks	01.02.86	9M, 8F, 1j, 17sp	

5. *L. mariae*

Municipality	Locality	Substrate	Date	No Sp
BRUGGE	Ws W mole	large blocks	11.05.87	2M, 2F, 2j
(ZEEBRUGGE)	id.	id.	01.88	8M, 6F, 7sp