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**On the trophic role of the blue mussel (*Mytilus edulis* L.)
in a Baltic coastal ecosystem and the fate of
the organic matter produced by the mussels**

N. Kautsky

Askö Laboratory, Institute of Marine Ecology
University of Stockholm, Stockholm, Sweden

Abstract

Mytilus totally dominates the animal biomass on Baltic hardbottoms since most predators and competitors are excluded due to low salinities. Experiments failed to prove the presence of scavengers on moribund mussels. Since predation is largely lacking, weakened individuals are not removed from the population and these dying mussels respire up to 80% of their meat weight before death, resulting in a drastically reduced energy flow from mussels to destruents. Apart from a considerable output of reproductive products to the pelagic system and an export of shell organics to sediment bottoms, the adult *Mytilus* population seems to constitute a "dead end" in the food web.

Introduction

The blue mussel, *Mytilus edulis* totally dominates the animal biomass in the Baltic proper, colonizing bottoms from the algal belts at the water surface down to about 35 – 40 m depth where hard substrates become scarce. Although the northernmost records of *Mytilus* in the Baltic (Fig. 1) are from the Quark (63°N) (BERGH 1964), the mussels rapidly become less abundant north of the Åland Sea due to decreasing salinities. In the southwestern part of the Baltic, *Mytilus* is again less dominant due to predation mainly by *Asterias rubens* L. and *Carcinus maenas* L. which can still tolerate the low salinity there. Between these areas, over the larger part of the Baltic proper, the euryhaline *Mytilus edulis*, although dwarfed by the salinity stress, occupies alone a niche which is normally shared by many suspension-feeding species. The general absence here of both heavy predators and competitors for space often results in overcrowded mussel populations limited by intraspecific competition for food and space (KAUTSKY, 1981 a, b). Such permanent establishments of near "monocultures" of animals over larger areas which predators fail to exploit seem to be an exceptional feature in natural marine ecosystems, but are well known in experimental systems where predators have been excluded (e.g. PAINE 1971, 1974, MENGE 1976).

In this paper an attempt is made to quantify the predatory pressure on a Baltic *Mytilus* population and to discuss the trophic role and the fate of the organic matter produced by the mussels.

The standing stock and the population dynamics of *Mytilus*

This investigation was carried out in the primary research area of the Askö Laboratory situated about 70 km south of Stockholm and comprising 160 km² of an outer

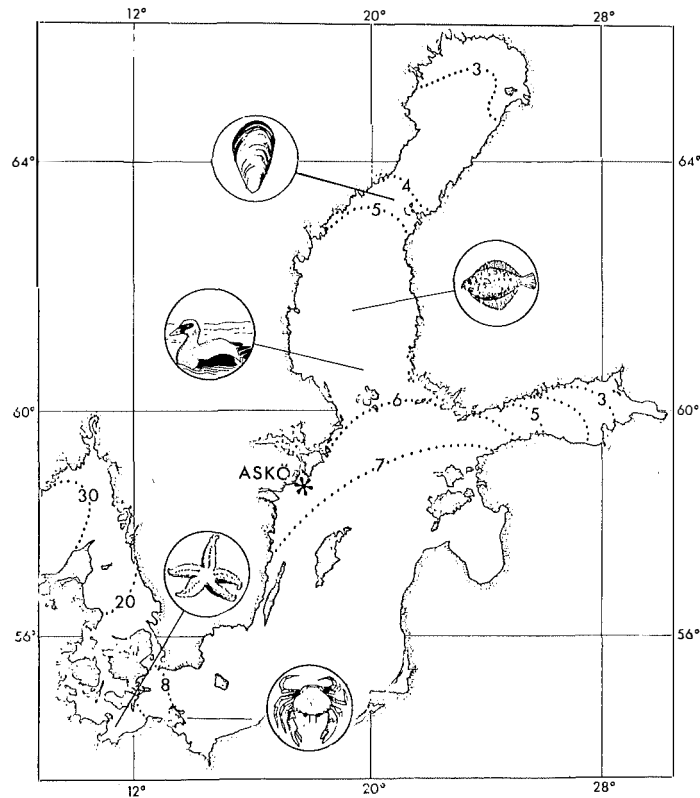


Figure 1

Map of the Baltic Sea with surface water isohalines (dotted lines) and innermost distribution limits of *Asterias rubens*, *Carcinus maenas*, *Platichthys flesus*, *Mytilus edulis* and innermost major breeding area of *Somateria mollissima*.

archipelago area, with a salinity of about 6.5 ‰. Approximately half the bottoms here down to 25 m are hard bottoms, with 86 % of the animal ashfree dryweight made up by *Mytilus edulis* and a total biomass in July–August amounting to about 10 200 metric tons dryweight including shells if *Mytilus* occurring on soft bottoms are also included (JANSSON and KAUTSKY 1977, KAUTSKY and WALLENTINUS 1980). Of this biomass about 1500 tons dryweight is meat (~ 750 tons org.C) and the rest, or about 8 700 tons dryweight, is shell. The shells contain mainly inorganic matter, but the organic content of 6.2 % (KAUTSKY unpubl.) means that a total of 270 tons org.C. or one quarter of the total organic matter is bound in the shell matrix.

In ten years of diving in the study area, no major fluctuations between years in the distribution and abundance of *Mytilus* have been noted (KAUTSKY unpubl.). Despite recruitment, growth and mortality, there are indications that the total standing stock of the population is also rather constant during most of the year, maintained at a food- and space-limited saturation level of 1 500 tons meat (KAUTSKY, 1981 a, b).

Only during April–May is there a considerable increase in the condition of the mussels leading to an 80 % rise in the total meat weight of the population (KAUTSKY 1981 a, b).

This whole increase, amounting to 600 tons org.C, can be attributed to the build-up of the gonads, which triggered by the increase in water temperature around the beginning of June, is released in the form of reproductive products.

The total standing stock of the mussel population can thus be divided into three essential parts (Fig. 2): the gonads which are built up annually and then released, and the more constant pools of mussel meat and shell organics.

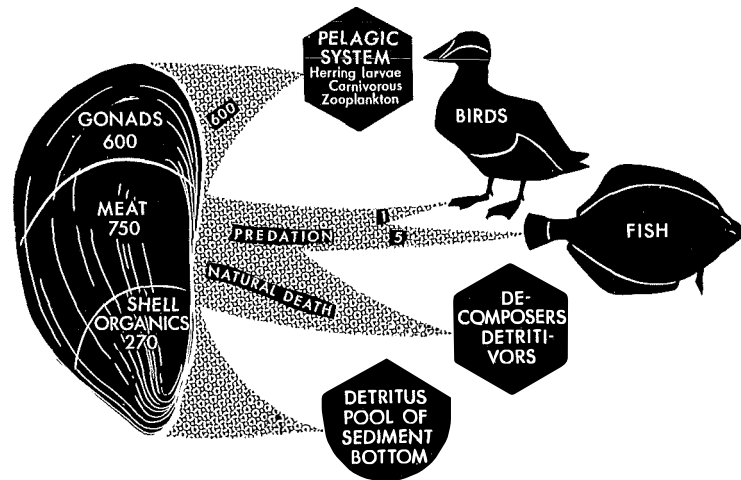


Figure 2

Showing the total standing stock of *Mytilus* gonads, meat and shell organics respectively in the Askö primary research area (tons org.C · 160 km⁻²) and the fate of these different fractions (tons org.C · 160 km⁻² · year⁻¹); see text.

The fate of the organic matter produced by the mussels

Export of reproductive products to the pelagic system

The already mentioned decrease in mussel condition in late spring indicates an annual input of up to 600 tons org.C to the pelagic system as eggs and larvae. This means that up to about 4 g org.C · m⁻², corresponding to as much as half of the annual zooplankton production in the area (JOHANSSON and SKÄRLUND, in prep.), is released to the pelagic system over a few weeks at the beginning of June. These values, however, only indicate the release of reproductive products from the mussel population and do not indicate how much actually enters the pelagic system and is not immediately sedimented back to the bottoms. As this input, however, coincides with the hatching and growth of herring larvae (ANEER and NELLBRING 1980) and since mussel larvae have been found to constitute a large part of the gut content of herring larvae (SCHNACK 1972), it probably plays a very important role, both to herring and other carnivorous zooplankton.

Predation on the adult stock of *Mytilus*

As mentioned earlier, the major invertebrate predators on adult *Mytilus* in more saline areas, i.e. *Asterias*, *Carcinus*, *Thais* etc., are excluded from most of the Baltic and the predators still present are thus limited to certain bird and fish species.

In the Askö area the Eider duck, *Somateria mollissima* L., is by far the most important bird feeding on mussels. Bird censuses have shown there to be about 500 pairs nesting in the area giving rise to about 750 surviving juveniles each season. The adults have been estimated to spend in total about 105 000 „bird days” in the area and the juveniles about 60 000 (B. ALMQVIST, pers. comm.). Using a daily consumption value of 300 g fresh weight of mussels for the adults (BELOPOLSKII 1961) and an estimated value of 100 g fresh weight for the juveniles, this would mean a total annual consumption of mussels by Eider ducks in the Askö area of 37.5 tons fresh weight, which corresponds to 2.2 tons shellfree dryweight (~ 1.1 tons org.C). Other mussel-eating birds nesting in the area viz. Velvet Scooters (*Melanitta fusca* L.), Tufted Ducks (*Aythya fuligula* L.) and Goldeneyes (*Bucephala clangula* L.) take only minor amounts of mussels compared to the Eiders. A quantitatively important mussel-eating bird in the Baltic is the long-tailed Duck (*Clangula hyemalis* L.) which, however, occurs only occasionally within the area. Only about 1 ton org.C. can therefore be estimated to be taken by birds in the Askö area (Fig. 2).

The main mussel predator among fish seems to be the flounder (*Platichthys flesus* L.). Results from purse seining indicate a standing stock of 27 tons wet weight (5.4 tons dryweight) in the area (ANEER et al. 1978) which, with an average daily food requirement of 1.5 % of the body dryweight (ARNTZ 1978), gives an annual food requirement by *Platichthys* corresponding to about 9 tons shellfree dryweight of mussels (~ 4.5 tons org.C).

Although *Mytilus* constitutes a major food item for flounder in the Askö area (LORD 1969) it also utilizes other food items, mainly *Macoma balthica* (L.) especially when *Mytilus* has a low nutritive value after spawning. At this time of the year *Platichthys* have even been observed to prefer *Macoma* despite the fact that the flounder migrates then to the shallow hardbottoms and is often in fact found in the middle of the *Mytilus* beds by divers (KAUTSKY unpubl.).

Some smaller fish e.g. eelpout (*Zoarces viviparus* L.), especially that part of the population living on rocky bottoms, also eat mussels but since this is not a commercial species very little is known about it and its role is therefore very uncertain. Cod (*Gadus morhua* L.) also takes minor amounts of *Mytilus* (NYQVIST 1969) but in total the yearly consumption of *Mytilus* by demersal fish does not exceed 10 tons shell free dryweight (~ 5 tons org.C) (Fig. 2).

Dead mussels as food for scavengers

Since death by predation is insignificant, “natural” death from age, parasitic infection or starvation due to competition for food must instead be of major importance. This would result in mussel carcasses for consumption by expected scavengers in the area, such as some fish and amphipod species, planarians and *Nereis diversicolor* O.F. Müller, as has been noted in intertidal mussel clumps on the British coast (EMSON 1977).

To investigate the occurrence of such potential scavengers on the mussel bottoms in the Baltic and to see how fast mussel carcasses disappear, a baited cage experiment was designed. A 30 cm wide 1 mm mesh nylon sieve was placed at 7 m depth in the *Mytilus*-red algal belt and 10 forced-open mussels with cut adductor muscles were placed loosely in the sieve together with a stone serving as a weight and as a shelter for those small fish expected to be attracted. 10 opened mussels each were also placed in 2 net bags with 0.7 and 2.5 mm mesh respectively, in order to discriminate between the scavenging effects of very small animals (e.g. Amphipoda, *Planaria*, *Nereis* etc.)

and predation by fish which had free access only to the mussels placed in the open sieve. This arrangement was put out for one night at the end of April after which a net bag was placed around it and it was taken to the laboratory for analysis. Quite astonishingly, nothing had happened and all the mussels were still untouched. The experiment was then repeated with an exposure time of three weeks.

Even after this time period, most surprisingly again nothing had happened and all mussels were still living and fresh. They had, however, spawned although spawning had not yet started in the surrounding natural population.

This experiment was carried out twice more between the middle of May and the end of June. After these periods about two thirds of the mussels were still living although some of them were in bad condition with very thin mantles. The remaining third were half rotten and stinking, but none of the shells were empty indicating that no scavenging had taken place. In this respect, there appeared to be no difference between the mussels in the net bags and those openly exposed.

No accumulation of macrofaunal animals was noted around the mussels and about the normal composition of species and numbers were found, i.e. plenty of Amphipoda spp. a few *Hydrobia* spp. and *Planaria* spp. On one occasion (period 3), two specimens of *Prostoma obscurum* Schultze (Nemertini) and three individuals of *Praunus flexuosus* (O.F. Müller) (Mysidacea) were also caught. It is uncertain whether these animals were attracted by the remains or merely present by accident.

Transport of matter to the sediment bottoms and terrestrial systems

As already stated, about one quarter of the total standing stock of organic C of the *Mytilus* population in the area is bound in the shells. This matter is unavailable to predators and if devoured it passes through the gut together with the calcareous part of the shell. The shells of Baltic *Mytilus* are thin and comparatively badly calcified, leading to a rather quick dissolution of the calcareous part of dead shells leaving a thin sheet of periostracum containing most of the shell organics. Currents carry away these periostraca which finally settle on the sediment bottoms where they can often be found in great quantities making up 3–5 % of the sediment volume sampled by the Van Veen grab (CEDERWALL, pers. comm.). On these bottoms the periostraca form a pool of very slowly disintegrating organic matter. In the long run, however, most of this matter will be made available to the food chains again, and will probably, together with drifting macro-algae, have a stabilizing effect on the benthic system by ensuring at least some food supply to benthic animals when the strongly fluctuating input from the pelagic system is at a minimum.

Parts of the living mussel population, especially those occurring in the upper littoral or those attached to *Fucus vesiculosus* risk being scraped off by ice and storms and tossed ashore to become food objects of e.g. gulls and badgers (*Meles meles* L.) (P.-A. SKOOG pers. comm.) or they may be carried by drifting algae to deeper soft bottoms where they may be drowned in the sediment, or if they land on erosion bottoms they may survive as the sparse and patchy *Mytilus* population found on these bottoms (ANKAR and ELMGREN 1976) which probably has no own recruitment.

General discussion

As mentioned earlier, the fate of the mussel biomass that is represented by the reproductive products and the shell organics can be accounted for fairly easily (Fig. 2). The rest of the standing stock (750 tons org.C) which is found as mussel meat is only

protected by thin shells and could thus be readily used by carnivores in the system. The evidence presented in this paper, however, indicates that only very little of the standing stock is used by macro-consumers in the food chains. As there is obviously plenty of food easily available, other factors would appear to limit an increase in predator populations. It seems as if some of the few species which have overcome salinity problems, can, at least during parts of the year, choose from other more energy-rich food items.

Although the predatory pressure exerted by seabirds and fish is very small, it will probably have a positive effect on the food- and space-limited mussel population by thinning out the dense stock and thus increasing production. A more important effect on the system, however, might be that the predation increases diversity by allowing other competitively inferior species e.g. benthic macroalgae to colonize the bottoms. Such effects have been discussed by e.g. PAINE (1974), but have not yet been shown to be valid for the Baltic.

The most striking feature, however, is the absence of scavengers in the system. In a true marine system opened mussels, as in the cage experiment, would have been taken by fish or crabs within a few minutes, as was observed on shallow sandy bottoms (ERIKSSON et al. 1975) and in a comparative experiment carried out in the rocky sublittoral of the Swedish west coast (KAUTSKY, unpubl.).

How is it then that such large, easily accessible, energy parcels are left unused in the Baltic? Are dead mussels really so rare that no species has adapted to utilize such a resource? This last question may sound strange on reflection since empty shells are quite common, especially after spawning (KAUTSKY, unpubl.) and must be evidence of natural death, since the known predators among birds and fish in the Baltic swallow the mussels whole and do not leave any empty shells as e.g. *Asterias* and *Thais* would do.

There are indications however, that natural death in Baltic *Mytilus* is a very slow process, sometimes involving long periods of up to a couple of months of "negative growth" when individual mussels can in fact respire away their own biomass by up to about 80 % before dying (KAUTSKY 1981 a, b). The baited cage experiment, where the mussels spawned and decreased in weight, also supports this. Most of this respired energy is lost from the system. Large amounts of nutrients will, however, be regenerated and recirculated to the primary producers of the benthic and pelagic systems (KAUTSKY and WALLENTINUS 1980). A similar process probably also takes place in mussels of true marine ecosystems, but here weakened individuals will continuously be removed by the predators present.

Apart from drastically reducing the total energy flow from mussels to destruenters in the Baltic this respiration process results in smaller, less tempting energy parcels and scavengers e.g. fish might prefer to predate directly on the unlimited supply of living, thin-shelled, Baltic mussels which are only loosely attached by byssus threads.

Thus, since predation and scavenging are obviously limited and the mussels to a large extent seem to respire their own biomass the standing stock of adult Baltic *Mytilus* can be said to constitute a sort of "dead end" or "blind alley" in the food web.

A parallel to this can be drawn with other ecosystems with organisms which are not preyed on for some reason, such as e.g. echinoderms which often constitute "dead ends" in food webs. In these systems energy drains due to respiration can also be suspected of being of great significance and should be accounted for in ecosystem energetics.

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