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Trends in littorinid research in Belgium (Mollusca, Gastropoda, Prosobranchia)

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Summary

This paper reviews the actual knowledge on the five *Littorina* species that live on the Belgian coast. *L. saxatilis* and *L. littorea* are common, while *L. obtusata, L. mariae* and *L. neglecta* show a local distribution. Furthermore, the Belgian populations of *L. saxatilis* are characterized by low densities, a considerably reduced shell colour polymorphism, early maturation and a relatively high gene flow between populations. Prospects for further research are commented.
Key-words : *Littorina*, Prosobranchia, faunistics, population genetics, polymorphism, Belgium.

Résumé

Cet article revoit la connaissance actuelle des cinq espèces du genre *Littorina* vivant en Belgique. *L. saxatilis* et *L. littorea* sont communes, tandis que *L. obtusata, L. mariae* et *L. neglecta* ont une distribution locale. Par ailleurs, les populations belges de *L. saxatilis* sont caractérisées par des densités basses, un polychromatisme de la coquille fortement réduit, une maturation prématurée et un échange de gènes relativement haut entre populations. Les possibilités pour la recherche future sont discutées.
Mots-clefs : *Littorina*, Prosobranchia, faunistique, génétique de population, polymorphisme, Belgique.

Introduction

According to a recent revision of the classification of the Littorinidae (REID, 1989), the genus *Littorina* 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 shores, but which may be found in estuaries and mangroves too.

The systematics and taxonomy of this genus have undergone important changes after the discovery that some classical species are in fact complexes of sibling forms. They were reviewed by FRETTER & GRAHAM (1980), RAFFAELLI (1982), SMITH (1982), WARMOES (1987) and WARMOES *et al.* (1989).

According to most authors (see HELLER, 1975 ; SACCHI, 1975 ; HANNAFORD-ELLIS, 1978, 1979 ; RAFFAELLI, 1979), the group of *L. saxatilis* (OLIVI, 1792) *s.l.*, or rough winkles, comprises four species : *L. saxatilis s.s.* (including the former *L. tenebrosa* (MONTAGU, 1803) and in part *L. rudis* (MATON, 1797)), *L. neglecta* BEAN, 1844, *L. nigrolineata* GRAY, 1839 and *L. arcana* HANNAFORD-ELLIS, 1978. *L. obtusata* (LINNAEUS, 1758) *s.l.*, the flat winkle, was split by SACCHI & RASTELLI (1966) in *L. obtusata s.s.* and the dwarf species *L. mariae* SACCHI & RASTELLI, 1966 (both including in part *L. littoralis* (LINNAEUS, 1758) and *L. palliata* (SAY, 1821) ; see also GOODWIN & FISH, 1977). With *L. littorea* (LINNAEUS, 1758) and *Melarhaphe neritoides* (LINNAEUS, 1758), a total of eight littorinid species are thus presently known in Europe.

However, *L. arcana* is not accepted by some authors (e.g. CAUGANT & BERGERARD, 1980), while, recently, it appeared that *L. neglecta* could be an ecomorph of *L. saxatilis* (JOHANNESON & JOHANNESON, 1990 a, b).

Furthermore, there are large differences in reproductive biology between the species. *M. neritoides* and *L. littorea* have planktonic eggs and larvae, while *L. nigrolineata, L. arcana, L. obtusata* and *L. mariae* are oviparous and *L. saxatilis* and *L. neglecta* ovoviviparous.

The about 65 km long Belgian coast completely lacks natural rocky intertidal sites, but men has provided a number of artificial substrata such as dikes, piers, fences and breakwaters, which are suitable to the most tolerant rocky shore organisms. Because of severe environmental stress (high exposition to waves and wind, and lack of shelter), the flora and fauna of these substrata is poor, as compared to that of natural sites (DARO, 1969).

This is probably the main reason why the Belgian coast has been somewhat neglected by malacologists during the past fifty years. With respect to the *Littorina* species, only some faunistic records can be found in the literature (e.g. VONCK, 1933 ; LELOUP & MILLER, 1940; VERSTRAELEN, 1966). Recently, the author started a more profound study of the genus in Belgium ; the preliminary results of this study are reviewed in this paper.

Faunistics of the Belgian Littorinidae

WARMOES *et al.* (1989) have demonstrated that five *Littorina* species live on the Belgian coast, namely *L.*

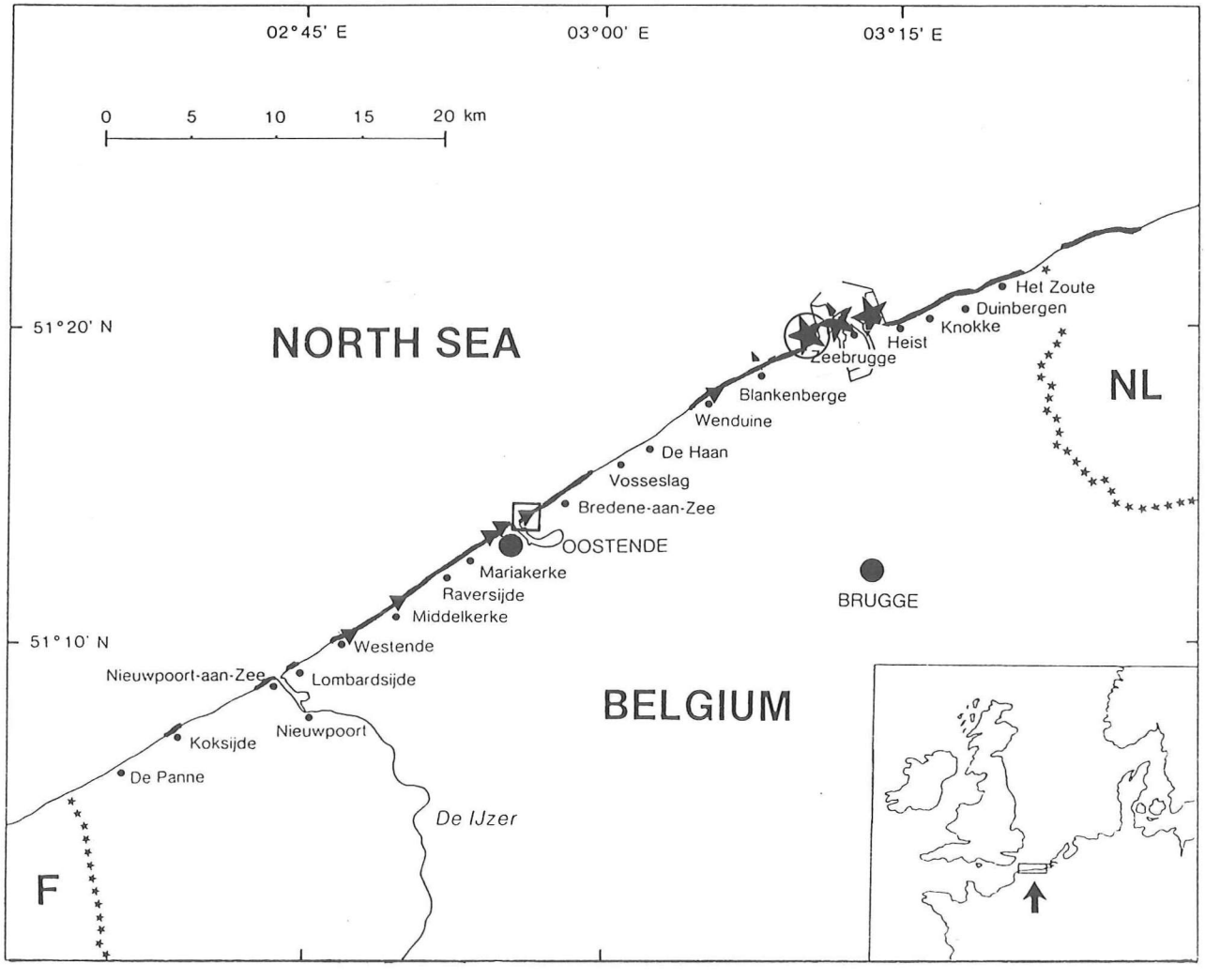

Fig. 1 - Map of the Belgian coast showing the localities visited by the author. Bold line : parts of the coast where breakwaters were built ; triangles : dike in contact with the sea at high water ; stars : populations of L. obtusata ; *open circle : population of* L. mariae ; *open square : population of* L. neglecta. L. saxatilis *and* L. littorea *were found on nearly all hard sustrates examined.*

littorea, L. saxatilis, L. obtusata, L. neglecta and *L. mariae*, the latter two being new to the Belgian fauna. *L. arcana, L. nigrolineata* and *M. neritoides* were not found. For *M. neritoides* this is somewhat odd, as this species was regularly found in northern France and the Netherlands (STOCK, 1975) and has a planktonic stage. *L. littorea* can be found on nearly all intertidal hard substrata, while *L. saxatilis* is unexpectedly common in Belgium and seems to be a rapid coloniser of new suitable substrata. In spite of its ovoviviparous reproduction, the species may be much more mobile than hitherto believed, at least along shallow sandy coasts. *L. neglecta* was found with certainty only on a concrete block in Oostende, which is completely overgrown by the barnacle *Semibalanus balanoides.* However, many intermediates with *L. saxatilis* were found ; this emphasizes the doubtful status of *L. neglecta.*

L. obtusata and *L. mariae* have a very local distribution because they live on large brown weeds (*Fucus* spp.), which are not common on the Belgian coast. While *L. obtusata* can be found on both *F. spiralis* and *F. vesiculosus, L. mariae* is restricted to the lower part of the *Fucus* belt and was found only on *F. vesiculosus.*

When we compare the Belgian populations of *L. saxatilis* and *L. obtusata* with the populations of natural rocky coasts, such as those of Brittany (France), it is striking that they show much lower densities. This is possibly explained by the nature of the substratum and a high predation rate by birds.

Survival rates of winkles have been shown to be related to the availability of cracks and holes in the substratum (RAFFAELLI & HUGHES, 1978), and the breakwaters and dikes could be less rich in micro-sheltered niches for the snails. Snails sitting on the open surfaces are both more easily detached by waves and more vulnerable to predation from birds. Accordingly, on the Belgian coast, substrata with deeper cracks and more (dead) barnacles seem to support higher densities of *L. saxatilis.*

Population densities of Belgian *L. obtusata* seem to fluctuate remarkably over the years, but the causes of this phenomenon are still unknown.

Finaly, it is striking that Belgian *L. saxatilis* matures early. Mature animals with a shell height of 3 mm are

not exceptional. Probably this is an adaptation to the small shelter places (mainly dead barnacles) on the breakwaters. Most animals have between 5 and 10 penial glands, which is much less than in rocky shore populations. Belgian *L. neglecta* shows 3 to 7 penial glands.

Shell colour polymorphism

In comparison with other regions, Belgian *L. saxatilis* and especially *L. obtusata* show a strongly reduced shell colour polymorphism. This may possibly be caused by visual selection (predation), pollution, lower salinities, poor weed cover, absence of some weed species and geographical isolation (WARMOES *et al.*, 1989). Although it is likely that several factors are involved, we do not know, at present, which factors are predominant.
The crypsis shown by *L. saxatilis* and the high numbers of overwintering Turnstones (*Arenaria interpres*) and Purple Sandpipers (*Calidris maritima*) on the Belgian coast, both consuming large quantities of small winkles (FEARE, 1966 ; BECUWE, 1971 ; PRATER, 1972 ; PETTITT, 1975), seem to point to a preponderant role for visual selection in this species.
While both crabs and birds undoubtedly consume large 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.*

Population genetics and dispersal

The genetics of Belgian populations of *L. saxatilis* have been studied by JOHANNESON & WARMOES (1990). The other species occurring in Belgium were not yet analysed by electrophoresis.
Although the difference is not large, the Belgian populations of *L. saxatilis* are about 8% less heterozygous than populations from natural rocky coasts. It is likely that these populations have passed through bottlenecks either when founded, or when the breakwaters were rebuilt, but a rapid expansion in population size after the introduction to a new site may limit the genetic loss to less than 10% (JANSON, 1987).
No relationship was found between genetic and geographic distances between the Belgian populations of *L. saxatilis*, although such relationship was found along 300 km of Swedish shore (JANSON, 1987). Furthermore, the differences between the Belgian populations are rather small. This suggests that the gene flow between sites is higher in Belgium than in Sweden and that individuals may be transported over longer distances along the Belgian coast. The explanation for this may be that dispersal mechanisms are different between the Belgian and Swedish coasts (the latter being atidal and having deeper waters).
However, which dispersal mechanisms are actually involved, remains to be investigated. Transport by tidal and coastal currents seems important along the continuous shallow sandy coast of Belgium. Individuals of *L. saxatilis* may be dislodged from the substratum and shoved to another site. The species is very tolerant to environmental stress of different kinds and will likely survive some weeks of passive rolling along a sandy bottom. Furthermore, transport by birds, ships or drifting weeds are possible dispersal mechanisms.

Conclusive remarks

Although the present knowledge on the Belgian *Littorina* populations is still very fragmentary, it is already clear that many deviations from the "normal" situation, mainly known from the rocky coasts of Brittany (France) and the (western) British Isles, can be found in this area. These peculiarities are :
- the many intermediates between *L. saxatilis* and *L. neglecta* ;
- the early maturation of *L. saxatilis* ;
- the reduced polymorphism of *L. saxatilis* and *L. obtusata* ;
- the extreme low densities of most *L. saxatilis* populations.

The causes of these deviations are difficult to assess, but we believe that (at least) three factors could play an important role : the small tidal range in the Channel, as compared to that of the Atlantic coasts ; the specificity of the isolated, artificial habitat in a hostile environment and the important predation pressure to which the winkle populations are subject.
A more profound study of the different species in the Channel is needed and in this context particular attention should be paid to population ecology and genetics, demography and anatomy. Moreover, generally spoken, not much is known on the biology of *L. obtusata* and *L. mariae* ; these species should receive more attention from littorinologists in the years to come.
There is also urgent need for more experimental work on *Littorina*. This should focus on quantitative measurements of transport rates between populations, dispersal mechanisms, visual selection and the precise effect of bird and crab predators on the winkle populations. The discrete, artificial substrata of the Belgian coast, with well-defined populations of *Littorina*, offer excellent opportunities to conduct these investigations.

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