D. J. Jellyman.

NEW ZEALAND MARINE DEPARTMENT
TECHNICAL FISHERIES REPORT
NO.11.

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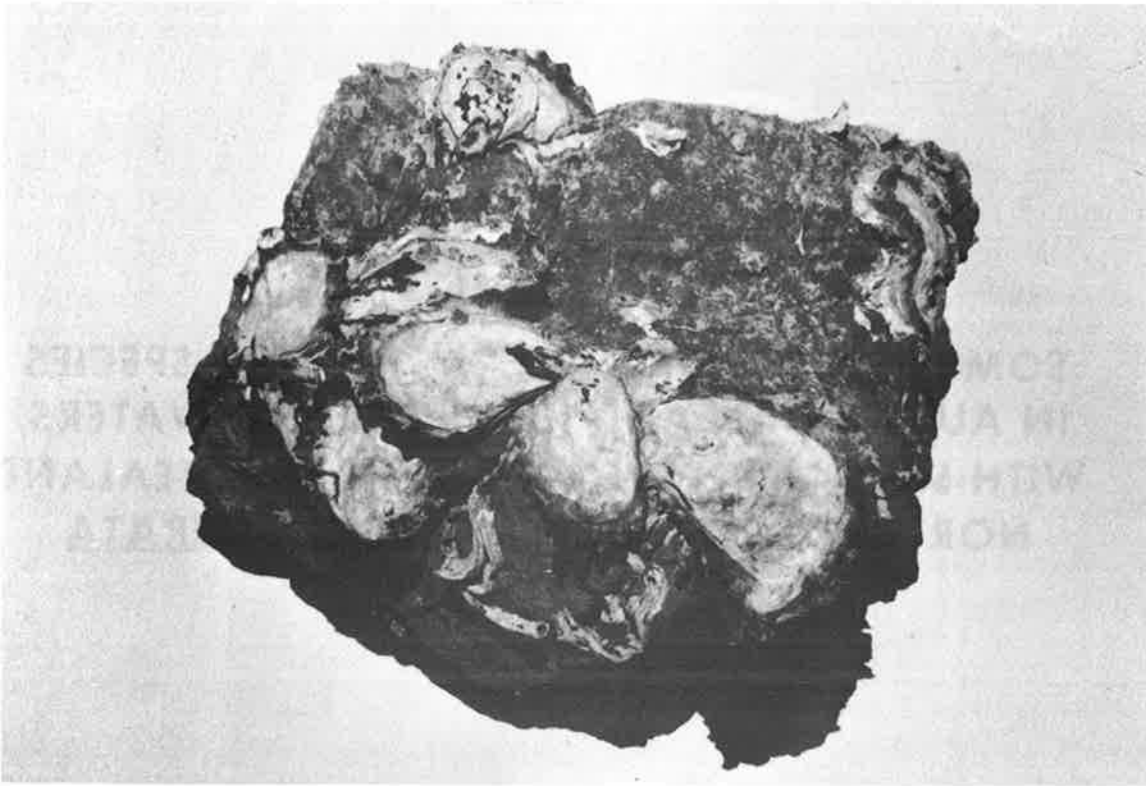

Fig. 1. Adult *Crassostrea glomerata* growing naturally on a stone substrate.

ABSTRACT

At the present time there is in New Zealand an encouraging, growing interest into the cultivation of rock oysters in the northern part of the North Island. With this interest, however, has come the realisation of how little is actually known of the habits of this species of oyster, and how much the cultivation to date has depended on the trial-and-error adaptation of the methods used overseas.

In an attempt to present a realistic situation of such knowledge, this report has been compiled entirely from the published data specific to *Crassostrea glomerata*, the Auckland rock oyster, and *C. commercialis*, the Sydney rock oyster regarded as allied to, if not the same as, the Auckland one. The report has but a humble purpose - it is intended as a compromise between supplying information by way of introductory data for workers contemplating a scientific study into this oyster, and as information most likely to be of use and interest to persons wishing to attempt cultivation.

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LIST OF ILLUSTRATIONS

ACKNOWLEDGEMENTS

I wish to acknowledge with thanks Mr J.W. Brodie, Director of Oceanographic Institute and Acting Director of Research Fisheries Laboratory, who suggested a study of this nature; Mr A.C. Kaberry, Director of Fisheries, and Mr B.T. Cunningham of the Marine Department who offered advice and helpful criticism with the manuscript. I also wish to thank Dr R.K. Dell for identifying mussel specimens, and Mr F.E. French, District Inspector of Fisheries, Auckland, for making available his meticulous records of the departmental experiments into oyster cultivation and the photographs included in this report other than figs. 1, 3, 4, 9 and 11 which have been obtained by courtesy of National Publicity Studios, Auckland. Special thanks are due to the late Mr H.S. Valentine, the Inspector of Fisheries at Whakapirau, Mr M. Howell, late of Victoria University, Wellington, the former librarian at the Fisheries Laboratory, Mrs J.M. Banfield, and the librarians at the Turnbull Library and the Dominion Museum Library.

INTRODUCTION

The living oysters are subdivided into three main "groups" each represented by a particular genus with its characteristic shell morphology, anatomy and reproductive stages. The three genera are Ostrea, Crassostrea and Pyenodonta.

OSTREA

This genus includes the common flat oysters such as O. edulis Linnaeus, the edible European mud oyster, and the New Zealand Foveaux Strait O. angasi Sowerby.

Features:

Valves more or less circular in outline, and not deeply cupped.
Muscle scar near the centre, and not coloured.
No promyal chamber, so only a single passage for the exhalant current.
Eggs relatively large; up to 1,000,000 per gonad incubated in the inhalant chamber.
Larval shell, or the prodissoconch, inequivalve with two teeth at each end of the hinge plate.

In nature these oysters occur in large numbers, forming extensive colonies in shallow water which may be wholly or partially exposed at low water of spring tides.

CRASSOSTREA

These are the cupped oysters and are represented by the New Zealand northern rock or Auckland oyster, C. glomerata, and include the Sydney rock oyster, C. commercialis; the American oyster, C. virginica; the Portuguese oyster, C. angulata; and the Japanese oyster C. gigas, to name a few.

Features:

Oyster elongate, markedly inequivalve.
Left, or lower, valve deeply cupped, often with markedly corrugated edges.
Muscle scar nearer the shell margin than to hinge, and usually deeply pigmented.
Promyal chamber present, providing an additional passage for exhalant current on right side.
Eggs small; may exceed 50,000,000; and are not incubated.
Larval shell somewhat asymmetrical; the 2 unequal valves with 2 teeth at each end of hinge plate.

These oysters are the most numerous, most successful, and by far the most important commercially of modern oysters. Their structure enables them to withstand wide fluctuations in environmental conditions, especially the lowered salinities, so that they are able to live in less saline but often nutritionally richer waters of estuaries and other inshore waters.

PYCNODONTA

This is a most distinctly shaped oyster found all over the world in relatively deep or open seas, and in water of full salinity. Although edible the species are seldom easily accessible, and certainly never occur in sufficient numbers to justify collection on commercial scale. They will not, therefore, be discussed further.

Some of the workers, namely Thomson (1953) who have studied the Sydney oyster *Crassostrea commercialis*, consider that the Auckland *C. glomerata* is merely the neozelanic form of its Sydney counterpart, and since as yet no studies have proved them wrong this report will present as fully as possible first, the account of the Sydney oyster, and then any differences to it in the New Zealand species. For comparative purposes general information on some other *Crassostrea* species is included at the end of most sections, but it should be borne in mind that such material is general only and is not an earnest effort to make a detailed comparison with the species of most interest in this report. It has not been possible to make a concentrated study of the numerous papers on these other species.

A list of references and a bibliography have been included at the end of the report. These again are specific to *C. commercialis* and *C. glomerata*.

DISTRIBUTION

Crassostrea glomerata, the commercially important rock oyster of Northern New Zealand, and *C. commercialis*, which extend along the eastern shores of Australia, are closely allied and sometimes claimed as the same species. They are described as being of tropical origin since in the southern hemisphere they thrive above the S. lat. 38°. Essentially estuarine animals, they are found in more saline conditions, but here their growth and general development are impaired both physically and physiologically. Likewise, they are species preferring an environment sheltered from direct action of waves and prolonged exposure. Consequently, these rock oysters show relatively little variation in pattern of distribution in response to these factors.

C. commercialis Iredale and Roughley - the Sydney Rock Oyster.

This rock oyster has been found under a variety of conditions. Generally, however, it is a species restricted to the east coast, with its geographical optimum limit extending from the Tropic of Capricorn to the border between New South Wales and Victoria. It does grow, and quite prolifically, north of Rockhampton, but owing to the great rise and fall in tide and heat of tropical sun the shell remains stunted and crinkled and the oyster is of little commercial value. Abingan Inlet appears to be as far south as the rock oyster grows naturally. When several bags were brought from New South Wales to Broughton River, South Australia, the oysters grew very well. This was also the case at Coffin's Bay, Nepean Bay and Kangaroo Islands. There was a question, however, as to whether these oysters would propagate in the new surroundings. Thomson (1952) states that the oysters taken to South Australia, Western Australia and Tasmania have not acclimatised.

Roughley (1925) considered the oyster to be Ostrea cucullata and as such described its distribution as being along the west coast of Australia from S. lat. 30° northwards and along the east coast as far south as Gippsland Lakes in Victoria. In 1933, following the recognition of the distinction between O. cucullata and O. commercialis, Roughley (1933) revised the distribution, stating that the oyster appears to be confined to the east coast.

The oyster is chiefly an estuarine form, growing best in an environment of fluctuating salinity, but it ranges from the surf-swept extremity of ocean reef to the innermost recesses of mangrove forest. In Queensland it is spread over extensive level banks that are more or less uncovered at low water, while Dakin, Bennett and Pope (1948) describe Saxostrea commercialis in New South Wales as reaching a high zone of intertidal shore with a fairly sharp zoning - a character brought out very conspicuously in the estuaries.

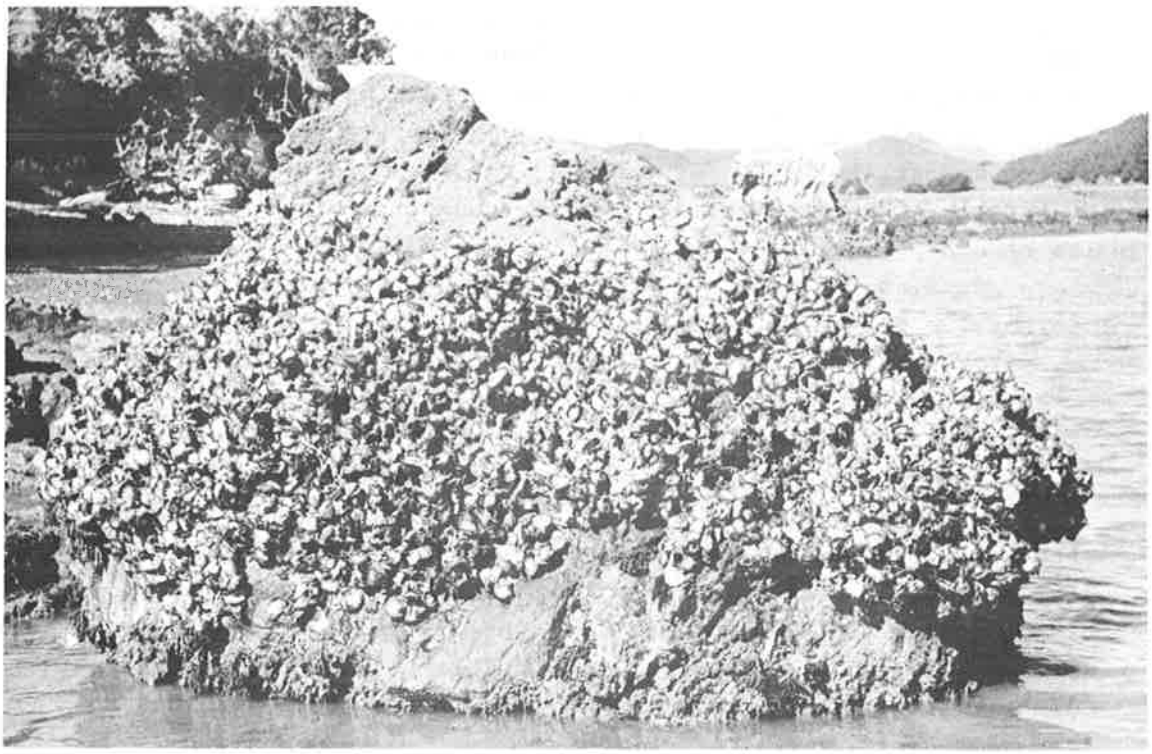


Fig.2. Natural Oyster Zone,
Bay of Islands.

The oyster is also found in almost all the ports of the State where it attaches itself to the wharf piles. In Port Jackson the oyster reaches its greatest abundance in the lower part of the intertidal zone and occurs to the extent of being rated a fouler (Wood and Allen, 1958). Hedley (1913) found it to range vertically from the mean tide level to several fathoms, with the optimum at the half tide mark.

C. glomerata Gould - the Auckland rock oyster.

The New Zealand northern rock oyster, or the Auckland rock oyster, is common throughout the northern North Island of New Zealand. It has been recorded at various locations under varying generic and specific names since middle 1800s, and some of the more specific references are introduced here.

Ecologically the oyster forms a distinct belt (as shown in Fig.2) between tide marks, ranging vertically from beds experiencing 22% exposure (Dellow, 1950) to those submerged at all times. The shells may be scattered about in dense clusters or may cover the entire surface of the belt, as at Takapuna (Auckland, New Zealand), where Oliver (1923) records them to cover the surface in a belt one metre wide and 6-10 c.m. deep.

Like Oliver, Hedley (1919) regarded the Auckland species as C. cucullata. He considered it to be here at the extremity of it range in New Zealand, growing near and below the water mark, its aspect so changed as to appear to be another species. Nonetheless, the rock oyster has been recorded farther south - as O. cucullata in rock pools at Tauranga by Oliver, who found it to be rare in that area, and as O. glomerata at Lyall Bay (Wellington) by Iredale and Mestayer (1907). There is no other data to collaborate the latter finding. Saxostrea glomerata is also found at the Chathams, in the upper tidal rocky zone (Powell, 1947; Dell 1960).

In an ecological study of Narrow Neck Reef (Waitemata), Dellow (1950) notes S. glomerata to form a conspicuous, sharply delineated belt, consistent at a level with vertical range of 10.2 - 3.6 ft between the M.H.W.N. and M.L.W.N., 6.5 ft above the M.S.L. with an estimated exposure of 92-21.3%. In another ecological study in Hauraki Gulf, Dellow (1955) finds S. glomerata in a prominent belt for 2 ft below the M.S.L., in regions where there is a certain amount of protection from direct wave action. Most adjacent islands are inhabited by the oyster along their southern and western shores, and it is "physiognomic in sheltered harbours and bays of Western Great Barrier and Coromandel Peninsula, and hard rock faces in the upper Firth of Thames". Dellow notes that the oyster fades out at Te Puru, Howick, Little Barrier, Sugar Loaf Rocks, and north-east of Great Barrier - a feature correlating with the oyster's sensitivity to excessive sedimentation and movable stones or boulders, aeration and surf pounding.

Cranwell and Moore (1938) in the published results of their study of intertidal communities of the Poor Knights Islands, mention finding a small group of oysters in a pool in spray zone. The oysters were attached very firmly by a broad base to odd boulders lying in the water; were small 35 x 27 x 20 mm; and apparently were most nearly allied to O. heffordi. But since O. heffordi is normally an oyster of southern New Zealand and since the authors refer to these specimens as undescribed species fairly common in Hauraki Gulf, there is the possibility of their being distorted, stunted specimens of C. glomerata. An interesting feature is that the oysters were found nowhere else on the island, except in this particular pool. It has not been possible to obtain further data in this instance.

The most recent work on the Auckland oyster is that of Rainer (1964) which is based on the study of oysters at Kaipara Harbour, on the west coast of the Northern North Island, and especially at Whakapirau - a shallow drowned river valley with deeply indented shorelines and extensive sand and mud flats exposed at low tide. Kaipara is one of the larger oyster producing centres of the North Island, where substantial quantities are harvested commercially.

Other better known species of Crassostrea include:
C. virginica (Gemlin) - the American oyster.

"Ranges extensively off the Atlantic coasts from the Gulf of St. Lawrence along the shores of North America into the Gulf of Mexico and further south to Panama as well as around the West Indian Islands. This covers an unusually wide range of temperature. It is an extremely abundant species and, like the Portuguese oyster in Europe and the Japanese oyster C. gigas, is the basis of a great industry, being cultivated on a large scale." (Yonge, 1960).

C. gigas Thunberg - the Japanese oyster

".... widely distributed around the shores of Japan and Korea, and is successfully exported as "seed" to the Pacific coast of the United States and Canada and to Australia" (Yonge, 1960).

C. angulata Lamarck - the Portuguese oyster

"Occurs along the east and south coasts of Portugal and Spain. In 1868 it was imported into France where it now forms large natural beds at the mouths of the Gironde and the Charente. It is cultivated on a vast scale in France and is important for relaying on British oyster beds along the east coast and in the mouth of the Thames. There it grows well but, owing to the lower temperature seldom breeds. However, from time to time during hot summers it does spawn and spat may settle and grow." (Yonge, 1960).

C. cucullata Boon

".... the common rock oyster of the tropical Indo-Pacific, abundant around the shores of India and along the east coast of Africa and extending into the eastern Mediterranean." (Yonge, 1960).

SHELL MORPHOLOGY

EXTERNAL

Valves:

From all accounts there do not appear to be any visible differences in the morphology of Crassostrea glomerata and C. commercialis.

The oysters are recognisable by the markedly inequivalve appearance: the lower, or left, valve is deep, cup-shaped, and moderately crenulate; the upper, or right, valve is opercular, moderately flattened, and folded towards the lip to fit the crenulations of the lower valve.

The rock oyster is an adherent species attaching itself to a hard substrate by the left valve at about 3 weeks of age, and in nature remains there for the rest of its life. For the first year or so the left valve grows very closely connected with at least half its area to the substrate, but later the edges of the valve bend sharply up from the rock surface, and the shell assumes a cup shape.

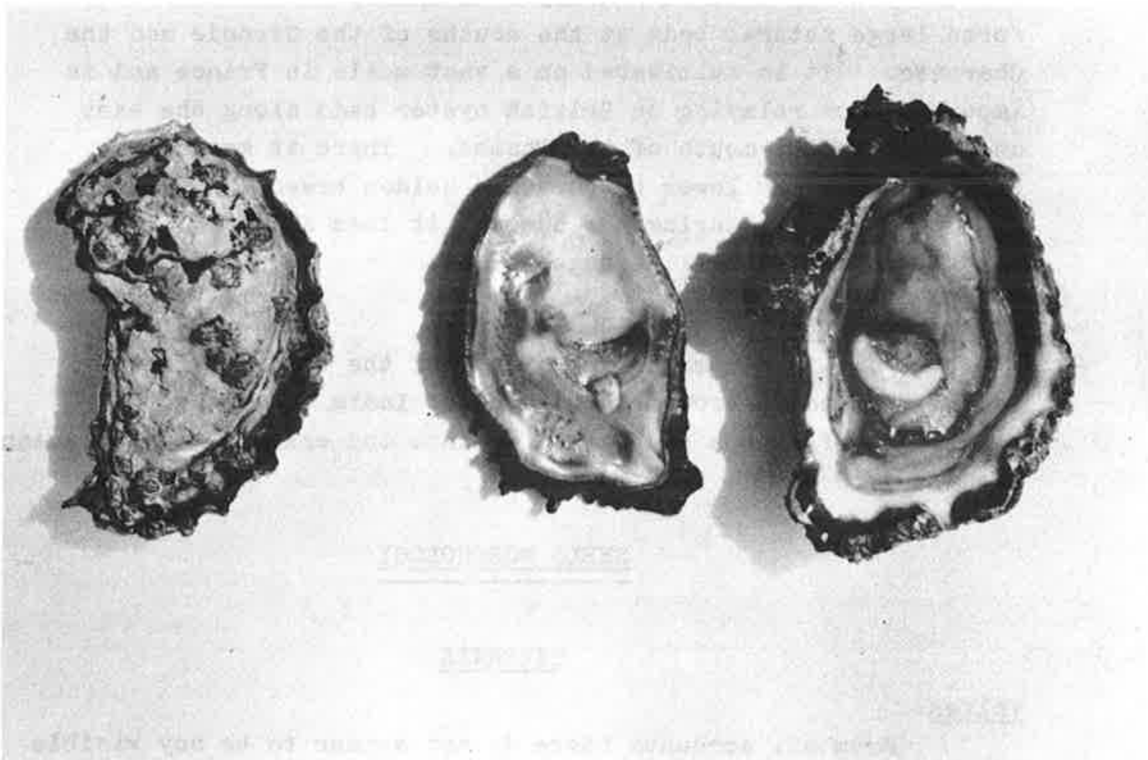


Fig. 3. External and Internal morphology of C. glomerata

The opening and shutting of the shells is performed only by the upper valve which in overcrowded conditions may itself grow attached to a neighbouring rock or oyster.

Shape:

Basically, the bivalve is slightly elongate, and often somewhat crescentic in shape (See fig. 3). Any further shape is determined by the immediate environment in which it grows - the type of substrate, the overcrowding, the degree of salinity of water, the amount of exposure. Thus, for instance, in saline exposed positions oysters may be thick-shelled, stunted, much crumpled and even spiked, while in sheltered estuarine waters they may grow rapidly into thin-shelled smooth specimens 3" - 4" long. In some specimens the lower valve is sharply ribbed, and as well sharply ridged in transverse, the latter presumably indicating intensive sporadic growth following quiescent periods. The growing portion of the shell, approximately 3 mm wide, is laminate and extremely brittle, and is usually broken off in the dead shells found on beaches.

Colour:

The external colouration is variable from bluish-black to greyish-white in older specimens. There is usually an indefinite blue-black or purple border along the margin of both valves, and intermediate forms often show radial rays extending from the hinge to the lip on the upper valve. Removal of the horny outside layer of a shell through the abrasion by water or weathering, or the usual intense populisation of the upper shell by barnacles, result in the removal or at least masking of most of the colour, and the shell then appears typically greyish-white mottled with dark purple.

Hinge:

In their account of Ostrea commercialis Iredale and Roughley (1933) describe the hinge line as being short, but all the subsequent literature refers to its being moderately wide, except in specimens from crowded conditions where it may be short. The hinge plate is moderate, and the ligament blue-black in colour drying to brown and brownish-black.

INTERNAL

Valves:

As with other molluscs the inside of the shell (See fig. 3) is conspicuous in its pearly sheen. The relief is a modified inverted replica of the outside with depressions occurring chiefly where the gonad and the muscle are found. Muscle scar is conspicuous, and in older oysters has a purple band around the lip edge. Growth ridges, conspicuous on the outside of some oysters, are absent though in some cases slight indentations appear to follow the line of growth. Frequently, in the lower valve there is a recess under the hinge, reflected on the outside in a prominent curved "beak".

Muscle Scar:

The muscle scar of the posterior adductor muscle is broadly lunate in shape, whitish in colour, but frequently with bluish or creamy markings especially on the upper valve. Often, instead of a single muscle depression, the scar is seen to consist of a number of distinctly directed concentric bands which appear to trace the dorsolateral displacement of the muscle towards the lip of the shell. This is particularly evident in the upper shell. Each band, on average, is about 2.3 mm wide, but 7-8 mm bands have been found in shells in which the overall length of the upper shell is 7.2 and 7.8 cm respectively. On the lower valve, the scar is usually seen to consist of two main subequal areas - those marking the "catch" and "quick" parts of the adductor, although closer examination discloses a greater number of bands.

Denticles:

Along the edge of the upper valve, and especially immediately on either side of the hinge, there is a row of small denticles which are reflected in a number of pits in corresponding arrangement along the edge of the lower valve. These denticles are a fraction of a millimetre long, spaced at irregular intervals, and extend with decreasing density for about a half to two thirds of the length of the shell.

Colour:

The colour of the inside of shells is generally a dirty white, often with bluish black or brown inclusions, especially in the upper valve. In oysters recently killed and scraped out, there is a general yellowing of the valves, but this soon weathers away. A brownish coloured rim newly covered with nacreous secretion - the growing portion of the shell - is found along the growing edge of either shell, and again is more evident in the upper valve. The oysters growing low on the shore or subtidally tend to have no internal pigmentation at all (Rainer, 1964).

Larval shell:

Rainer (1964) describes the prodissoconch as typically *Crassostrea* type, being inequivalve, somewhat asymmetrical, with 2 teeth on either side of the provinculum, interior ligament well away from the provinculum. The hinge is short, and the ligament interior.

FEEDING

This is an aspect of oyster study that has been well studied in Europe and America but, if published literature forms the criterion, has been badly neglected in New Zealand and Australia. For the most part, therefore, it is assumed that Crassostrea glomerata and C. commercialis have feeding habits similar to those of the oyster of America, Japan and Europe.

Oysters feed on organic detritus, diatoms, flagellates, larvae of various marine organisms, plant particles and such. Food particles are swept up with a current of water into the oyster, and are then moved by ciliary action along gill filaments to the labial palps. Sheets of mucus, produced so long as the oyster feeds, strain out small food particles from the water, and the particles are then moved by cilia to the mouth. If the oyster is disturbed, gills may continue pumping water, but the secretion of the mucus sheet stops.

A revolving crystalline style, formed in the stomach when the oyster is submerged, disappears when the oyster is exposed, and quickly reforms when the oyster is submerged again and opens its shell. According to earlier workers this style is present only in the oysters that had been feeding. Hence, some consider that its presence or absence marks the health condition of the animal, the absence signifying that something is amiss with the oyster. (Korringa, 1952).

FOOD TYPES

C. COMMERCIALIS:

In a study of food types of oysters at the George's River and at Hawkesbury River, Roughley (1926) found that the two very small unicellular organisms which he could not identify and which formed the bulk of the stomach content of Ostrea elongata and O. edulis, formed but a very small portion of the stomach content of Crassostrea commercialis. The remainder consisted of diatoms, in particular Pleurosigma, Navicula, Coscinodiscus and Bacillaria, and also sponge spicules, confervae, portions of epidermis of larger algae, fragments of larval crustacea, and minute sand grains. On several occasions considerable numbers of infusoria, probably Tintinnopsis, were also found, but these are considered to have been swept in with the current when they were already dead and still suspended in waters.

C. VIRGINICA:

It has recently been recognised that the labial palps, of at least Crassostrea virginica, are capable of great discrimination in selection of food particles, involving factors other than just their size and shape (Korringa, 1952). Examples noted are derived from the experiments in which oysters were fed with yeast cells and plankton organisms of the same size and in which the yeast cells were refused, and also from the experiments in which oysters were fed with a dilute suspension of mixed plankton culture into which a little of the culture of red Chromatium perta was added. In the latter experiment, the oyster ingested the bulk of the plankton mixture, but rejected almost solely Chromatium. Korringa assumes, provisionally, with the experimenters that in the labial palps there are probably specialised cells which act as chemoreceptors and which refuse certain organisms probably on the basis of their secretions.

FEEDING TIMES

C. COMMERCIALIS:

Roughley (1926) considered that feeding in C. commercialis went on during both tides, although it was almost invariably found that more food was obtained on the flood tide than on the ebb. The reason for this, he thought, might have been either that sufficient food had been obtained for the oyster's requirements during the flood tide and, therefore, food was rejected on the ebb tide, or that food may be more abundant on the flood than ebb tide. He writes ".... the gills continue to pass the food forward towards the mouth so long as the oyster remains open, and after many observations, I have come to the conclusion that it remains open just as long on the ebb tide as on the flood. Therefore, if the food is as abundant on the ebb as on the flood tide, considerable quantities must be rejected by the palps."

C. VIRGINICA:

According to American workers working with C. virginica, feeding is not limited to any part of the tidal cycle nor to any time of day or night, so long as the salinity of water remains high and fairly constant throughout the tidal cycle. With temporary lowered salinities as, for instance, during the low tide further up the river, oysters appear to stop feeding so long as the low salinities prevail. (Korringa 1952).

ENVIRONMENTAL EFFECTS

C. COMMERCIALIS:

In his study of oyster mortality on George's River, Roughley (1926) concluded that three main factors contributed to variation in the volume of food consumed by the oysters - the temperature of the water, the direction and temperature of the wind, and the state of tide. He confirmed earlier findings that oysters will not open to feed at temperatures at or below 50°F (10°C) basing this statement on the fact that in the oysters opened on two occasions when the temperature was 48°F and 50°F and tide about half flood the food present was negligible. At high temperatures more food was recovered from the stomachs than at lower temperatures, "provided that the wind was in the same direction, and the state of the tide the same." The direction and the temperature of the wind were important in as far as their effects on cooling or heating the water and possibly thus creating turbulence.

C. VIRGINICA:

In studies with C. virginica, temperature has been found to affect the rate of pumping in that little pumping occurs below 30°C (37.4°F); the rate increases from 8°C - 16°C (46.4° - 60.8°F); is steady between 16° - 28°C (60.8° - 82.4°F) and markedly decreases above 34°C (93.2°F) when the oyster shows signs of distress. It should be remembered, however, that while pumping is not strictly indicative of feeding, feeding does not occur without pumping (Korringa, 1952).

Low pH values, resulting in nature by an influx of acid swamp water or by industrial pollution, also reduce rate of pumping. Oysters appear to pump normally at a pH of 7.75 (Korringa).

Silt and other turbidity creating substances, even when in quantities as low as 0.1 gm per litre of sea water, seriously reduce the ratio of pumping (to 40% of normal value in this example) with the effects demonstrated in the vigorous shell movements and expulsion of large quantities of pseudofaeces. Reduction in pumping rate occurs and as well, in an experimental study with C. virginica, the oysters "became sluggish in response to stimuli, as if some toxic product had exerted an influence. Dangerous quantities were 300/ml for Euglena, 75,000/ml for the smaller Nitzschia closterium, and 2,000,000/ml for the very small

Chlorella .... transferred to normal sea water, the oysters resumed their normal rate of pumping after some time" (Korringa, 1952). It was concluded that in dense cultures of plankton there must be present a toxic substance, probably metabolic products of the micro-organisms. In another experiment, oysters fed with a Chlorella suspension demonstrated considerable and irregular fluctuation in filtration off of the organisms which apparently could not be correlated with the concentration of the organisms administered.

Korringa (1952) mentions a find by American workers of a hitherto unreported factor naturally present in sea water and which is found to stop the rate of pumping in C. virginica when present in quantities less than 4.8mg/l of sea water. At high temperature (28°C) (82.4°F), the threshold value may be as high as 12mg/l. Designated tentatively as a carbohydrate, it is not destroyed by boiling, but its quantity will drop sharply if sea water is stored at 25° - 30°C (77° - 86°F), for more than 4 days.

SEASONAL EFFECTS

C. COMMERCIALIS:

In the European flat oyster, O. edulis, it has been repeatedly found that only a remarkably small amount of food is ingested during the winter. In rock oyster, however, difference between summer and winter feeding is negligible, there being occasions when "little or no variations can be seen" (Roughley, 1926). Roughley considered that such difference in feeding habits is probably due to the difference in the temperature of water in which the oysters grow.

The greater amount of food consumed by the oyster in warmer periods may be attributed to the increase of metabolism, of general activity, and to the development of a relatively enormous reproductive organ in the cells of which nutrient must be stored to nourish the embryo in its early stages of cell division. During the winter, oysters greatest activity is that of enlarging its shell, "the constituents of which are probably obtained, not from the food, but from the water."

There appears to be no published data either on the feeding habits or food types of the Auckland rock oyster.

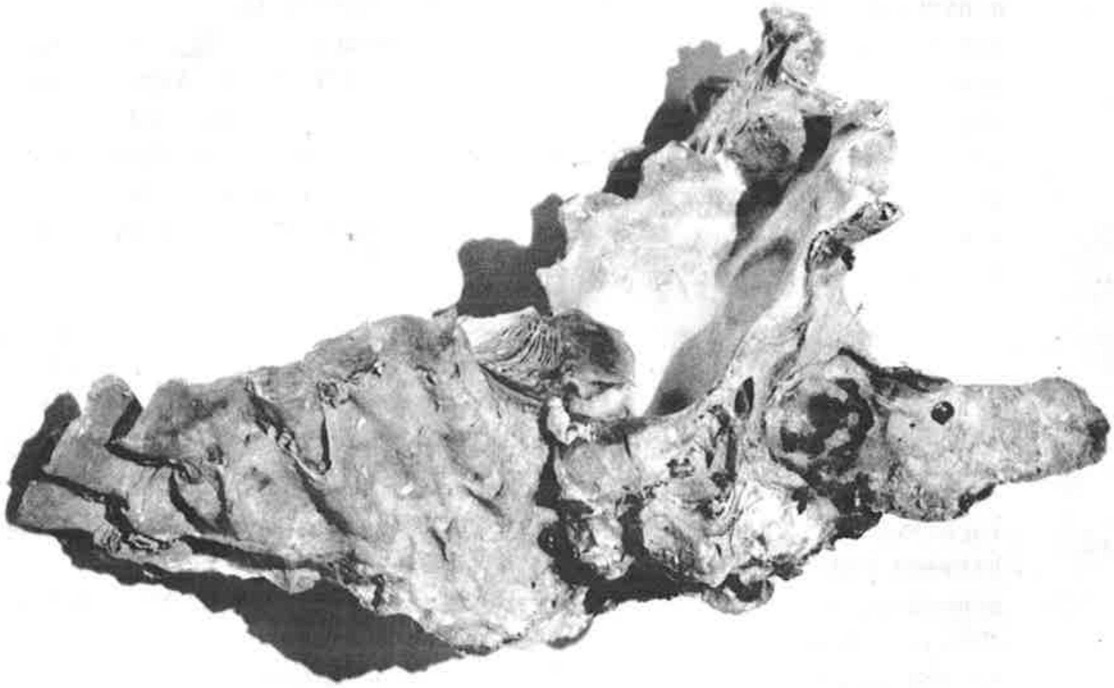


Fig.4. Successive crenulated "growing edges" in C. glomerata.

GROWTH

The growth is regarded as both the increase in the size of the shell and the increase in weight of the soft body. Increase in the size of shell is seen externally by means of the growth edge, another conspicuous dark-coloured brittle border (See fig.4.). Although this aspect of oyster study has been comparatively well studied all over the world, published data on the Sydney and Auckland rock oysters is again scarce.

C. COMMERCIALIS:

Roughley (1925) observes that the growth from early straight hinge stages is rapid so that by the time the larva attaches itself to a suitable substrate (about 2-3 weeks after fertilisation) it is approximately 1/75th of an inch long. It grows rapidly, its lower shell remaining in close contact with the substrate for approximately 12 months. Then, the edge farthest from the hinge of the lower shell begins to grow upwards and away from the substrate, and the depth of the oyster increases largely.

In 1933, Roughley published a paper in which he writes of an experiment he performed on the rate of growth of the embryo, and gives the following figures. At 34 hours after fertilisation, the larvae appeared with a straight hinge and average measurements of 20 larvae were length 67/u x depth 53/u, with a hinge length of 45/u. At 5 days, the above measurements averaged 75/u x 58/u, and 50/u respectively. A fully grown larva was approximately 330/u long, while the average depth of newly attached spat was 216/u.

For growth at later stages, Saville-Kent (1893) notes that the oysters attached to cement-coated split paling reached approximately 1" in shell diameter at 3 - 4 months, and about 2" at 5 - 6 months. This is now seen as a somewhat generous statement, and most workers are of the same opinion as Wood and Allen (1958) that just after settlement the embryo shells are under 1/16" across and in six months reach an approximate length of 1-1¼"m normally reaching the full marketable size of 3" across or slightly more in about 3 years. However, under favourable conditions of food, temperature, and salinity an oyster may reach that size in 2 years. According to Marine Department records, the New Zealand oyster seems to take 5 - 7 years to reach the same size.

Effect of Salinity:

From general literature and Roughley's (1933) paper it is apparent that while the release of gonadial products and spat settlement are more favourable under conditions of high salinity, the oysters transferred to waters of lower salinity grow much more rapidly than they would in their previous environment.

In practice this has been demonstrated in the cultivation at Port Hacking where most of the adult oysters are stunted, with hard crinkled shell and numerous close layers of growth. If allowed to remain there, their development is extremely slow and, in fact, only a small percentage reaches marketable size. However, when removed to the more blackish waters of George's River fresh, healthy growth appears and the oysters double their size in the course at about 12 months. In one particular case when this practice was used, the oysters were found to be ready for market in one year and nine months (Roughley, 1922).

C. GLOMERATA:

The latest study into the growth of our rock oyster is that by Rainer (1964) in which he attempted to study the growth in relation to annual and seasonal variations, to the position of oyster on the shore, and to the environmental factors.

Larvae:

Rainer found four size groups in larval stages: 85 - 160/u, early umbo; 160 - 245/u, late umbo; 245 - 300/u; mature, and over 300/u, eyed, "measurements being taken from the umbo to the opposite point of the prodisso-conch".

Spat:

The most important single factor in the variation of growth rates at different shore levels is probably the amount of submersion experienced at each level. Growth of spat at higher levels (2.5m) was found to be less than at lower levels, possibly due to heating and desiccation and the oysters' efforts to overcome them. At the same time, there was a differential growth rate among the spat protected completely from insolation and the spat exposed. Thus, for instance, at 2.5m the mean length of protected spat at 7 weeks was 3.31mm while that of exposed 2.21mm.

At lower levels, the difference was not as obvious due to the greater abundance of food competitors on sheltered surfaces and the reduced amount of insolation experienced.

Silting had little effect on spat growth at Whakapirau because of the high current speeds, whereas in Hargreaves Basin it appeared to reduce growth rates considerably.

In spat growing subtidally, growth rates were found to be directly related to water temperatures in the range of 12 - 20°C (59oF) (53.6o - 68°F). The growth curve was sigmoid, with the greatest steepness near 15°C. Here, too, the maximum length increment, at 19.5°C, (67.1oF), increased gradually from approximately 2mm per week when spat first settled to 3mm per week when a length of 10 - 12 mm was reached. Therefore, the rate of which decreases slowly with increasing size.

Post-Spat:

In investigating the growth during the remaining life of the oyster, Rainer used length-width measurements of attached oysters *in situ* and free oysters in trays.

In attached oysters, Rainers notes, growth follows the same broad trend as in spat but with three features:-

1. There is an apparent decrease in growth rate in low level oysters compared with higher level ones. This could be due to the combined effects of the changed direction of growth, resulting from the up-lifting of the oyster shell for almost perpendicular to substrate, and the exposure to desiccation resulting from this.
2. A reduction in growth rates occurs during mid-summer, which could be due either to lowered food intake, associated with lowered phytoplankton concentration, or instrumental error.
3. A negative growth is evident during winter, particularly in older oysters. Smaller oysters continue to grow, but at a reduced rate. In tray oysters, weight increase was measured as well as the shell dimensions. The results of the latter was not reliable owing to damage done to the shell by high water currents. Weight increment was irregular but continued throughout the year. It was greater in summer than in winter, and was greater at lower levels than higher. Some of the variations in weight increments may be associated with spawning.

Growth rates:

In slower-growing oysters, Rainer found growth can be directly related to width within an age class, and, inversely, to weight within a length class. In faster growing oysters, periodic variations occur with increasing length and weight, and appear to represent age classes.

Another apparent relationship is that of growth rates and sex ratios "there being a higher proportion of females to males above the mean of an age group than below" with an increasing tendency to femaleness with increasing size.

C. VIRGINICA

American workers have found that the growing period of this oyster is only eight months of the year, with maximum length increase occurring in mid summer. (Korringa, 1952).

Growth does not occur below 7°C, (44.6°F) and volume increment is greatest at about 21°C, 69.8°F) (Rainer, 1964).

Growth rates vary from 3" in 4 - 7 years in the Maritimes, to 4" - 5" in 1.4 years in Florida.

C. GIGAS:

The main growth period is from September to February but growth in winter does not stop entirely even when temperatures are well below 10°C (40.°F) (Thomson 1952).

Mean length of this oyster in Tasmania is 9.4cm at the end of three years, and in Washington waters (U.S.A.) 10cm for the same time.

REPRODUCTION

While the reproductive system of the oyster is simple, its whole reproductive process is complex and as yet not fully understood.

Crassostrea species are oviparous i.e. their sex products are liberated into water where the fertilisation occurs, in contrast with Ostrea species in which the fertilisation occurs inside the oyster and larvae are liberated into water. The larvae spend 2 - 3 weeks in a free state before settling on a firm substrate and becoming spat. From this stage they rapidly metamorphose into adults in which the maturation, including the sexual maturation, is largely dependent on such environmental conditions as the availability of food, temperature of water, density of the water.

The Crassostrea species investigated so far, exhibit alternate sexuality (Rainer, 1964) which means that they usually produce sex products of only one sex a year, but in their early years they can act as either male or female and it is impossible to predict from one sexual phase what the succeeding phase will be.

The reproduction, therefore, can be regarded as a process with four phases - spawning, pelagic stage, settlement, and sexual maturation.

From an oyster cultivator's point of view, this is the most important process in the life of oyster, since it is during certain phases of this stage that the cultivating operations intervene in the natural order of things.

SPAWNING

When the gonad is ripe and the environmental conditions favourable, release of gonadial products is induced either by sharp fluctuation in water temperature and or by chemical means. The latter is thought to involve the presence of sperm in water in the case of spawning female oysters, and the presence of sperm and eggs in the case of males, as well as a wide range of organic compounds. In Japan, a substance similar to those has been found in a variety of green seaweeds and this adds force to the suggestion of one American worker that natural spawning may be stimulated on the first instance by some substance released by the plant plankton. (Yonge, 1960).

Spawning is usually incomplete - some sex products remain in the gonad and are absorbed slowly and replaced by the developing nutritive tissue over winter in preparation for the development of sex products in spring.

C. COMMERCIALIS:

In this oyster, spawning may occur almost the whole year round, although generally there are two chief spawnings - one in spring and one in autumn.

In New South Wales, the process reflects this irregularity in that with the warming of water in spring the gonad develops rapidly and may become fully mature by mid-December; spawning then occurs during abnormally high tides around Christmas, with possibly another spawning activity in late summer. If, however, the spring has been abnormally cool, the development of the gonad is relatively slow and spawning may then occur in January or April or even May. At other times it can be observed as a partial process throughout the summer months, with some light intermittent spawnings in winter. Because of the variety of local conditions on the east coast of Australia, some workers feel that it is not possible to specify either a temperature threshold or an appropriate date for the commencement of spawning of Australian oysters (Dew and Wood, 1955). Generally, however, spawning is found to occur when temperatures are in the 71° - 76°F range.

Roughley (1933) observed that on one occasion spawning began when the daily water temperatures became greater than 70oF and following the day when the water temperatures dropped to 68oF. More precisely, on this occasion the temperature of water at the surface was 70°F and at the bottom 68°F. However, since the oysters had appeared ready to spawn days before and, in fact, fertilisation did occur when the eggs and sperm were mixed, he suggested that physical conditions other than just the temperature must play a part in governing the spawning impulse, probably tidal habitat of the system and the consequent rapidity of the water temperature fluctuation.

Density of water at the time of the above spawning was 1.0195 at the surface and 1.020 at the bottom. The tide was spring, 3 - 4 hours on the ebb. Past observations showed that the heaviest spawnings on the New South Wales coast occur at spring tides, both at full and new moon periods, with surface water temperatures at 70°F. and heavy seas outside as well.

During spawning, eggs and sperm are released at short intervals in the form of a white cloud. Eggs diffuse quickly, while sperm are inclined to hold together for a short time as well-defined milky streaks.

Once the spawning begins it will continue even if the oyster is bared by the tide or handled roughly. However, the oyster is at this time more sensitive to exposure than usual and mortality occurs much quicker at this period if it is deprived of water.

Spawning periods are very short - in the above instance Roughley notes that from the time the oysters began expelling sex products it took only an hour for the water to become practically clear again over the spawning beds.

At the completion of the process, great exhaustion of the oyster follows to the extent that sometimes it cannot even close its shell.

Cleland in 1950 estimated that 15,000,000 ova are produced per gonad in one season (Korringa 1952).

C. GLOMERATA:

Apparently no direct data exists on the spawning in this oyster. Rainer (1964) deduced from the spat settlement data that in the 1962 - 63 season major spawning activity occurred in late January and mid-March when the mean sea temperatures were higher than 21°C (69.8°F).

C. VIRGINICA:

As most of these oysters often grow in water of considerable depth and are, therefore, never exposed by tide there is a certain uniformity of sexual development and a more regular spawning. Spawning generally occurs at temperatures above 70°F, and although the oyster may spawn at 68°F, or even 59°F, the process is more active between 75° - 85°F. It has been demonstrated that there is no definite temperature level at which spawning is impossible (Korringa 1952). As well, there appears to be a latent period between the critical temperature and the actual release of gonadial products even though the oysters may be morphologically and physiologically ripe. Some workers have suggested that it is possible that temperatures prevailing during the period of gonad maturation determine the temperature at which the first spawning will take place, even though such temperatures may be lower than the ones at which spawning normally occurs. Others claim that there is evidence for the existence of physiological spawning varieties which come into action at different temperature levels. Some oysters have been found to be ripe and yet they did not spawn for considerable time; these oysters could not beinduced to release their products even under laboratory conditions. (Korringa, 1952).

In spawning there appears to be mutual stimulation of both sexes involving two substances - a soluble hormone-like substance, and an active principle associated with protein, diantlin, which exerts its influence on oysters of both sexes in all seasons, and precedes actual spawning (Korringa, 1952).

pH values during spawning of this oyster have been found to range usually from 7.8 to 8.2. Failure to spawn at low tide when water temperature is higher than the critical level, is thought to be due to low alkalinity at this stage of the tide (Roughley, 1933).

The oysters do not feed while spawning.

C. GIGAS:

There is one spawning season a year - when the temperatures are generally around 77°F. Oysters have been observed spawning about 30 - 40 minutes after they became submerged to a depth of one foot by water on flood tide. It is thought by one Japanese worker that the impetus causing the stimulus to spawn is the fresh current of flood tide. (Roughley, 1933).

C. CUCULLATA:

The optimum temperature along the coast of Bombay for spawning is 80° - 87°F, and the optimum density of the water approximately 1.020. (Roughley, 1933).

C. ANGULATA:

Little appears to be known apart from the fact that when salinities as high as 29°/oo - 32°/oo prevail the oyster cannot get rid of its eggs. Under such conditions only 5% of the eggs produced are normal, while the oyster itself suffers and may die. (Korringa, 1952).

PELAGIC LIFE

As yet it has not been possible to determine precisely the duration of this stage in either *C. glomerata* or *C. commercialis* although from comparative studies with other oysters it is believed to last about 2½ - 3 weeks from the time of fertilisation to the settlement. And although the physical development of the larva up to the actual settlement has been easier to follow and the stages are known, there is again conjecture as to the duration of each of these stages.

Very soon after fertilisation the zygote begins to divide into a number of cells without, at first, increasing in size. In a few hours minute hairs, or cilia, develop at one end of this cluster of cells and the embryo can now swim by vibrating the hairs. Its movement, however, is very limited compared to the power of water current.

After a day or two, shells begin to form on either side of the embryo and rapidly grow downwards until the whole animal is covered completely. The shells are united at the hinge, which at this stage is straight, and can be opened or closed "at will". Portion of the ciliated body, the velum, can be protruded beyond the rim so that movement is continued.

It is at this stage that the embryo begins to feed, and with this achievement reaches the status of larva.

Further development is rapid as the larva increases both in size and in specialisation of its organs. When it reaches about 1/150th of an inch in length the shells (as in the case of C. commercialis) begin to grow upwards about the hinge. The left shell grows somewhat more rapidly than the right one creating an asymmetry - a feature characteristic of the oyster larvae.

At the same time, a further locomotor organ is developed - the foot. This cilia-covered organ when protruded from the shell extends and with its tip attaches itself to an object. It then contracts and thus pulls the rest of the animal after it. The main purpose of the foot is to enable the larva to exercise some degree of selectivity once it finds itself on potential substrate.

Other organs to develop include gills, mouth and alimentary tract, and two muscles of which one will be absorbed when the larva becomes attached.

The salient physical features of the larva, then, are the velum and the foot both of which are important in the final selection of a suitable substrate provided, of course, that the larva is in the first place carried by the water current to a location where suitable materials for attachment are present.

At the end of the larval period the larva must attach itself to a solid substrate or die. Some workers consider this critical period to be 2 days. The attachment is by the left valve and the spat, as the larva is now called, will remain in that place for the rest of its natural life. Its free existence is finally terminated with the loss of the now redundant velum and foot.

C. COMMERCIALIS:

Roughley (1933) observed, in field, that the sizes of free-swimming stages range from 0.05 - 0.06mm and up to 0.229mm when the eggs are first released to approximately 330/u when the larvae are fully grown. At attachment, larva is approximately 1/75th of an inch long. The interim sizes in the stages development are 175/u when the umbo is developed, and 230/u when the foot is first seen to protrude in the smallest of specimens. The length-depth ratio of the larva is that up to 300/u the length is equal to the depth, and after 300/u the depth is greater than the length.

Four interesting experiments are described by Roughley in the same paper - the effect of water density on the embryonic development, the effect of water temperature on the same, the rate of growth of the embryo, and the rate of movement of the embryo. In the first experiment, on the water density, Roughley found that the rate of development decreased with the lowering in water density. Thus in density of 1.021 free-swimming stage was reached in 8 hours, in 1.005 in 9 hours, in 1.011 in 10¼ hours, while in 1.005 at the end of 21 hours only 50% of the eggs were observed to be fertilised and in these very little development had taken place. No free stage was developed in the last case.

The experiment on the effect of temperature demonstrated that in a sample with the initial temperature of 77°F and the mean temperature calculated at 78°F free swimming stage was reached in 6 hours, while in the one with the initial temperature of 64°F and the mean temperature at 62°F the same stage was reached in 22 hours. Density of the water in both cases was 1.016.

The study of the rate of growth of the embryo was initiated with fertilisation at water temperature of 70°F and density of 1.021. Seven hours later, a small percentage of free-swimming embryos was seen on or near the bottom of the beaker. At 8 hours, a number of embryos were observed at the surface. A quarter of an hour later numerous white columns of embryos were seen extending from the surface of the water downwards. This, Roughley observed to be characteristic of the embryonic stage of the oyster - "the embryos are continually swimming from the bottom to the surface, where they remain for some time attached to the surface film, before making their way again to the bottom." At 9 hours, the great bulk of the embryos were free swimming. 34 hours after fertilisation, the first embryos completely covered with shells and with a straight hinge were seen; the average measurements of 20 larvae at this stage were 67/u in length, 53/u in depth, and 45/u in hinge length.

The rate of movement was studied under miscroscope, the criterion used being the length of time it took the embryos to swim the full length of the micrometer scale (1/31st of an inch). On this basis it was calculated that at 24 hours embryos averaged : 39"/hour, at 30 hours 58"/hour, and at 69 hours 46"/hour.

In nature, however, it is presumed that the vitality and activity of the embryos would be greater since such conditions as aeration, etc., would be better.

It should be borne in mind that most of the information known on the larval development and behaviour in this oyster has come from experimental work and relatively little from direct observation in field. Therefore, data from the experimental findings should be accepted only as the approximate of that in nature, since in nature there are likely to be influences of which a worker may not be aware, which he therefore cannot duplicate in his controlled observations, and which therefore influence the end result of his observations.

Roughley believed that the younger larvae move continually from the bottom to the surface of the water and as they get older they tend less and less to come to the surface. This was evident from the fact that surface catches of older larvae decreased in proportion to their size, and by the fact fully developed larvae and those approaching full development were more abundant near the bottom than at the surface. This would probably be partially explained by the development of the photo sensitive pallial eye and the resultant negative photo-taxis exhibited by the larvae.

The vertical movement of the larvae is in opposition to the horizontal movement caused by the water currents which carry the animals back and forwards, so that the eventual position of the larvae at settling may be at quite a distance from the parental beds. The action of water current in such case explained why Roughley found predominance of larvae "in situations where the currents, by the contour of the land, form eddies."

Vertical distribution of the larvae was also observed; indirectly, by Dew and Wood (1955) during their study of periodicity of fouling organisms in Sydney Harbour. They found that lamellibranch larvae, chief of which were <u>C. commercialis</u>, preponderated in the plankton tows taken in a series of 24-hour periods at 2-hour intervals starting from October, and that there were three daily peaks occurring between the hours of 9-11 a.m., 1-5 p.m., and 1-5 a.m. There was some irregularity of time which did not correspond with tide, and when they tested the relationship of plankton catches to the time of day, the results further confirmed the significance of this ratio to that of plankton catch and state of tide. The authors suggest that insolation cannot be the cause of the irregularity in plankton catches since one of the major peaks occurred during the day.

C. glomerata:

From two groups of serial plankton samples taken over 24-hour periods at Whakapirau, Rainer (1964) has managed to group larvae into 4 size groups - early umbo 85-160/u; late umbo 160-245/u; mature larvae 245-300/u; and eyed larvae 300+/u. Larvae below the length of 85/u were not retained by the relatively coarse sampling equipment.

Rainer finds the numbers of larvae to show large variations associated with tidal cycle. Highest concentration is found near high water, with a smaller maximum, chiefly of eyed larvae, near the low water. Little, if any correlation is seen with the current speed. These variations appear consistently in all size groups including the eyed larvae.

At night there is little difference in the vertical distribution of the mean numbers of mature and eyed larvae per sample at any depth, but in the day time eyed larvae show tendency to aggregate at the lower levels. The numbers of samples at lower levels are, however, small. Such distribution, however, may not be directly related only to the absolute light intensity.

Turbidity, also, appears to influence the distribution as seen by the concentration of larvae near the bottom during the high light intensity of the day and low turbidity at high tide, while at low sun and higher turbidity, and also at the high tide, larvae are closer to the surface. Equivalent samples at high tide at night show regular distribution from top to bottom.

There appears to be no evidence that larvae cease to swim above the current speed of 15 cm/sec.

C. virginica:

The development has been observed to be most successful around the water temperatures of 70°F.

Under experimental conditions when water temperatures were 80°F, free swimming stage was reached in 4 - 5 hours after fertilisation. By following the growth and development of the oyster larvae in the plankton, one Canadian worker has estimated pelagic lift to last 30 days at temperature of 18°C (64.6°F), 26 days at 20°C (68°F), and 24 days at 21°C (69.8°F) (Korringa, 1952).

This apparently is longer than is usually recorded for U.S. waters where larvae settle at a smaller size than in Canadian waters, but no figures are given.

The size of the egg is on average 0.05mm. The embryo becomes fully covered with shell 24 - 36 hours after fertilisation when its length is 0.06mm. Umbo begins to show prominently at the larval length of 172/u, and the fully grown larvae is 386/u on the average. At all stages its length exceeds its depth.

Under experimental conditions the eggs have been found to develop at salinities 15°/oo - 29°/oo.

Some workers have found no relation between the vertical distribution of larvae and the tidal cycle, nor any evidence that larvae in advanced stages of development are more common near the bottom during periods of rapid tidal flow, and are as a result widely dispersed by the tidal currents. However, when there are considerable differences in salinity and current velocity at short distances in both vertical and horizontal directions when larvae, at all stages, do not flow past a given point uniformly distributed, but are very unevenly distributed both in vertical and horizontal direction. (Korringa, 1952).

One worker considers that when the larvae begin feeding they are probably selective in their food, and in the absence of proper quality and quantity of the food in plankton may perish before reaching metamorphosis.

C. gigas:

Optimum water temperatures for the larval development have been found to be 73°- 79°F and the optiumum density 1.017 - 1.021 (Roughley, 1933). Salinities in some commercial areas vary from 30°/oo - 32°/oo in summer.

Under experimental conditions, larval life has been observed to last 23 days at temperatures fluctuating between 73° and 90°F and density approximately 1.019 - 1.021. Under natural conditions the rate of development is probably considerably faster. (Roughley, 1933).

The size of the egg is on average 0.05mm.

The shell is completely developed at 3 - 4 days when the length of the embryo is 0.06mm, the depth 0.07mm, and the hinge length 0.04mm. Umbo begins to show prominently at the larval length of 172/u. In length-depth ratio, the length is greater than depth up to 100/u, and the depth is greater than length from 100/u to 280/u. Larva is fully grown at the length of 280n. (Roughley, 1933).

Successful larval development has been found to coincide with the occurrence of large numbers of Monas (Korringa, 1952).

Fig. 5. Two year old specimens of C. glomerata which had settled too heavily on the limited surface.

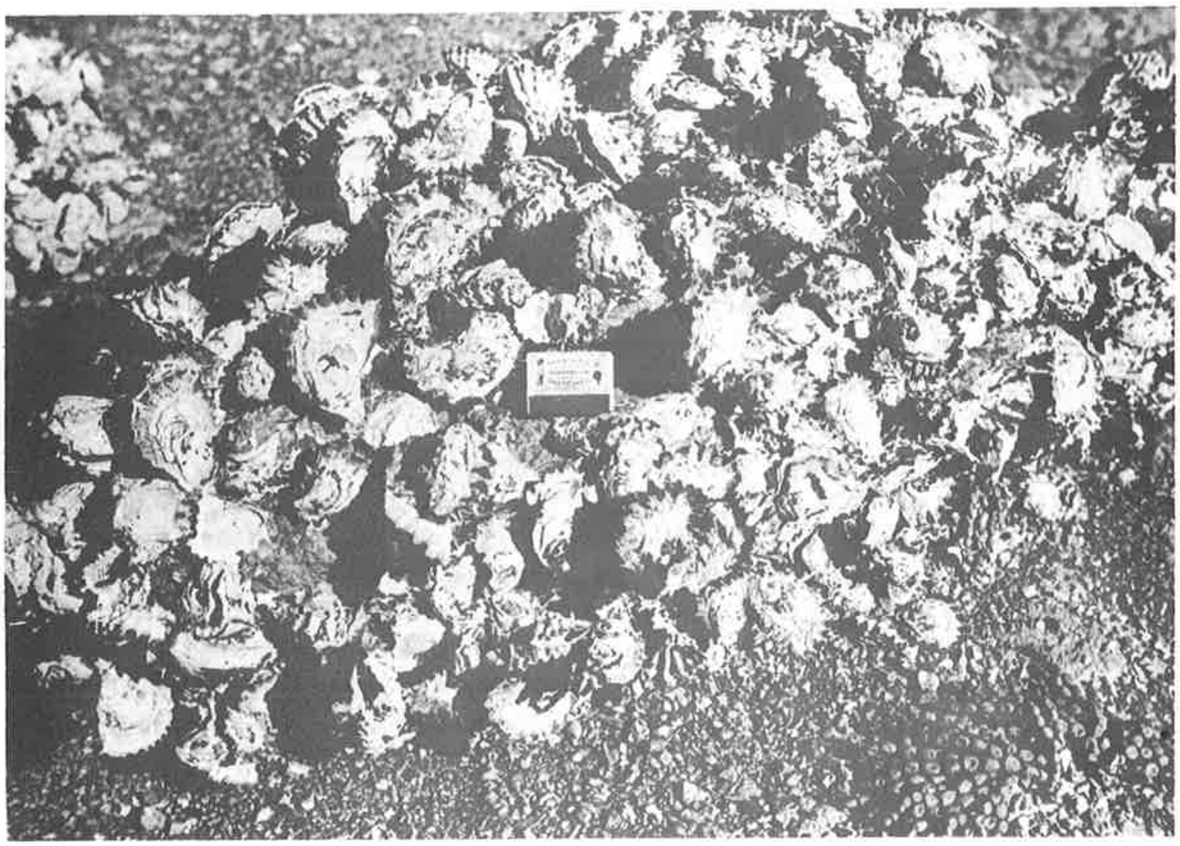


Fig. 6. Ideal fixing of oysters. (C. glomerata)

SETTLEMENT

Towards the end of its pelagic phase the larva is ready to settle. It is equipped with organs sensitive to light and gravity and with two locomotor organs (velum and foot) by means of which it selects, in a limited way, the most suitable place for permanent attachment. It swims around until it comes into contact with a potential substrate when it withdraws its velum and creeps about with its foot, exploring. The larva may repeat this process several times before it finally attaches itself. The attachment is by the deeper, or left valve, and once this is accomplished the larva is called spat.

Factors influencing the choice of place for settlement are varied - there is the isolation, the current speed, the type of surface and the cleanliness of it. Oyster larvae prefer a clean surface, but also a surface on which there is a certain amount of growth of bacteria, diatoms, and hydroids. Another factor is the gregariousness, demonstrated by the ready settlement of larvae to surfaces to which others are already attached.

Once the larva becomes attached, its velum and foot are no longer needed so that they both degenerate and are absorbed. The spat begins to grow rapidly in close contact with the surface and soon assumes adult characteristics in the development of both the shell and internal anatomy.

C. commercialis

Influences on the Selectivity of Attachment Place:

Roughley (1933) observed that larvae seek to find attachment on the under surfaces of objects in water or in the local depressions of the upper surfaces where there is more chance of surviving the abrasive action of the tides and currents. This choice of under surface is governed by the fact that sedimentation and large fluctuations in heat are considerably reduced in such positions. Both of these factors appear to cause spat mortality on the upper surfaces in the tidal zone. Roughley considers that great numbers of larvae possibly first alight on the upper surface, but that they tend to crawl underneath. Another cause for such preference could be the negative photo-taxis exhibited by the larvae in its mature stage. This is the result of the development of the pallial eye which has been demonstrated to be sensitive to light. Since the eye develops within 24 hours of attachment it is reasonable to expect that it influences greatly the setting during daytime hours.

Thomson (1950) reported on a study on the orientation of culch material in relation to spat and in the above paper discusses its application to the effects of illumination, orientation and force of the current, time of immersion of culch, silt and slime, and predation. As culch he used a series of fibro-cement slats arranged one above another. Results show that:

- A greater number of oysters settles on the slats less than ½" apart than when the slats are 1" apart. As well, in the former case, spat are evenly distributed about the surface, while in the latter case spat are clustered in the centre of the slats.
- Catch is greater when the slats are ½" apart and their longitudinal axis is parallel to the water current than when the slats are further apart and their axis is at right angles to the current. This is probably explained by the fact that when the slats are parallel to the current they provide more opposition to the flow of water.
- While the number of spat is greatest on the horizontal portion of a broad surface, the spat are more evenly distributed on the vertical position. For cultivation purposes, therefore, broad slats arranged vertically in the water would ensure best catch.
- The evidence of negative phototropism is provided by the fact that the numbers of spat are greatest on the under surfaces of the slats, next on the vertical, and finally on the upper surfaces. Spat numbers on the vertical and upper surfaces decrease in numbers toward the source of illumination. As well, there is more spat when the distance between the slats is reduced to less than ½" and therefore the amount of light is less.
- Larvae require relatively slack water for setting. This is seen from the greater numbers of spat in the central area of closely packet slats - an area where normally relatively little disturbance occurs both horizontally and vertically.

- Silt and slime prevent larvae from setting on the affected surfaces, and these are usually upper surfaces. Slime could be regarded as a secondary effect of light since the growth of the photosynthetic algae is encouraged by the light. The time, or the length, of the immersion of culch, therefore, is one of the critical aspects of oyster cultivation. Predation by other animals e.g. fish, is lessened if the slats are bundled closely.

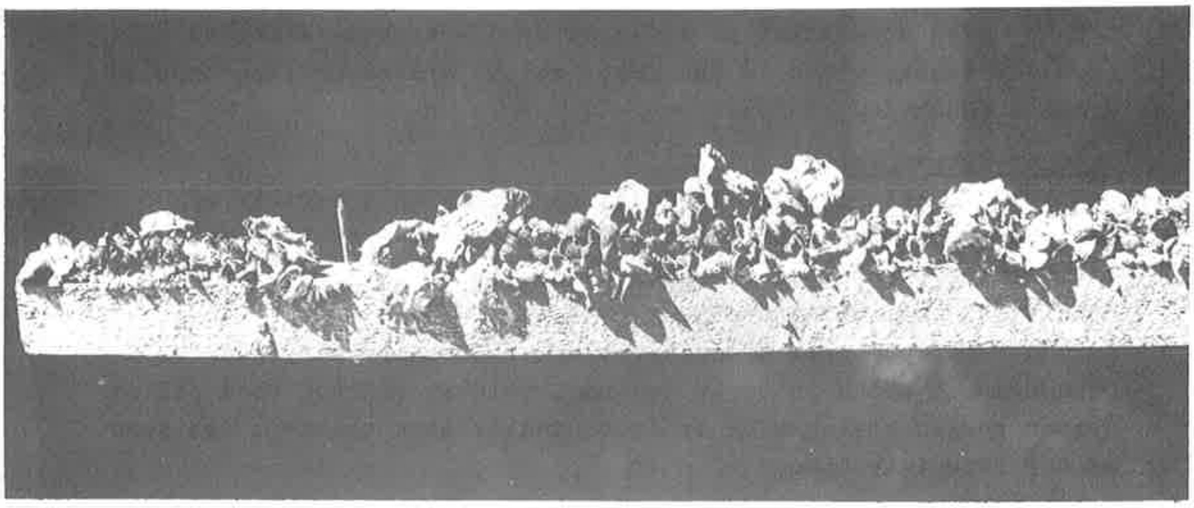


Fig. 7. Oysters and competitors grown from spat caught on the under side of stakes (which have been turned over for photographing).
Kaipara Harbour

Angle of Attachment:

In measuring the angle of attachment with goniometer eye-piece Roughley (1933) states "the medium line of spat, i.e. the line of apposition of the right and left valves, lies at an angle varying from 27 to 32 degrees, while the angle of the upper surface of the right valve lies at an angle of about 56 degrees".

Attachment:

The attachment is effected by a substance secreted from the byssus gland in the foot, which hardens in less than 10 minutes (Roughley, 1933).

Type of Substrate:

In nature, spat is found to settle on a variety of substrates ranging from rocks to shells of dead or live molluscs to mangrove plant roots, provided that other environmental conditions are satisfactory.

For purposes of cultivation, when uniformity and cheapness of culch is to be desired, sticks, treated wood paling oyster shells string wire or loose inside wire netting, are some of the materials used.

General:

Saville-Kent (1893) noted that an abundant fall of spat commonly follows after an advent of flood - that freshwater apparently acts as a pronounced stimulus in such case. There appears to be no more recent comment on this factor.

C. GLOMERATA

Selectivity of attachment place:

Rainer's (1964) findings suggest that in Kaipara there is a considerable vertical range, with no apparent direct relationship between the numbers of spat and shore height or maximum concentration of shore oysters.

More spat are found on the under-surfaces than on the upper, with the numbers on the under surfaces averaging 6.8 times more spat than those on the upper. This is especially evident when upper and lower horizontal surfaces are compared (See fig.7) but it is also present on the upper and lower obligue surfaces. Differences in an experiment cannot be attributed entirely to the silting. In an experiment on attachment to fouled surfaces, settlement was found to be greater on minimally - fouled culch although, apparently, it will occur on fouled culch when all other available surfaces are thickly covered with spat.

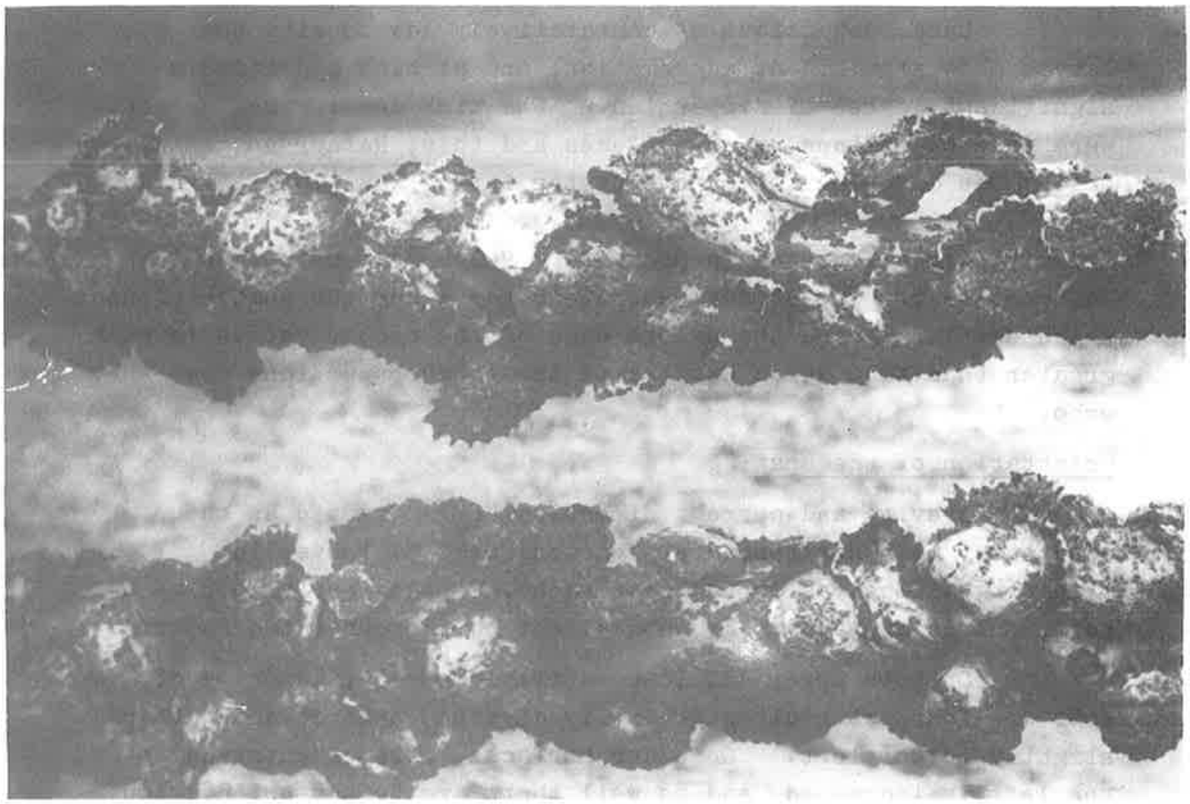


Fig.8. Auckland rock oysters growing naturally on horizontal wooden posts, Parua Bay.

Under conditions of comparatively low density the larvae show significant aggregation, and at high densities a significant degree of dispersion. The high density measurements were made on oblique under-surfaces and this, Rainer suggests, may be why the distribution of the oyster larvae was close to randomness.

Gregariousness is present. Rainer suggests that the "attractive principle" may be protein based for the number of spat which settles around the smooth edge of the oyster valves is much greater than that which settles on the rougher portions near the umbo.

Orientation of the spat:

Gravity and current direction are suggested as the apparently main environmental features used by larvae in orienting themselves during settlement. Light may also play a part, but it appears to be subservient to the other two factors.

On both upper and lower surfaces at 45^o, majority of spat are found with umbos generally directed upwards and perhaps slightly to the left. On under surfaces, this orientation to the left is increased, and as well there are "other orientation peaks along the axis of the angle (90^o and 270^o) and directly downwards (180^o)" (Rainer, 1964).

Type of Substrate:

As in Australia, a wide variety of materials have been tried : sandstone rock, concrete and spauls, iron rods and bars, pumice concrete posts, concrete slabs with blue metal chips, treated and tarred pine sticks. Pumice concrete posts have been found very good for the growth of oysters, but tannalised pine battens easiest to handle and more economical.

C. VIRGINICA:

Setting is by far the heaviest near the bottom and more so when depth is 5 to 10 feet rather than 30 feet or more. This is considered to be due probably to the greatly reduced speed of current near the bottom.

SEXUAL MATURATION AND DIFFERENTATION

Spat grows rapidly into an adult, its internal organs progressively developing and assuming the characteristics and functions of the adult oyster. One exception to this parallel development is that of the reproduction system which "awaits the onset of sexual maturity, usually about the first year, before beginning to take shape" (Yonge, 1960).

When the reproductive system is formed eventually, it is found that all the species so far investigated are protandric hermaphrodites i.e. the initial sexual phase is male although the oyster as it matures further, can change its sex at different seasons with the change occurring from male to female or vice versa. This appears to be largely dependent on the environmental conditions, e.g. the availability of food, because under optimal conditions this phase can be completely suppressed. It is considered that the metabolic activity of the oyster may be associated with the development of the gonad, for the higher metabolic rate made possible by good feeding appears to favour development of ovaries, and conversely, lower metabolism appears to be associated with male condition. The production of sperm, therefore, is less demanding on the animal than is the production of eggs where the yolk is needed to supply the needs of early development in embryo. The oyster, therefore, is capable earlier of coping with the development of sperm than with the development of eggs.

At the same time, however, the "primary gonad of the oyster is bisexual, with one sex usually predominating over the other after a juvenile hermaphrodite phase. This dominance is not always complete, however, and functional hermaphrodites are occasionally found" (Rainer, 1964).

In <u>Crassostrea</u> spp., the sexual phase is generally established at the beginning of the breeding season and usually remains stable for the duration of that season. At the completion of the current spawning season the sexual products which have remained in the gonad are absorbed and the organ then functions to produce nutritive tissue in preparation for the eventual development of the sex products in the next season.

When the gonad is fully differentiated and developed just before the spawning and the gonadial products are almost ready for release, the gonad is very swollen and the oyster normally fills the entire shell cavity. It is at this stage that it is regarded as being in "good condition" for the market.

Under suitable environmental conditions, the ripe ova and sperm are extruded through the gonoducts and into the exhalant chamber of the oyster from where they are released to the outside. The oyster is then said to spawn.

C. Commercialis

Following many years' work on this oyster when he noticed that females usually predominated in the samples, Roughley (1933) made a special examination of 3,000 oysters to determine the ratio of females to males. The oysters were picked and examined during the months of January and February, 1927. The resulting ratio averaged 73% females to 27% males. AS well, Roughley found that very young oysters were usually males - a feature which pointed to sex change. He followed this with an examination of a further sample of 100 oysters taken from 5 different localities, and whose age was estimated to be no more than 14 months. 77 out of these proved to be males. This last lot of oysters were examined at the beginning of February. During the following month, Roughley received and examined further batches and found a small percentage functioning as females, which indicated that the oysters may have spawned as males and had now begun to develop ova. A detailed miscroscopic examination of five specimens containing both ova and sperm suggested that the development of sperm either precedes the development of ova, or that the two are developed concurrently.

These findings rejected the view held to date, that the sexes in this oyster are separate and that an oyster is either male or female throughout its life. However, at the time there was no evidence whether sex change occurs from females to males, or if some oysters do not change sex at all. As far as it is known this is still an intangible point.

Roughley also attempted to test the idea held by some workers on other species of Crassostrea that there is a tendency to femaleness with favourable nutritional conditions. He examined some oysters, including some of considerable age, from areas known to be very adverse for oyster development and presumed to be nutritionally very poor and, instead of finding males predominating as was expected, found females still outnumbering the males greatly.

It is of interest to note that Seville-Kent (1890) wrote of finding fully developed ova and sperm in oysters of approximately ½" diameter and whose age he estimated to be not more than 3-4 months.

C. GLOMERATA

There appears to be evidence for differential maturation rate with the males tending to differentiate earlier in the season than the females. Rainer (1964) considers that the best explanation for this is the increasing tendency to femaleness with increasing age. Thus, although the gonad may be present in the oyster's first summer its smears do not show presence of any mature sex elements, but in the second summer, or even later in slow-growing oysters, sperm appear in the gonad which is as yet comparatively poorly developed. It appears that most males show signs of a mature gonad at the flesh weight of 0.2 - 0.4 gm. Females, on the other hand, do not normally appear in the intertidal populations below a fleshweight of 2.5 - 3.0 gm. Their age at this time is approximated at 2 years.

Generally, there is a preponderance of males in the smaller size groups in all samples at various shore levels, the numbers of males decreasing with the increasing size. The relationship of weight to sex is evident also in older age groups, when the females tend to be larger within an age class.

Rainer found evidence of the better nutritive conditions required by females for maturation in that females at low levels tend to mature faster than those at high levels, presumably because they experience increased feeding times. Subtidally growing oysters may even develop directly into females in their second summer as seen from the examination of 43 spat out of which 22 were undifferentiated, 19 were males, and 2 were females. Their mean flesh weight was 0.3, 0.6 and 0.62 gm, respectively.

Hermaphodrites, apparently functional, were found but only either well before the breeding season or among oysters in which the sexual differentiation was accelerated in winter by heating at 30°C (86°F) for 6 weeks. Most of the hermaphrodites in nature, were found at about the level of 3 metres above the datum in mid-November, and one was also found in September at about 2 metres However, Rainer considers that since they were functional hermaphrodites their presence indicates more the unstable nature of the sex determining mechanisms of the oyster than a relationship to the time of the year at which sex is determined.

Using gonad smear technique, Rainer suggests that immediately after spawning, dedifferentiation occurs. It is a rapid process exemplified by the fact that approximately 4 weeks after the main 1962-63 spawning, when the water was still at a mean temperature of 23oC (73.4°F), 3 out of 57 oysters from the 3m level gave no indication of sex. A period of unknown duration follows, and then redifferentiation occurs, more rapidly at the low levels than at high - in a sample of 94 oysters taken from the level of 1.3m in early May (approximately three and a half months from the main spawning) more than a quarter had apparently mature gametes with approximately equal numbers of both sexes.

Rate of differentiation of sexes in relation to shore heights is also present, that of females being much slower at higher levels than that of males. Thus by about the middle of August at the levels of 3m, half of the sample of 26 oysters were found to have differentiated, all of them as males. By middle of November, with the mean temperature c.a. 18°C (64.4°F), differentiation was complete at all levels and at all sizes. The next two months or so were spent in the elaboration of the gonadial products before the spawning.

C. VIRGINICA

Sex change in adult oysters tends to occur late in October and in winter, shortly after the spawning season and after intensive proliferation of the connective tissues when it is difficult to distinguish males from females. The gonad may then mature with the rise in water temperatures in spring. However, under experimental conditions, an apparently normal development of gonad is found to proceed in the winter season if the temperature of water is raised, and even if little food is given. In the case of raising water temperatures, one worker has found that only about half the males and a third of the females could be induced to spawn without the additional influence of a chemical stimulus - a sperm in the case of females, and sperm and ova in the case of males (Yonge, 1960). However, in one set of experiments when the temperature was used as the experimental stimulus, in oysters placed in water at 15°C (59°F) sperm were found in the gonads after 15-20 days, and after 30 days some of the females were found to contain fertilisable eggs; spawning could be induced after 35 days. Similarly, at temperatures of 20°C (68°F) and 25°C (77°F) sperm were found after 10 and 5 days respectively, and fertilisable ova after 15 and 9 days respectively. Oysters brought from the dormant winter stage into water of 30°C (86°F) developed ripe sperm in 3 days and some fertilisable eggs in 5 days. (Korringa, 1952).

This temperature factor, therefore, is probably one of the main reasons for the variety of maturation and spawning time experienced by the species. In southern districts of U.S. features of both sexes have been found in very young and still immature specimens. For instance, in the warm waters of Louisiana one worker has found among 10 oysters under 28 days old 2 mature females and 4 mature males, the smallest mature female measuring only 9.0 x 7.5 mm. (Korringa, 1952).

Considerable delay has also been found to occur in the maturation of the gonad due to tissue starvation in oysters living under conditions of seriously depressed salinity.

There is evidence of inter-related controlling factors which determine the total number of the eggs and larvae to be produced in any one season. These factors include the type or the combinations of stimuli required before the spawning is to proceed, the reversal of sex (although one sexual phase often persists for a number of years), the numbers of breeding oysters and the related nutritional conditions. Another feature noticed is the thickness of the gonadial tissue which varies not only from year to year but also from place to place. In the latter case, the thickness appears to be influenced by the depth at which the oyster lives, as exemplified by the difference in oysters living at the depth of 10 feet in which the gonadial tissue is almost twice that of oysters living at 30 feet. (Korringa, 1952).

Reversal of sex from female to male in specimens of various ages has been found by one worker to be 12.8%. (Rainer, 1964).

C. GIGAS

An abundance of food appears to tend towards the development of a preponderance of females, while a lack of food tends towards the development of males. This theory has been derived from the observation of this species on both good and poor fattening grounds. Oysters used were in one-winter and two-winter batches. In the one-winter batch from the poor grounds, ratio of females to males was 100 : 116, and in two-winter 100 : 155. In those from the good grounds, the same ratio in the one-winter batch was 100 : 95, and in two-winter 100 : 73. The worker concluded that there was correlation between the sex ratio and the amount of food available.

The same worker in 1929 studied the sex change in oysters passing from one-winter to two-winter stage. In the one-winter group there were more females than males. Only 24% of the total number of oysters had changed sex, but sex change had occurred both from males to females and vice versa. The worker concluded that it is probable that at the beginning of every new spawning season, the sex differentiates independently of the sex of the preceding season, and that protandry does not occur (Roughley, 1933).

C. CUCULLATA

In one study, a worker found that among the normally healthy oysters 56% were females, 41% males, and 3% hermaphrodite.

However, among the oysters infested with the pea-crab (Pinnotheres) only 10% were females while 83% were males and 7% hermaphrodite. He suggests that the sex change in the oyster is influenced by the infestation of the pea-crab and is the result of either the reduction of food supply of oyster, or the change in the affected oyster's metabolism. (Roughley, 1933).

PARASITES : DISEASES

This section is taken entirely from the studies of C. commercialis which at times has been attacked by such diseases as "Winter Mortality" and pests like mudworm. These have subjected the Australian oyster industry to threats of considerable depletion - a factor responsible for their study. In New Zealand, oyster cultivation has to date been only on a comparatively small scale and these problems have apparently not yet been encountered. However, on several occasions mortality of the Auckland oysters without an apparent cause had been noticed, and it is quite possible that these diseases and some of the parasites do infest this oyster, but that as yet they have not been identified.

The direct consequence of many parasites and diseases is not yet established although it is fairly certain that they at least lower the resistance of oyster to further infections or changes in the environmental effects, and it is supposed that some may actually be lethal.

WINTER MORTALITY

A disease causing serious losses to the oyster industry in New South Wales, it is found to occur in oysters grown by any of the usual methods of cultivation. Most of the information on this has come from a paper by Roughley (1926) in which he studied an outbreak on oyster beds on George's River in 1924-25.

Causes:

The actual cause has not yet been determined, but in the incidence described by Roughley was suggested to be probably due to a combination of factors including water and air temperature changes, quantity and type of food, plankton, algae, "slime" (Echinocarpus, probably E. sordidus), and parasites, perhaps, the whole process having been initiated by the low winter temperatures which lowered the resistance of the oysters to the extent that any subsequent infection by bacteria was facilitated. (Roughley, 1926).

Symptoms:

In the above incidence, ulceration was noticed on labial palps, gills, and inner surfaces of the mantle, in the gonads, liver, stomach and muscle. In fact, there appeared to be a fairly definite ratio of ulceration to mortality.

Means of spreading:

Probably by water, although Kesteven (1941) observes that since a considerable number of parasites have at times been found in oysters on the eastern coast of Australia, it is possible that they are directly responsible either for the actual disease or for the lowering of resistance on part of oysters. Roughley (1926) however, believed the occurrence of winter mortality to be a normal annual event, with only the intensity of it varying from year to year, and from place to place.

Control:

Roughley (1926) suggested raising the oysters in wire-netting trays during the months from June to September so that at least some, if not all oysters so treated may be saved.

Kesteven (1941) recommends cleanliness and efficiency in cultivation as the best combat measures.

General:

By 1941 when Kesteven published his paper on the economic aspect of oyster cultivation, nothing more was known of this disease. No more recent publications on the topic have been sighted.

POLYDORA CILIATA

It appears that the effects of the infection by this parasite first became known in New South Wales in 1870, when so many oysters were destroyed that it forced the cultivation to foreshores where the infection could be controlled. Prior to this date, cultivation was carried out on shelly or gravally bottom never bared by tide. Gradually the worm spread from river to river until by 1925 (Roughley, 1933) few rivers were sufficiently free from it to allow cultivation below low tide level.

The cultivation on Georges River was the first to be seriously affected. In 1889, mud worm increased with such alarming rapidity that for the whole of that year only 4 bags of oysters were marketed. Yet the disease was first recorded in the area only in the previous year, 1888, when a total of 138 bags were marketed.

Distribution:

From half tide level to moderately deep water, though chiefly on mud flats about the low water mark. Whitelegge (1890) found the oysters lying loose or partially buried in mud to be particularly attacked while the oysters somewhat raised above the mud and attached to a solid substrate were comparatively free.

Means of Entry:

Worm larvae are swept in with the water and attach themselves to the shell by the head. They do not burrow into the shell (Whitelegge, 1890).

Means of Attack:

Whitelegge notes that only larvae attack the oysters - adults do not even attempt to enter the shell. Larva attaches itself to either valve, and especially near the margins in the anterior part of the animal where it is in close proximity to the inhalant or food current of the oyster. It immediately starts constructing a tube, at the rate of $\frac{1}{4}$" per hour, through which it collects a large quantity of mud and thus forms a soft blister on the shell.

Yonge (1960) states that the worm gives an appearance of seeking a crevice and backing into it and at the same time enlarging it, possibly by a combination of chemical attacks on calcium carbonate by acid and mechanical scraping by the hard bristles.

Effect on Oyster:

If the oyster is healthy, it immediately and rapidly lays down a thin layer of shelly matter, sealing off the worm and its patch of mud. However, if the oyster is unhealthy, the deposition of shelly matter is very slow, and the worm can accumulate mud and grow more quickly than it is covered. In such cases, the infection may so spread that eventually it fills up the whole of either valve so that there is no room left for the oyster.

The death of the oyster is brought about chiefly by the decomposition of mud after the death of the worm. Also the diseased oyster becomes so sensitive to any disturbance that it can keep its shell open for only short times and the quantity of food it receives during these times is inadequate. To aggravate this further, any food that is swept in may be further greatly diminished if 20-30 worms have access to the water current. Yonge (1960), however, states that while the precise mode of feeding in the worms is not known, in no case is parasitism involved or probably even any competition for the same food.

Control:

2 methods are suggested:

(a) Placing infected oysters in fresh water. This kills the worm and also some oysters, probably because of the putrescent germs developing in the mud after the worms die.

(b) Keeping oysters out of water for 2 weeks then placing them in salt water for several days. This appears to destroy the worms and leave the oysters in a healthy condition.

General:

The New South Wales Commission of Fisheries, in their Annual Report for 1898 recorded that long dry weather appears to facilitate greatly the increase of the disease. It is also suggested that the death of the oyster is due to exhaustion resulting from the repeated laying down of the shelly matter over the numbers of worm that keep on entering the oyster. This disease proved such a nuisance to the State, that it was even suggested a Bill be introduced compelling lessees to keep their oyster beds free of the worm.

Yonge considers the Australian species of the worm to be P. websteri, the same species that is found on Atlantic and Pacific coasts of North America.

BUCHEPHALUS:

Occurrence:

A parasitic trematode found in the gonads of C.commercialis as cercaria of Gasterostomum on five occasions (Roughley, 1933). No species is given, but it is mentioned that in Europe, according to one European worker, G.gracilescens develops cercaria known as B. haimeanus in the digestive diverticula and genital organs of Ostrea, Cardium, Tapes, etc.

Symptoms:

Gonads of the host contain either no sexual products or only a few degenerating eggs.

Life History:

In Europe, cercaria larvae leave these molluscs and infect fish such as haddock, whiting, cod, etc., where they encyst in the intestine, and emerge as larvae which grows into the adult Gasterostomum when the host fish is eaten by angler fish.

Incidence:

In Europe the ravages of the worm are inconsiderable. Infection has been reported in C. virginica as about 1% and Roughley (1933) states that it is apparently far less common in the Australian oyster.

Intermediate Hosts:

Intermediate and final fish hosts in Australia are not known.

Leptoplana australis - The Wafer.

"The turbellarian worm .... is thought to cause much damage to oyster life, but in what manner it kills the oyster has not been definitely determined. It is commonly found feeding on the meats of recently dead oysters, and is of course blamed for their death, but it is difficult to see how entrance can be gained inside a live oyster. However, its frequent association with dead oysters places it under grave suspicion, and it is, therefore, destroyed whenever found". (Roughley, 1925).

PREDATORS

The oyster spends only a minimal part of its life free in water, and yet it is this stage that forms it most hazardous period. Physical environmental factors such as wind, water currents, temperature, availability of settlement surfaces, influence the dispersion and fertilisation of the sex products and the dispersion and settlement of larvae. At the same time, some of the animals which contribute to the ecological environment of the adult oyster become predators on its progeny already at this stage and continue to pester it well into its adulthood.

As the oyster grows it becomes subjected to an increasingly greater variety of predators so that in the end its feeding, growth and reproduction are influenced in some malevolent way by representatives of almost all the classes of the animal kingdom.

All the predators described are derived from literature on Crassostrea commercialis, with the exception of Lepsiella scobina which attacks C. glomerata.

Bird Pests:

Very little published material exists relating to the feeding habits of birds and the destruction of oyster population - Saville-Kent (1893) mentions the oyster catcher Haemotopus longirostris and some cranes as being predators of the Australian oyster.

Fish Pests:

Roughley (1925) reports the damage done by these fish pests to be considerable, with the only means of protection afforded to the oyster cultivation being to fence off the leases with stakes or wire netting.

Mullet: (Mugil, spp.)

Owing to the feeble development of its teeth, mullet is capable of attacking oysters only when they are still soft-bodied creatures of microscopic size, and does so by straining the eggs and larvae out of the water.

Common toadfish or toado (Spherioides hamiltoni):

Considered as the greatest of fish pests, these fish have teeth modified into a kind of beak resembling that of a parrot and with which they can crush the shellfish.

Bream (Sparus australis):

The bream uses 2 sets of teeth to get at its prey - a set of canines with which it wrenches the oyster from its attachment, and a set of molars adapted to crushing the shells.

Stead (1930) notes that the common black bream is considered to be the "archdestroyer" of oyster spat in its first and second years.

Eagle ray (Myliobatis australis):

This is generally reported to be one of the worst enemies of the adult oyster. Provided with two plates of teeth, it can crush oysters of 2" or more in circumference.

Crabs

The Australian oyster grower "frequently suffers much loss from the onslaughts of the mangrove crab (Scylla serrata), a large species, deep greenish brown in colour, which may attain a width of two feet overall. The oysters are crushed between the powerful nippers, most of the damage being done at night. While the young oysters suffer most at the hands of this crab, fully grown specimens are by no means immune, particularly if their growth has been rapid and their shells not very thick and hard. The visits of the crab are periodical, and if concentrated in considerable numbers, a whole bed of oysters may be destroyed in a few days. The only remedy so far devised is to improvise fences to keep them off the leases" (Roughley, 1925).

Starfish:

These usually confine their activities to more mature oysters, and generally to those near ocean estuaries or during times of high water density.

Method of Attack:

In a recent article by Croft (1964), it is stated that a starfish excretes a poison in front of the inhalant syphon of the oyster causing the oyster's muscular control to weaken and the valves to gape. This follows the theory of the Japanese workers who claim that a substance formed in the stomach of the starfish and introduced with the inhalant current into the mantle cavity of the oyster, causes muscle paralysis and consequent gaping of valves. However, others claim that the starfish wraps itself round the oyster and with its numerous tube feet exerts a series of sudden pulls on the valves. This causes the muscle to weaken so that the valves can be pulled further apart, and the predator's stomach protruded into the shell.

Starfish can eat 20 - 25 oyster spat or 2 - 3 large oysters a day.

Though these pests are destructive in Australian waters, it appears they are not nearly so bad as in oyster beds in America where, for instance in Long Island Sound, damage, including the cost of remedies, has exceeded one million dollars in a single year (Yonge, 1960). An able account of the study done in this field up to early 1950 is provided by Korringa (1952).

Distribution:

Preventative measures lie in the determination of the distribution and hydrological optima of the pest. For instance, studies on the effects of reduced salinities on Asterias forbesi, the American starfish, indicate that this animal occurs normally in waters with salinities of 18°/oo - 32°/oo. While it can endure very low salinities for a few hours, salinities under 18°/oo have in the long run injurious effects on the starfish, with the lower the salinity the shorter the tolerance period.

Another aspect studied is the critical distance between a starfish and its potential prey. Some workers claim that a starfish can detect and move directly toward a concentration of oysters less than 40 feet away, while others consider that it must be very close to its prey before it moves directly towards it.

Prevention:

Remedies proved effective are those directed to the systematic destruction of the adult predators. One of the methods used in Canada and United States is that of spreading finely granulated quicklime over oyster beds at approximately 500 lb to an acre. This causes rapidly spreading lesions in the delicate skin membrane of the starfish and ultimately leads to its death (Korringa, 1952) while at the same time it does not appear to affect oysters. The most commonly used method in the United States is mopping, whereby long tangles of mops pulled in rows over oyster beds collect thousands of starfish, which are then killed with steam, and later used as fertiliser.

At the other end some workers consider that artificial ways of preventing starfish attacks on oysters may be unnecessary, that their abundance is entirely governed by natural conditions. (Korringa, 1952).

Borers or Drills:

As with most other predators, the effect of the drills on the oyster diminishes as the oyster shell grows thicker with age. Hence these animals, which comprise the most important oyster predators, cause most damage among oysters of up to 2 years of age.

Method of Attack:

Borers destroy their prey by drilling a hole through the shell and into the body of the oyster. The flesh of the prey is then scooped out by the proboscis. Drilling is done mainly by mechanical means, though some workers consider that at least in some drills a chemical secretion is produced in an "accessory proboscis" in the foot which aids in the process.

Destructive potential:

Under experimental conditions, it has been found that newly hatched drills (Urosalpinx spp). attacking C. virginica devour 1.39 young oysters of 3 - 7 mm length per day, while medium-sized specimens kill one 2" oyster every 3 weeks, but more if oysters are smaller. (Korringa, 1952).

Distribution and Prevention:

Oyster borers are most common where the salinity of the water is fairly high; they cannot withstand water of low salinity and are, therefore, found in greatest numbers near the mouths of rivers or in those streams into which little fresh water flows. This, fortunately, frequently represents one natural means of preventing overcrowding of oysters - under natural conditions young oysters are very much more numerous in these water than in waters of lesser salinity and high sedimentation and, therefore, a far greater number of oysters may settle on limited surfaces than can ever grow to maturity owing to their overcrowded conditions. In these cases borers are useful in that they rapidly thin out the spat.

Studies on the effect of temperature on the distribution of drills in America (Mosalpina spp.) indicate that the drills are active at temperatures above 11°-12°C (51.8°-53.6°F) and that their reproduction occurs at about 20°C (68°F). Drills fed experimentally on spat 10-30mm in diameter stopped feeding at 5°C (41°F) and fed only spasmodically at 10°C (50°F). Above this temperature, rate of feeding increased with the maximum occurring at 25°C (77°F) when each drill consumed on the average 3 spat every 2 weeks. (Korringa, 1952).

Roughley (1925) describes 3 species of boring whelks found on the coast of New South Wales.

The Common Borer (*Xymene hanleyi*)

"........ grows to a length of about an inch, and deposits its eggs in dome-shaped capsules about ⅛th of an inch in diameter; these it attaches to the surfaces of oyster shells or stones". It is apparently by far the most prevalent of borers and few, if any, rivers are entirely free from it.

The Black Borer (*Drupa marginalba*)

"........ of about the same size as the preceding, but characterised by blunt protruberances, black in colour".

The Hairy Borer (*Cymatium parthenopeum*)

"........ a larger species which attains a length of four inches and deposits its eggs in a parchment-like case held firmly against the under surface of the shell ..... This borer makes a comparatively large hole and is capable of penetrating the shells of adult oysters".

New Zealand Oyster Borer (*Lepsiella scobina*)

This (See Fig.9) is the chief predator of the northern rock oyster of New Zealand. It occurs throughout New Zealand, and appears to be at its most destructive around the half tide level. The borer attacks mainly young oysters, but often is seen to attack even the largest specimens when it has been observed to pierce a shell in 45 minutes (Powell, 1947). Graham (1943) records it attacking rock oysters in Manukau Harbour where in approximately four hours it may drill a hole of about 1/16 of an inch in diameter. As with other borers, it is far less tolerant of silting and lower salinities and therefore occurs in much lower numbers in estuarine areas than in fully marine ones.

In marine conditions, therefore, the vertical range of the oyster is fully equalled by that of *Lepsiella*, and it is here in particular that the slow-growing oysters high on the shore are easily attacked. Under estuarine conditions oysters extend above *L. scobina* and "quite dense populations may form even near the level of high water heap" (Rainer, 1964).

Control Measures

Each year a great deal of effort is put into the destruction of borer in the areas where oysters are grown for market. There appear to be 2 effective measures:

1. Systematic destruction of the predators and their egg capsules. It is preferable to remove the drills before the egg-laying begins. Marine Department annual reports detail departmental expenditure involved in the process.

2. Removal of young oyster spat to areas where the drills are rare or non-existant. Waters of high salinity are condusive both to the life habits of drill and to the oyster spat settlement. But oyster growth is more rapid under conditions of low salinity. Therefore, in removing the settled culch from the areas of high salinity to those of low, a dual purpose is accomplished simultaneously.

Dark Rock Shell (Lepsia Laustrum)

An active carnivorous species it forces open oysters and other bivalves by inserting the tip of its own shell as a wedge (Powell, 1947).

White Rock Shell (Neothais scalaris)

Another of predators having done untold damage to the commercial oyster harvest (Dellow, 1955).

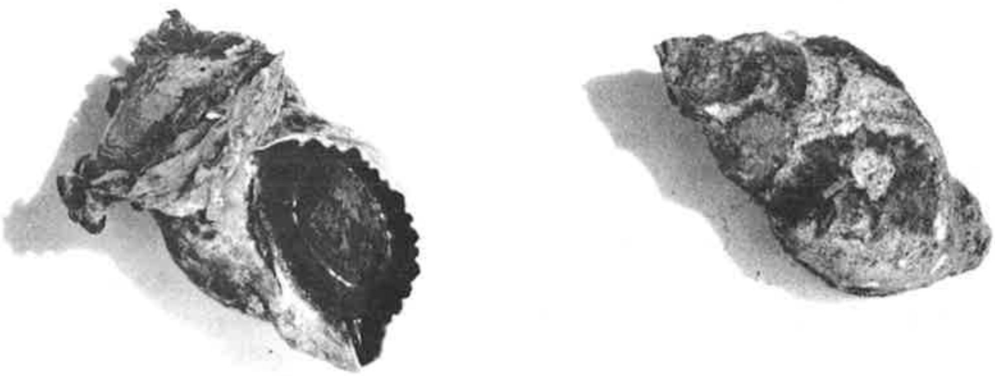


Fig. 9. Lepsiella scobina, the New Zealand oyster borer.

MORTALITY

In a previous section it was mentioned that sometimes mortality occurs in oysters without having any observable causes, but which can be suspected as having been caused by either an animal organism or a combination of physical and biological factors. In this section, for the want of better placement, two further aspects are included.

Inherent Inviability:

This is a factor for which there is evidence to show that it causes mortality in some larvae of *C. commercialis* no matter how favourable the environmental conditions may be. Kesteven (1941) writes ....."a certain proportion of larvae of each spawning cannot survive because..... there is some lethal factor in their constitution which kills them. There is nothing which could be done to save such stock, and proper measures must be those designed to reduce the nonviable proportion of offspring." The measures suggested are the elimination of all poor and neglected stock, the establishment of brood stock beds, and the establishment of spatting areas. As to subsequent mortalities, Kesteven continues ...." It is probable, although as yet no evidence is available they are in part due to inherent physiological weakness because of which the individuals cannot survive the ordinary ranges of water conditions".

Algae:

Unlike predators and parasites which actively cause the death of the oyster through their own process for survival, algae are "passive" in their destruction of the oyster beds. One of the studies done in this aspect is that by Roughley (1926) in which among the many factors studied as possible cause of the oyster mass mortality on George's River was the effect of algae known as "slime" (*Ectocarpus*, probably *E. sordidus*) which covered massively the oysters at the time. Although an experiment to determine its toxicity failed to give positive results, Roughley felt that this isolated experiment could not be accepted as proof that the weed did not kill the oysters.

In the same report Roughley writes of incidences of mortality caused by periodic invasion of Port Macquarie by large quantities of fine red algae (*Falkenbergia*). At times the weed, suspended in water, was so dense that with receding tides it formed thick deposits over oyster beds where it putrified and liberated sulphuretted hydrogen in sufficient quantities to kill many of the oysters.

COMPETITORS

Related to predators, but with more passive habits, are animals and plants which do not eat or otherwise exploit oysters but compete with them for place and food. These include barnacles, mussels, sponge and Ascidian growths, and seaweed. Some of these not only eliminate available settlement space, but also settle on the oysters themselves and/or envelope them. (See Fig. 9 & 10).

The competition begins at larval stages and is especially serious when larvae are those that settle on similar surfaces and at the same time of the year as the oysters.

Common small barnacle or acorn barnacle (Elminius modestus)
Distribution: Found all round New Zealand coasts as well as Tasmania, Victoria, and New South Wales, it is proving to be the most serious of Australian pests. The white, star-shaped barnacles cluster in thousands in the intertidal zone on anything that will afford a base of attachment including oysters themselves. Breeding is continuous throughout the year, and therefore its larvae settle both before and after oyster spatfall.

Control: In America it has been found that spraying spat collectors with a concentration of D.D.T. results in notably greater settlement of oyster spat. It has been noticed that while the D.D.T. inhibits early growth of the spat subsequent growth more than compensates for this (Yonge, 1960).

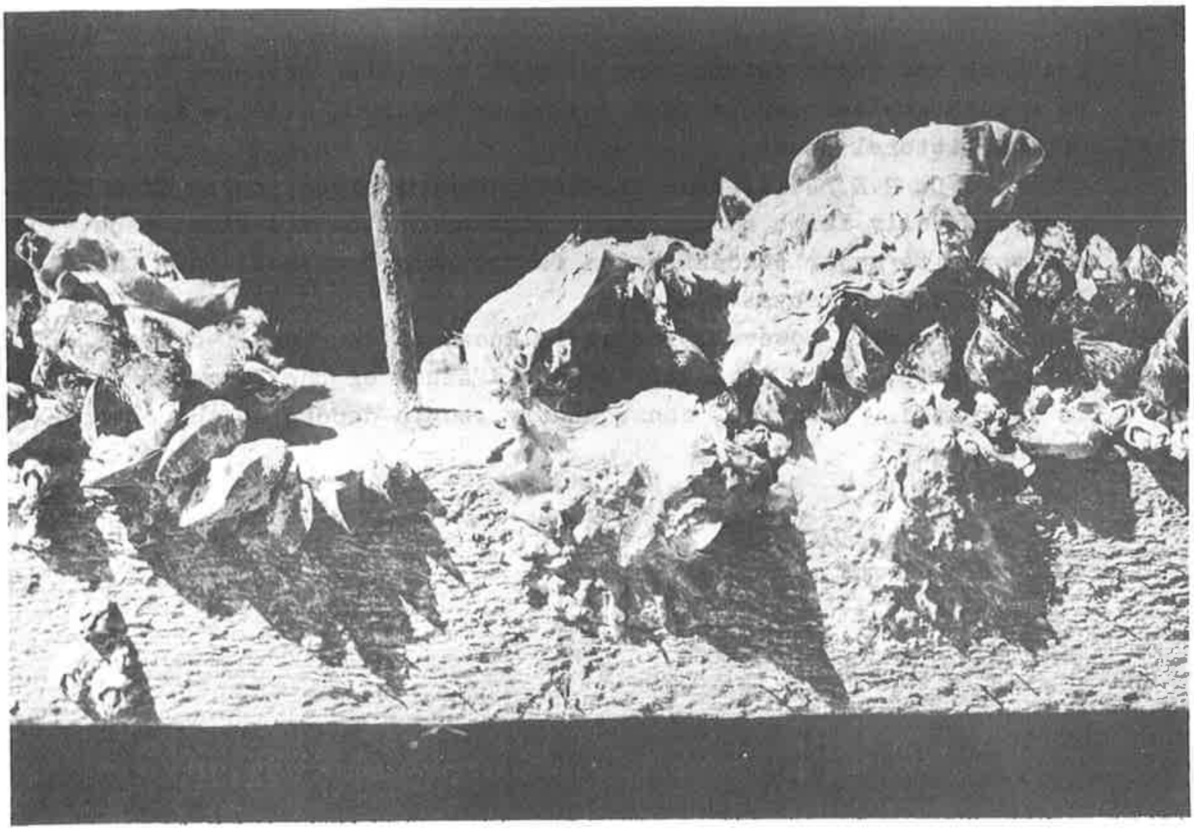
ALGAE:

These are plants found at the same or similar vertical distribution on the shore, and include Arthropyzenia (Cranwell and Moore, 1938) Caulacanthus spinellus, Centroceras clavulation, Gelidium caulacanthum, Gelidium caulacanthum, Hormosira (Dellow, 1955).

MUSSEL: (Modiolus neozelanious)

This shellfish has only recently become regarded as a possible potential nuisance to the rock oyster in the northern New Zealand when it was reported in one area as having settled heavily on the oyster culch (wooden battens in this case). Apparently there is no record of the effects of its infestation of natural oyster beds.

Knox (1954, Trans. Roy Soc. N.Z., 81:204) in a report on ecological study in Banks Peninsula records that the mussel, found at M.H.W.N. and E.L.W.N., is extremely tolerant of the wide range of environmental conditions. It occurs on all type of substrate, and tolerates exposure from 85% to 40%. It can also withstand



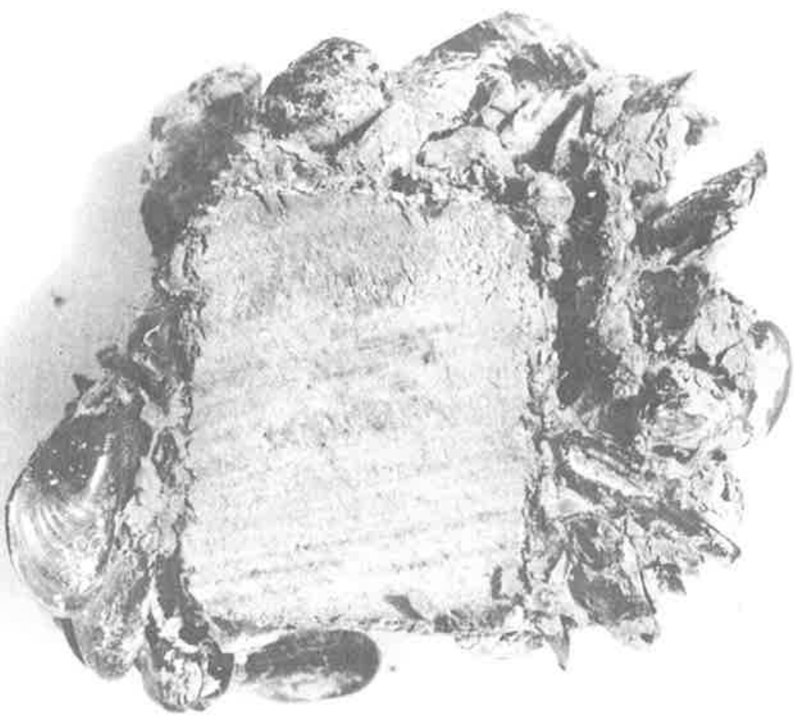


Fig.10. Competition for space - C. glomerata and its competitors. Note the heavy settlement on the under-surface of the stake (since turned over). Kaipara Harbour.

Fig.11. Cross-section view of a densely settled stake.

brackish and muddy waters, and as well tolerates coverage by sand to a much greater degree than any other dominant sessile animals of the littoral zone.

Dr R.K. Dell, in a personal communication, notes that the mussel usually forms bands fairly high up in the mid-tidal zone, and that its major concentration is probably somewhat above the level of the rock oyster band.

In all, however, little is known of the mussel-oyster relationship, and a necessary specific study of the former's habits is indicated. Control, consequently, would depend on the outcome of the study.

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WELLINGTON NEW ZEALAND

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