

# ON THE ECOLOGY AND DISTRIBUTION OF THE PARASITIC COPEPOD *MYTILICOLA INTESTINALIS* STEUER

by

P. KORRINGA

*Rijksinstituut voor Visserijonderzoek, IJmuiden*

Prior to 1950 very few scientific papers had been devoted to the parasitic copepod *Mytilicola intestinalis* Steuer. Early in this century Steuer discovered this parasite in mussels collected at Trieste. He described genus and species in detail and added some notes on its biology (STEUER, 1902, 1905). Shortly after, PESTA (1907) told us more about the development of its larvae. Next, there are some scattered records of its being detected here and there along the coastline of the Mediterranean, but never beyond that sea. Treatises on parasitic copepods or on molluscan parasites like those of DOLLFUS (1927), MONOD and DOLLFUS (1932), van OORDE-DE LINT and SCHUURMANS STEKHOVEN (1936), and PELSENEER (1929) did not make mention of its occurrence along the coastlines of Atlantic Ocean and North Sea. PELSENEER (1929) warned us, however, against too hasty conclusions, since malacologists usually did not look after parasites, whereas parasitologists had not yet made an overall survey of all potential molluscan hosts. Then CASPERS (1939) found this parasite in mussels in the Eastfrisian coastal waters, and ELLENBY (1947) recorded it from the Blyth estuary (Northumberland). COLE told us later (1951) that a single specimen had been found in Southampton as early as 1937, but that this finding had not been published.

That 1950 was a turning point, and that many *Mytilicola* papers did appear in the next 15 years should not be ascribed to a sudden interest of taxonomists, parasitologists or zoogeographers in parasitic copepods, but merely to its becoming a species of great — be it negative — economical importance. The disaster which struck the thus far flourishing Zealand mussel industry through a regular explosion of *Mytilicola* (KORRINGA, 1950) sounded a warning, and the colloquy held at Paris, February 8-9, 1951, led to a concerted attack on the gaps in our knowledge of

the biology of this species and of the interrelationships between the parasite *Mytilicola intestinalis* and its host, the mussel, *Mytilus edulis*.

The more important points in question can be formulated as follows:

(A) Is *Mytilicola intestinalis* really the causative agent of the dramatic events in Zealand, and of the extensive mussel mortalities observed in the coastal waters of East Frisia, and later in the Whitstable area?

(B) Should the observed explosion of *Mytilicola* be considered as of epidemic (epizootic) nature, or is *Mytilicola* a new intruder in the waters of Western Europe? In the first case its realm will probably be of short duration, whereas in the second case it may never disappear again, like has been observed after the intrusion of several marine organisms in European waters.

(C) If *Mytilicola* is an intruder, where did it come from, and why did we never hear about its deleterious activities there? How did it spread to its new environment and where can we expect its arrival in the near future?

(D) What is the ecological range of *Mytilicola intestinalis* and which ecological factors limit its distribution and abundance?

(E) Why is the present distribution of *Mytilicola intestinalis* of such a disjunct nature and why did *Mytilicola*, despite its pelagic larvae, not yet reach all the major mussel beds of Europe? What can this teach us for the proper management of our mussel industries?

A critical appraisal of all the information published since that fatal year 1950, supplemented by my own practical experience in this field, leads me to formulation of the following answers to the questions listed above:

(A) DOLLFUS (1951) was virtually the only scientist who pleaded "not guilty" for *Mytilicola intestinalis*. But we can hardly blame him: he was so fond of parasitic copepods that he simply could not bear the thought of their doing serious harm to, or even kill, other creatures. Faced with the facts, especially with the results of physiological investigations carried out by MEYER and MANN (1950, 1951), Dollfus admitted reluctantly that *Mytilicola* could lead to loss of condition and weakening of its host, but he insisted that the final blow, which leads to death of the host, should be ascribed to an unknown pathogenic agent invading mussels of reduced resistance.

We know now that this cannot be true. Many investigators demonstrated that *Mytilicola* does affect its host adversely and that proportional to the number of parasites per host (ANDREU, 1963; BRIENNE, 1964; CHEW et al., 1965 (*Mytilicola orientalis* in *Crassostrea gigas*); COLE and SAVAGE, 1951; KORRINGA, 1950, 1952, 1954; MEYER and MANN, 1950, 1952; ODLAUG, 1946 (*Mytilicola orientalis* in *Ostrea lurida*)). Using an accurate method to determine the condition index of mussels (KORRINGA, 1955) I demonstrated myself (KORRINGA, 1951, 1952) how sensitive the Dutch mussels are: even the effect of one single parasite per host was measurable, and the condition appeared to decrease proportionally to the number of parasites per mussel. ANDREU (1960) even expressed this in a formula: the fresh weight of a shucked mussel is according to him  $8.98 - 0.0943 \times$  the number of parasites; but we should consider that this formula cannot have an overall validity; it varies with the size of the mussels, the activity of the parasite as determined by water temperature and by the general feeding conditions for the mussel.

That neither GENOVESE (1959) nor HRS-BRENKO (1964) could demonstrate a clear-cut effect of *Mytilicola* on the condition of its host does not prove that the Mediterranean mussel (*Mytilus galloprovincialis*) does not suffer at all from this parasite. Had they used larger samples and more heavily infested mussels, and had they analysed those with more accurate methods to determine the condition index, they would no doubt have found an adverse effect of the parasite on its host. The possibility should, however, not be excluded that the Mediterranean mussel shows a different degree of vulnerability than the Atlantic

mussel. This not in the sense that copepodids of *Mytilicola* would more readily penetrate the Atlantic mussels than the Mediterranean ones, but rather in terms of LAMBERT's supposition (1951) that *Mytilus galloprovincialis* might in the course of time have developed anti-bodies against the toxins exuded by *Mytilicola*. Careful physiological observations might demonstrate that, but the lean mussels, bearing several parasites we saw in the Etang de Berre and in the Grau d'Agde (KORRINGA and LAMBERT, 1951) indicate already that the difference in sensitivity between Atlantic and Mediterranean mussels cannot be very great.

For the same reason WILSON (1938) could not measure the effect of *Mytilicola orientalis* on *Crassostrea gigas*, but later workers (CHEW et al., 1965) did demonstrate that a somewhat heavier infestation does adversely affect the condition of that oyster.

That also the growth of mussels is closely related with the degree of infestation has been demonstrated (KORRINGA, 1953). THEISEN (1965) tells us of a distinct growth ring indicating in Limfjord mussels the period of heavy infestation with *Mytilicola*.

The physiological observations by MEYER and MANN (1950, 1952) and MEYER-WAARDEN and MANN (1954a) clearly demonstrate what really happens: even in case of light infestations the filtration rate is reduced so that less food can be collected, whereas the metabolic rate increases, as demonstrated by a growing oxygen consumption. In severe cases the mussels become extremely lean, and death may follow (KORRINGA, 1950, 1952; WAUGH, 1954). This latter especially when the mussels are 100% infested and carry on an average 10 or more parasites each, and this at rather high water temperatures. But the most remarkable thing is that as soon as the number of parasites diminishes or low water temperatures reduce their activity, even the leanest mussels, at first sight in moribund condition, recover. This would not be the case when pathogenic agents other than *Mytilicola* invaded: the lean mussels rendered vulnerable by *Mytilicola*'s attack (KORRINGA, 1952, 1954, 1957). Several authors assert that the mussels suffer definitely less under for them favourable conditions: plenty of food, water poor in silt, low water temperatures (ANON., 1956; HEPPER, 1955; KORRINGA, 1954a).

Just how *Mytilicola* exerts such a deleterious effect on its host is not precisely known. FLEURY et al. (1951) and LAMBERT (1952) assume that *Mytilicola* excretes some toxic substance which exerts an ill effect on the host, as do so many parasites. The better the general ecological conditions for the host, the less

they will suffer from the toxins, and the more vigorous the activity of the parasite at higher water temperatures, the more serious the effects.

It is interesting to mention here that very young mussels (usually under 20 mm in shell length) rarely or never carry *Mytilicola* in their intestinal tract, and that in the same lot of mussels the number of parasites is usually proportional to the shell length (ANDREU, 1960; GRAINGER, 1951). This latter could easily be explained in terms of the volume of water filtered by individual mussels of different size.

(B) When Caspers found *Mytilicola* in the German Wattenmeer, he thought that this species might have been overlooked there thitherto. Meyer and Mann, carrying out *Mytilicola* investigations in the German coastal waters since 1950, have repeatedly stressed their opinion that *Mytilicola intestinalis* is autochthonous on the European coastlines of the Atlantic Ocean and in the North Sea, but that it normally occurs so sparsely that it never drew the attention of taxonomists, naturalists, and fisheries biologists. The numbers found in the Büsum and Friedrichskoog area, due East of the Elbe estuary (1 to 2% of the mussels infested, usually with 1 parasite each) should represent the normal level, incapable to do any harm to the mussels. The mass-development observed in the Eastfrisian Wattenmeer in 1950 and 1951 is according to them of truly epidemic (epizootic) nature. A rare combination of some ecological factors must have favoured *Mytilicola's* reproduction so much that its population suddenly reached a level endangering the well-being of the mussels. These epidemic features of *Mytilicola's* mass-development warrants that its realm will be of short duration only. Within a few years at most, the *Mytilicola* population will have dropped to its old inconspicuous level, and soon the mussel population in the German Wattenmeer will be back on its former high level (MEYER, 1951; MEYER and MANN 1950, 1951, 1952; MEYER-WAARDEN, 1953; MEYER-WAARDEN and MANN, 1954, 1954b).

It is true, that lack of data is no proof that a certain organism does not occur in a given place, especially not in inconspicuous organisms like intestinal parasites. Since mussels have been used on a large scale for biological laboratory work, especially in England (from the very Blyth estuary where *Mytilicola* was found by Ellenby in 1947!) and Holland, it seems strange, however, that no one ever found the blood-red *Mytilicola* there. Where thousands of mussels have been opened and cut up year after year for sanitary control purposes, as in Holland, it is incredible that *Mytilicola* would never have been observed

during those practices had *Mytilicola* occurred there in even a low percentage of the mussels (KORRINGA, 1951).

It is also true, that some marine organisms with an inconspicuously low level of population density may suddenly appear in incredible numbers, apparently because a given combination of environmental factors accidentally favoured their reproduction. We have seen this in the coastal waters of Holland and Germany in the year 1965 in the Bryozoan *Electra pilosa*. Such tremendous fluctuations in population density can be expected in species which have a very narrow ecological amplitude in at least part of their life cycle. It always concerns species with small but very numerous eggs.

*Mytilicola* is not such a species; it has relatively few (200 to 300) eggs of fairly large size. The eggs contain so much yolk that the pelagic larvae can develop into copepodids without uptake of food (GRAINGER, 1951). Moreover *Mytilicola* has a very wide ecological range in all its developmental stages. It needs not wait for a very special set of ecological factors to be able to reproduce profusely. Since 1950 it reproduces year after year with considerable success in the Zealand estuaries and in the Eastfrisian Wattenmeer, but has hitherto never been seen in the Dutch Waddensea west of Ameland and in the Schleswig-Holstein waters north of Büsum, though we do not know of any environmental conditions basically different there.

Time gave the correct answer to the assumption of Meyer-Waarden and Mann: their forecast that *Mytilicola* would soon drop again to its original low level in Zealand and in the German Wattenmeer did not come true! *Mytilicola* may fluctuate somewhat from year to year, but as long as there were plenty of mussels, their population never dropped to a really low level since the year 1950!

The transplantation experiments described by MEYER-WAARDEN and MANN (1954b) simply demonstrate that any parasite-free mussels brought into the infested Jade estuary soon get their share of parasites, and their observation in Italy (1954a) that the local mussels in the Lago di Ganzirri (Sicily) did not become infested after introduction of a commercial consignment of *Mytilicola*-bearing mussels from La Spezia is not at all an argument in favour of the epidemical nature of *Mytilicola's* mass-developments elsewhere. They describe themselves the rather abnormal hydrographical conditions in this lagoon which no doubt will unfavourably affect all pelagic larvae.

It is interesting to note how Meyer-Waarden and Mann halt between two opinions. The supposed epi-

demical character of *Mytilicola's* local mass-occurrence would render it perfectly safe to transplant infested mussels to areas where evidently conditions do not favour the development of the parasite, and they really advocate this for Italy, based on their observations in the Lago di Ganzirri (1954b). In Germany, however, they did everything within their power to prevent transplantation of infested mussels to the Schleswig-Holstein waters, where *Mytilicola* does not occur at all. This is an excellent management pattern in my opinion, but it does not tally at all with the supposed epidemical nature of *Mytilicola's* flourishing.

Considering the prolonged duration of *Mytilicola's* mass-development in Zealand and in the Eastfrisian Wattenmeer, and its complete absence in many other important mussel areas in the immediate vicinity, I have every reason to reaffirm my opinion (KORRINGA, 1950, 1951, 1951a, 1951b) that *Mytilicola* is a new intruder in the waters of western Europe and that we cannot count on its rapid disappearance or on its population dropping to an insignificant level. Where *Mytilicola* does occur in a very limited percentage of the mussels only, it does not really thrive there. It can only persist in those places through a repeated influx of pelagic larvae from nearby centres with heavier infestation. A real colonization is only possible where quite a few male and female *Mytilicola's* of about the same age meet each other inside their hosts, and this is impossible at infestation rates of 1 and 2% only.

I therefore agree with HAVINGA (1951) that *Mytilicola intestinalis* is a new intruder in the coastal waters of western Europe, following *Crepidula fornicata*, *Petricola pholadiformis*, *Eriocheir sinensis*, *Urosalpinx cinerea*, and *Elminius modestus*. We will never get rid again of any of those!

(C) It is not always easy to trace the path new intruders followed, but in case of *Mytilicola's* invasion in Zealand it is quite evident that Zealand mussel farmers are to blame for it. Some of them have illegally fished mussels on the Ranzelwatt, south of the Isle of Borkum, in the early spring of 1948. These mussels have been relaid in the Zandkreek, a rather narrow body of water with very limited flushing and a heavy population of mussels. One could not have thought of a better place to put them if one wanted to promote *Mytilicola's* development! The Ranzelwatt mussels were at that time already heavily infested with *Mytilicola*, but neither the Zealand mussel farmers nor the Dutch fishery authorities knew that in 1948!

As early as 1949 *Mytilicola's* population rose alarmingly in the Zandkreek, leading to mortality of the mussels in September, and from there spread all over the Zealand mussel plots, which process has been closely followed, but could not be stopped. I launched the hypothesis (KORRINGA, 1950) that *Mytilicola* is not autochthonous in the German Wattenmeer but that it must have been brought there in mussels attached to ship's hulls from the Mediterranean, where it occurs naturally in many a place. We later found *Mytilicola* in mussels attached to ship's hulls in Mediterranean ports (KORRINGA and LAMBERT, 1951) and the observations made by several investigators on the British Isles fully confirm that *Mytilicola* is easily transported this way. It has repeatedly been stated that especially ships brought to ship breaking yards are vehicles for a variety of fouling organisms. Since ship breaking yards are usually situated in estuaries and inlets with a limited flushing, *Mytilicola* gets a fair chance to invade eventual local mussel populations (ANON., 1966; BOLSTER, 1954; BULL, personal communication; GRAINGER, 1951; HOCKLEY, 1951; THOMAS, 1954). The peculiar disjunct distribution of *Mytilicola* in British, Irish, and Scottish waters can easily be explained that way. Therefore, transportation of *Mytilicola* to the German coastal area in mussels attached to ship's hulls in some year preceding 1939 seems quite plausible. In the 'thirties ships often stayed long in ports, and Wilhelmshaven, Cuxhaven and some other ports nearby natural mussel beds will then certainly have seen heavily fouled ships coming in.

Shipping is, however, only one way *Mytilicola* can travel. We have already seen that shiploads of *Mytilicola*-infested mussels are sometimes transferred to mussels beds elsewhere. LELOUP (1951) tells us that *Mytilicola* was brought to the Bassin de Chasse at Ostend with infested Dutch mussels, and LAMBERT (1951) recorded that the same holds good for the Rade de Brest (France) where *Crepidula* arrived the same way, at the same time. Frequent and almost uncontrollable transportation of young mussels and consumption mussels along and to the coasts of France saw to a rapid expansion of *Mytilicola's* range there. LAMBERT (1951), BRIENNE (1960, 1962, 1964) and BRIENNE and PAIRAIN (1966) inform us on the whereabouts of *Mytilicola* along the French coastlines in the course of time.

It is important to note here that although the mussel, *Mytilus edulis*, is the major host of *Mytilicola intestinalis*, some other molluscs may become infested too, be it, as a rule, less heavily than the mussel.

BAIRD et al. (1951) found it in oysters, and I found it repeatedly in Oosterschelde oysters myself. CHEW et al. (1964) state that *Mytilicola orientalis* is neither very selective in searching a host. This latter parasite has been found in several species of molluscs on the American Pacific coast, and it has once been imported from Japan in consignments of oysters (WILSON, 1938). I feel therefore sure that *Mytilicola's* sudden arrival in the western sector of the Limfjord (THEISEN, 1964) had something to do with importation of Zealand oysters for relaying. Any places where fouled ships come in and any sites where living shellfish, included mussels used for bait, originating from other localities, may be thrown in the water, can expect some day *Mytilicola's* arrival.

The third way *Mytilicola* travels is by means of its own pelagic larvae. But this does not bring it very far. Only where a nearly uninterrupted bed of mussels makes it easy to find a host, *Mytilicola* will spread without difficulty. As soon as obstacles such as a large river or a zone devoid of mussels have to be cleared, *Mytilicola* usually fails. Some larvae may get across safely, but even if they find a host there, the chance of meeting a specimen of the opposite sex in the intestinal tract of the same host is very limited, indeed. Without that nothing happens, and since *Mytilicola's* life span is quite short, it soon dies in virginal state. To both sides of an area of high population density we may observe such intrusion zones, where a few parasites find a host, but which do not easily develop into a focus of colonization.

The question remains why *Mytilicola* never made so much havoc among the Mediterranean mussels that complaints were heard. It has been assumed that *Mytilus galloprovincialis* could have become more resistant to this parasite in the course of time (FLEURY et al., 1951), but there is as yet little evidence to support that view. Laboratory experiments carried out with both *Mytilus edulis* and *Mytilus galloprovincialis* failed to show such a natural immunity of the latter species (HEPPER, 1955). Until it has been demonstrated that the Mediterranean mussel suffers less from *Mytilicola's* presence in its intestinal tract than the Atlantic mussel, I am inclined to ascribe the absence of complaints in the first place to the smaller chances *Mytilicola* gets in the Mediterranean centres of mussel culture to build up a dense population. Usually, mussels are grown there in hanging cultures and are therefore already considerably less vulnerable than mussels grown on the bottom — as will be explained below — and further, growth is rapid in the Mediterranean area and mussels usually are in a given

season quantitatively brought to the market, often leaving the culture areas completely devoid of adult mussels for a couple of months. This makes it virtually impossible for *Mytilicola* to build up a dense population by several generations in sequence. It usually has to start all over again from a limited parent stock at the beginning of the new growth season (KORRINGA and LAMBERT, 1951).

(D) Without any doubt *Mytilicola intestinalis's* ecological range is very wide in all its developmental stages. For the sake of clearness I will deal with several ecological factors one by one.

As far as *water temperature* is concerned, *Mytilicola* is by no means a sensitive creature. It has been kept under laboratory conditions for 36 hours at 30°C., and survived (FLEURY et al., 1951). It is not killed by prolonged periods of low water temperature. It survived several severe winters in the Eastfrisian Wattenmeer (a.o. 1939-1940, 1940-1941, 1941-1942, 1946-1947, 1955-1956, 1962-1963). During the last mentioned winter the sea water was in the Oosterschelde (Holland) for over 70 days in succession -1.4°C. the freezing point of sea water of the local salinity. No sign that this did hurt *Mytilicola*. It may seem amazing that a species originating from the Mediterranean can survive such low water temperatures, but the natural distribution of a species reflects by no means its potential range (KORRINGA, 1951). The larvae too are a quite hardy breed. In laboratory experiments they survived after having been kept at 0°C. for 4 days (BOLSTER, 1954). In nature they will not be faced with such low water temperatures, for reproductive activities (hatching of eggs, development of nauplii) have not been observed at water temperatures lower than about 7°C. From that level upwards the larvae will develop (HELDT, 1950). GRAINGER (1951) reports that development to the first copepodid requires only some 40 hours at 13 to 14°C., but that this process is considerably slower at about 9°C. In nature active reproduction and invasion of mussels with young parasites has been observed from 7°C. upwards. Therefore, no clear-cut seasonal pattern in reproduction can be observed in waters where temperatures fluctuate between 10°C. and 18°C. throughout the year as in Galicia (ANDREU, 1963). BRIENNE's note (1964) that reproduction of *Mytilicola* requires a water temperature of 18°C. to 20°C. must be erroneous.

As far as *salinity* is concerned *Mytilicola* is certainly a hardier creature than its host, the mussel. It can stand a very wide range of salinities, from slightly brackish water to salinities so high that they rarely

occur in nature (FLEURY et al., 1951; KORRINGA, 1951). But not only adult *Mytilicola*'s can survive in such a wide range of salinities. Its larvae too are far from sensitive in this respect. MEYER and MANN (1950) reported that the pelagic larvae of *Mytilicola* survive at salinities as low as 3‰! BOLSTER (1954) reared the larvae successfully at salinities between 20 and 35‰, though the best results were obtained at the higher salinities. Considering this wide range of salinities, it is the more surprising that several authors claim that *Mytilicola* seems to prefer a somewhat reduced salinity, and that it does not thrive at salinities prevailing in open sea (BOLSTER, 1954; HEPPER, 1955; VILELA and MONTEIRO, 1960). This conclusion is based on the unmistakable fact that in estuaries *Mytilicola* flourishes especially in the middle section. Lower infestation rates are found both further upriver and in the downriver section of the estuary, close to the open sea. This phenomenon has, however, nothing to do with a salinity preference as such, but is brought about by the numbers of *Mytilicola* larvae passing over the mussels per 24 hours, which determines infection hazards. ANDREU (1963) saw clearly that it is not a preference for reduced salinities which makes *Mytilicola* abound inside the estuaries.

Not many data are available on oxygen requirements (FLEURY et al., 1951), but everyone who has carried out laboratory experiments with *Mytilicola* can confirm that it can stand very low oxygen levels for a prolonged period, which is not surprising for an intestinal parasite with red blood pigmentation. A sojourn out of water, which forces the mussel to switch over to an anaerobic style of living does not seem to harm *Mytilicola* at all, it does not suffer when its host is already moribund. The pelagic larvae do not yet possess the red pigment which might render them more exacting in this respect than the adult parasites.

*Food* is often the limiting factor in early developmental phases of many marine organisms. Laboratory experiments have demonstrated that it is easy to rear the larvae of *Mytilicola* and to make them infect a host without offering any food at all. GRAINGER (1951) states therefore that the pelagic larvae need no food at all. Evidently the rather large eggs contain sufficient yolk to cover the needs of the early developmental stages.

*Light* is a factor of little importance in this species, which is not surprising for an intestinal parasite. Interesting is, however, that the nauplii show a positive phototaxis (HOCKLEY, 1951; MEYER and MANN, 1950). This can promote their distribution by tidal currents,

which show higher velocities in the surface layers. The first copepodid reveals, however, a marked tendency to move to deeper water layers, this rather by geotaxis than by negative phototaxis.

This typical reaction of the copepodid brings the factor *depth* into the picture. *Mytilicola* larvae move to the bottom layers in search of a host. The result of this behaviour is that the mussels occurring directly on the bottom become more heavily infected than those living in higher water layers. Therefore, mussels attached to poles or rocks reveal a lower degree of infestation than those not raised from the bottom under otherwise exactly the same conditions, whereas mussels attached to floating objects, such as buoys, are usually almost free of parasites (CASPER, 1939; HEPPER, 1955; HOCKLEY, 1951; MARTEIL, 1960; MEYER and MANN, 1950) Therefore "bouchot" and raft culture systems will render better results in *Mytilicola*-infested areas. Hence a recommendation (ANON., 1956) to experiment with mussel "bouchots" in England.

The remarkable fact that on one and the same mussel plot the rate of infestation is distinctly higher in a deeper section than on a shallower part, even when the latter is never exposed at low tide (KORRINGA, 1954) should be explained in terms of the number of larvae descending to the bottom from the layers of water above them. If the larvae are quite evenly distributed, as can be expected in an area with rather strong tidal currents, there are more of them above a deeper bottom section than above a shallow part close by. The effect of water depth has been noted by other authors too (MONTEIRO and FIGUEIREDO, 1959).

*Water currents* are also of considerable influence on the whereabouts of *Mytilicola* larvae. ANDREU (1963) tells us that in the hanging cultures of Galicia the infestation rate is about the same at all depths where strong currents prevail. Evidently the larvae are quite evenly distributed there. Where currents are slower there is a marked tendency for heavier infestation in the mussels attached to the lower ends of the ropes.

That *tidal currents* and *flushing pattern* do affect the distribution pattern of *Mytilicola* is not surprising. In the seaward section of an estuary the water carrying *Mytilicola* larvae is considerably diluted with water from the open sea, free of *Mytilicola* copepodids. Therefore, mussels living in that section of the estuary are less liable to become infected than those higher up in the estuary. In the upriver section of the estuary, on the other hand, where a river

exerts its influence, the mussels will part of the time (roundabout low water) be bathed in water devoid of copepodids. Therefore this section does also show a lower infestation rate. If it concerns an inlet or an estuary with very limited influx of river water, the section furthest away from the sea may show the highest infestation with *Mytilicola* (ANDREU, 1960). On open coastlines *Mytilicola* larvae will easily be carried away by the currents to an area where no mussels occur. If the mussels are moreover attached to rocks close to the surface of the sea, they usually escape heavy infestation. This pattern offers a simple explanation for the many observations that *Mytilicola* abounds in middle sections of estuaries, in ports and inlets, in partly enclosed sheltered areas with limited flushing, but that it is always less numerous in mussels on open coastlines and in seaward sections of inlets and estuaries (ANDREU, 1960; BRIENNE, 1964; MARTEIL, 1955; MEYER-WAARDEN and MANN, 1954b; MONTEIRO and FIGUEIREDO, 1961; VILELA and MONTEIRO, 1958, 1960).

It has sometimes been stated that *wave action* and *strong currents* would endanger the pelagic larvae of *Mytilicola* and/or would make it difficult for them to find a host. MEYER-WAARDEN and MANN (1954a, 1954b) assume that therefore mussels on the open rocky coasts of Italy never carry many parasites. BOCQUET and STOCK (1957) surmise that the larvae will be endangered where strong currents and breaking waves prevail, which would explain the lower degree of infestation on more exposed sections of the coast of Brittany as compared with more sheltered places, but in a footnote they make a change of front and explain that the dilution with offshore water will reduce the concentration of larvae considerably in the more open sections, and that this may lead to lower levels of infestation there. BOCQUET & STOCK's idea that the degree of infection is inversely related to the degree of exposition, was statistically proved by KLEETON (1963) for *Trochicola*, a genus related to *Mytilicola*. She demonstrated that around a small island in the Bay of Morlaix (France), statistically significant differences existed in the percentages of hosts infested, although the numbers of larvae per cubic unit of sea water is presumably alike all around the island. The numbers of larvae per unit of water have, however, not been ascertained. The more exposed belt has a significantly lower infection percentage than the more sheltered side of the island. I agree, however, with ANDREU (1960) who states that current velocity as such is not the factor bringing

about the typical distribution pattern in an estuary or inlet.

Of other environmental factors mention can be made of *pollution*. Caspers already wondered whether slightly polluted water would not favour *Mytilicola*. Leaving aside whether an intestinal parasite can notice slight pollution of the water in which its host is bathed, we can answer Caspers that high infection rates often coincide with reduced salinities and pollution in many ports and estuaries, but that flourishing of *Mytilicola* is not in causal relation with these factors.

It is interesting to note here KEY's observation (1965) that *Mytilicola* larvae are easily killed by free chlorine (15 min. at 5 p.p.m.), whereas adult *Mytilicola*'s need a higher dosis. Free chlorine is not found in natural sea-water, but this information is useful when volumes of water in storage tanks must be deinfected before being discharged into the open water.

It is good to note in the ecological section of this paper that the rather short *life-span* of *Mytilicola* sometimes makes it difficult to keep up a high population level. Observations in the Dutch mussel districts led me to the conclusion that 9 to 10 months is the main life-span here, included several cold winter months. Where water temperatures are higher, the life-span is definitely shorter. ANDREU (1963) carried out transplantation experiments and found that many *Mytilicola*'s had already disappeared 3 months after transplantation, and that virtually all of them were dead after 6 months. It can be concluded that the life-span evidently is shorter than 6 months in Galicia. Though under favourable conditions *Mytilicola* will produce the first batch of eggs when only 7 weeks old (KORRINGA, 1954, 1954a), the short life-span may account for considerable fluctuations in population density in the course of the year. That in the Zealand waters *Mytilicola* produces either 2 or 3 generations per year, according to a late or early onset of spring, is of course of considerable effect on the population density in late summer (KORRINGA, 1952).

Unfortunately, we are still rather poorly informed about the factors of influence at the moment a copepodid invades a host. At present most authors assume that the larvae are passively carried into the branchial chamber of the host with the water the filter feeders draw in. This makes it rather difficult to understand why they occur in so much greater numbers in mussels than in other filter feeding molluscs though *Mytilicola* is not fully host-specific. HEPPEL's laboratory experiments (1953) demonstrate that *Mytilicola* can

settle and develop in the intestinal tract of *Mytilus*, *Ostrea*, *Cardium*, *Paphia*, and even *Crepidula* as filter feeding Gastropod, but not in *Scrobicularia*, *Chlamys*, *Pecten*, and *Macoma*. MEYER and MANN (1950) could not find any chemotactic reaction of the larvae on more or less diluted mussel juice. BOCQUET and STOCK (1963) surmise that the host in which the mother lives may condition the larvae in such a way that they will actively search for the same biochemical atmosphere when selecting a host. CARTON (1963, 1964, 1966a, 1966b) amply demonstrated such biochemical influence on copepod larvae of the genera *Sabelliphilus* and *Lichomolgus*, using Davenport's classical experimental method. However this may be, there is not yet sufficient experimental evidence to understand why most of *Mytilicola's* larvae enter mussels, and only few of them other filterfeeding molluscs. Another interesting question is why *Mytilicola's* often are not distributed over a certain batch of mussels according to the probability curve. Even at rather low infestation percentages one may find an occasional mussel carrying many more parasites than their congeners of similar size and background. This must have something to do with the behaviour of the larvae when searching for a host. Do they congregate in some manner or is there some chemical or other attraction which makes them decide where to enter?

(E) We are well informed about the evolution of *Mytilicola* in western Europe in recent years through the concerted action of fisheries biologists in several countries (ANDREU, 1960, 1963, 1965; BRIENNE, 1960, 1962, 1964; BRIENNE and PAIRAIN, 1966; FIGUEIREDO, 1961; LELOUP, 1960; LELOUP and LEFEVERE, 1952; MARTEIL, 1955, 1960; MASON, 1961; THEISEN, 1965; THOMAS, 1954; VILELA and MONTEIRO, 1958; WAUGH 1954). LELOUP's paper (1960) is accompanied by a map which gives a good overall picture of the observations up to that year. The map presented in the leaflet entitled "Protecting British Shellfisheries" (ANON., 1966) gives in a thick black line the coasts where *Mytilicola* is present now, but the disjunction of its spreading within this area is insufficiently shown. Moreover, the Schleswig-Holstein coastline should still be considered as completely free of *Mytilicola* from Büsum up to the Limfjord. How *Mytilicola* slowly spread in western direction from the Eastfrisian Wattenmeer by sending its pelagic larvae along with the tidal currents has been told in a series of papers (KORRINGA, 1952a, 1953, 1954). It finally managed to settle in sufficient numbers behind the easternmost islands in the Dutch Waddensea to estab-

lish new, selfsupporting colonies, and since then threatens to invade the western section of the Waddensea, where mussel farming is carried out on a large scale. The boundary is now the western tip of the isle of Ameland.

It is clearly understood now why *Mytilicola* is not present in overwhelming numbers in all mussels living on the coastlines it reached on ship's hulls or hidden in shellfish transferred to other areas. *Mytilicola* has a very wide ecological amplitude, but the limiting factor is that a male and a female of the same developmental stage must meet in the intestinal tract of one and the same host before reproduction can take place. Since *Mytilicola's* life-span is short, a single specimen cannot wait long for the arrival of a mate. Since the numbers of eggs produced are moreover remarkably low for a parasite, the large number of copepodid larvae required for a successful invasion of a new area can only be expected where considerable quantities of infested mussels occur, and where water currents will preclude too great a dilution of the larvae before the new hosts are reached. The extent of the production of larvae, which depends on the number of mated adult parasites in the area under consideration, the dispersal of the larvae with tidal and other currents, and the availability of hosts, preferably on or close to the bottom, together with its short life-span, are the factors limiting *Mytilicola's* numbers and bringing about considerable fluctuations in its population density, not only from place to place, but also from month to month, and from year to year (ANDREU, 1963; BOLSTER, 1954; GRAINGER, 1951; HOCKLEY, 1951; KORRINGA, 1952, 1954; MARTEIL, 1960).

Though very heavy infestations can lead to poor condition and even to death of the host, it is very well possible to continue the cultivation of mussels in presence of this parasite. One has to think in quantitative terms, and to see that the production of *Mytilicola* larvae is kept within bounds, and to preclude that too many of the larvae produced find a host. This means in practical terms that the extent of the production of mussels for the market should be restricted and adjusted to local hydrographical conditions, that the mussels should sojourn as short as possible in the dangerous area, that where growth is fast the older generation of mussels should be taken away quantitatively before putting the new generation of mussels into the water, that mussel farming raised from the bottom should be practised where possible, and that too dense concentrations of mussels should be avoided. Advice and instructions along these lines

have been given in several countries (ANDREU, 1963, 1965; BRIENNE, 1964; KORRINGA, 1954a; MOREAU and TROCHON, 1964).

Where *Mytilicola* does not yet occur, all possible efforts should be made to avoid its introduction on the fouled hulls of vessels or with consignments of infested shellfish from elsewhere. It seems that broad estuaries, like that of Elbe and Rhine, form an excellent obstacle for its spreading, but also stretches of coast devoid of mussels are barriers which are difficult to surmount.

*Mytilicola's* distribution has much in common with that of another intruder, *Crepidula fornicata*, and in several cases both of them even travelled together!

A realistic attitude, stating frankly that once *Mytilicola* arrives there is little chance of getting rid of it again, is in the interest of the shellfish industry greatly to be preferred above dissemination of the view that fluctuations in natural conditions are to blame for mass-development of pests like *Mytilicola* and *Crepidula*, and to forecast that they will disappear again in due course. In the field of fisheries such cases of wishful thinking, obscuring man's own deleterious effect on the stocks of fish and shellfish, have too often led to delay in carrying out the necessary scientific investigations and to frame methods of control before it is too late.

SUMMARY

Critical appraisal of the literature data on *Mytilicola*

*intestinalis*, combined with personal experience in this field, led to formulation of answers on a series of questions re the ecology and distribution of the parasitic copepod *Mytilicola intestinalis* Steuer.

It is confirmed that *Mytilicola* has been the causative agent in extensive mussel mortalities. The explosion of *Mytilicola* in several places on the coastlines of North Sea and Atlantic Ocean should be explained in terms of *Mytilicola* being a new intruder in these waters. There is no ground for the view that a special set of ecological conditions saw to the explosive development of the autochthonous species *Mytilicola intestinalis*, normally existing in small numbers only.

*Mytilicola intestinalis* has a wide ecological range in all phases of its life cycle. The number of hosts living in a given volume of water, together with the amount of flushing of that water, is the main factor governing the number of parasites per host. Since two individuals of opposite sex have to meet in the intestinal tract of one and the same host, some scattered pelagic larvae cannot easily lead to establishment of a new focus of infection. Stretches of coast devoid of mussels form an almost unsurmountable barrier against the natural spreading of this parasite. It is usually man, through his multiple activities, who should be held responsible for the invasion of mussel areas previously devoid of *Mytilicola intestinalis*.

REFERENCES

ANDREU, B., 1960: Un parasito del mejillón. Propagación del copépodo parásito *Mytilicola intestinalis* en el mejillón de las rías bajas. Revista Econ. de Galicia, 1-7.  
 - 1963: Propagación del copépodo parásito *Mytilicola intestinalis* en el mejillón cultivado de las rías gallegas (NW de España). Investigación Pesq. 24, 1-20.  
 - 1965: Biología y parasitología del mejillón gallego. Las Ciencias Madrid 30, 107-118.  
 ANON., 1956: Control of *Mytilicola* in mussels. Min. Agric. Fish & Food, Lab. Leaflet N.S. 9.  
 - 1966: Protecting British Shellfisheries. Min. Agric. Fish & Food, Lab. Leaflet N.S. 10.  
 BAIRD, R. H., G. C. BOLSTER & H. A. COLE, 1951: *Mytilicola intestinalis* Steuer in the European flat oyster (*Ostrea edulis*). Nature, Lond. 168, 560-561.  
 BOCQUET, CH., & J. H. STOCK, 1957: Copépodes parasites d'invertébrés des côtes de France. Trav. Stn biol. Roscoff N.S. 8, 233-239.  
 - 1963: Some recent trends in work on parasitic copepods. Oceanogr. Mar. Biol. Ann. Rev. 1, 289-300.  
 BOLSTER, G. C., 1954: The biology and dispersal of *Mytilicola intestinalis* Steuer, a copepode parasite of mussels. Fishery Investigations Ser. II, 18 (6), 1-30.  
 BRIENNE, H., 1960: *Mytilicola intestinalis* Steuer dans les moules de la Baie de l'Aiguillon. Sci. Pêche 87, 1-6.  
 - 1962: Evolution de l'infestation des moules de la Baie de l'Aiguillon par *Mytilicola intestinalis* Steuer au cours de l'année 1961. Sci. Pêche 106, 1-5.  
 - 1964: Observations sur l'infestation des moules du Per-tuis Breton par *Mytilicola intestinalis* Steuer. Revue Trav. Inst. Scient. Pêch. marit. 28, 205-230.  
 BRIENNE, H., & R. PAIRAIN, 1966: Distribution de *Myti-*

- licola intestinalis* Steuer le long des côtes françaises. Sci. Pêche 149, 1-6.
- CARTON, Y., 1963: Etude de la spécificité parasitaire chez *Lichomolgus actiniae* D.V. (Copépode Cyclopoïde). C.R. Acad. Sci., Paris 256, 1148-1150.
- 1964: Spécificité relative à l'intérieur de l'espèce *Stellicola clausi* (Rosoll), Copépode cyclopoïde parasite des deux Stellérides *Marthasterias glacialis* (L.) et *Asterina gibbosa* (Penn.). Arch. Zool. exp. gén. 103 (N. & R., 1), 13-19.
- 1966a: Etude du comportement et de la spécificité parasitaire de *Sabelliphilus sarsi* Claparède, Copépode parasite de *Spirographis spallanzani* Viviani. Bull. Mus. nation. Hist. nat. (2) 37 (5), 807-817.
- 1966b: Spécificité parasitaire de *Sabelliphilus sarsi* parasite de *Spirographis spallanzani*. Arch. Zool. exp. gén. 107 (3), 427-443.
- CASPERS, H., 1939: Über Vorkommen und Metamorphose von *Mytilicola intestinalis* Steuer (Copepoda paras.) in der südlichen Nordsee. Zool. Anz. 126, 161-171.
- CHEW, K. K., A. K. SPARKS & S. C. KATKANSKY, 1964: First record of *Mytilicola orientalis* Mori in the California mussel *Mytilus californianus* Conrad. J. Fish. Res. Bd. Canada 21, 205-207.
- 1965: Preliminary results on the seasonal size distribution of *Mytilicola orientalis* and the effect of this parasite on the condition of the Pacific oyster, *Crassostrea gigas*. J. Fish. Res. Bd. Canada 22, 1099-1101.
- COLE, H. A., 1951: Le *Mytilicola* en Angleterre. Revue Trav. Inst. scient. Pêch. marit. 17, 59-61.
- COLE, H. A., & R. E. SAVAGE, 1951: The effect of the parasitic copepod *Mytilicola intestinalis* Steuer upon the condition of mussels. Parasitology 41, 156-161.
- DOLLFUS, R. PH., 1927: Notules sur les copépodes parasites de la faune française. Bull. Soc. zool. Fr. 52, 119-121.
- 1951: Le Copépode *Mytilicola intestinalis*. A. Steuer peut-il être la cause d'une maladie épidémique des moules? Revue Trav. Inst. scient. Pêch. marit. 17, 81-83.
- ELLENBY, C., 1947: A copepod parasite of the mussel new to the British fauna. Nature, Lond. 159, 645-646.
- FIGUEIREDO, M. J., 1961: Enquête sur le parasitisme des moules par le copépode *Mytilicola intestinalis* (Steuer) en 1961. ICES Council Meeting 1961, Doc. 148.
- FLEURY, G., P. LUBET & J. LE DANTEC, 1951: Note sur le *Mytilicola intestinalis* Steuer. Anns pharm. fr. 9, 569-574.
- GENOVESE, S., 1959: Sulla presenza di *Mytilicola intestinalis* Steuer (Copepoda parasitica) nel Lago di Ganzirri. Atti Soc. pelorit. Sci. fis. mat. nat. 5, 47-53.
- GRAINGER, J. N. R., 1951: Notes on the biology of the copepod *Mytilicola intestinalis* Steuer. Parasitology 41, 135-142.
- HAVINGA, B., 1951: *Mytilicola intestinalis* in relation to other invasions of aquatic animals. Revue Trav. Inst. scient. Pêch. marit. 17, 77-80.
- HELDT, M. J. H., 1950, 1951: Observations sur *Mytilicola intestinalis* Steuer, parasite des moules. Revue Trav. Inst. scient. Pêch. marit. 17, 33-40. Bull. Soc. Sci. nat. Tunis. 3, 57-62.
- HEPPER, B. T., 1953: Artificial infection of various molluscs with *Mytilicola intestinalis* Steuer. Nature, Lond. 172, 250.
- 1955: Environmental factors governing the infection of mussels, *Mytilus edulis*, by *Mytilicola intestinalis*. Fishery Investigations, London Ser. II, 20 (3), 1-21.
- HOCKLEY, A. R., 1951: On the biology of *Mytilicola intestinalis* (Steuer). J. mar. biol. Ass. U.K. 30, 223-232.
- HRS-BRENKO, M., 1964: *Mytilicola intestinalis* as a parasite of mussels in natural beds and artificial rearing places of the eastern Adriatic. Acta Adriatica 9, 161-165.
- KEY, D., 1965: Interim report on the tolerance of *Mytilicola intestinalis* (Steuer) to solutions of free chlorine and its use in limiting the further spread of the parasite. ICES Council Meeting 1965, doc. 90.
- KLEETON, G., 1963: Corrélation entre la fréquence de *Trochicola entericus* Dollfus, 1914, et les conditions du milieu. Proc. Kon. Ned. Akad. Wet. Amsterdam, (C) 66 (1), 70-73.
- KORRINGA, P., 1950: De aanval van de parasiet *Mytilicola intestinalis* op de Zeeuwse mosselcultuur. Visserij-Nieuws 3 (7) suppl. 7 pp.
- 1951: Over *Mytilicola intestinalis* (Copepoda parasitica) en enkele andere ongewenste vreemdelingen in onze wateren. Vakblad voor Biologen 31, 63-74.
- 1951a: Le *Mytilicola intestinalis* Steuer (Copepoda parasitica) menace l'industrie moulière en Zélande. (Traduction de Korringa 1951b). Revue Trav. Inst. scient. Pêch. marit. 17, 9-13.
- 1951b: *Mytilicola intestinalis* Steuer (Copepoda parasitica) threatens the Zealand mussel industry. ICES Council Meeting 1951, Shellfish Comm.
- 1952: Epidemiological observations on *Mytilicola intestinalis* Steuer in the Zealand waters. ICES Council Meeting 1952, Shellfish Comm.
- 1952a: Epidemiological observations on the mussel parasite *Mytilicola intestinalis* Steuer, carried out in the Netherlands 1951. Annales Biol. 8, 182-185.
- 1953: Epidemiological observations on the mussel parasite *Mytilicola intestinalis* Steuer, carried out in the Netherlands 1952. Annales Biol. 9, 219-224.
- 1954: Epidemiological observations on the mussel parasite *Mytilicola intestinalis* Steuer, carried out in the Netherlands 1953. Annales Biol. 10, 197-200.
- 1954a: De biologische achtergrond van de recente structuurverschuivingen in onze mosselcultuur. Visserij-Nieuws 7 suppl. 18 pp.
- 1955: Qualitätsbestimmungen an Miesmuscheln und Austern. Archiv für Fischereiwiss. 6, 189-193.
- 1956: Epidemiological observations on the mussel parasite *Mytilicola intestinalis* Steuer, carried out in the Netherlands 1954. Annales Biol. 11, 184-186.
- 1957: Epidemiological observations on the mussel parasite *Mytilicola intestinalis* Steuer, undertaken in the Netherlands 1955. Annales Biol. 12, 230-231.
- KORRINGA, P., & L. LAMBERT, 1951: Quelques observations sur la fréquence de *Mytilicola intestinalis* Steuer (Copepoda parasitica) dans les moules du littoral méditerranéen français. Revue Trav. Inst. scient. Pêch. marit. 17, 15-29.
- LAMBERT, L., 1951: Le "Cop Rouge" (*Mytilicola intestinalis* Steuer) sur les côtes de France. Revue Trav. Inst. scient. Pêch. marit. 17, 51-56.
- 1952: Un parasite de la moule, le Cop Rouge (*Mytilicola intestinalis* Steuer). La terre et la vie 1952 (3), 15 pp.

- LELOUP, E., 1951: Sur la présence de *Mytilicola intestinalis* Steuer le long des côtes de Belgique. Revue Trav. Inst. scient. Pêch. marit. 17, 57-58.
- 1960: Distribution de *Mytilicola intestinalis* Steuer le long des côtes européennes. ICES Council Meeting 1960, Doc. 13.
- LELOUP, E., & S. LEFEVRE, 1952: Sur la présence dans les eaux de la côte Belge du Cirripède *Elminius modestus* Darwin, 1854, du Copépode parasite *Mytilicola intestinalis* Steuer, 1902, et du Polychète *Merckeriella enigmatica* Fauvel, 1922. Bull. Inst. r. Sci. nat. Belg. 28 (48), 1-12.
- MARTEIL, L., 1955: Répartition actuelle de *Mytilicola intestinalis* Steuer sur la côte sud de Bretagne. ICES Council Meeting 1955, Doc. 58.
- 1960: *Mytilicola intestinalis* Steuer sur la côte sud de Bretagne. ICES Council Meeting 1960, Doc. 30.
- MASON, J., 1961: The distribution of *Mytilicola intestinalis* (Steuer) in Scottish waters in 1961. ICES Council Meeting 1961, Doc. 75.
- MEYER, P. F., 1951: Epidemische Erkrankungen der Miesmuschelbestände in Nordwesteuropa. Fischereiwelt 3, 82-83.
- MEYER, P. F., & H. MANN, 1950: Beiträge zur Epidemiologie und Physiologie des parasitischen Copepoden *Mytilicola intestinalis*. Arch. für Fischereiwiss. 2, 120-134.
- 1951: Recherches allemandes relatives au *Mytilicola*, Copépode parasite de la moule, existant dans les Watten allemandes 1950-1951. Revue Trav. Inst. scient. Pêch. marit. 17, 63-74.
- 1952: *Mytilicola*-Epidemie 1951/1952. Fischereiwelt 4, 136-137.
- MEYER-WAARDEN, P. F., 1953: Investigations into *Mytilicola intestinalis* and its attack upon the German *Mytilus* stock in 1952. Annales Biol. 9, 218-219.
- MEYER-WAARDEN, P. F., & H. MANN, 1954: Der Befall von *Mytilus edulis* durch *Mytilicola intestinalis* in den deutschen Wattengebieten 1950-1953. Ber. dt. wiss. Kommn. Meeresforsch. 13, 347-362.
- 1954a: Untersuchungen über die Bestände von *Mytilus galloprovincialis* an der Italienischen Küste auf ihren Befall mit *Mytilicola intestinalis* (Copepoda parasitica). Boll. Pesca Piscic. Idrobiol. 8, 5-24.
- 1954b: Ein weiterer Beitrag zur Epidemiologie von *Mytilicola intestinalis* (Infektionsversuche). Arch. Fischereiwiss. 5, 26-34.
- MONOD, TH., & R. PH. DOLLFUS, 1932: Les copépodes parasites de mollusques. Anns Parasit. hum. comp. 10, 132-157.
- MONTEIRO, M., & J. DE FIGUEIREDO, 1959: Présence du "Cop Rouge", *Mytilicola intestinalis* Steuer, dans les moules de l'estuaire du Tage 1959. ICES Council Meeting 1959, Doc. 113.
- 1961: Note sur la répartition de *Mytilicola intestinalis* Steuer dans l'estuaire du Tage. Notas Estud. Inst. Biol. mar. Lisb. 22, 1-13.
- MOREAU, J., & P. TROCHON, 1964: Evolution en fréquence et en intensité de l'infestation des moules par *Mytilicola intestinalis* Steuer dans le bassin Marennes-Oléron pour la période 1960-1963. Cultures Marines 14 Oct. 1964, 12-13.
- ODLAUG, T. O., 1946: The effect of the Copepod *Mytilicola orientalis* upon the Olympia oyster, *Ostrea lurida*. Trans. Am. microsc. Soc. 55, 311-317.
- OORDE-DE LINT, G. M. VAN, & J. H. SCHUURMANS STEKHOVEN, 1936: Copepoda parasitica. Tierwelt der Nord- und Ostsee 90, 73-197.
- PELSENEER, P., 1929: Copépodes parasites de mollusques. Anns Soc. r. zool. Belg. 59, 33-49.
- PESTA, O., 1907: Die Metamorphose von *Mytilicola intestinalis* Steuer. Z. wiss. Zool. 88, 78-98.
- STEUER, A., 1902: *Mytilicola intestinalis* n.gen.n.spec. aus dem Darne von *Mytilus galloprovincialis* Lam. Zool. Anzeiger 25, 635.
- 1905: *Mytilicola intestinalis* n.gen.n.spec. Arb. zool. Inst. Univ. Wien & Zool. Stat. Triest 15, 1-46.
- THEISEN, B. F., 1964: *Mytilicola intestinalis* Steuer in Danish waters. ICES Council Meeting 1964, Doc. 103.
- 1965: *Mytilicola*-en snylter i blåmuslinger. Skr. Danm. Fisk. og Havunders. 25, 21-24.
- THOMAS, H. J., 1954: The distribution of *Mytilicola intestinalis* (Steuer) in Scotland. Annales Biol. 10, 200-202.
- VILELA, H., & M. C. MONTEIRO, 1958: Présence de copépodes chez *Mytilus edulis* L. ICES Council Meeting 1958, Doc. 87.
- 1960: Infestação de mexilhões, *Mytilus edulis* L., do rio Tejo, pelo copépode *Mytilicola intestinalis* Steuer. Boln R. Soc. esp. Hist. nat., Biol. 58, 375-388.
- WAUGH, G. D., 1954: The occurrence of *Mytilicola intestinalis* (Steuer) on the East coast of England. J. Anim. Ecol. 23, 364-367.
- WILSON, C. B., 1938: A new Copepod from Japanese oysters transplanted to the Pacific Coast of the United States. J. Wash. Acad. Sci. 28, 284-288.