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Chromosomy partenogenetycznego, telytokicznego ryjkowca
*Eusomus ovulum* Germ. (*Curculionidae, Coleoptera*). —
*The chromosomes of the parthenogenetic and thelytokian
weevil* *Eusomus ovulum* Germ. (*Curculionidae, Coleoptera*).

Mémoire
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(Plate 18)

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The problem

The cytology of parthenogenetic weevils was the subject of
research by *Suomalainen* (1940, 1945, 1947), *Seiler* (1947) and
*Mikulska* (1949, 1950). Recent studies concerned the genera:
*Otiorrhynchus* Germ., *Polydrosus* Germ., *Sciophilus* Steph., *Trachyphloeus* Germ., *Strophosomus* Steph., *Barynotus* Germ.. Parthe-
ngenesis is also known in the genus *Eusomus* (*Smreczyński*
1949) not studied cytologically till now.
In Poland there occurs the species *Eusomus ovulum* Germ., widely distributed over Central Europe. In the south-east, one finds besides this form another *Eusomus beckeri* Tourn., commonly held to be a different species. Penecké for instance regards it as vicarious with *E. ovulum* in the District of Bucovina. However, its specific peculiarity is not certain. The characteristics cited by Penecké for *E. beckeri*, do not, according to Smreczyński, allow the exactly distinction between this form and *E. ovulum*. To set aside these doubts cytological studies of both forms might contribute some results.

From the results of recent studies emerges the fact that the parthenogenesis of the weevils is a geographical one. The bisexual forms usually occupy other areas than the parthenogenetic ones, although there are some exceptional cases of the coexistence of both forms in the same area. With the parthenogenesis is usually connected the polyploidy. Suomalainen (1940) was the first to observe it in some weevil genera. The grade of polyploidy may be different in various species, or even in the various forms of one species (e.g. *Otiorrhynchus scaber* L.).

Studies dealing with the origin of the geographic parthenogenesis in weevils must be based upon cytological research, carried out on a great number of forms, deriving from many localities.

As the chromosome relations of genus *Eusomus* were up to now not known, and having had the opportunity to gather rich material of *E. ovulum* in the environs of Kraków I decided to study the chromosomes of this species.

**Material and methods**

The insects studied were collected in the years 1948, 1949, 1950 and 1951 in the neighbourhood of Kraków, in the locality Pynchowice on the river dyke of the Vistula. The beetles appeared here very abundantly on leguminous plants. (*Lotus corniculatus* L., *Papilionaceae*) and on grasses, but in a somewhat confined area, that is on a dyke segment of southern exposure 70 m long. On the opposite side they appeared very seldom. The collections in the years 1948 and 1949 and 1950 were especially rich. A few minutes of plant sweeping of the dyke gave more then 100 specimens. Single specimens were collected in the vicinity or in other parts
of the dyke. In four spring seasons there were gathered a total of more than 600 specimens. The genital organs of about 500 specimens were dissected. All proved to be females. The spermatozoa were never found in the genital tubes. An attempt to breed from a part of the specimens in the laboratory was made. The weevils were put into glass containers, with the bottom fitted with lignine or earth, or in small wooden boxes. Food plants were placed in small glass jars filled with water, or set directly with the roots in earth. Pieces of lignine wetted with water maintained a suitable humidity in the containers.

The weevils laid the eggs most frequently between the layers of lignine, more rarely on the walls of the containers or between the leaves of food plants. The oviposition began after midnight most often in the dawn between 4 and 8 a.m. The number of eggs laid was from 30 to 70, mostly about 50. Eggs were laid in single layers, quite irregularly, only exceptionally in rows.

The eggs have a spherical ellipsoid shape, their dimensions being: length ca 0.7 mm, width ca 0.25 mm.

The chromosomes were observed in the somatic cells of the ovary, in the blastodermic cells and in the course of maturation divisions in oocytes clustered in the conducting tubes of the ovary.

The reproductive organs were prepared in Ringers solution and fixed in Bouins fluid (laboratory temperature or heated to +60°C) and also in Carnoy fluid. The use of Carnoy fluid allowed one to get clear pictures in the eggs, but for the fixing of delicate ovary tissues Bouins fluid proved to be better. The laid eggs were fixed in heated Bouins or Carnoy fluids.

The peeling off of the eggs from the chorion proved superfluous in the case of this species. The eggcover in Eusomus is very thin, notably thinner than in Otiorrhynchus, and does not give special trouble when making microtome sections.

The piercing of the laid eggs was attempted before the fixing. It appeared, however, that the freshly laid eggs have so thin and delicate a cower, that under lightest pressure they break and the contents flows out.

Trouble in getting freshly laid eggs came also from another side. The weevils for egg laying entered between tightly pressed layers of lignine where they had to be controlled. When the lignine layers were expanded and thus loosened, the beetles refused to lay. After
removing the lignine, to force them to lay eggs in other places, they refused to lay at all. In spite of a scrupulous inspection of plants and soil, there were no laid eggs to be found, whereas in the ovaries of the beetles masses of eggs were to be observed.

In a few cases only some eggs were found on the walls of the containers or on food plants, but their position time was not controlled.

A larger number of eggs laid was obtained, but only two hours after laying. The eggs were pierced after 1-minute action of fixing fluid. Further the normal technique was applied. For embedding paraffine of + 58°C melting point was used. The sections were of 6, 10 and 14 μ. As staining methods carmine, Heidenhains ironhaematoxyline and Feulgen method were used. All drawings were made under the microscope using Abbé's camera and Spencer Hom. Immersion 1·8 mm n. a. 1·25 and Zeiss Comp. Oc. Nr 18, with the exception of Fig. 9 made with Oc. Nr 4 (10 ×).

**Chromosomes in the somatic cells**

Numerous mitoses were observed in the follicular cells of the ovary as well as in the blastoderm.

The germarium of *Eusomus ovulum* is built similarly as in *Polydrosus mollis* Ström (Leńkowa 1950) and in *Ottorhynchus salicis* Ström (Mikulska 1950) of two pairs of egg tubes. The apical part of the tube filled with trophocytes is narrower at its base. In this narrowing there occurs the oocyte zone. The oocytes concentrate here forming a ring in the circumference of the tube. They wander from here into the interior of the tube. When wandering they become surrounded by small follicular cells, which divide intensively (Fig. 11).

The determination of the chromosome number in the follicular cells is rather difficult. They lie in dense plates, whose diameter is about 5 μ. Many of them were examined and counted. The results are given below:

<table>
<thead>
<tr>
<th>Chromosome number:</th>
<th>28</th>
<th>29</th>
<th>30</th>
<th>31</th>
<th>32</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plates number:</td>
<td>12</td>
<td>16</td>
<td>15</td>
<td>15</td>
<td>10</td>
</tr>
</tbody>
</table>

It is evident that the chromosome number of different plates balanced around 30. This balancing may be produced by the variability of this number, affected by fragmentation or fusion together
of single chromosomes, cases also occurring in other weevils (Suomalainen 1940), but it might also be due to the difficulty in discerning each single chromosome. The chromosomes are a little

Fig. 1. Metaphase of follicular division.
Fig. 2. Chromosomal plate in late prophase. 30 chromosomes visible, of that number 3 V-shaped.
Fig. 3. Chromosomal plate shown from side. V-shaped chromosomes on the border of plate. Not all chromosomes visible.
Fig. 4. Chromosomal plate shown from the side. Spindle radiation form an elongated ribbon. Not all chromosomes visible.
Fig. 5. Chromosomal plate in polar view. Black chromosomes in one preparation, contoured chromosomes of next preparation (Fig. 6).
Fig. 6. Two chromosomes shown contoured in fig. 5 were found in next section.

elongated and the majority have the shape of straight bars, or they may be of a ribbon-like shape. Several elements are distinctly larger. Figure 1 shows the metaphase of a follicular cell. As we see
an exact analysis of the size and shape of chromosomes is possible. Only some parts of each single chromosome lie in one plane. In the plate presented two elements are distinctly larger than the remainder. It seems that the third element lies beneath the others. The two elements mentioned above have the shape of a V. The cleft dividing the two arms is sharply marked in both of them. The remaining elements have the shape of straight or bow-like bent rods (bars), but differ in size. The attempts to distinguish homologous chromosomes did not give results in any case.

One thing is certain after these observations, namely that the chromosome number in the somatic cells of the ovary is $30 \pm 0-2$ and probably three elements differ from the remaining ones in shape and size.

Somatic mitoses were observed also in the blastodermic cells. The eggs are laid in the metaphase of maturation division. In the preparations from eggs fixed 2 hours after laying several blastomeres in egg cross-section are already visible, and several hours later (4–5, depending on the temperature of the environment) the stratum of blastomeres is just formed. In these periods numerous divisions may be found. However, similarly as in follicular cells, the exact determination of number and shape of chromosomes is impossible. The plates are very small, $5 \mu$ in diameter, and the chromosomes pressed together. It is possible to observe the presence of c. 30 elements, 2 or 3 of which seem to be larger.

**Chromosomes in maturation divisions**

The first phase of maturation division were observed in the eggs lying in the dilatation of the egg tube, i.e. in the calyx. The eggs are there in the late prophase in the period of spindle forming, or in meiotic metaphase. The early stages of prophase must pass very quickly. Having examined many preparations (several hundreds) I did not meet any early prophase. The eggs lying in calyces are already more advanced in development, whereas the oocytes sliding towards the calyx in my preparations were still in the stage of interphase. They are perhaps cases of developmental stoppage described already in other parthenogenetic weevils. Altogether 75 series of ovarian eggs were sectioned, and of them 27 examined in exact detail.
Late prophase

The chromosomal plate, in the youngest stages observed by me, was placed very near to the surface of the egg in the polar-plasma, whose layer is at this point a little thicker and forms a distinct homogenous patch among the surrounding yolk globules. The plate lies usually on the side of the egg (Fig. 12), having also sometimes an apical position. The plane of the plate is perpendicular to the egg surface. The plate is elongated its contour being ± oval or triangular. The length of the plates in this stage is about 12 \( \mu \) (up to 15 \( \mu \)), the width 5 \( \mu \). The spindle is not yet visible here. I counted very many plates of that kind. The number of chromosomes in those that could be counted was 30. Figure 2 shows such a plate 30 chromosomes are visible here. The parts of protoplasm next to the chromosomes are in the preparation lighter than the rest, it seems as if the chromosomes had a lighter cover (dyed with iron haematoxyline). Among 30 chromosomes 27 have the shape of more or less spheroidal globules. Three chromosomes are distinctly larger, having a V-shape. In the point of two arm connection a lighter shade is distinctly visible. The V-shaped chromosomes lie in the circumference of the plate. Two of them lie beside one another, the third on the opposite side of the plate. The chromosomes in most of the plates observed had a similar position. In a few cases only were the chromosomes differently arranged, having all three V-shaped chromosomes on one side of the plate, all lying together. Such a position was found in 3 cases out of 57 examined. In all other 54 cases the position of the chromosomes was as described above. When comparing the number of chromosomes in the prophase of meiosis with those in the somatic cells we see that it is the same. In both cases there occur 30 (or about 30) elements. Thus it may be concluded that the chromosomes do not form pairs.

In bisexual weevils, as we know from the exact investigation of Suomalainen, in the prophase of the first maturation division, the chromosomes occur as gemini. The number of visible elements becomes normally reduced to one half. In parthenogenetic weevils in the genera: Polydrosus, Otiorrhynchus, Strophosomus, Trachyploea, Sciophilus, Barynotus (Suomalainen 1940, 1947, Siebler 1947) there does not exist any conjugation of chromosomes, and individual chromosomes occur in the prophase of the maturation
division as single elements. This only maturation division is an equation division. The reductional division may take place only in the fragmentary form (Seiler 1947). As is evident from the observations upon the chromosomes of *Eusomus ovulum*, neither in this species does the conjugation take place in the prophase of maturation division. The chromosomes in the prophase are visible as single elements.

**Divisional spindle**

In the stage of formation the spindle stands tangentially to egg surface. The spindle radiations are arranged in the shape of a small barrel, or they form a widely extended ribbon. Figures 3 and 13 shows a barrel-like spindle. In this plate, seen from the side, not all elements are visible. In the borders of the plate, however, there are distinctly marked larger chromosomal elements. At the one end of the widely extended chromosomal row there lie two V-shaped chromosomes, the third holds its position at the opposite end.

The chromosomes do not lie in a straight line. A distinct break of the chromosomal line is visible here. In another case (Fig. 4) the chromosomal row is yet larger, the radiations of the spindle forming thus a long ribbon. Also here the »breaking« of the chromosomal line is to be observed but is less distinctly expressed.

This »breaking« visible in many plates seen from the side, indicates that the chromosomes lie in fact on two planes which incline one to the other at a certain angle. The angle is an obtuse one. This is probably the reason why in preparations even 15 μ thick the chromosomes of one plate (during polar observation) are often divided between two preparations. Such a situation is shown in Figure 5 and 6. In Figure 5 we see the chromosomes which are to be found in one preparation to the number of 28. At the end of the plate we see two V-shaped chromosomes. For a complete plate set they are lacking one small and one V-shaped chromosomes. They are visible in the next preparation (Fig. 6). The same situation is shown in Figures 14 and 15.

**Metaphase**

In this stage the plate becomes more compact, the chromosomes aggregate more tightly and are more difficult to distinguish.
Almost all the chromosomes are visible in a single preparation (in polar observation and 10 \(\mu\) thickness). The spindle has usually the shape of two cones touching closely with the bases (Fig. 7). The chromosomal row is equalized.

The size of plates and chromosomes balances in fairly wide margins. There occur plates twice as small as in the preceding stage.

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Fig. 7. Spindle in the metaphase stage.
Fig. 8. The plate in the stage of metaphase.
Fig. 9. The plate shown from the side. Diverging of chromosomes is visible.
Fig. 10. The plate shown from the side. Diverging of chromosomes is visible.

(Fig. 8). A similar phenomenon was observed by Suomalainen, who held it to be connected with the age of the plate ("Auch die Grösse der Chromosomen und der Platte selbst varieirt in den verschiedenen Metaphaseplatten erheblich... Dies scheint vom Alter der Metaphaseplatten abzuhängen, und zwar so, dass die Chromosomen der jüngeren Platten grösser sind. Die Chromosomen konzentrieren sich also während der Metaphase.) My observations would appear to confirm this supposition.
The V-shaped chromosomes are placed always in the circumference of plates, usually two together, the third aside, exceptionally all lying side by side as shown in Figure 8. Out of 50 metaphasal plates examined, in which it was possible to observe the position of V-shaped chromosomes, in only 2 were all three aggregated side by side.

The number of chromosomes in the metaphasal plates was also 30. In many cases it was possible to observe longitudinal furrows on chromosomes.

**Gonomery**

Suomalainen (1940) called attention to the phenomenon of gonomery in weevils. It is expressed by differentiation in the range of plates in polyploidal forms. In many cases the chromosomes of one oocyte were aggregated not in one, but more plates. Single plates contained one or more basic complexes. Separated plates often lay in various planes (Suomalainen 1940, p. 77, fig. 56).

I did not observe in *Eusomus ovulum* such sharply differentiated pictures of gonomery. However, the position of the chromosomes described in former chapters, often in the prophase of the matura
tion divisions, showed complete analogy with the phenomena described by Seiler in *Otiorrhynchus sulcatus* F. In this species, in the maturation division, Seiler observed an odd arrangement of chromosomes... »Sie sind manchmal fast einreihig in langer Linie aufgestellt... Auch sieht die Spindel bei sulcatus anfangs oft mehrpolig aus und die Abb. 6 und 7 könnten aufgefasst werden als Doppelspindeln, je mit einer diploiden und einer haploiden Platte, wobei die Ebene beider Platten in stumpfem Winkel zueinander stehen« (Seiler 1947, p. 95 and 96).

Also in other parthenogenetic insects multipolar »Verschmelzungspindeln« are known. They are exactly described by Seiler in *Solenobia*. »Während der ersten Furchung laufen bei *Solenobia triquetrella* automiktische Vorgänge ab. Die bestehen darin, dass je zwei Furchungskerne miteinander verschmelzen. Bevor das aber geschieht, bildet jeder Kern eigene Spindel aus, die Chromosomen stellen sich in die Äquatorialplatten, die im Begriffe sind sich zu vereinigen, zunächst noch in beliebiger Orientierung zueinander sich befinden, im Extrem senkrecht aufeinander stehen. (S. 1947, p. 97). Narbel (1946) described similar phenomena in *Apteronia*
helix, Sieb. and recently this problem with regard to Solenobia triquetrella F. R., has been discussed by Seiler and Gesner (1950).

Seiler holds that the pictures obtained in Otiorrhynchus sulcatus are traces of the rudiments of gonomery.

As formerly shown in Eusomus ovulum there often occur multipolar spindles. The chromosomes in the maturation prophase and in the period of spindle formation lie most often in two planes inclined together at an obtuse angle. This was shown in Figures 3, 4 and 13. It is more clearly visible Figures 17 and 18. Agreeing with the opinion of Seiler concerning Otiorrhynchus sulcatus, I presume it is rudiment of gonomery occurring often in other parthenogenetic species of weevils.

Discussion

The basic chromosomal number is not known in any bisexual representative of the genus Eusomus. In this genus besides E. ovulum and E. beckeri mentioned in the introduction, there are described 20 species distributed in central and south-eastern Europe, and central and northern Asia. To the parthenogenesis of E. ovulum attention was called first by Smreczyński (1949). The sexual dimorphism in representatives of this genus is weakly expressed. Professor Smreczyński supposes however that (on the bases of external pattern) the Central European ones should be also parthenogenetic.

Concerning East-European and Asiatic forms any information (with the exception of the parthenogenesis of E. beckeri as mentioned above) are lacking. Moreover, E. beckeri is held by Smreczyński (1949) to be an aberration of E. ovulum.

In accordance with recent systematic views, nearest to Eusomus should be placed the genera: Sciaphilus and Sciaphobus Daniel. Sciaphobus is represented by 20 species, whose cytology has not yet been studied. In the genus Sciaphilus 2 species have been described: Sc. costulatus Kiesw. and Sc. asperatus Bonsd. The first lives in the Pyrenees, the other is common in the whole of Europe. The cytology of Sc. asperatus has been investigated by Suomalainen.

1 For all data concerning representatives of the genus Eusomus, Sciaphilus, Sciaphobus, and the opinion concerning their systematic position I am indebted to Prof. S. Smreczyński head of Dept. of Zoology, Jag. Univ. to whom I express my thanks for this help.

It appears that this parthenogenetic species of weevil is triploidal, at least in the territory of Finland. In the eggs of _Sc. asperatus_ only one reduction division takes place. The chromosomes form in the period of division a long, narrow plate lying on the surface of the egg. On the chromosomes there is a sharply visible divisional furrow, thus they have the appearance of small buns. In one oocyte Suomalainen noted two metaphasal plates, one diploidal, the other haploidal. The chromosomes have before the division a spheroidal shape and after the division they become elongated. The chromosome number in the maturation divisions, as in somatic mitoses in the blastoderm, was 33. The basic chromosome number of this species is the same as in other bisexual and parthenogenetic weevils of genera: _Polydrosus, Otiorrhynchus, Barynotus, Trachyphtloeus_ and _Strophosomus_, namely 11.

As shown above, in _Eusomus ovulum_ in the somatic cell divisions it was possible to observe the presence of c. 30 chromosomes. About three of them were larger differing from the others in shape. In the maturation division there occurred 30 chromosomes, and of this number 3 V-shaped ones, distinctly larger than the others. The »breakings« of the chromosome plane observed many times, is probably the rudiment of the gonomery in this species. These facts allow the presumption that _Eusomus ovulum_ is a triploid with basic chromosome number _n_ = 10. The chromosomal complex should include 9 small and 1 large V-shaped chromosomes. As is known, there exist some cases of the formation of V-shaped chromosomes by the fusing of two rodlike ones, as an effect of meiotic disturbance (Robertis, Nowiński, Saez 1948, White 1945). Keeping this in mind, it might be possible to deduce the basic chromosome number as from 10 to 11. It is however, only a presumption not based on any fact. The basic chromosomal number _n_ = 11 is not a rule for weevils. In _Calandra granaria_ L for instance (Inkmann) it is _n_ = 12.

It should be noted that many peculiarities in the course of maturation divisions in _E. ovulum_ bring to mind that of _Sciaphilus asperatus_. The plates of the late prophase and early metaphase are very extended just as in _Sciaphilus_. The chromosomes in these stages are, in comparison with the other species, in both species mentioned above more dissipated (compare Fig. 64 of Suomalainen 1940, p. 83.). Not till then do the chromosomes aggregate
Also the shape of the chromosomes is similar with the exception of 3 V-shaped ones. In ready metaphasal plates before definitive division the chromosomes are spheroidal, proportionally small and furrowed in a bread-like manner.

As in other parthenogenetic weevils there do not exist in *E. ovulum* chromosomal conjugations. The division, the pro- and metaphases of which run still at the time when the oocytes prevail in the ovary, is probably an equational division. Here it should be noted that some pictures observed by the author in some oocytes, provoke the question as to the existence of a rudimentary reduction division. These are shown in Figure 9, 10 and 19. They remind us of the rudimentary reduction division of *Otiorrhynchus sulcatus* described by Seiler (1947, p. 95 and 98, figs 5b and 8). Closer analysis however leads to the doubt whether in this case in *E. ovulum* one was not dealing with the picture of plate rotation. Having not the pictures of anaphases at my disposal I could not decide this question. Thus it was impossible to determine the spindle position in the subsequent phase. Only the chromosome number was fixed at about 30.

In the preparations of the most recently laid eggs, about 2 hours after laying, a few blastomeres could already be observed in a cross-section in the middle among the yolk globules, and on the circumference of the egg one polar nucleus in the metaphase. This picture was observed many times. The spindle of the polar nucleus was perpendicular to the egg surface. Between the preceding and the last stage there should take place a rotation of the spindle of 90°. It is difficult to decide at which moment this occurred.

In the presence of only one polar nucleus, evidence may be seen that there exists only one maturation division.

This first note concerning the chromosomal conditions of *Eusomus ovulum* does not one obviously allow, to put forward suppositions as to the origin of the parthenogenesis of this species. The chromosomal number of the forms living in other territories, as also of other species of this genus should be investigated. It may well be that the question of peculiarity of *Eusomus beckeri* might be elucidated by cytological studies.

**Summary**

1. The parthenogenetic, thelytokian weevil *Eusomus ovulum* Germ. possesses in somatic mitoses $30 \pm 2$ chromosomes.
2. In the prophase of the maturation division there occur 30 chromosomes. The chromosomal conjugation does not exist.

3. The chromosomal set is composed of 27 small more or less spheroidal chromosomes, and 3 distinctly larger, V-shaped ones.

4. At the time of forming the spindle, the chromosomes arrange themselves in a long row. It is broken near one end. The chromosomes are in this period arranged in two planes inclining towards each other at an obtuse angle.

5. V-shaped chromosomes lie always in the circumference of the plate, usually 2 side by side, the 3rd on the opposite border; only exceptionally are they aggregated all together.

6. *Eusomus ovulum* is probably a triploid with basic chromosome number \( x = 10 \).

7. The division observed is probably the only maturation division being an equational one.

Bibliography


Explanation of figures

11. Fragment of longitudinal section across apical chamber of the ovary, with visible oocytes (o) and follicular cells (f). (Heidenhain iron-haemat.).

12. Longitudinal section across an oocyte separated from the ovary with visible chromosomal plate (mp). (Heidenhain iron-haemat.).

13. Photograph of plate in the period of metaphase. (Heidenhain iron-haemat.).

14. Photograph of the plate shown on fig 5. (Heidenhain iron-haemat.).

15. Photograph of chromosomes shown on fig. 6. (Heidenhain iron-haemat.).

16. Photograph of the plate in the period of metaphase (Heidenhain iron-haemat.).

17. Chromosomal plate with chromosomes aggregated on two planes. (Heidenhain iron-haemat.).

18. Chromosomal plate shown from the side with distinct «breaking» of chromosomal row. (Heidenhain iron-haemat.).

19. Photograph of the plate shown in fig. 9. (Heidenhain iron-haemat.).

Introduction.

There are two important fishery problems closely connected with the valley dams, viz. the migration of the fish through the fishladders on the one hand, and the migration of the fish through the various channels of water stations on the other.

The solution of the first problem has been found by establishing fishladders based on a chamber system enabling the fish to migrate along the flumes that have been partitioned away between the valley dams. These arrangements proving most useful for fishery, however,