NOTES ON *AURELIA AURITA* Lamarck

by J. Mauchline.

ABERDEEN

INTRODUCTION

These notes were prepared while acting as a student assistant at the Marine Laboratory, Aberdeen.

Aurelia is an abundant jellyfish on the Scottish fishing grounds, and elsewhere, and in order to help assess the importance of its influence on the fisheries it is desirable that the published data, or references to data, should be collected together. The object of these notes, then, is to review the literature on *Aurelia aurita*, emphasis being laid on feeding, breeding and distribution. I am indebted to Dr. J. H. Fraser of the Marine Laboratory for suggesting the work to me.

Aurelia aurita LAMARCK (1816) is a Scyphozoan Coelenterate belonging to the family *Ulmaridae* of the order Semaeostomeae. PERON and LESUEUR (1809) named it *"Aurellia"* but only a few authors (i.e. MAYER, VAN DER MAADEN, VERWEY, HORRIDGE) have used this form in past years and Lamarck's version will be used in this work.

Some of the physiological papers mentioned deal with *Aurelia flavidula*, the New England variation of *Aurelia* which KRAMP (1942) proposes to call *Aurelia aurita* var. *flavidula*. According to him the European form should be called *Aurelia aurita* forma *typica* and this is the form also found in certain parts of the Indo-Pacific region. STIASNY (1919, 1922) discusses the forms *Aurelia aurita* vars. *colpota*, *maldivensis*, *labiata*, and *flavidula*. BROWNE (1909), in the results of the Scottish National Antarctic Expedition gives a short account of *Aurelia solida*. HAECKEL (1880) gives an account of *Aurelia aurita*, *colpota*, *flavidula*, *marginalis*, *hyalina*, *labiata*, *clausa*, *limbata* and includes an extensive bibliography on each form. Bigelow (1938) also deals with this aspect.

The distribution data of *Aurelia* in Faroes, Shetlands, and round the coasts of Britain have been mostly extracted from the cruise reports of the research vessels of the Scottish Home Department, Marine Laboratory, Aberdeen. An extensive list of distribution literature is included in the list of references at the end. Also included in the literature are the papers of GILCHRIST (1937) and BUHK (1939) which deal with the rearing of *Aurelia aurita* in an aquarium.

Aurelia aurita shows a high degree of variation but variants are easily recognised as *Aurelia aurita*. Starved specimens, however, are often unrecognisable superficially and have often been placed in a new species (DE BEER and HUXLEY 1924). It has been suggested that *Aurelia* would be a source of easily obtained material suitable for variation studies.

There is a quantity of suggestion but a lack of concrete facts in the literature concerning the relations between *Aurelia* and fish. In the Faroes region and off the south coast of Finland there are reports that shoals of *Aurelia* clog the nets, often damaging them to such an extent that fishing in these regions becomes unprofitable. Most of this literature has been derived from trawlermen's reports, accounts of scientific experiments and observation being scarce.

LIFE HISTORY

The fertilised egg develops into the free-swimming planktonic planula larva which, after a short period, settles on a hard substrate and develops into the scyphistoma. This scyphistoma becomes transformed into a number of free-swimming ephyrae stages by strobilization. From these ephyrae develop the sexually mature medusae which are then distributed by the ocean currents.

a) Egg, Blastula, Gastrula and Planula

The gonads, which are of endodermal origin, are located in the floor of the gastric cavity. The eggs in the ovary are separated by a single layer of cells from the enteric cavity from which they obtain the necessary food for growth.

Once growth is initiated, the egg cells increase rapidly in size and food is stored in their cytoplasm for future use. HARGITT (1920) discusses the size relationship between the growth of the egg cells and their nuclei. JORGENSEN (1910) in Sponges, SCHAXEL (1910a, 1911b) in Coelenterates, (1910b) in Ascidians, and (1911b) in Echinoderms, discuss the effect of chromatin liberation into the cytoplasm of the eggs and its relation to their growth. TSUKAGUCHI (1914) questioning SCHAXEL (1911a) postulates all cytoplasmic granules to be, not of two kinds, but one - namely mitochondria.

The eggs are liberated from the ovaries into the interradial grooves whence they are taken to the genital pouches situated near the edges of the free margins of the oral arms. MINCHIN (1889) gives an account of the attachment of the eggs to the oral arms. Here fertilisation takes place, the sperm, liberated into the sea by the male medusae being drawn into the mouth with the food particles. Segmentation of the egg is very irregular and may be equal or unequal. The blastula formed is ciliated (HOLLOWDAY, 1951) and may escape from the parent medusa at this stage of its life history or may continue development to the planula stage inside the genital pouches before starting its independent existence.

Gastrulation is achieved by various methods. These are discussed by SMITH (1891) and HYDE (1894); CONKLIN (1908) shows a relationship between the various types of gastrulation. BERRILL (1949) discussing gastrulation in coelenterates in general, shows that in those species with small eggs (below about 0.13 mm. in maximum diameter) gastrulation takes place by ingression of cells at one pole; in those with large eggs (over about 0.23 mm. in diameter) by invagination without regression; in those of intermediate size by varying combinations of these two. The gastrula is also ciliated and HOLLOWDAY (1951) suggests that this serves to prevent these young stages from sinking to the bottom before the planula stage is developed. Before the planula is fully developed, i.e. before the blastocoele becomes filled by invaginating or ingressing cells, the nematocysts may develop in the cnidoblastic cells of the ectoderm.

The planula shows small variations in shape and appearance (HOLLOWDAY, 1951). At this stage the independent existence of these young forms usually commences, and they leave the genital pouches, having attained a size of about 0.26 mm. After a number of hours of planktonic existence (HOLLOWDAY notes about 48 hours) they settle on some solid object on the bottom in fairly shallow water, e.g. 1-2 m. in Mariage Fjord (USSING, 1927), 4-5 m. in the Finnish coast (WIKSTRÖM, 1932), possibly always less than 20 m. (BIGELOW, 1928).

b) Scyphistoma

The planula become attached by their anterior end, and develop into scyphistomas. In all scyphopolyps the nature of the substratum is probably of survival importance; KRAMP found scyphistomas of *Cyanea capillata* on stones, shells and algae; MOORE (1937), USSING (1927) and WIKSTRÖM (1932) found *Aurelia* scyphistomas on living *Mytilus* and *pecten* shells.

Aurelia, however, may not show a scyphistoma stage at all but may develop into an ephyra by direct development from the gastrula (HAECKEL, 1881). This takes place only in the case of the largest eggs where the blastocoele cavity is not completely filled with endodermal cells after gastrulation is complete, with the result that the cells are crowded at one end and, on growth of the cells taking place, enlargement of the gastrula takes place in the transverse plane as opposed to the polar axis which is the normal plane when the cavity is filled; thus instead of the body becoming longer, it widens at one end and eight ectodermal lobes appear which slowly develop into the arms of the ephyra. AGASSIZ (1862), GOETTE (1893) and DELAP (1905) have studied a similar phenomenon in *Pelagia*.

Through the work of CLAUS (1877) and TEISSIER (1925) it has been shown that in *Chrysaora*, *Haliclystus* and possibly in *Aurelia* the blastula and planula are able to increase in size without the usual progressive morphogenesis. The gastrodermis of Coelenterates has ingesting properties and it is postulated (BERRILL 1949) that these young stages have retained or regained these properties.

When the pear-shaped planula settles, a depression appears at the distal end which causes pressure on the underlying endoderm and thus brings about the formation of the first pair of gastric pouches. The endodermal derivation of these pouches was much discussed by GOETTE (1887), CLAUS (1892), HYDE (1894), BIGELOW - see MAYER (1910), and HADZI (1907) but appears now to be accepted. After the partial formation of the second pair of pouches the mouth breaks through on a proboscis and the oral tentacles form. The formation of the tentacles takes place in a fixed manner; they develop either in the sequence 2, 4, 8, 16, or more rarely 3, 6, 12, etc., the secondaries appearing midway between the primaries which are equidistant from one another, the tertiaries midway between the secondaries and primaries, and so on. As BERRILL (1949) points out, this may be the general method of development of tentacles throughout the whole group as similar phenomena in Haliclystus (WIETRZYKOWSKI, 1912), Cyanea (PEREZ, 1922) and Mastigias (UCHIDA, 1926) were found.

According to HOLLOWDAY (1951) about 30 hours after settlement of the planula the typical form of the scyphistoma can be recognised and it can be seen that, contrary to the opinion of some previous workers, some cilia still remain between the bases of the tentacles and on the oral surface and are still actively beating five days after the planula has become attached.

When the scyphistoma, also known as a polyp or hydratuba, has attained 16 tentacles, it grows in size without much morphogenesis though in some fully developed scyphistomas as many as 30 tentacles may be found. In the fully grown polyp, which at this stage attains a height of about 5 mm., just below the hydranth, or head of tentacles, four septa are found each perforated by an ostium; these ostia form the gastral-ring sinus. On further increase in body length, new ostia form under these and when the constrictions in the polyp take place to form ephyra rudiments they do so between these, the ostia later aiding in the formation of the gastral cavities of the ephyrae (PERCIVAL, 1923).

When a scyphistoma is ready to strobilate, i.e. to produce one or more ephyrae, succeeding constrictions form in rings down the body, beginning below the hydranth and continuing well down the stalk but never as far as the pedal stolon. Often as many as 14 rings form but numbers up to 30 have been recorded (LAMBERT, 1935). The number of ephyrae formed seems to be proportional to the feeding and growth of the scyphistoma which shows itself phenotypically in the shape and depth of its column (BERRILL, 1949).

PERCIVAL (1923) gives embryological accounts of the formation and morphology of the longitudinal muscles of the polyp, discussing the formation of the manubrium from the strand connecting the two ephyrae rudiments, and the development of the peristomial pits and gastral filaments.

From each segment, or area between two ring-constrictions, there soon appear eight protrusions, each containing a diverticulum of the enteron. From the end of each protrusion a further lobe develops and this contains a diverticulum of the enteron which develops into a tentaculocyst or marginal sense organ. When the ephyrae rudiments have fully developed (see PERCIVAL, 1923; BERRILL, 1949) separation from the scyphistoma takes place. This comes about most probably by strong muscular action of the circular and radial muscle bands, causing the connecting strands between the ephyra and the one below it to sever close to the exumbrellar surface (HERIC, 1909). The columella (PERCIVAL, 1923) breaks almost simultaneously, thus releasing the ephyra.

The following times of strobilation have been put forward; November (HEROUARD, 1920); February or March (AGASSIZ, 1862; DELAP, 1905); April (HARGITT, 1910); autumn (HOLLOWDAY, 1951); winter (HALISCH, 1933); and December to March (LAMBERT, 1935). LAMBERT puts forward the following factors as conditions of strobilation; 1. a copious supply of the right food; 2. a critical temperature, and 3. a continuance of the food and oxygen supply during the critical period. HAGMEIER (1930 states that strobilation takes place below 9-10°C; in north-west Europe the strobilization temperature is stated to be between 4° and 11°C (VERWEY, 1942). In Norwegian and Danish waters, and possibly off Holland, ephyrae are found not only in spring but also in autumn, which would suggest that there is a second period of strobilization when the temperature falls to the critical range.

BERRILL (1949) discusses the physical factors involved more fully and VERWEY (1942), who bases his discussion on VAN DER MAADEN'S (1942) results, discusses these phenomena with reference to the Baltic.

The whole process of strobilisation is metamorphic in that according to CHUIN (1930) it involves histogenesis, histolysis, and phagocytosis. There are, however, irregularities in the budding off of the ephyrae. Some of the lower ephyrae rudiments may develop tentacles and after liberation move about for a short time before settling on the bottom, where they develop a stalk and pedal disk. Scyphistomas may also be formed by the oral disk which, when budded off, may settle down and form a stalk. Other irregular methods of scyphistoma formation and strobilisation are discussed by HEROUARD (1920a, 1920b) and PERCIVAL (1923).

When the ephyrae are all budded off the strobila then the temperature may have risen above the critical strobilating range and, according to HAGMEIER (1930) the scyphistoma will be able to produce buds and stolons. These develop from the lower part of the polyp stalk and may be of four types (GILCHRIST, 1937). BERRILL (1949) describes five forms of buds and stolons, three of which are applicable to Aurelia and a fourth possibly so. One of these, the fig-type bud, grows out from the polyp stalk, a hydranth developing on the side proximal to the parent hydranth and a stolon, by which it attaches itself to the substratum, from the other. By contraction of the stolon the budded polyp is drawn from the parent.

Another, the pedal stolon, grows straight out from the upper stalk and becomes attached by its distal end, reinforcing the attachment of the parent polyp's base. HEROUARD (1911) and GILCHRIST (1937) discuss this base and the production of the cementing substance. BERRILL (1949) describes the origin and development of stolons and their reconstitution on damage. HEROUARD (1911), PEREZ (1922), and HALISCH (1933) using Chrysaora and GILCHRIST (1937) using Aurelia describe their functions of attachment and locomotion.

The stolonic bud differs in that the development of the hydranth is often delayed until after attachment.

The hydra-type bud grows out forming a hydranth at its distal end and remains attached to the parent for a considerable time before the development of a pedal stolon at its base and consequent separation from the parent takes place.

Studies on regeneration and reconstitution of polyps, buds, and stolons have been made by HEROUARD (1921), HALISCH (1933), GILCHRIST (1937), BERRILL (1949), and CHILD (1951). The main conclusion from the studies would appear to be that there is a pronounced apico-basal gradient of growth potential in the polyp.

Studies on the nervous system have been made by KOMAI (1942) who could find no evidence of a nervous element in the scyphula of Aurelia.

According to PERCIVAL (1923) the ectoderm of the scyphistoma is ciliated between and on the tentacles and also on the proboscis. Food, in mucous chains, can be observed moving up to the mouth and along to the ends of the tentacles which bend over to the mouth transferring the food to the proboscis. It is then carried down to the enteron by the ciliated lining of the proboscis. Exhalent and inhalent functions of these cilia tracts in the proboscis can be carried on simultaneously, the inhalent channels being on the interradial ridges and the exhalent on the perradial angle. There is a strong current running from the base of the strobila to the uppermost ephyra; this is brought about by the aboral surfaces of the developing ephyrae which are ciliated and on which the currents move to the ends of the lappets.

The scyphistomae also feed by using the nematocysts on the tentacles. Infusoria (GEMMILL, 1921), copepods, decapod larvae, larval molluscs, more rarely young fish and other small plankton organisms (LEBOUR, 1923) are impaled by the nematocysts and the tentacles flick quickly towards the mouth immediately the prey touches them. CHUIN (1929) has made a study of the digestive vacuoles of the scyphistoma.

An interesting paper on cannibalism among the scyphistomae by KHALAF-EL-DUWEINI (1945) recounts how the attacker, with wide-open mouth, envelops its fellow scyphistoma, finally taking it wholly into its enteron.

c) Ephyra

Most ephyrae, when liberated from the stobila, have eight lappets and eight marginal sense organs. The sense organs are each situated at the end of an arm between the two arm lappets. The manubrium at first is a simple, four-cornered tube; the stomach gives rise to protrusions forming 16 unbranched, radiating canals going to the bell periphery, tentacles, and marginal sense organs or rhopalia. The tentacles grow in the eight adradial spaces. The manubrium then develops the mouth arms by extension of the four perradial corners of the lips and the peripheral ring canal develops by the radial canals forming T-shaped branches and the lateral branches of the Ts joining to form one continuous canal. Canals grow in from this ring canal, fusing with the eight perradial and interradial canals, making them branched in appearance.

Variation in the morphology have been studied by BROWNE (1894 and 1895a) who finds that the irregular ephyrae have no survival value over the normal but that the ratio of normal to abnormal forms remains constant over many years. LOW (1921) studied the production of abnormal ephyrae and their abnormalities quantitatively.

The ephyrae arms are provided with numerous stinging cells which, when prey comes against them, release their poison-carrying cnidotrichs. GEMMILL (1921) has made a detailed study of the feeding of ephyrae and finds that infusoria striking any part of the exumbrellar and subumbrellar surfaces of the arms and the periphery of the bell tend to be carried to the lappets where the greatest concentration of stinging cells is to be found. After release of the cnidotrichs and consequent impalement of the prey, mucous or other colloidal matter, produced most probably by cells of the lappets, impedes any attempt of escape. The ephyra arms then generally all stop beating and the prey-bearing arm and the manubrium bend towards each other, the prey being transferred to the manubrium. GEMMILL thinks the prey is carried down into the stomach by a "Central-manubrial current which is compensatory to the exhalent currents produced by ciliary action in the floor of the mouth angle grooves", but, according to him, this may not be the whole explanation.

The arms and manubrium have co-ordinated flexibility, being able to adjust their movements in relation to each other to handle awkwardly trapped prey. The diet of Aurelia ephyrae is, according to GEMMILL, infusoria chiefly, nauplius larvae and minute copepods occasionally, and according to DELAP (1905) Obelia, Phialidium, small copepods, fish eggs, and, as the ephyra increases in size, small ctenophores, pteropods and big Calanus. LEBOUR (1922) states that four-day old ephyrae feed on young fishes and crab zoeae. She found that when no young fishes were present amphipods, crab zoeae, and other crustacea, even small copepods and medusae, were taken.

ADULT MEDUSA

1) Anatomy

The adult medusa has a bell-diameter of 140 mm. to 250 mm., a height of 50 mm. to 90 mm., and a gonadal radius of about one third that of the bell-radius (MAYER, 1910). The bell is circular in shape except for eight small, interradial and radial notches in which the sense organs are situated. These organs are each composed of an exumbrellar ocellus formed from ectoderm, a subumbrellar pigmented eye derived from both ectoderm and endoderm, and a crystalline concretion of ectodermal origin. The four radial mouth arms have their eight free edges much convoluted with a median groove between them on the ventral side of the arm. The arm- and bell-edges have many hollow tentacles richly supplied with nematocysts. The four interradial, horseshoe-shaped gonads lie in the floor of the gastric cavity and according to GOODEY (1909) four interradial grooves on the floor of the stomach cavity carry the products from the gonads to the convolutions of the oral arms. The stomach is four-lobed and bounded by the gonads; from it eight unbranched adradial, four branched radial and four branched interradial canals arise and run out to the peripheral ring canal at the bell margin.

Variations from the normal form of Aurelia are fairly common. BALLOWITZ (1899) gives an account of these and summarises the literature up to that date. BROWNE (1895a, 1901) gives an account of the variation in the number of tentaculocysts, radial canals, and gonads and tries to relate the variations to each other. McINTOSH (1910) discusses the work of BROWNE (1901) and HARGITT (1905), estimating the percentage of individuals with various abnormalities. Other papers on variation in Aurelia are BROWNE (1894), DUNKER (1894), HERDMAN (1894), SORBY (1894), UNTHANK (1894), AGASSIZ and WOODWORTH (1896), HARGITT (1901) and McINTOSH (1911). STEINER (1935) gives an account of degeneration in the ephyra and medusa.

Scyphozoa in general, and Aurelia in particular, can live in sea water of a wide range of pH values. Sea water usually has a pH around 8.0 to 8.2; pH above or below these values cause the bell pulsations to increase in speed and finally stop (THILL 1937). Dilute sea water has no adverse effect on Aurelia, the medusae being found in the Baltic where salinity is 0.6‰ (BEADLE, 1943, SEGERSTRÅLE, 1951) and in other areas where salinity is over the average value (about 3.2%). The body fluids of Aurelia are in equilibrium with sea water and when the medium is dilute, then the body fluids are correspondingly dilute. Studies on these effects have been made by BENAZZI (1933), HESSE (1940), HYMAN (1940), and on Aurelia in artificial sea water by WIEDEMANN (1950).

The water content of the medusa is a much discussed subject in the literature. KRUKENBERG (1880) postulated that the medusa contained 95.34% water and had a dry weight of only about 4.66%. BATEMAN (1933) then stated the water content to be 99.1%. LOWNDES (1943) critisizing GORTNER (1938) and HYMAN (1938) showed the chemical composition of Aurelia to be "About 96% water, 3% salts, a trace of fat, /the amount being dependent on the state of the gonads/," only about 4% is said to be protoplasm. Reasons are given for drawing the above conclusions, LOWNDES (1942), and the method of distillation under xylol, which he used for his determinations, is described by LOWNDES (1940). Other workers in this field were MACALLUM (1903), MOEBIUS (HYMAN, 1938), THILL (1937), HYMAN (1938) gives a good summary of all the literature up to that date. ROBERTSON (1949) gives a general account of osmotic regulation in marine invertebrates and puts forward the results of his analyses of tissue fluid:

	Mg./gm. water						mg./l.	
	Na	K	Ca	Mg	Cl	SO_4	Protein	H_2O
Mesogloeal tissue								
Fluid I	10.45	0.411	0.390	1.235	19.65	1.458	0.4	981
Fluid II	10.42	0.397	0.383	1.240	19.82	1.043	0.9	981
I after dialysis	10.59	0.380	0.408	1.270	19.00	2.642	0.4	981
II after dialysis	10.52	0.385	0.406	1.251	19.08	2.656	0.9	981
Sea water	10.55	0.382	0.404	1.273	19.02	2.655	-	983

He sums up as follows: "The mesogloeal fluid of Aurelia showed the following compositions (expressed as percentage of concentration in the dialysed fluid): Na, 99%, K 106%, Ca 96%, Mg 97%, cl 104%, SO_4 47%.

This regulation seems to be brought about by elimination of sulphate and accumulation of potassium by the epithelium bounding the mesogloea, with resultant alteration in the remaining ions in conformity with osmotic equilibrium between the jelly and sea water." HENSCHEL (1936) also did work on the chemistry of Aurelia.

The respiration rate was worked on by THILL (HEILBRUNN 1944); he found the medusa to consume 0.0034 to 0.005 c.c/gm./hr. of oxygen at 13° to 17°C. MAYER (1914) studied the reactions of the medusa to increase of temperature.

HORRIDGE (1953) confirms the work of SCHAFER (1878) showing that there is a nerve network, visible under phase-contrast or oblique illumination. He made a study of the properties of this system at each contraction of the bell and showed that an impulse at any one point of a nerve consists of a single excitation. The bell pulsations are controlled by the marginal sense organs (ROMMANES, 1885) which each tend to send out impulses at differing rates from each other, but the one with the fastest rate controls the rest. ROMMANES and MORSE (1911) studied the reactions of the bell when deprived of one or more marginal sense organs. The rhythmic pulsations of the bell have been studied by BETHE (1908) and VERESS (1938) and neuro-muscular actions and responses to stimulation by BULLOCK (1943) and by PANTIN and DIAS (1953). LEE and MORSE (1910) put forward an explanation for the "summation of stimuli" effect which ROMMANES found on applying a series of electrical stimuli to the medusa. WOOLLARD and HARPMAN (1939) confirmed the work of SCHAFER (1878) and BOZZLER (1927) by showing the presence of synapses in the nerve net. The nerve of the medusa, therefore, has been found to conduct stimuli at a constant rate which has been stated to be 23 cms. per second without fatigue or decrement, thus producing the rhythmical pulsations of the bell which continue for long periods.

Other important studies on the nervous system of medusae have been made by BOZZLER (1926a, 1926b), HORSTMANN (1934a, 1934b), STEINER (1934) and VAN DER MAADEN (1939); SCHEERE (1948) gives an excellent general summary.

Aurelia medusae feed by entangling food particles in mucous, the food chains then being transported by ciliary mechanisms, external and internal, to the gastric cavity. The internal ciliation has been described by WIDMARK (1913) and the external by ORTON (1922). Food is collected by the submarginal tracts of cilia on the oral arms and is carried to the stomach via the mouth and gastro-genital canals. The ciliated surface of the exumbrella, of the area between the lappets, and of the subumbrella also collect food, taking it to the circular food groove and food pouches. When it reaches the gastric pouches, some digestion takes place before the internal currents carry it into the various canals (WIDMARK, 1913). There are oral arm basal tracts of cilia beating in the opposite direction to the submarginal tracts and these carry excretory matter, which has been delivered to them by the perradial canals and interradial and gastro-oral arm canals, to the exterior.

Studies on the gastro-vascular system of Aurelia have been made by WIDMARK (1911, 1913) and WETOCHIN (1926).

2) Feeding

ORTON (1922) concludes that adult Aurelia feed on coarse and medium plankton, supplemented by a smaller amount of finer plankton. In the stomach contents of the specimens he examined he found the following: "Gastropod larvae of Crepidula and others, Oyster larvae (black spat), Copepods of various species including Calanus and Harpactids, Epicaridian larvae in fair quantity, larvae of Cirrepedes and Copepods, Cypris larvae of Balanoids, young Polychaetes especially Polydora, a good number of Rotifers, algal threads, green and brown, in one case with a large colony of Vorticellids attached, eggs of Polychaetes or Rotifers, eggs and tadpoles of Ciona and other ascidians, nematode worms, tintinnoids, a number of diatoms of several species, and some sand grains."

LEBOUR (1923) examined specimens between 20 mm. and 25 mm. in diameter and found their food to consist of chiefly crab zoeae and some other coarse and medium plankton, including one young flatfish. She states that no fish have ever been recorded in the stomachs of Aurelia over 30 mm. diameter and that when she kept Aurelia of 60 mm. diameter in a tank with young fish, none of the fish were attacked. Aurelia below 30 mm. diameter, if kept in a tank in company with young fish, consume them all. SOUTHWARD (1949) states that the communications between the mouth and gastric pouches are wide in the very young Aurelia but become very narrow grooves as the medusa grows in size. This may partly explain the change from macrophagous feeding of the young stages to the strictly plankton feeding of the older stages. Southward is continuing his work on the feeding of Aurelia. An interesting paper by FOX and PANTIN (1944) discusses the pigments in Coelenterates in general; the chemical and physical properties are elaborated and mention of Aurelia aurita is made.

GEOGRAPHICAL AND SEASONAL DISTRIBUTION

Aurelia aurita is a cosmopolitan species, and it is found in almost all European seas. It can become acclimatised to live very near to its lethal temperature in the surface of the tropics or to withstand being frozen solidly into ice, but in either case loses its resistance to temperatures at the other end of the scale (MAYER, 1917). It has not been recorded from the east coast of Greenland so far, but has been found from Iceland and west Greenland (KRAMP, 1942), Faroes, Shetland and the sea area between Faroes, Shetland and the north coast of Scotland. Specimens have been collected in the Atlantic from around the position 60°45'N 9°30'W in July. In the latitude of Faroe they are further to the west of this position, individuals having been caught as far as 11°W in the month of September. It has been found around Rockall in July but has not so far been recorded from the surrounding areas.

Specimens have been collected from the Hebrides and Clyde sea area. In the Clyde, the ephyrae appear in late February (MARSHALL, 1925) and the mature adult medusae are found in August and September; Aurelia occurs off the north-west coast of Ireland and in the Irish Sea. According to MOORE (1937) ephyrae were found in the hatching ponds at Port Erin, Isle of Man, in January and February 1908, and in the laboratory aquarium in March, 1901. BROWNE (1895b), records that Scyphistomas were found on a pecten shell in Bay Fine in August 1892. Scyphistomas occur in Port Erin aquarium tanks throughout the year (MOORE, 1937b).

At Plymouth, scyphistomas have been recorded from June to March, strobilating from January to March. The ephyrae are common from March to April, the young medusae then appearing in greatest quantity in June. The medusae, being carried by the currents, make their appearance in the English Channel towards the end of summer. On the Dutch coast, the medusae are numerous from mid-May to mid-June, as the ephyrae make their appearance in February (VERWEY, 1942; VAN DER MAADEN, 1942).

Aurelia is found on the east coast of Britain, ephyrae being recorded off the Northumbrian coast in April (SANDERSON, 1930) but more likely making their first appearance earlier. The adults are found from March to November in the Firth of Forth, off the Tay mouth, up the Aberdeenshire coast, in the Moray Firth, extending up the northern coast to John O'Groats and Orkneys. Towards the end of the summer they are carried further out into the North Sea, occurring midway between England and Denmark in September and October, and have been collected from 2°E between latitudes 56°N and 61°N in October. The medusae occurring midway between the Shetlands and Norwegian coasts have probably originated from the shoals around Shetland.

Aurelia is found towards the north of the Norwegian coast but does not extend into true Arctic regions (VERWEY, 1942), and there appears to be an absence of time data on the appearance of the various stages of Aurelia in this area. It would appear, however, that they occur earlier in the year in the southern limits of their North Sea distribution than in the northern areas, and this also applies to times of disappearance in the autumn. This autumnal disappearance has been a disputed topic in the literature; some authors hold that after liberation of their sexual products the medusae disintegrate. The Aberdeen laboratory, however, has records of Aurelia medusae in late November and December in the Faroe-Shetland region. Fishermen assured EVANS and ASHWORTH (1909) that Aurelia were sometimes found in the trawls during winter and in the 12th Report of the Fishery Board of Scotland (part iii p.49) it is mentioned that near the Isle of May on 18th January, 1893, a few Aurelia were caught in "Garland's" Trawl. Most recent authors seem to be agreed that some Aurelia pass the winter in deeper water in the northern limits of their distribution but no medusae have yet been recorded in winter in their more southern habitats.

The bulk of the medusae, however, are budded off as ephyrae in the spring and, having liberated their sexual cells, die during the period August to November when they may drift seawards or on to the shores, a process of disintegration taking place in both cases.

An interesting paper by DAVIDSON and HUNTSMAN (1926) puts forward evidence postulating that the disintegration of masses of these medusae in Passamaquoddy Bay is possibly the direct cause of an autumn increase in the Phytoplankton in that area due to the fertilising action of their decay.

The temperature of the water controls the time of appearance of the ephyrae in the spring in the various localities. The temperature also controls their time of appearance at the surface and some authors are of the opinion that young medusae, if the surface of the water is still below a certain temperature, attach themselves to the bottom for a period (VERWEY, 1942).

According to the observations of MAYER (VERWEY, 1942), CALHOUN (1945) and HYMAN (1940) the medusae are active at the surface from the late afternoon on into the first half of the night. They then sink deeper and remain down in the morning hours. If, however, the sky darkens during the morning and stormy weather is prevalent then the medusae do not rise even though the light conditions are favourable. Other reports state that Aurelia is found at the surface in bright sunlight and I have observed them thus in the Firth of Clyde in August. For further information VERWEY (1942) should be consulted.

An extensive literature exists on the distribution of Aurelia in the Baltic. In recent decades there has been an increase in the salinity of the Baltic which has made it a favourable habitat for the medusa. Aurelia has consequently spread up as far as and into the Gulf of Finland and has been reported reproducing near Tvärminine at the mouth of the Gulf. A similar spread eastwards has taken place in the case of the American form of Aurelia aurita which has, in the last few decades (it is thought since 1910) colonised the west coast of Greenland.

The following, especially Verwey and Hela, are good reference papers for the Baltic area: BOGUCKI (1933), WIKSTRÖM (1936), VERWEY (1942), KÄNDLER (1950), HELA (1951) and SEGERSTRÅLE (1951).

KRAMP (1924) notes that CARUS (1884) found Aurelia in the following localities in the Mediterranean: Nice, Naples, Sicily, Trieste, west coast of Asia Minor, and Alexandria. GRAEFFE (1884) found examples in the Adriatic sea during February, March, and April, and occasionally as late as June. Aurelia is also recorded from the Bosphorus and Black Sea.

Thus Aurelia is found around all the European coasts except the most northern parts of the Norwegian coast and possibly the most northern part of the Baltic; late in the summer it is carried by the currents out from the coasts and in winter a few specimens may still be obtained in deep water, in the more northern limits at least of its distribution.

RELATIONS BETWEEN AURELIA AND FISH

a) Commensalism

There are frequent references in the literature to the commensal association of young fish with jellyfish, referring either mostly or exclusively to Cyanea; e.g. DAMAS (1909), KRUMBACH (1928, 1930), LUNEL (1883). Aurelia seems to be much less attractive, possibly because its lesser size or great transparency makes it a less adequate shade, or possibly because its vertical movements make such a commensalism unsuitable. Although DAMAS (1909) suggests that the commensalism with Cyanea may form an important part of the life history of various gadoids it does not seem likely to be essential (HJORT and DAHL, 1900). Young fish may find food there in the amphipods such as Hyperia which are often commensal with jellyfish, living on food in the mucous strings and this has thus been suggested as beneficial to both parties as the young fish will help to control the numbers of amphipods feeding at the expense of the medusae.

HJORT and DAHL (1900) do refer to Aurelia, particularly in connexion with a "jellyfish stage" of whiting (p.118), but are convinced that the jellyfish are not essential to the development of whiting or other gadoids. The literature refers chiefly to cod, saithe, whiting and Caranx, but Scottish investigations show that Onos up to about 40 mm. is one of the most abundant fish associated in this way, Aurelia not so often being the host as Cyanea.

b) Effect on fisheries

On the fishing grounds around Faroes, shoals of Aurelia appear in late summer and become so numerous that the fishermen are forced to move to other grounds. The following account has been synthesised from skippers' reports. The first appearance of medusae - Cyanea at first - in sufficient numbers to present difficulties to trawling in 1952 was reported in the second week of May on Faroe Bank; there the nuisance was described as "great slithers, brownish in colour and over four feet in diameter". At this time the summer fishing had not commenced at Faroes but the large brown jellyfishes seemed to disappear and were absent when the Faroes daylight fishing reached its intensity at the beginning of June. Fishing continued until about the third week of July when catches were falling in amount and skippers were reporting new slithers, this time Aurelia, on these grounds, but the numbers of Aurelia were not then sufficient to affect the actual fishing.

By the first week of August fishing was found to be best at night and reports of these slithers were still being made; in the first week of September they were stated to be present in large quantities. At this time, however, they were still in the surface waters and, therefore, not having much effect on trawling. A week later large numbers of jellyfish, presumably still Aurelia, were reported on the Myggenaes grounds and about 25th September it was said that the best grounds were off Sumbo, but at this time bad weather and medusae were impeding fishing. By the end of September fishing was becoming slack all around Faroes and in mid-October all craft found fishing unprofitable in this area and were forced to leave. By the end of October the North Faroese grounds were badly affected but the southern grounds had improved. In mid-November reports of the disappearance of the "slithers" from the Faroese grounds came from the skippers and by 20th November the catches had greatly improved on those of the previous weeks.

On almost exactly the same date in 1953, that is, the third week of July, the first reports of "slithers" (Aurelia) were made. A week later they had commenced to gather in quantity and the trawler skippers on the grounds reported a decline in the amount of fish obtainable. By the end of the first week of August, Aurelia were present in shoals and fishing craft were taking longer to fill their holds before returning to port. On the west Faroese grounds, but not on the east, skippers stated that in their opinion the Aurelia were now found at all depths, including the bottom, with the result that the shoals of fish "scattered". On 20th August they were reported "on the sea bed and 'scaring' off shoals on all but the south-east grounds off Fuglo and south of Sumbo Holm"; the end of August saw the end of the summer fishing in this area with shoals of fish very scarce. The catches did not improve until the medusae disappeared.

In these two years Aurelia appeared on the Faroese grounds about the third week of July but in 1952 did not seriously hamper fishing operations until mid-September. The first grounds reported as affected were those on the west side, followed by a spread to all others. From the evidence the southern grounds are free from the medusae first, the northern grounds last.

These jellyfish can be present in immense quantities and some skippers state that almost immediately the trawl goes down it becomes filled; when hauled to the surface the cod-end is usually burst open due to the weight of jellies. Not only is the cod-end filled but a good part of the bag as well, and the square is often also burst open. Very few fish are found in the net even if it is fairly intact but whether the fish are still on the grounds or not cannot be stated with certainty. If the net is very soon clogged with Aurelia it would form a solid mass dragged along the bottom and no fish are likely to enter even if they are present on the bottom. The fish may still be present in the area but dispersed above the bottom, as even if Aurelia is spread through the various water layers there will still probably be an aggregation at the bottom with less dense areas above, to which the fish might move. A pelagic trawl for fish off the bottom would not be likely to be successful as the jellyfish distributed throughout the layers would still clog the net, and the fish would not be congregated at any particular depth.

There is a variability of the time when the slithers become a serious menace; sometimes it is as early as August, sometimes as late as October. Always, however, they increase in numbers in the surface waters for a period, then more deeply possibly as the upper layers become heavily populated less plankton food is available. When they sink the trawling is affected and catches diminish. The plankton also becomes temporarily reduced but this would not cause any immediate ill effect on the bottom living organisms which are the food of the commercial white fish.

If the fish do move elsewhere, although this seems unlikely, and food shortage is not the prime factor, do these masses of Aurelia emit some substance which affects the fish, or affects the fish through affecting the bottom fauna? Or is it that the Aurelia are so numerous as to be competitive for living space? If the fish do move off the ground where do they move to and do they always proceed to the same area? These are questions which still require an answer.

The available evidence seems to indicate that the Aurelia population at Faroe is self-contained. Aurelia is not reported from the east coast of Greenland, and I have found no records of its occurrence midway between Iceland and Faroe, so that origin from the west seems unlikely. The current systems involved preclude colonisation from the North Sea, or Norwegian coasts, and although there might be occasional opportunities for colonisation from the west Irish or Scottish areas the timing of the appearance of Aurelia at Faroe would appear to be too regular - only records from two years are given here, but the fishermen's evidence over many years suggests such a regularity.

The rocky topography of the Faroese coast is ideal for the development of Aurelia scyphistomas and, as conditions there would be relatively uniform, all the scyphostomas would tend to strobilate about the same time. The circulating current system round Faroe would then distribute the ephyrae to the fishing grounds where they first become noticed because of the size they have then attained.

The only reference in the literature to this problem that I can find is a mere mention of it in Rae (1947).

Almost the same problem is present in the Gulf of Finland each year. Hela (1951) in summing up his list of reports in the changing population density of Aurelia in the different areas says:

"These reports, although disagreeing in some details, plainly show that (1) since about 1940 the eastern border of the regular occurrence of Aurelia has shifted considerably further eastwards (Kaunissaari, Tessjö), that (2) apparently at the same time the abundance of Aurelia has generally increased also in other areas (possibly excepting the southern part of the southwestern archipelago), and that (3) particularly in autumn 1949, Aurelia has been found in some localities in the east (Klamila, Tammio) where it has never been seen before as far as is known. The Aurelia's found in the eastern part of the Gulf of Finland, on the other hand, may have their origin in the southern part of the Gulf, where they most likely occur in greater abundance, and further to the east, owing to the greater salinity, than on the northern coast. Also it is worth noting the reports that during warm summers Aurelia is possibly more than usually numerous."

Among the above summarised reports are the following .... "Tammisaari: Tofö, since 1921; not found for a long time previously: occurs now yearly. A peak appeared between 1943-47, causing harm to the regular fishing. In 1948-49 the number was reduced; Skedö, increasing occurrence since 1939. It has become a menace to fishermen because during windy weather it enters the net fish-traps set for pike, causing the death of the pike; ....."

He goes on to give the following reports which are also worth quoting as they show the similarity between this area and the Faroes region.

"EK. Pyhtää: Kaunissaari; Aurelia was first seen in summer 1940 after strong south winds in the first half of August. This slimy animal sometimes got entangled in the fishing nets in such large quantities that the latter often looked as if they had been taken out of a fruitcooking pot. Thereafter it has appeared usually in August after hard south and southwest winds, though it is not certain whether it occurs every summer. Even last summer it appeared about the same time. When the weather becomes cold, it disappears. We fishermen have noticed that where it is very numerous the herring and sprat do not thrive.

U. Tammisaari: Skedö; they are small about midsummer, but grow bigger towards the end of November when the autumn storms wash a great number of them on to the shores, and the rest disappear to an unknown fate, only to reappear about midsummer of the following year still more numerous, as a great annoyance to the fishermen because the net fish-traps become so packed with them that the hoops break when the traps are examined.

U. Tammisaari: Halstö; as the wind drove it towards the fishing places, whitefish catching was still hampered about December 1, 1949.

V. Hiittinen; I remember well that Aurelias have appeared since my childhood, first small ones in the spring, but already during the summer they grew bigger. They occur in large amounts at first near to the surface but later in the autumn they sink deeper. Last autumn (1949) I found Aurelia still very numerous in my large fish-traps at the end of November.

A. Hammarland: Tillholm; Aurelia has occurred here for many years and increases year after year. It is impossible to fish with herring nets in August; they become packed with Aurelia."

Here again they first are found in the surface waters but later are found deeper. Whether they are found throughout the depths or when they "sink deeper" they disappear from the surface is not stated. Trawling is not directly mentioned in the above reports, net fish-traps and surface herring nets being discussed. In the third report, from Tammisaari, "Whitefish catching" is mentioned and this must involve a demersal net, possibly a trawl but more likely the Danish seine net.

One point is clearly expressed in the reports in this paper, namely, that the greatest numbers of medusae are found in the warmest summers with plenty of sunlight. The successful survival of Aurelia would depend first on the presence of a suitable substratum for the settlement of the planulae larvae, and on the presence of the necessary nourishment, and later on the water reaching the critical temperature, to enable the strobilisation of the scyphistomas to take place successfully and yield a maximum number of ephyrae per strobila. Thus if the water temperature should rise earlier one year than another, the medusae would be expected to appear earlier. In Faroese waters the inshore water temperatures were higher in May, June and July 1953 than in the corresponding months in 1952. In 1953 the medusae were plentiful enough to affect the fishing in the first week of August, in 1952 with colder temperatures the medusae did not hamper fishing until mid-September.

In HELA (1951) there are two reports referring to herring and sprat, and LUCAS and HENDERSON (1937) also suggest that where Aurelia is numerous the herring are scarce.

There appears to be a lack of direct scientific observations as opposed to reports from trawlermen which, though very helpful, are sometimes insufficiently detailed, or vary quite considerably. In Faroe, data on water temperatures, sunlight, times of appearance and disappearance of Aurelia would be required over a period of a few years before any general conclusions could be drawn. Some scientifically constructed experiments should also be made to find out if and why herring or other fish avoid masses of Aurelia; this survey of the literature has yielded few definite conclusions on this topic.

REFERENCES

AGASSIZ, A. and WOODWORTH, W. McM., Variations in Aurelia. Bull. Mus. Comp. Zool. at Harvard College, Vol.30, No.2, 1896.

AGASSIZ, L. Contributions to the Natural History of the United States of America, 4, 1-380, Boston, 1862.

BOLLOWITZ, E. Uber Hypomerie und Hypermerie bei Aurelia aurita LAM. Arch. für Entwick. der Organismen Bd. VIII, pp.239-52, 1899.

BATEMAN, J. B. Water Content of Medusae. Science, N. Y., 77, 2002, 1933, p.451.

BEADLE, L. C. Osmotic Regulation and the Faunas of Inland Waters. Biol. Rev. Cambridge, 18, 4, 1943, pp.172-83.

BEER, G. R. de, and HUXLEY, J. S. Dedifferentiation and Reduction in Aurelia. Q. J. M. Sci., London, 68, 1924, pp.471-79.

BENAZZI, M. l'influenza dell' aqua di mare diluita sui movimenti ritnici delle meduse. Bull. Zool. Torino 4, 1933, pp. 211-19.

BERRILL, N. J. Developmental Analysis of Scyphomedusae. Biol. Rev. Cambridge, 24, 4, 1949, pp.393-410.

BETHE, A. Die Bedeutung der Blektrolyten für die rhythmiscen Bewegungen der Medusen. I. Teil die Wirkung der Seewasser enthaltenen Salze auf die normale Meduse. Pflüger's Arch. f. d. ges. Physiol. 124, pp.541-77, 1908.

BIGELOW, R. P. The Anatomy and Development of Cassiopea xamachana. Mem. Boston Soc. Nat. Hist., 5, p.193, 1900.

BIGELOW, H. B. Scyphomedusae from the Arcturus Oceanographic Expedition. Zoologica, N.Y., 8, 1928, pp.495-524.

Plankton from the Offshore Waters of the Gulf of Maine. Bull. U.S. Bur. Fish. Washington, 40, (2), 1, 1928, pp.1-509.

Plankton of the Bermuda Oceanographical Expeditions, VIII. Medusae taken during the years 1929 and 1930. Zoologica, N.Y. Zool. Soc., XXIII, 5, 1938, pp.99-187.

BOGUCKI, M. Sur le cycle evolutive de l' Aurelia aurita L. dans les eaux polnaises de la Baltique. Fragmenta faun. Mus. Zool. Polon. 2, 1933, pp.117-19.

BOZZLER, E. Sinnes- und nervenphysiologische Untersuchungen an Scyphomedusen. Z. vergl. Physiol. 4, pp.137-89, 1926a.

Weitere Untersuchungen zur Sinnes- Nervenphysiologie der Medusen. Erregungen, Funktion der Randkorper, Nahrungsaufnahme. Z. vergl. Physiol. 4, pp.797-817, 1926b.

Untersuchungen über das Nervensystem der Coelenteraten. Z. vergl. Physiol. 6, pp.255-63, 1927.

BROWNE, E. T. Medusae of the Scottish National Antarctic Expedition (Scotia). 1902-1904. R. Soc. Edin. Trans. Vol. XLVI, 1909.

Aurelia aurita. Nature, London, Vol. 1, p.524, 1894.

On the Variations of the Tentaculocysts of Aurelia aurita. Q. J. M. Sci., (N.S.), 37, pt.3, p.245 1895a.

Report on the Medusae of the L. M. B. C. District. Fauna Liverpool Bay, Rep., IV, p.371, London 1895b.

Variation in Aurelia aurita. Extr. Biometrica Vol. 1, No.1, Oct. 1901.

BUHK, F. Aufzucht von Ohrenquallen, Aurelia aurita L., im aquarium. Wschr. Aquar. Terrarienk. Braunschweig. 36, 1939, pp.433-35.

BULLOCK, T. H. Neuromuscular Facilitation in Scyphomedusae. J. Cell. Comp. Physiol. 22, pp.251-72, 1943.

CALHOUN, J. B. J. Tennesee Acad. Sci. 20 (2), pp.228-32; (3), pp.291-308; (4) pp.373-78, 1945. 21 (2), pp.208-316; (3) pp.281-91, 1946.

CARUS, J. V. Prodromus faunae mediterraneae, Vol.1, 1884.

CHILD, C. M. Physiological Dominance in the Reconstitution of the scyphistoma of Aurelia. Physiol. Zoöl. 24, 1951, pp.177-85.

CHUIN, T. T. Sur les vacuoles digestives chez le scyphistome. C. R. Soc. Biol. Paris 102, 1929, pp.825-27.

Le cycle evolutive du scyphistome de Chrysaora. Trav. Stat. biol. Roscoff, 8, 1, 1930.

CLAUS, C. Studien über Polypen und Quallen den Adria. Denkschr. Akad. Wiss. Wien. 1877.

Ueber die Entwicklung des Scyphistoma von Cotylorhiza, Aurelia, und Chrysaora, 1-11, Arb. zool. Inst. Univ. Wien. Vol. 9, pp.85-128, Vol.10, pp.1-70, 1892.

CONKLIN, E. G. The Habits and Early Development of Linerges mercurius. Publ. Carneg. Inst. No. 103, p.153, 1908.

DAMAS, D. Contribution a la biologie des Gadides. Rap. et Proc. Verb. Cons. Perm. Int. Explor. Mer, X, 3, 1909, pp.1-277.

DAVIDSON, V. M. and HUNTSMAN, A. G. The Causation of Diatom Maxima. Trans. R. Soc. Canada, XX, V, 1926.

DELAP, M. J. Notes on the Rearing in an Aquarium of Aurelia aurita l. and Pelagia perla. Rept. Fish. Ireland 1905, Sci. Invest.

DUNKER, G. Ueber ein abnormes exemplar von Aurelia aurita. Arch. Naturgesch, Jahrg. lx, p.719, 1894.

EVANS, W. and ASHWORTH, J. H. Some Medusae and Ctenophores from the Firth of Forth. Proc. R. Physic. Soc. Edin. 17, 1909, pp.300-311.

FOX, D. L. and PANTIN, C. F. A. Pigments in Coelenterata. Biol. Rev. Cambridge, 19, 4, 1944, pp.121-34.

GEMMILL, J. F. Notes on the Food Capture and Ciliation of Aurelia Ephyrae. Proc. R. Physic. Soc. Edin. Vol. XX, 1921, pp.222-225.

GILCHRIST, F. G. Rearing the Scyphistomas of Aurelia in the Laboratory. In P. S. Galstoff and others 'Culture Methods for Invertebrate Animals', p.143, Ithaca 1937.

Budding and Locomotion in the Scyphistomas of Aurelia. Biol. Bull. Wood's Hole, 72, pp.99-124, 1937.

GOETTE, A. Entwicklungeschichte der Aurelia aurita und Cotylorhiza tuberculata. Abh. Entwick. der Thiere 4, 1887.

Vergleichende Entwicklungeschichte von Pelagia noctiluca. Re. z. wiss. Zool. 55, p.645, 1893.

GOODEY, T. A further Note on the Gonadial Grooves of a Medusa, Aurelia aurita. Proc. Zool. Soc. London, 1909, Vol.1, pp.78-81.

GORTNER, R. A. Outlines of Biochemistry. London: Chapman & Hall, 2nd Ed., p.276, 1938.

GRAEFFE, E. Uebersichte der Seethierfauna des Golfes von Triest. III Coelenteratea. Arb. Zool. Inst. Wien., Tom. V, Heft 3, 1884.

HADZI, J. Einige Kapitel aus der Entwicklungeschichte von Chrysaora. Arb. Zool. Inst. Univ. Wien. 17, pp.17-44, 1907.

HAECKEL, E. Das System der Medusen, Bd. 1, Heft 2. System der Acraspeden. [1880].

Metagenesis und Hypogenesis von Aurelia aurita. Ein Beitrag zur Entwicklungeschichte und zur Teratologie der Medusen. Jena, 1887, 4to, 36 pp.

HAGMEIER, A. Die Züchtung verschiedener wirbelloser Meerestiere. Abderhalden's Handbuch d. biol. Arbeitsmethoden. Abt. IX, 5, pp.552-72, (Scyphozoa: pp.553-63). 1930.

HALISCH, W. Beobachtung an Scyphopolypen. Zool. Anz. Leipzig, 104, pp.296-304. 1933.

HARGITT, C. W. Variation among Hydromedusae. Biol. Bull. Vol. 2, No. 5, pp.221-255. Boston, 1901.

Variation among Scyphomedusae. J. Exper. Zool., Baltimore, Vol. ii, pp.547-84. 1905.

HARGITT, C. W. and G. T. Studies in the Development of Scyphomedusae. J. Morph., 21, pp.217-62. 1910.

HARGITT, G. T. Germ cells of Coelenterates, VI General Considerations, Discussions, Conclusions. J. Morph. 33, 1920, pp.1-59.

HEILBRUNN, L. V. Outline of General Physiology. Saunders. 1944.

HELA, I. On the Occurrence of Jellyfish, Aurelia aurita, on the south coast of Finland. Arch. Soc. 'Vanamo' 6, No.1, 71, 1951.

HENSCHEL, J. Untersuchungen über den chemischen Sinn der Scyphomedusen Aurelia aurita, und Cyanea capillata und der Hydromeduse Sarsia tubulosa. Wiss. Meersuntersuch Abt. Kiel (N.F.) 22, 1936, pp.21-42.

HERDMAN, W. A. Pentamerous Aurelia. Nature, London, Vol. 1, p.426, 1894.

HERIC, M. Zur Kenntnis der Polydisken Strobilation von Chrysaora. Arb. Zool. Inst. Wien. Vol. 17, pp.95-108, 1909.

HEROUARD, E. Sur le mode de fixation au soles des scyphistomes par des tonofibrilles. Paris Bull. Soc. Zool. 36, pp.15-19. 1911.

Les monstres doubles du scyphistome. C.R. Acad. Sci. Paris, 170, 5, pp.295-98. 1920a.

Existence of Bistrobilisation; sa signification et ses consequences. Bull. Soc. Zool. Paris, 45, pp.162-69. 1920b.

Retablissement de l'equilibre de correlation par laceration chez le scyphistome. Bull. Soc. Zool. Paris, 46, pp.68-72. 1921.

HESSE, R. Osmoregulation als- Energie-verbrauch. Jahrb. Preuss. Akad. Wiss. Phys.-Maths. Kl. 1940, pp.79-80.

HJORT, J. and DAHL, K. Fishing Experiments in Norwegian Fjords. Rep. Norwegian Fish. Mar. Invest., Vol. 1, No.1, 1900. pp.1-215.

HOLLOWDAY, E. D. Planula, Hydratuba, and Ephyra Stages of the Common Jellyfish. Microscope 8, 8, 1951, pp.193-98.

HORRIDGE, A. An Action Potential from the Motor Nerves of the Jellyfish, Aurelia aurita Lamarck. Nature, London, 171, 4348, p.400. 1953.

HORSTMANN, E. Untersuchungen zur Physiologie der Schwimmbewegungen der Scyphomedusae. Pfleuger's Arch. 234, 1934, pp.406-20.

Nerven- und Muskelphysiologische Studien zur Schwimmbewegung der Scyphomedusen. Pfleuger's Arch. 234, 1934, pp.421-31.

HYDE, I. H. Entwicklungeschichte einiger Scyphomedusen. z. wiss. Zool. 58, pp.531-65. 1894.

HYMAN, L. H. Water Content of Medusae. Sci. 87, pp.166-67. 1938.

Observations and Experiments on the Physiology of Medusae. Biol. Bull. Wood's Hole, 79, 2, 1940, pp.282-96.

JÖRGENSEN, M. Beiträg zur Kenntnis der Eibildung, Reifung, Befruchtung, und Furchung bei Schämmen (Syconen). Arch. f. Zellforsch. Bd. 4, 1910.

KÄNDLER, R. Jahreszeitliches Vorkommen und unperiodisches Auftreten von Fischbrut, Medusen und Dekapodenlarven im Fehmarnbelt in den Jahren. 1934-43. Ber. deutsch. wiss. Kom. Meeresforsch. Stuttgart N.F. 12, 1, 1950, pp.49-85.

KHALAF-EL-DUWEINI, A. Cannibalism in Aurelia. Nature, London, 155, 3933, 1945, p.337.

KOMAI, T. The Nervous System in Some Coelenterate Types. 2. Ephyra and Scyphula. Annot. Zool. Jap. 21, 1942, pp.25-29.

KRAMP, P. L. Danish Oceanographical Expedition 1908-1910. Vol. II. Coelenterata. 1924.

The Godthaab Expedition, 1928. Medusae. Medd. Grønland, 81, 1, 1942, pp.3-168.

KRUKENBERG, C. F. W. Über den Wassergehalt der Medusen. Zool. Anz. Leipzig, 3, p. 306, 1880.

KRUMBACH, T. Scyphozoen. Deutsch. Tierwelt, 4, 1928, pp.161-188.

Scyphozoa. Tierwelt Nord. v. Ostsee, IIId, 1930, p.1-88.

LAMBERT, F. J. Jellyfish. The Difficulties of the Study of Their Life History and Other Problems. Essex Nat., 25, 2, 1936, pp.70-86.

LEBOUR, M. V. The Food of Plankton Organisms I. J. Mar. Biol. Assoc. Plymouth, (N.S.), 12, 1922, pp.644-47.

The Food of Plankton Organisms, II. J. Mar. Biol. Assoc. Plymouth, (N.S.), 13, 1923, p.70.

LEE and MORSE Nervous Stimuli. Proc. Soc. Exper. Biol. and Medicine, New York, Vol. 7, p.38, 1910.

LOW, J. W. Variation in Ephyrae of Aurelia aurita. Proc. R. Physic. Soc. Edin., Vol.XX, pt.5, 1921, pp.226-35.

LOWNDES, A. G. Rapid Determination of Water in Animals and Plants. Nature, London, 148, pp.594-95, 1940.

Percentage of Water in Jellyfish. Nature, London, 150. pp.234-35, 1940.

Some Applications of the Displacement Method of Weighing Living Aquatic Organisms. Proc. Zool. Soc. London, (A), 113, 1943, pp.28-43.

LUCAS, C. E. and HENDERSON, G. T. D. On the Association of Jellyfish and Other Organisms with Catches of Herring. J. Mar. Biol. Assoc. Plymouth, (N.S.), 21, 1, 1936, pp.293-304.

LUNEL, G. Sur un cas de commensalism d'une Caranx et d'une Crambessa. Rec. zool. suisse, Bd. 1, 1883.

MAADEN, H. VAN DER. Über das Sinnesgrübchen von Aurelia aurita Linne. Zool. Anz. Leipzig, 125, 1939, pp.29-35.

Beobachtung über Medusen am Strande von Katwijk aan Zee (Holland) in den Jahren 1933-37. Arch. Neerland Zool. 6, (4), pp.347-62, 1942.

MACALLUM, A. B. J. Physiol. 29, pp.213-41, 1903.

MARSHALL, S. M. A Survey of Clyde Plankton. Proc. R. Soc. Edin., 45, 1925, pp.117-41.

MAYER, A. G. Medusae of the World, Vol. III. Carnegie Inst. Publ., 109, 3, 1910.

Papers from the Tortugans Laboratory of the Carnegie Institute, 6, 1, 1914.

Report upon the Scyphomedusae collected by the United States Bureau of Fisheries' Steamer 'Albatross' in the Phillipine Islands and Malay Archipelago. Smithsonian Inst., U.S. Nat. Mus., Bull. 100, 1 (3), 1917, pp.175-233.

McINTOSH, D. C. Variation in Aurelia aurita. Proc. R. Physic. Soc. Edin., Vol. XVIII, No. 2, pp.125-43, 1910.

Note on Variation in the Jellyfish, Aurelia aurita. Ann. Scot. Nat. Hist., 20, pp.25-29, 1911.

MINCHIN, E. A. Note on the Mode of Attachment of the Embryos to the Oral Arms of Aurelia aurita. P. Z. S. 1889, pp.583-85.

MOORE, H. B. Marine Fauna of the Isle of Man. Proc. L'pool. Biol. Soc., 50, 1937a, pp.38-57.

Marine Fauna of the Isle of Man. University of Liverpool Press, 1937b.

MORSE, Pulsations in Scyphomedusae Deprived of their Marginal Sense Organs. Sci., New York, 31, pp.544-45, 1911.

NETCHAEFF, A. and NEU, W. Aurelia aurita L. und Pilema (Rhizostoma) pulmo Haeck. im Schwarzen Meer und im Bosphorus. Zool. Anz. Leipzig, 129, 1940, pp.61-63.

ORTON, J. H. Mode of Feeding of Jellyfish, Aurelia aurita, on the Smaller Organisms of the Plankton. Nature, London, 110, 1922, pp.178-79.

PANTIN, C. F. A. and M. VIANNA DIAS. Rhythm and After-discharge in Medusae. An. Acad. Brazil Cienne, 24, (4), 1953.

PALMEN, E. Untersuchungen über die Strömungen in den Finnland umgebenden Meeren. Soc. Scient. Fenn., Comm. Phys.-Maths., 5, 12, pp.1-94, 1930.

PERCIVAL, E. On the Strobilisation of Aurelia. Q. J. M. Sci. London, 67, 1923, pp.85-100.

PERON, F. and LESUEUR, C. A. Tableaux des caracteres generiques et specifiques des toutes les especes de Meduses connues jusqu' a ce jour. Ann. Mus. d' Hist. Nat., Tome 14, 1809.

PEREZ, C. Observations sur la multiplication gemmipore d' une scyphistome. Bull. Biol. 56, pp.244-74. 1922.

RAE, B. B. Review of the Scottish Lemon Sole Fishery at Faroe with Special Reference to the Years 1933 to 1938. J. Cons. Inter. Explor. Mer, Vol. XV, No. 1, 1947, pp.61-68.

RENTON, R. M. On the Budding of the Scyphistoma. Proc. Zool. Soc. London, 1930, pp.893-96.

ROBERTSON, J. D. Ionic Regulation in Some Marine Invertebrates. J. Exper. Biol. Cambridge, 26, 2, 1949, pp.182-200.

ROMMANES, G. J. Physiological Studies. Inter. Sci. Series, Vol. 49, 1885.

SANDERSON, A. R. The Coelenterate Plankton of the Northumbrian Coast during the Year 1924. J. Mar. Biol. Assoc. Plymouth, 17, 1930, pp.219-32.

SCHAFER, E. A. Phil. Trans. R. Soc., 169, p.563, 1878.

SCHAXEL, J. Die Eibildung der Meduse Pelagia noctiluca. Festschr. R. Hertwig. Bd. 1. 1910a.

Die Morphologie des Eiwachstrums und der Follokelbildungen bei den Ascidien. Arch. f. Zellforsch., Bd.4, 1910b.

Das Verhalten der Chromatins bei Eibildung einiger Hydrozoen. Zool. Jahrb., Abth. Anot. Bd.31, 1911a.

Das Zusammenwirken Zellbestandteile bei der Eireifung, Furchung und ersten Organbildung der Echinodermen. Arch. f. mikr. Anat., Bd. 76, pp.543-607, 1911b.

Plasmastrukten, Chondriosome und Chromidien. Anat. Anz., Bd. 39, 1911c.

SCHEERE, B. T. Comparative Physiology. Chapman & Hall Ltd., London, 1948.

SEGERSTRALE, S. G. The Recent Increase in Salinity of the Coasts of Finland and its Influence upon the Fauna. J. Cons. Int. Explor. Mer, 17, 1951, pp.103-10.

SMITH, F. Gastulation of Aurelia flavidula. Bull. Mus. C. Z. XXII, No. 2, pp.115-25, 1891.

SORBY, H. C. Symmetry of Aurelia aurita. Nature, London, Vol. 1, p.476, 1894.

SOUTHWARD, A. J. Ciliary Mechanisms in Aurelia aurita. Nature, London, 163, 4144, 1949, pp.536.

STEINER, G. Sense organs in Aurelia aurita L. Biol. Zbl. Leipzig, 54, 1-2, 1934, pp.102-5.

Über eine eigenartige Degeneration bei Ephyren und Medusen von Aurelia aurita. Zool. Anz. Leipzig, 109, 1935, pp.176-81.

STIASNY, G. Die Scyphomedusen Sammlung de Naturhistorischen Reichsmuseum in Leiden. II. Zool. Mededeel., Leiden, V, 1919, pp.66-99.

Die Scyphomedusen-Sammlung von Dr. Th. Mortensen nelst anderen Medusen aus dem Zoologischen Museum der Universität in Kopenhagen. Papers from Dr. Mortensen's Pacific Expedition 1914-16, XII. Vidensk. Medd. nat. For. Kjøbenhavn, 73, 1922, pp.513-55.

STORROW, B. Young Herrings and 'Jellyfish' at Cullercoats. Naturalist, London, No. 780, 1922, p.18.

TEISSIER, L. and G. Quelques observations sur les Jeunes scyphistomes de Chrysaora hysoscella (L). Bull. Soc. Zool. Fr., 50, p.412-19, 1925.

THILL, H. Beiträge zur Kenntnis der Aurelia aurita (L). Z. wiss. zool. Leipzig, 150, 1937, pp.51-96.

TSUKAGUCHI, R. Über die feinere Struktur des Ovarialeies von Aurelia aurita L. Stockholm Geol. För. Forg. 35, 1914, pp.407-38.

UCHIDA, T. Anatomy and Development of Mastigias papua. J. Fac. Sci. Tokyo Univ. (Sect. 4, Zool.), 1, 45, 1926.

UNTHANK, H. W. Aurelia with Pentamerous Symmetry. Nature, London, Vol. 1, p.413, 1894.

USSING, H. Bidrag til Aurelia aurita's Biologi i Mariagerfjiord. Vidensk. Medd. Naturb. Foren. Kjφbenhavn 84, 1927, pp.91-106.

VERESS, E. Studien über die rhythmiscen Bewegungen der Medusen. Allat. Kozlem. Budapest, 35, 3-4, 1938, pp.153-70.

VERWEY, J. Die Periodizitat im Auftreten und die aktwin und passuren Bewegungen der Quallen. Arch. Neerland Zool. 6, (4), pp.363-468, 1942.

WIEDEMANN, Ed. Die Haltung der Ohrenqualle, Aurelia aurita L., in künstlichen Seewasser. Zool. Gart. Leipzig, 16, 5, 1950, pp.186-87.

WETOCHIN, I. A. Ueber die Arbeit des Fluninerepitels des Gastovascularsystem der Meduse Aurelia aurita (L). Lam. Travaux de la Stat. Biol. de Murman, Vol. I, 1926.

WIDMARK, E. M. D. Ueber die Gastrovaskularströmungen bei Aurelia aurita L. und Cyanea capillata Eschr. Zool. Anz. 38, pp.378-82, 1911.

Über die Wasserströmungen in dem Gastrovaskularapparat von Aurelia aurita L. Zs. Allg. Physiol., Jena, 15, 1913, pp.33-48.

WIETRZYKOWSKI, W. Recherches sur le development des Lucerniaires. Arch. Zool. exp. gen. (5), 10, 1, 1912, pp.1-95.

WIKSTRÖM, D. A. Beobachtung über die Ohrenquallen (Aurelia aurita L.) in den Scharen S.W.-Finlands. Mem. Soc. Fauna Flora Fennica 8, 1932, 33, pp.14-17.

Iakttagelser om öronmaneten (Aurelia aurita L.) i S.W.-Finlands skärgard. Mem. Soc. Fauna Flora Fennica II, pp.216-26, 1935.

WOOLARD, H. H. and HARPMAN, J. A. Discontinuity in the Nervous System of Coelenterates. J. Anat. London, 73, 1939, pp.559-62.

SUPPLEMENTARY REFERENCES TO PAPERS ON DISTRIBUTION

BASSINDALE, R. Invertebrate Fauna of Southern Shores of the Bristol Channel and Severn Estuary. Proc. Bristol Nat. Soc. (4), 9, 2, 1941, pp.146-55.

BIGELOW, H. B. Medusae and Siphonophorae Collected by the U.S. Fisheries Steamer 'Albatross' in the North-west Pacific, 1906. Proc. U.S. Nat. Mus., Vol. 44, 1913, pp.1-119.

Plankton of the Bermuda Oceanographical Expedition. VIII. Medusae taken 1929-30. Zoologica, New York, 23, (2), 1938, pp.99-189.

BROWNE, E. T. Scyphomedusae. Fauna and Geography of the Maldive and Laccadive Archipelago, ii, Supple. I, 1905, pp.958-72.

BURGERS, J. M. Over de Poliepen van de Oorkwal. Levende. Nat. Amsterdam, 48, 11-12, 1944, pp.129-133.

CLEVE-EULER, Quantitative Plankton Researches in the Skager Rak, Pt.1; K. Svenska. Vet. Akad. Handl., 57, No. 7, Stockholm, 1917, pp.1-130.

DAWYDOFF, C. Observations sur la faune pelagique des eaux indochinoises de la mer de Chine meridionale. Bull. Soc. Zool. Fr., 61, 1937, pp.461-84.

DEMEL, K. Etudes sur la faune benthique et sa repartition dans les eaux polonaises de la Baltique. Arch. Hydro-biol. Ichthiol. Suwalki, 9, 3-4, 1935, pp.239-311.

GESSNER, F. Hydrographie und Hydrobiologie der Brackwässer Rugens und des Darss. Keil Meeresforsch, 2, 1937, pp.1-20.

HARGITT, C. W. Variations among Scyphomedusae. J. Exper. Zool., Baltimore, Vol. II, (1905), 4, pp.547-84.

The Medusae of the Woods Hole Region, Mass. Bull. U.S. Bur. Fish. Vol. XXIV, 1904, (1905), pp.21-79.

KORSCHELT, E. Vergleichende Entwicklungesgeschichte der Tiere. Vol. 1, pp.158-220. Jena, 1936.

KRAMP, P. L. Medusae in Greenland Waters. Kjøbenhavn Nath. Medd. 65, 1913, pp.257-286.

Medusae Collected by the Tjalfe Expedition. Videns. fra. Dansk. nat. For. Kjøbenhavn, Bind. 65, (1913), pp.257-86.

[Scypho-] Medusae, Ctenophora, and Chaetognatha of the Great Belt and Kattegat in 1909. København Medd. Havundeo Ser. Plankton, I, Nr.12, 1915, pp.1-20.

Polypdyr (Coelenterata) II. Gopler Danmarks Fauna 43, 1937, pp.1-223, Kjøbenhavn.

Medusae of the North Atlantic. Danish Ingolf Expedition, Copenhagen, 5, 14, 1947, pp.1-66.

KÜNNE, C. Über als "Fremdlinge" zu bezeichnende Grossplankton ten in der Ostsee. Rapp. Cons. Explor. Mer. Copenh., 102, 2, 1937, pp.1-7.

MENON, M. G. K. The Scyphomedusae of Madras and the Neighbouring Coast. Bull. Madras Govt. Mus., 3, 1, 1930, pp.1-28.

PERRIER, R. La Fauna de la France. 1A, pp.8-64, 118, Paris, 1936.

POWELL, A. W. B. Natural Animals of New Zealand. Auckland, 1947.

PURASJOKI, K. J. Korvamedusen, Aurelia aurita L., Lisääntymisalne Laajenemassa. Arch. Soc. Zool. Bot. Fein. 'Vanamo', 2, 1942.

RANSON, G. Scyphomeduses provenant des Campagnes du Prince Albert 1er. de Monaco. Res. Camp. Sci. Monaco, Fasc. 106, 1945, pp.1-92.

Resultats Scientifiques des Croisieres du Navire-ecol belge "Mercator" IV. 2. Medusen. Mem. Inst. R. Sci. nat. Belg. (2), No. 33, 1949, 00. 121-58.

RAO, H. S. Notes on the Scyphomedusae in the Indian Museum. Rec. Ind. Mus., Calcutta, 33, 1931, pp.25-62.

STIASNY, G. Die Scyphomedusen-Sammlung des "Musee Royal d'Histoire Naturelle de Belgique" in Brüssel. Mem. Mus. Hist. nat. Belg., 42, 1930, pp.1-29.

Über einige Scyphomedusen von Puerto Galera, Mindoro (Philippinem). Zool. Meded. Leiden, 9, 1926, pp.239-48.

Die Scyphomedusen der Snellius Expedition. Verh. Akad. Wet. Amsterdam, Sect. II, 34, 6, 1935, pp.1-44.

Scyphomedusae. Scient. Rpts. John Murray Exped., 1933-34, 4, 7, 1937, pp.203-42.

Die Scyphomedusen. Dana Rpts. Copenhagen, 4, 18, 1940, pp.1-28.

STIASNY, G. and MAADEN, VAN DER. Über Scyphomedusen aus dem Ochotschischen und Kamtschatka Meer Nebst einer Kritik der Genera Cyanea und Desmonema. Zool. Jahrb. Jena (Syst.) 76, 1943, pp.227-66.

THIEL, M. E. Scyphomedusae Bronns Klassen. u. Ordnungen Leipzig 2. Bd. 2, Abt., 2 Buch. Liefg, 1-3, 1936, pp.1-480.

UCHIDA, T. Medusae in the Vicinity of the Amakusa Marine Biological Station. Bull. biogeogr. Soc. Tokyo, 8, 10, 1938, pp.143-49.

USSING, H. Bidrag til Aurelia aurita's Biologi i Mariagerfjord. Vidensk. Medd. nat. For. København 84, 1927, pp.91-106.

VALKANOV, A. Notizien über die Brackwasser Bulgariens. 2. Versuch einer hydrographischen und biologischen Eforschung derselben. Ann. Univ. Sofia, 32, 3, 1936, pp.209-341.

REFERENCES NOT AVAILABLE TO THE AUTHOR

CHILD, C. M. Oxidation-reduction Indicator Patterns in 3 Coelenterates. Physiol. Zoöl., 24, 1951, pp.97-115.

FRIEDMANN, OTTO. Die Postembryonale Entwicklung von Aurelia aurita. Zool. Anz. Leipzig, Vol. XXIV, 1901, pp.567-68.

GOETTE, A. Über die Entwicklung der Aurelia aurita und der Cotylorhiza barbonica. Zool. Anz. Leipzig, 1885, viii, pp.554-56.

[Ivanova] Cleavage of the Egg of Aurelia aurita in the White Sea. C. R. Acad. Sci. Moscow, N.S., 65, 4, 1949, pp.589-91.

KRUMBACH, T. Scyphozoa. Grimpe. v. Wagler. Die Tierwelt der Nord. u. Ostsee, 17, 1930, Teil 3d, pp.1-88.

LAMBERT, F. J. Observations on the Scyphomedusae of the Thames Estuary and their Metamorphosis. Trav. Stat. Zool. Wimereux 12, 1935, pp.281-307.

LE DANOIS, Ed. Coelenteres du Plankton etc. 1912. Paris Bull. Soc. Zool., 38, 1913, pp.13-25, 27-34.

SCHAFER, W. Fossilisations Bedingungen von Quallen und Leichen Serrekenbergiana Frankfurt, 23, 4-6, 1941, pp.189-216.

SHRAMLIK, E. Beobachtung an Medusen. Zool. Jahrb. Jena. (Allg. Zool.), 61, 1945, pp.296-336.

V. SIEBOLD Beiträge zur Naturgeschichte der Wirbellosen Tiere über Aurelia aurita. Danzig, 1839.

WILL, L. Ueber Hungerreduktion bei Aurelia aurita Sitzberg. Naturf. Ges. Restoch. (3), 1, 1927, pp.66-69.

YASHNOV Medusae of the North Seas of U.S.S.R. Moscow, 1948.

28.4.55