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ON THE SUPPOSED COMPULSORY RELATION BETWEEN OVIPAROUS OYSTERS AND WATERS OF REDUCED SALINITY

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It is a well-established fact that flourishing natural beds of oviparous oysters of any description are often located in waters of somewhat reduced salinity. It will suffice to mention the tremendously rich beds of the Portuguese oyster, *Crassostrea (s. Gryphæa) angulata*, in the Gironde estuary, and the prolific beds of the American Atlantic oyster, *Crassostrea virginica*, in the delta of the Mississippi river. Oviparous oysters not only seem to thrive best in rather shallow waters, but typical estuarine conditions prevail in almost any place where these varieties of oysters are abundant.

Oyster farmers all over the world know very well that the oviparous oysters can be reared with success in many a place where the larviparous flat oysters could not live. Oysters of the genus *Crassostrea* can live and thrive on a rather soft and muddy bottom, whereas the flat *Ostrea* oysters require a much firmer subsoil ; oviparous oysters can stand prolonged exposure to the air (in both hot and cold weather) far better than the larviparous oysters ; further, *Crassostrea* oysters can grow and fatten in waters so turbid and silt-laden that flat oysters would suffer or die there. But more striking still is the ability of the oviparous oysters to live and thrive in waters of reduced salinities (*e. g.* 12-20 per 1,000), whereas flat oysters require salinities of some 23 per 1,000 and higher for their well-being. It is therefore possible to grow oviparous oysters in many waters where the cultivation of flat oysters would be absolutely impossible. Where both types of oyster are grown in one and the same body of water (as *e. g.* in the Bay of Arcachon, France), the oystermen select the deeper beds with harder subsoil and clearer water of higher salinity for the planting of flat oysters, and may use the shallower beds with softer subsoil, and more turbid water of reduced salinities for the oviparous oysters. It is even a general practice among the oyster farmers of Japan and Australia to transfer the spat of oviparous oysters, collected in the saline and clear waters close to the sea, to beds higher up in the estuary, where the water is of lower salinity and greater turbidity, because the oysters will grow and fatten better there.

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It has been scientifically established that oviparous oysters are especially adapted to life in brackish and turbid waters :

Careful laboratory experiments carried out by LOOSANOFF and SMITH (1949) on the rate of pumping in the American Atlantic oyster, *Crassostrea virginica*, demonstrated that this oviparous species can be normally active in waters of salinities which cannot be tolerated by flat oysters (12 to 20 per 1,000). They found it possible to get this oyster accustomed even to a much lower salinity than prevails in the water in which they were grown ; in these experiments oysters could be kept in water of a salinity of 7 per 1,000 for a prolonged period. LOOSANOFF (1950) also demonstrated that *Crassostrea virginica* is capable of withstanding sharp changes in salinity without experiencing serious physiological injuries. It is evident that the American Atlantic oyster is a very euryhaline species, indeed.

Similar observations have been made on the turbidity factor. NELSON (in litt. 14-3-1956), discussing his 1931 observations at Plymouth, states that during increasing turbidity the flat oyster, *Ostrea edulis*, soon became distressed, and tried in vain to rid itself of excess sediment by vigorous shell movements, whereas the oviparous oysters *Crassostrea angulata* and *C. virginica* could be observed to filter apparently normally in water of much greater turbidity still. NELSON (1921, 1923) found the American Atlantic oyster able to feed rapidly in waters bearing as much as 0.4 g. of suspended matter, dry weight, per litre ! In other terms (NELSON, 1938) in water " so turbid that a bright silver coin disappears in a cupful when exposed to the sun at noonday ". LOOSANOFF and TOMMERS (1948) studied the feeding behaviour of the American Atlantic oyster in water laden with silt and other turbidity-creating substances under laboratory conditions, and demonstrated the amazing achievements of this creature.

If the ability to live in waters of different and even rapidly changing salinities is primarily a physiological question, the way oviparous oysters can cope with excess silt and turbidity is also based on anatomical features. Flat oysters are easily smothered when too much sand or silt is deposited on the very site where they settled as a tiny spat on a fairly large piece of cultch, just because they are completely incapable of moving from the spot, but many oviparous oysters are in a position to displace the hinge part of their shells over a distance of several cm, and can thus often escape from certain death (KORRINGA, 1956, p. 318 and Plate XII, fig. 2).

The observations of YONGE (1936) and NELSON (1938) are also very instructive. They found that oysters, lacking the siphons so characteristic for many other lamellibranchs living on or in soft bottoms, show a wide area over which food material can be drawn into the inhalent cavity, and a similar wide aperture at the aboral side. This would expose them to a serious danger from clogging the feeding and respiratory mechanism and from encroaching sediment, were it not promptly removed. Adjustment of the place of admission of the incoming current by the pallial curtain, ciliary activity, and sudden contractions of the adductor muscle are means by which all types of oysters can cope with excess sediment. A characteristic feature of oviparous oysters is the presence of the promyal chamber, discussed in detail by NELSON (1938). This promyal chamber offers great advantages in the fight against silt. Virtually all the water passing the right demibranchs anterior to the adductor muscle makes its way out via the promyal chamber, and not via the epibranchial chamber beneath the adductor muscle as is the case in flat oysters. Not only is this a shorter way, but it also places the oyster in a position to blow out any bottom deposits which may encroach in the vulnerable aboral part of the shell aperture above the adductor muscle. Another, and perhaps even more important advantage of the promyal chamber is the possibility it opens for displacement of the adductor muscle in a direction away from the hinge, as so much less space is required for the epibranchial chamber. This in its turn ensures a considerably better leverage, so that the size of the " catch " muscle can be reduced, which leaves space for an elarged " quick " muscle. This is exactly what one finds in oviparous oysters (YONGE 1936, NELSON 1938). A greater " quick " muscle placed in a position with better leverage ensures a very efficient mechanism to get rid of excess silt by vigorous and frequent shell movements. More recently MENZEL (1955) summarized the various reasons why *Crassostrea* is so well adapted for feeding in waters of high turbidity.

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All these adaptations to life in water of reduced salinity and high turbidity has led to the assumption that oviparous oysters are therefore typical denizens of brackish water; that water of reduced salinity is the only suitable habitat for them; that they are at least during the most sensitive part of their life incapable of standing water of high salinity. It was RANSON especially who expressed such a view repeatedly. According to him (RANSON 1940, 1943) the Portuguese oyster, *Crassostrea angulata*, cannot thrive in water of a salinity over 31 per 1,000, and cannot get rid of its sex products at salinities over 29 per 1,000. RANSON claims further (1941, 1943, 1948, 1949) that larvæ of oviparous oysters cannot develop normally in waters of the salinity prevailing in the open sea. According to him oysters of the genus *Crassostrea* require salinities under 23 per 1,000 for a normal development of the larvæ. In his 1948 paper RANSON states with greater precision that the larvæ of *Crassostrea angulata* and *C. gigas* require a salinity between 18 and 23 per 1,000 for their well-being, those of *C. virginica* even 12 to 19 per 1,000. This without adducing experimental data to prove his case. The explanation given is : « L'équilibrium intracytoplasmique de cet œuf est tel que l'imbibition de la phase hydrophile commence seulement lorsque la salinité du milieu extérieur est relativement basse. C'est pourquoi le développement de l'œuf n'a lieu que dans des eaux de densité 1010-1018 » (RANSON, 1948). In framing his ideas on the evolution of oysters RANSON (1943) sticks rather dogmatically to the complete impossibility for the oviparous oyster to develop normally in high salinity waters. He believes that such a profound modification of protoplasmatic reactions would be required for a purely marine species to migrate into the coastal waters with reduced salinities, that the oviparous oysters cannot possibly have originated from oysters living in deeper water with higher salinities, but must have lived in coastal waters from the Cretaceous.

In his efforts to explain several obvious discrepancies between his dogmatic theories and the practical experience of the oystermen, Ranson comes to some far-fetched explanations :

In almost any site where setting of oviparous oysters has been observed in waters of high salinity, Ranson postulates subterraneous wells which have locally reduced the salinity to the low values he considers as compulsory for the larvæ of these oysters.

Considering the high salinity prevailing in the Bay of Arcachon and the large scale on which Portuguese oysters are collected there with tiles, Ranson assumes that all this spat must be attributed to larvæ born in the rather brackish Gironde estuary and washed into the Bay by the currents while in a rather advanced stage of development : " Par ailleurs, les courants de jusant refoulent sur la côte landaise et particulièrement dans le Bassin d'Arcachon quelques éléments des eaux de la Gironde et y entraînent des larves d'Huîtres portugaises qui se fixent sur les collecteurs. Ce ne sont certainement pas les Huîtres déposées dans le Bassin qui ont donné les larves en question, les conditions requises pour la reproduction n'y étant pas réalisées " (Ranson, 1949). He does not, however, present any data on currents, salinities or larvæ in different developmental stages to support his view.

On the assumption that the larvæ of all oviparous oysters can develop only in water of reduced salinities, Ranson (1951) concludes that the spat of *Crassostrea margaritacea* setting on tiles in the Knysna Lagoon (Cape Province, South Africa) must have come from parent oysters living as far away as Tuléar on Madagascar, where natural beds of this species exist under estuarine conditions. These larvæ would have to make the journey carried by the ocean currents (and that presumably in rather brackish pockets of water!) over some 2,000 to 3,000 km. ! The speed of the Agulhas current being well under 90 km. per day, this journey cannot even be completed within the regular 3 weeks larval development requires.

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From the observations I have made in many an oyster area I cannot agree that there is any truth in Ranson's assumption that the larvæ of oviparous oysters can develop only within a rather narrow range of salinities, viz. 18-23 per 1,000 for *Crassostrea angulata* and *C. gigas*, and 12-19 per 1,000 for *C. virginica*. On the contrary, there is every reason to assume that the larvæ of oviparous oysters have, so far as salinity goes, a very wide ecological range, indeed. It is true that the American Atlantic oyster, *Crassostrea virginica*, may develop and settle well in waters of reduced salinity (e. g. in the upper parts of the Chesapeake Bay ; in some areas in the delta of the Mississippi river), but perfect larval development and profuse setting in the same species may very well occur in waters of higher salinities (e. g. Long Island Sound, 27-28 per 1,000 ; Beaufort, North Carolina, salinity well over 30 per 1,000 ; Port

Aransas, Texas, 36 per 1,000). *Crassostrea rhizophoræ* settles profusely in waters of 33 to 44 per 1,000 in Puerto Rican waters (MATTOX, 1949); *C. madrasensis* at Madras in waters of a salinity over 30 per 1,000 (PAUL, 1942). The larvæ of the Japanese oyster, *Crassostrea gigas*, evidently develop very well in Mangoku-Ura inlet, an important area for the production of seed-oysters, though salinities are here 32-33 per 1,000 during the summer months (IMAI et al., 1951), which is considerably higher than the 18-23 per 1,000 RANSON considers as the adequate range for this species.

For the Bay of Arcachon it suffices to mention the numerous observations on oyster larvæ made by the staff of the Institut des Pêches, which clearly reveal that the larvæ of Portuguese oysters may occur there in fair numbers and in all developmental stages. It is certainly not true that only larvæ in advanced developmental stages are washed into the Bay after having spent their days of early development in the Gironde estuary.

As far as the larvæ of the South African oyster, *Crassostrea margaritacea*, are concerned, I have adduced convincing evidence through personal observations (KORRINGA, 1956), which demonstrates that perfectly healthy larvæ of this oyster, in all developmental stages, can be found in the inshore countercurrent in waters of about 36 per 1,000 salinity. Without any doubt they were born from parents living nearby in great numbers in the intertidal zone, partly in deeper waters without appreciable admixture with fresher water.

That adult oviparous oysters can thrive only in waters of reduced salinity is definitely not true. Everybody who has seen the perfect growth and fattening of Portuguese oysters in the Etang de Thau (France) at salinities over 34 per 1,000 or the fat oysters living attached to rocks on the South African coast at salinities of about 36 per 1,000 will be convinced on this point.

This does not mean, however, that places where high salinities prevail always give a better growth and fattening than waters of reduced salinity. For, in several cases, estuarine waters are definitely richer in food than purely oceanic waters, and thus offer better conditions to the oysters. Oyster farmers are well aware of this for they often transfer the spat collected close to the sea in clear water of high salinity to more brackish water higher up in the estuary, because food is more abundant there. Such a practice is carried out on a large scale in Matsushima Bay, Japan (verbal information given by Prof. IMAI), and also in the Port Stephens Lagoon, Australia (information provided by Mr. A. SALM at Salt Ash; compare KORRINGA 1956, Plate XX). From this it can be concluded that larval development and setting in oviparous oysters may, indeed, be confined to a narrower ecological range than normal growth and fattening in the adult oyster, but that it is the young stages which require the higher salinities.

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From all these data I feel convinced that the relation between salinities and oviparous oysters can concisely be stated as follows:

Oviparous oysters are definitely more euryhaline than larviparous oysters. Not only are the adult oviparous oysters able to live and thrive in a much wider range of salinities than flat oysters, but also the larvæ of oviparous oysters are in a position to develop in a fairly wide range of salinities, even though the larvæ cannot tolerate such low salinities as the adults. Within this range factors other than salinity, especially the food factor, may determine whether or not a given body of water is suitable for larval development.

The best place for growth and development of adult oviparous oysters are often to be found within an estuary, in waters of reduced salinities. This is because the oviparous oysters are physiologically able to live normally in waters of reduced salinities, down to some 12 per 1,000, whereas flat oysters begin to suffer even at a level of about 23 per 1,000. Moreover oviparous oysters are so well adapted to life in silt-laden waters that they can take advantage of the high food content of such waters, even if the turbidity is so great that flat oysters could not possibly live there.

Many natural enemies and parasites of the oyster cannot tolerate the low salinities prevailing in many estuaries. Therefore general health and survival figures are often much better in the estuarine waters.

The low salinities as such do not bring any advantages, but it is the biological richness of estuarine waters and the escape from many parasites and predators which render many estuarine bodies of water so excellently suited to the oviparous oysters.

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Discussion.

M. Lubet. — Je me permets de signaler au Dr. KORRINGA l'existence d'un banc naturel d'Huîtres portugaises (*Crassostrea angulata* Lmk) dans le Bassin d'Arcachon. Ce banc naturel se trouve dans une zone d'estuaire (Estuaire de l'Eyre). Certes, les jeunes véligères peuvent se fixer aussi bien dans les zones à faible salinité qu'à salinité normale (32-35 pour 1.000). Mais je crois qu'elles présentent un tropisme qui les attire vers les zones de faible salinité. Des expériences entreprises au laboratoire d'Arcachon par M. ABOUL-ELA ont montré que leur croissance optimum s'effectuait pour des *p*H de 7,5.

D'autre part, je ne crois pas qu'il faille toujours invoquer pour expliquer la présence des bancs naturels d'Huîtres portugaises dans les zones d'estuaire, la régression du nombre des prédateurs dans ces zones. A Arcachon, on trouve sur ces bancs naturels, une grande abondance d'*Asterias rubens* et de *Polydora ciliata*.

M. Korringa. — L'existence d'un banc naturel d'Huîtres portugaises dans la partie Sud-Est du Bassin d'Arcachon est connue, mais d'après moi, il n'y a aucune indication que les larves ne puissent se développer ailleurs, dans le Bassin, ou bien se fixer exclusivement sur le banc naturel, dans une eau plus ou moins saumâtre. Les larves se trouvent dans tout le Bassin et la fixation sur les tuiles des ostréiculteurs et aussi sur les pinhiots (sorte de pieux placés autour des parcs) a lieu à maints endroits de salinité élevée, dans le Bassin et cela sur une grande échelle.

Polydora ciliata supporte des salinités diverses mais préfère un fond plus ou moins vaseux, et déteste du sable instable C'est pourquoi les *Polydora* peuvent bien être plus nombreux dans l'eau saumâtre vaseuse.

Il y a plusieurs autres organismes qui peuvent nuire à l'Huître, mais meurent par contact avec l'eau saumâtre ou l'eau douce, même si celle-ci n'est présente que quelques heures à marée basse, ou après des pluies importantes.

M. Bouxin. — Peut-être serait-il utile de mesurer l'intensité respiratoire de l'Huître en milieu saumâtre. Elle est vraisemblablement plus forte pour une proportion d'eau douce de 10 à 20 pour 100. Il doit s'ensuivre une augmentation correspondante dans le métabolisme et, par voie de conséquence, dans la croissance de l'Huître, au moins quand elle n'est pas trop vieille.

Mais je crois que dans les estuaires, notamment dans ceux qui correspondent à de petits cours d'eau, le rôle de l'eau douce est extrêmement important à un tout autre point de vue et contribue puissamment à permettre l'existence de populations florissantes de Lamellibranches.

Les Bivalves, en effet, peuvent très bien supporter pendant quelques heures, d'être plongés dans une eau de salinité très faible. Beaucoup de prédateurs en sont incapables. C'est, en particulier, le cas des Astéries, qui comptent parmi les plus redoutables. Il arrive, au bas des estuaires que les Astéries soient nombreuses au point d'y empêcher, en temps normal, l'établissement du moindre banc de Lamellibranches. Assez souvent, en hiver ou au printemps, il se met à pleuvoir pendant plusieurs jours de suite. La masse d'eau douce s'écoulant par l'estuaire, augmente alors énormément. Il en résulte qu'aux bas niveaux fréquentés d'ordinaire par les Astéries, une nappe d'eau douce peut baigner pendant près d'une heure à marée descendante, jusqu'à la fin de l'étale, une zone qui, normalement, aurait été baignée par une eau encore assez salée. Les Astéries, qui hantent cette zone, meurent toutes et l'estuaire en est provisoirement débarrassé. Il faut des semaines pour que les Astéries des régions voisines de la côte réapparaissent au bas de l'estuaire, des semaines pour qu'elles réoccupent en amont toute leur ancienne zone d'extension. Pendant ce temps, il peut s'établir dans les régions qu'elles ont dû délaisser, et aussi longtemps qu'elles ne les ont pas réoccupées en force, des peuplements de Lamellibranches, ce qui montre que, abstraction faite des prédateurs, ces régions offraient un ensemble de conditions de milieu favorable à la vie des Lamellibranches. D'autre part, sur les bancs habituels, ces animaux, n'étant plus gênés par les tentatives d'attaque des Astéries, font montre, pendant le même temps, d'une croissance plus régulière et plus forte.

Si l'on ajoute que les Astéries ne s'aventurent qu'avec une extrême répugnance sur les fonds de vase ou de sable fin, fonds très répandus dans les estuaires, on voit combien la combinaison de ces deux facteurs : salinité variable et nature du fond, peut être favorable aux Lamellibranches du point de vue de l'interéquilibre des espèces.

M. Korringa. — Nous n'avons pas fait d'observations concernant la respiration des Huîtres, mais une respiration élevée n'indique pas toujours une meilleure condition physiologique. Il est fort possible que la respiration monte parce que l'Huître doit travailler plus, par exemple parce qu'il y a dans l'eau plus de vase qui doit être éloignée fréquemment des branchies, ce qui est souvent le cas dans l'eau saumâtre.

La mort des organismes sur les coquilles des Huîtres est souvent un avantage, parce qu'on éloigne ainsi des compétiteurs pour leur nutrition. Les ostréiculteurs hollandais tuent par des produits chimiques, les Ascidies, Eponges, Bryozoaires, sur les jeunes Huîtres et sur les tuiles, pendant le second été, ce qui favorise la croissance de ces Huîtres. La mort des compétiteurs (et aussi des prédateurs comme les Bigorneaux perceurs et les Astéries dans l'eau saumâtre) est sans aucun doute, une explication logique du succès des cultures, dans les estuaires saumâtres.