ON THE DISTRIBUTION OF 'GONIONEMUS VERTENS' A. AGASSIZ (HYDROZOA, LIMNOMEDUSAE), A NEW SPECIES IN THE EELGRASS BEDS OF LAKE GREVELINGEN (S.W. NETHERLANDS) *

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INTRODUCTION

The ecosystem of Lake Grevelingen, a closed sea arm in the Delta area of the S.W.-Netherlands is studied by the Delta Institute for Hydrobiological Research. Average depth of the lake (surface area : 108 km^2; volume : 575.10^6 m^3) is small (5.3 m), as extended shallows occur, especially along the north-eastern shore. Since the closure of the original sea arm (1971), the shallow areas were gradually covered by a dense vegetation of eelgrass (*Zostera marina L.*) during summer. Fig.1. shows the distribution and cover percentages of *Zostera* in the lake during the summer of 1978. The beds serve as a sheltered biotope for several animals. The epifauna of *Zostera*, notably amphipods and isopods, represent a valuable source of food for small littoral pelagic species, such as sticklebacks and atherinid fish. The sheltered habitat is especially important for animals sensitive to strong wind-driven turbulence. From 1976 onwards the medusa of *Gonionemus vertens* A. Agassiz is frequently found within the eelgrass beds. The extension of the *Zostera* vegetation has evidently created enlarged possibilities for the development of the medusa (BAKKER, 1978). Several medusae were collected since 1976 during the diving-, dredging- and other sampling activities of collaborators of the Institute. In the course of the summer of 1980 approximately 40 live specimens were transferred into aquaria in the Institute and kept alive for months.

In this paper the occurrence of *Gonionemus vertens* A. Agassiz in Lake Grevelingen is discussed as well as the mechanism of its global and local distribution.

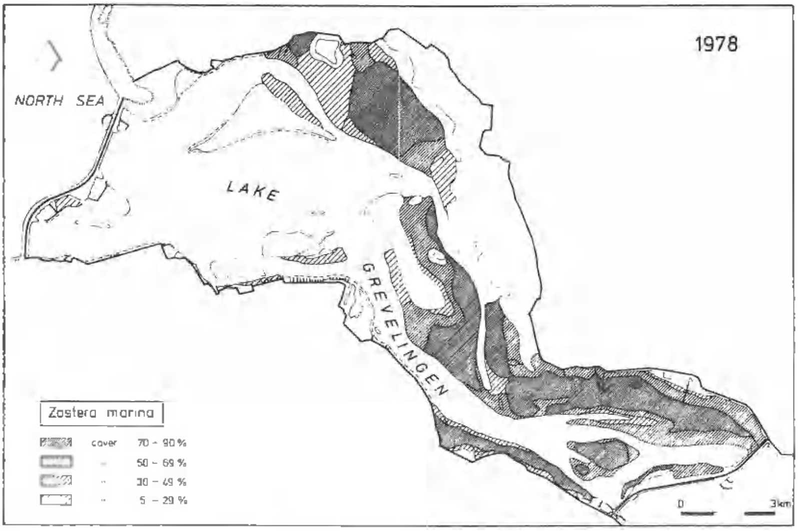

Fig.1. Distribution and cover percentages of *Zostera marina* in Lake Grevelingen in 1978 (after BOELÉ, in press).

THE MORPHOLOGY OF THE MEDUSA

For the systematic position of the species (class Hydrozoa, order Limnomedusae, family Olindiadidae) is referred to KRAMP (1961) who includes several forms (*G.depressus* GOTO, *G.agassizi* MURBACH and SHEARER, *G.murbachi* MAYER, *G.oshoro* UCHIDA and probably *G.vindobonensis* JOSEPH) in *G.vertens* A. AGASSIZ.

A few remarks are made about the morphology, see Figs.2 and 3. WERNER (1950 a) gives a detailed account of all morphological characteristics. For further details see MURBACH and SHEARER (1903),

* Communication no. 211 of the Delta Institute for Hydrobiological Research.

UCHIDA (1929), RUSSELL (1953), CHOW and HUANG (1958).

The umbrella is bell-shaped. Live medusae of Lake Grevelingen usually demonstrate a somewhat flattened umbrella, the height being smaller than the diameter.

Adult specimens of Lake Grevelingen reach 3-4 cm diam., in agreement with the dimensions reported by WERNER (1950 a). KRAMP (1961) mentioned 1.5 - 2.0 cm, but these data include a series of measurements of medusae cultured in aquaria and such animals generally use to remain smaller. The relatively larger diameter of adult medusae in Lake Grevelingen are an indication of the optimal development in the eelgrass meadows of the lake.

Live animals are beautifully coloured : radial canals dark-brown violet; ring canal much weaker violet; the gonads (sinuously folded on the radial canals) yellow-brown to red-orange; stomach with radial violet bands; mouth ending into 4 slightly crenulated white lips; umbrella margin dark gold-brown; bulbi of the marginal tentacles yellow-brown to orange; tentacle base with brilliant emerald-green spot.

The number of marginal tentacles is 60-80 (100-110 maximally, according to WERNER (1950 a). Completely extended, the tentacles reach a length of approximately twice the diameter of the umbrella. They bear numerous annular or spiral nematocyst clusters. At short distance from the distal end of the tentacle a conspicuous adhesive organ is found, causing the tentacle to kink.

The umbrella contains 1-2 marginal vesicles (with statocysts), situated between each 2 tentacles.

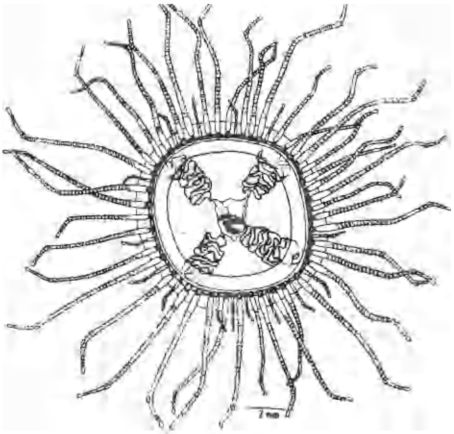

Fig.2. *Gonionemus vertens*, medusa (after CHOW and HUANG, 1958).

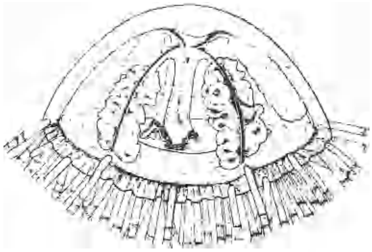

Fig.3. *Gonionemus vertens*, medusa (after WERNER, 1950a).

LIFE HISTORY AND HABITS

The medusae are dioecious, the males releasing sperm cells and the females shedding eggs into the surrounding water. RUGH (1929) found a production of 50-75,000 eggs per female. The fertilized egg develops to a ciliated larva, the planula. After a planktonic existence lasting some weeks it settles, attaching to the bottom (notably stones and shell fragments overgrown with algae) and transforms into a tiny polyp (of approximately 0.4 mm), surrounded by a gelatinous sheath covered with detritus. The solitary polyp phase has been described in detail by PERKINS (1903), WERNER (1950 b) and MIKULICH (1970). We did not yet discover this stage. The polyp is continuously able to produce vermiform buds (frustules) giving rise to new polyps. Consequently numerous polyps may occur in suitable biotopes after a couple of years.

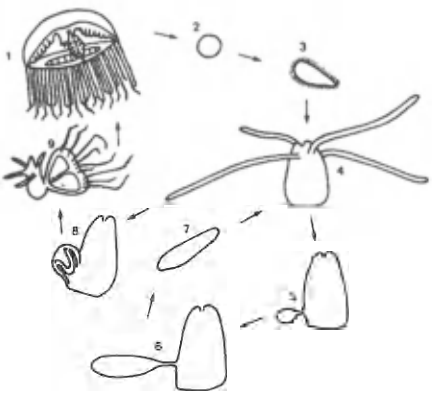

Fig.4. Life cycle of *Gonionemus vertens*. 1. adult medusa, ♀ or ♂ ; 2. fertilized egg; 3. Planula larva; 4. Polyp; 5/6 formation of a vermiform bud by the polyp; 7. released vermiform bud developing into a new polyp (4); 8. formation of a medusa bud by the polyp; 9. juvenile medusa, shortly before release. (Drawings mainly derived from PERKINS (1903), JOSEPH (1925) and MIKULICH (1970). Successive stages have not been figured proportionally).

When environmental conditions are becoming favourable, medusa buds are formed and the life-cycle is completed (Fig.4). The medusa stage is far more conspicuous, owing to its dimensions, colours and habits, than the very small and hidden polyp stage. Generally medusae were discovered in the lake when the eelgrass meadows grew out and water temperature rose above 17-18 °C. During the cold months of May and June 1980 conditions appeared unfavourable and modest numbers of medusae could be observed not earlier than in the beginning of August. During fall the medusae disappear when the *Zostera* plants die off.

A. Agassiz reported in detail (see RUSSELL, 1953) about the nature of the swimming movements of the animal. The species name refers to its peculiar habit of turning over when the water surface is reached and then sinking downwards on its back with all tentacles extended. His observations could be confirmed by divers in the eelgrass beds (Leewis, pers. comm.) and by ourselves, studying the species in aquaria with *Zostera*. When the medusa touches an eelgrass leaf it stops sinking, bends a few tentacles around the *Zostera* and remains attached by means of the adhesive pads. In this way the medusae are able to maintain themselves within a littoral vegetation, especially in a tidal area. This characteristic behaviour makes the *Gonionemus* medusa a littoral-bound species, which is exceptional as most Hydromedusae are truly pelagic (although neritic) stages. In Table I some data are listed in relation to the habitat of *Gonionemus* medusae. They may occur in tidal waters as well as in closed brackish to saline water bodies, but are always restricted to the shallow areas along the shores occupied by dense beds of submersed macrophytes and/or weeds. Inland waters of this type are inhabited especially by *Zostera*, but also *Ruppia, Potamogeton pectinatus* and green algae (*Ulva, Enteromorpha, Cladophora, Chaetomorpha*) occur. In tidal waters the medusae are found between the large brown algae (*Fucus, Laminaria, Himanthalia*) but, again, also in eelgrass (*Zostera, Posidonia, Phyllospadix*) meadows.

The sinking movement provides a remarkable catching capacity to the medusa. When all tentacles are fully extended in the radial plane, the animal is able to fish (also when resting) within an effective diameter of approximately 20 times the umbrella. Major food organisms are the smaller and larger crustacea moving between and along the eelgrass leaves, in Lake Grevelingen especially the isopod species *Idotea chelipes* (Pallas) and the amphipod *Gammarus locusta* (L.). Also WERNER (1950 a) stressed the importance of *Idotea* as food organism, based on a study of stomach contents of the medusae. MIKULICH (1970) moreover mentions some representatives of the microfauna, *i.e.* gastrotrichs and ciliates, as prey. TODD *et al.* (1966) indicate that also copepods and fish larvae are consumed. Using its adhesive organs, the medusa may even catch preys of its own dimensions, without taking the chance to be transported by its victim. JÄGERSTEN and NILSSON (1961) observed that young pipefishes were restrained by the medusa. Initially, we fed our animals naturally occurring isopods, but later (for practical reasons) small pieces of mussel meat were offered, with good results.

In nature the animals often appear to occur in swarms, possibly depending of an approximately synchronous formation of medusa buds by the polyps when a critical temperature level is exceeded. The occurrence in swarms may help the species to persist as chances of fertilization for the eggs are strongly increased. As a rule the animals are less active during daytime under strong illumination, resting then between the eelgrass leaves closer to the bottom. Against sunset they start performing the characteristic upward swimming and downward sinking movements. The hidden existence during the day makes it understandable that the medusa has remained undiscovered during long times. Very probably the animal has been overlooked in this way in several suitable and well-studied localities.

Because the medusa stage appears to be strictly limited to the summer months, we suppose that higher water temperatures are of decisive importance for its development. This was clearly illustrated during 1980, when the first medusae could be observed not earlier than late July. Even in August only modest numbers were counted. Water temperature remained abnormally low (15-16 °C) during 6 foregoing weeks, namely the whole month of June and the 2 first weeks of July. During preceding years many medusae had already been seen in June, when water temperatures rose earlier to the level of 17-18 °C.

MIKULICH (1970), studying the feeding behaviour of the polyp, observed that the animal immediately reacted when its tentacles or body surface were touched by nematodes. The worms sticked tightly to the tentacle, became (partly) paralyzed and were transported to the proboscis-like end of the mouth bending in the direction of the prey. Consumption of an adult nematode by the polyp lasted 2-3 minutes. Copepods, mites and ciliates, on the other hand, moved freely around and were seen to collide now and then with the polyps body and to creep along an extended tentacle without provoking any reaction of the polyp. The polyps, therefore, appear to feed exclusively on nematodes, not at all competing for food with the medusae which feed on a variety of organisms from other groups.

The polyps are able to survive for years and years without formation of medusa buds. A seawater aquarium in Vienna, in 1910 filled with water from the Adriatic (Rovinj), was found to contain medusae since 1917. (For these and more data in relation to findings of *Gonionemus* in aquaria : see JOSEPH, 1925; WERNER, 1950 a; EDWARDS, 1976). During all those years the contents of the aquarium were not changed : evidently, the polyps already present had waited to start development of medusae during that time. The minute polyps are extremely difficult to find and so escape easily the attention of the observer. It is not surprising, therefore, that many investigators, not succeeding to demonstrate the polyps in the natural habitat, tried to discover the animals in aquaria.

WORLD-WIDE DISTRIBUTION OF GONIONEMUS VERTENS

G.vertens has been known since 1859 when A. AGASSIZ (1865) described the species, occurring along the Pacific coast of North-America, from Puget Sound. Afterwards it has been observed frequently in the temperate to warm-temperate coastal regions of the entire North-Pacific Ocean, notably the Japanese and Chinese coasts (Fig.5). The Atlantic coast of North-America, on the other hand, shows remarkably few findings : the surroundings of Woods Hole only, in spite of the detailed inventories made in this area. In the Mediterranean Sea the species seems to thrive abundantly at the French coast only (Table I). However, the species must inhabit the Adriatic Sea, in view of the facts already mentioned about the occurrence of the medusa and/or the polyp stages in seawater aquaria at several places (Berlin, Prague, Vienna) filled with water from Rovinj. The successive NW-European findings (Table I) indicate that *G.vertens* has gradually become a common species here, especially in eelgrass meadows (JÄGERSTEN and NILSSON, 1961). However, reports are lacking from the French Atlantic coast south of Brittany, from the Spanish and Portuguese coasts and from western Italy (Fig.6). The distribution is peculiar and several authors have questioned its origin. For a detailed survey is referred to TAMBS-LYCHE (1964) and especially to EDWARDS (1976).

We compare the following data about occurrence, life history, propagation and habits of the species in connection with the 'erratic' (EDWARDS, 1976) pattern of distribution :

1. The species is endemic in the coastal North Pacific. The Atlantic area of occurrence shows large gaps (disjunct distribution), especially at the North American coast but also at the Western European coast. Circumarctic distribution, usual for species common to the Pacific and the Atlantic northern temperate area, is not found.
2. The medusae phase is strictly littroal, bound to eelgrass beds and algal belts.
3. Planula larvae have to be taken in account as possible distributional stages.
4. The polyp phase is solitary and very small, growing on stones and shells. *Gonionemus* may persist in a given locality in this stage, being able to multiplicate repeatedly by asexual budding of (vermiform) frustules.

The foregoing facts lead to the following assumptions :

ad 1. The distribution of *G.vertens* seems artificially influenced. Human action might be responsible for the distribution from the original area, the Pacific.

ad 2. Previous ideas about the distribution of the species via the medusa (TEISSIER, 1932) can be rejected in view of the strictly littoral character of this stage, of which even morphological details (*i.e.* the adhesive organs) indicate strong connections with macrophyte vegetations of shallow areas. Transportation of such stages by ocean currents, otherwise a normal way of dispersal for medusae, needs not or hardly to be considered.

ad 3. Planula larvae too are not supposed to play an important role in relation to the extension of the distributional range. Planulae may readily be able to assist in maintaining a once occupied suitable biotope

Fig.5. World-wide distribution of *Gonionemus vertens.*

locality	tidal currents	littoral vegetation	author
Gulf of Georgia, USA, Pacific coast	+	large brown algae	AGASSIZ, 1865
Woods Hole, Eel Pond, USA Atlantic coast	–	*Zostera marina*	PERKINS, 1903
Île Callot, Bretagne, France	+	*Himanthalia zone*	TEISSIER, 1932; 1950
Ostende, Bassin de Chasse, Belgium	–	*Ulva lactuca*	LELOUP, 1948
Villefranche s. Mer, French Mediterranean coast	+/–	*Posidonia*	PICARD, 1955
Rantum Becken, Sylt, German Wadden Sea	–	*Ruppia maritima*	WERNER, 1950a, b
Creek Rammekenshoek, Ritthem Walcheren, The Netherlands	–	*Cladophora fracta* *Potamogeton pectinatus*	LEENTVAAR, 1961
Gullmarfjord, Swedish Westcoast	+	*Zostera marina*	JÄGERSTEN and NILSSON, 1961
Hardangerfjord, Norway	+	*Laminaria zone*	TAMBS-LYCHE, 1964
Lagoon at Santa Barbara, California, USA, Pacific coast	–	*Enteromorpha*	TODD et al, 1966
Borgenfjord, Trondheim, Norway	+	*Fucus serratus* *Ceramium rubrum*	GULLIKSEN, 1971
Amur Bay, Sachalin N.W. Pacific coast	+	*Phyllospadix*	MIKULICH, 1970
Nice, French Mediterranean coast	+/–	'eelgrass meadows'	HAEFELFINGER, 1975
Lake Grevelingen, The Netherlands	–	*Zostera marina*	BAKKER, this paper
Harbour canal, Goes, id.	–	id.	id.

Table I. Some findings of *Gonionemus vertens* (medusa)

Fig.6. Distribution of *Gonionemus vertens* in Europe. Arrows: occurrence in nature (coastal tidal and stagnant brackish waters); dots: findings in seawater aquaria (after EDWARDS, 1976, modified and completed).

by developing polyps, the existing population of polyps becoming enlarged in this way. Explosive extension followed by occupation of new areas situated at very large distances from the old distribution center, however, seems unlikely for these stages. The same would hold for the polyp frustules and the medusa buds. Planulae and frustules are able to perform small-scale range extensions, via coastwise dispersal of the distributional area, but fail to explain the long-distance dispersal of *Gonionemus* from the Pacific to the Atlantic Ocean.

ad 4. Consequently, the sessile minute polyp must be of significance for the distribution. Contrary to the usual situation in Hydromedusae, it is this stage that seems most suitable for the explosive distribution in the case of *G. vertens*. Two plausible possibilities are offered, both pointing to human influences :

a.) Distribution by means of transported shellfish, notably oysters (EDWARDS, 1976; LELOUP, 1948).

b.) Distribution by means of shipping, the polyp participating in the fouling community of the ship's hull (TAMBS-LYCHE, 1964).

ad 4a. EDWARDS (1976), giving a detailed account of the history of the oyster culture, - trade and - transport in Europe since 1850, argues strongly that the original source of introduction of *Gonionemus* into Europe might be *Crassostrea gigas* (Thunberg), the Japanese oyster. These oysters have frequently been transported to Portugal, probably carrying the *Gonionemus* polyps to this country. From Portugal a lot of Portuguese oysters (*Crassostrea angulata* (Lamarck)) were exported, firstly to France (Bay of Arcachon), and afterwards to other European localities. Essential in this respect is the demonstrated identity of the Japanese and Portuguese oyster (a.o. MENZEL, 1974). European oysters, brought to the United States, finally, might account for the isolated mentions of *Gonionemus* at the Atlantic coast (Woods Hole and surroundings).

A severe objection to this hypothesis is that *Gonionemus* has never been reported from Portugal, neither from the Bay of Arcachon. Accounting for the circumstance that the last locality harbours a marine biological station, it seems very unlikely that the species, when present as medusa, might not have been detected here.

ad 4b. At first sight it seems less reasonable to assume an ocean transport of the polyp by ships, because *Gonionemus* was thought to be restricted to shallow waters, not permitting passage of large ships. However, a remarkable fact mentioned by EDWARDS (1976), but not discussed further by this author, reveals new possibilities for the distribution of the polyp. EDWARDS wrote (1976, p.258) : . . . . . 'I heard from Dr. P. F. S. Cornelius of the Coelenterate Section, British Museum (Natural History) that *Gonionemus* medusae had just been found, on 19 September 1975, in an aquarium at the museum, maintained at

15 °C by the Bryozoa Section (Miss P.L. Cook) . . . . . Search had revealed the presence of reproductive polyps on a dead shell of *Laevicardium crassum* (Gmelin) . . . The shell was part of a consignment of shell-gravel received by Miss Cook from Plymouth, dredged on 24 June 1975 on the offshore Eddystone grounds. No other polyps could be found. From information supplied by Miss Cook about the aquarium and its contents it is almost certain that the source of the *Gonionemus* was the shell gravel . . . . . '. EDWARDS only remarks that 'the occurrence of the species offshore is most unusual'. After my opinion however the foregoing throws a new light on the occurrence of the species in the polyp phase. The sessile benthic stage of *Gonionemus* evidently can be present in vital form in deeper water where the medusa due to the absence of vegetation cannot optimally thrive or maintain itself. This offshore occurrence strongly emphasizes the probability that the polyp is much more common on far more localities in shallower *and* deeper water, than the medusa. But when this is true this implies that the polyp may represent a member of the fouling community of large ship's hulls and in this way the distribution of the species can be extended on global scale. The isolated occurrence on the North American Atlantic coast, however, is best explained by EDWARDS' (1976) hypothesis.

When the polyps live also in deeper waters, frustules and medusa buds are likely to be distributed from these places too. The fate of the medusa buds will soon be sealed, unless they reach shallow areas with the accompanying vegetation. The vermiform buds however will spread in deep as well as in shallow waters due to currents, then settle and give rise to increased numbers of new polyps at both habitats. The possibility should thus not be excluded that shallow areas are colonized in this way from polyps partly inhabiting deeper waters.

When we consider that even many holozooplanktonic species, although easily transported by ocean currents, have not arrived at a cosmopolitan distribution (cf. v.d. SPOEL and PIERROT-BULTS, 1979), this cannot at all be expected in relation to littoral-benthic species possessing moreover a littoral-bound pelagic stage, such as *G.vertens*. The mechanisms inducing world-wide distribution, suggested by EDWARDS (1976) and TAMBS-LYCHE (1964), undoubtedly are of more significance than the restricted capacities of the species itself.

Thus : the exact mechanism of the large-scale range extension of *Gonionemus vertens*, influenced as it is by man, is still not quite clear. The species is indigenous in the North Pacific, the polyps here being probably present everywhere in shallower and deeper (coastal and offshore) seawater. Replacement of polyps to the North Atlantic (including the Mediterranean) was realized, either by means of shellfish transports or by transport as part of the fouling community of ships.

The littoral habits of life of the medusa and the minuteness of the solitary polyp, combined with the evidently non-obligatory formation of medusa buds by the polyp, stress the chance that *Gonionemus vertens* may occur in much localities during many and many years, without being observed. WERNER (1950 a) is right stating that the several isolated findings of the medusa in European waters indicate that the species meanwhile has become endemic here.

DISTRIBUTION OF *GONIONEMUS VERTENS* IN THE S.W.-NETHERLANDS

The first locality where *Gonionemus* was found in the Netherlands was the creek Rammekenshoek at Ritthem (Walcheren) (Fig.7). Its origin was a dike burst caused by bombings in 1944, closed after the war. LEENTVAAR (1960) obtained some specimens of the medusa and sent them for identification to KRAMP (1961). In 1950 Mörzer Bruyns (from LEENTVAAR, 1961) demonstrated much swimming *Enteromorpha* sp. and *Ulva lactuca* L. in the creek. During the following years these species decreased introducing a succession with *Potamogeton pectinatus* L. and *Cladophora fracta* (Dillw.) Kütz. Chlorinity in June 1959 amounted to 14 $^{0}/_{00}$. During the sixties occurrence of the medusa has not been reported. We are not certain that the medusa did not occur at all, but it is quite probable because intensive inventories were made during that period. After 1970 the vegetation of algae and macrophytes gradually disappeared and *Gonionemus* was not observed anymore.

The second locality, the harbour canal of Goes (Fig.7), was discovered in July 1976 by the author. Drainage water of the surrounding polders do not enter the canal as its level, being fully dependent of the tidal Eastern Scheldt via a sluice connection, is higher than that of the drainage area. Consequently, the canal water is characterized by high salinities, closely approaching those of the Eastern Scheldt. Along the shallow shores a *Zostera* vegetation extends to a depth of approximately 1 m.

Also since 1976, medusae of *G.vertens* have been observed regularly in Lake Grevelingen during summer. In 1964 the Grevelingen estuary had already been closed at the eastern side. During the period 1964-71 tidal conditions remained the same in the westernmost part, but in the eastern direction current velocities decreased accompanied by increasing transparencies of the water. During that time the small eelgrass beds in the eastern part met more favourable conditions and started gradually to extend their range. When the estuary was closed at the western side in 1971 and the tides completely disappeared, the growth of the beds increased drastically. In 1973 an area of 16 km^2 was covered with *Zostera*, in 1975 increasing to 28 km^2 in 1978 to 44 km^2, *i.e.* approximately 40 % of the total lake area (NIENHUIS *et al.*,

Fig.7. Distribution of *Gonionemus vertens* in the S.W.-Netherlands. I. Creek Rammekenshoek at Ritthem (Walcheren): finding of the medusa in 1960 only. II. Harbour canal Goes-Eastern Scheldt. III. Lake Grevelingen (eelgrass beds hatched). Between North- and South-Beveland the former (tidal) Zandkreek was situated (now Lake Veere). The dots represent the finding areas.

1980). It was not until 1976 that the first *Gonionemus* medusae were observed. In 1977 the animals were mainly seen in the oldest eelgrass meadows in the easternmost part. In 1978 they were found also in the strongly enlarged beds along the north-eastern shore (Fig.1).

The characteristic picture of the biotope preferred by the medusa of *Gonionemus vertens* emerging from the literature, is in agreement with the local situation in the S.W.-Netherlands. In the Eastern Scheldt, a sea arm with strong tidal movements and poorly developed eelgrass beds, the medusa is supposed hardly to be able to persist. So far approximately 15 Hydrozoa medusae species were observed in this basin and *G.vertens* is still lacking (which does not exclude that the medusa sometimes may occur in small numbers).

Present distribution in the S.W.-Netherlands is shown in Fig.7. The considerations given above with regard to the global distribution of the species, suggest that the polyp might be much more abundant than the medusa, notably in tidal (and previous tidal) waters. In this way the temporary occurrence of the medusa in the creek of Rammekenshoek can be easily explained. The polyp stage is supposed to be present 'everywhere' within the marine tidal reaches of the Delta area including the mouth of the Western Scheldt estuary. The dike burst in 1944 is thought to be responsible for the entrance and the occurrence in the creek after subsequent closure. (EDWARDS (1976), not accounting adequately for the complicated hydrography of the Dutch estuaries, supposed that relaying of oysters from the eastern part of the Eastern Scheldt to the Zandkreek between North and South Beveland might have been responsible for the occurrence of *G.vertens* in the creek. This is impossible, however, as the communication between Eastern and Western Scheldt via the Zandkreek was blocked already before 1870 and the oyster culture orginated after that date). After some years environmental conditions for the medusa became favourable, evidenced by the development of a littoral vegetation in the tidalless salt to brackish water and medusae appeared. During recent years the vegetation disappeared, probably caused by continuing eutrophication and decreasing transparencies of the water. At the same time medusae were not observed any longer. The strong connection between *Gonionemus* medusae and submerse vegetation is, again, clearly suggested. This agrees with data from other areas. During the period 1894-1930 *Gonionemus* medusae were found in numbers in the Eel Pond, Woods Hole (a small basin, connected with the harbour via an inlet). The 'wasting disease' of the Atlantic eelgrass beds (1931) infested also the *Zostera* vegetation of the Eel Pond and after its dying off no medusae were observed anymore (WERNER, 1950 a). Before 1931 the medusa perhaps occurred also in the then extended eelgrass beds of the Dutch Wadden Sea, but we found no indications for that assumption (personal information A. v.d. Werff).

It is not surprising that the medusa has been discovered not untill recently in the harbour canal of Goes, because the fauna has not been studied systematically. The seagrass-covered margins of the canal however are known to occur here since long times. Very probably the medusa has been overlooked here earlier.

The polyp may also have been present for years and years in the Eastern Scheldt, including the previous tidal Grevelingen estuary. Perhaps medusa buds occasionally are released from the polyps, but then the juvenile medusae easily will take the chance to be transported by the tidal currents to unfavourable areas, *i.e.* deeper water layers, where they will not be able to perform their characteristic feeding behaviour and soon will die. The environment of Lake Grevelingen, on the other hand, grew more and more suitable, due to the extension of the eelgrass meadows, after the closures of 1964 and 1971. Originally the first medusae, still in small numbers, will have contributed to an increase of the polyps population density and larger numbers of polyps will have resulted in increased numbers of medusae during the following summer a.s.o.

The dissemination of *Gonionemus* within Lake Grevelingen may be advanced further as a consequence of the strongly increased boat recreation. More and more smaller sailing- and motor-yachts arrived and anchored at shallow places, including the areas along and within the *Zostera* beds. Planula larvae as well as vermiform polyp frustules will have attached to the ships hulls, accelerating the gradual occupation of the total eelgrass area by the polyps.

It is impossible, afterwards, to unravel exactly the course of the spreading of *Gonionemus vertens* in the S.W.-Netherlands. In view of the sufficiently studied ecology of the species, however, the present distribution could be explained satisfactorily. *Gonionemus* has settled definitely in the Dutch Delta area, especially in the saline Lake Grevelingen. We may even expect that the range of distribution of the species in the lake will increase yet, as a consequence of the immigration of the Japanese brown alga *Sargassum muticum* (Yendo) Fensholt into the lake attached to stone sea-walls and rip-rap dams in the western part in 1980 (NIENHUIS, in press). This large brown alga probably penetrated from the sea via the sluices in the western dam. It is not primarily the species composition of the littoral vegetation that is decisive for the suitability of the environment for *Gonionemus* medusae, but the precense of a dense littoral vegetation *per se.* Consequently we must account for the possibility that the medusa in due time may spread along all the shores of the lake, irrespective the quality of the prevailing substrate.

SUMMARY

Data about morphology, life history and habits of *Gonionemus vertens* A. Agassiz (Hydrozoa, Limnomedusae) are given. The distribution of the species is treated in more detail, especially its mechanism in relation to large-scale (global) and small-scale (local) range extensions.

The species is endemic in the coastal North Pacific Ocean, possessing a strictly littoral medusa stage (bound to eelgrass beds and algal belts) and a very small sessile solitary polyp phase (attached to stones and shells).

The hypotheses trying to explain the spread to Western Europe and the Atlantic coast of North America strongly suggest human influences, *i.e.* distribution of the polyp via oyster transports (EDWARDS, 1976) and transport of the polyp as a member of the fouling community on ships hulls (TAMBS-LYCHE, 1964). Arguments pro and contra these hypotheses are evaluated. The occurrence of *Gonionemus* polyps in offshore waters, as mentioned by EDWARDS (1976) but not further discussed by this author, deserves more attention.

It is the assumed occurrence of the polyps in shallow as well as in deeper waters with strong tidal movements that explains satisfactorily the previous and recent findings of the medusa in the S.W.-Netherlands. The medusa has been found in the *Zostera marina* beds of the saline Lake Grevelingen. From 1976 onwards the abundance of the medusa increased synchronously with the extension of the eelgrass beds. Medusae were collected during the summer of 1980, fed with isopod crustaceans or mussel meat and kept alive for several months in seawater aquaria in the lab. Polyps have not yet been observed.

ACKNOWLEDGEMENTS

My thanks are due to J.A. van Duren, P. de Koeyer, A.J.J. Sandee and J.M. Verschuure who collected medusae during sampling excursions in and along the eelgrass beds and to G. Doornbos and F. Twisk who sampled the animals during fishing using a beam-trawl in the shallow areas bordering the beds. P.J. van Boven maintained the seawater aquaria and J.W. Francke fed the medusae. I thank J.A. van Duren and R. Leewis for litterature data and valuable discussions. A.A. Bolsius and J.A. v.d. Ende prepared the figures and miss M.J. de Dreu typed the manuscript. I am grateful to Dr. E.K. Duursma and Dr. P.H. Nienhuis for critical comments.

REFERENCES

AGASSIZ, A., 1865. In: F.S. Russell (1953), pg.401.

BAKKER, C., 1978. Some reflections about the structure of the pelagic zone of the brackish Lake Grevelingen (S.W.-Netherlands). Hydrobiol.Bull.12:67-84.

BOELÉ, F.E., in press. Verspreiding, biomassa en productie van het macrofytobenthos in het Grevelingenmeer. Stud.Rep.Delta Inst. for Hydrobiol.Res.

CHOW, T. and M. HUANG, 1958. A study on Hydromedusae of Chefoo. Acta Zool. Sinica 10:173-197.

EDWARDS, C., 1976. A study in erratic distribution: The occurrence of the medusa *Gonionemus* in relation to the distribution of oysters. Adv.Mar.Biol. 14:251-284.

GULLIKSEN, B., 1971. A new record of *Gonionemus vertens* Agassiz (Limnomedusae) in Norway. K.norske Vidensk. Selsk.Skr. 12:1-4.
HAEFELFINGER, H.R., 1975. Hydrozoën en schijfkwallen. In: B. Grzimek: Het leven der dieren, 2e druk. I. Lagere dieren, pg.215-16. Uitg. Spectrum, Utr. Antw.
JÄGERSTEN, G. and L. NILSSON, 1961. Life in the sea. G.T. Foulis, London, pg. 180-183.
JOSEPH, H., 1925. Zur Morphologie und Entwicklungsgeschichte von *Haleremita* und *Gonionemus*. Ein Beitrag zur systematischen Beurteilung der Trachymedusen. Zeitsch.wissensch.Zool. 125:374-434.
KRAMP, P.L., 1961. Synopsis of the medusae of the world. J.Mar.biol.Ass.U.K. 50:7-469.
LEENTVAAR, P., 1960. Een zeldzame kwal in de Rammekenshoek. De Levende Natuur 63:261-62.
LEENTVAAR, P., 1961. Two interesting invertebrates, *Limnadia lenticularis* (L.) (Crustacea Phyllopoda) and *Gonionemus vertens* A. Agassiz (Limnomedusae), found in the Netherlands. Zool.Med.Rijks Mus. Nat.Hist.Leiden 37(14):225-230.
LELOUP, E., 1948. Présence de la trachyméduse *Gonionemus murbachi* Mayer, 1901, à la côte belge. Bull.Mus.roy.Hist.nat.Belg. 24(27):1-4.
MENZEL, R.W., 1974. Portuguese and Japanese oysters are the same species. J.Fish.Res.Bd.Can. 31:453-56.
MIKULICH, L.V., 1970. Polyps of the poisonous jelly fish *Gonionemus vertens vertens* L.Agassiz and their behaviour. Transl. from Dokl.Akad.Nauk.S.S.S.R. 190(4): 979-82.
MURBACH, L and C. SHEARER, 1903. On medusae from the coast of British Columbia and Alaska. Proc.Zool.Soc.London 1903(2):164-192.
NIENHUIS, P.H., B.H.H. DE BREE and J.M. VERSCHUURE, 1980. Re-estimation of the primary production of eelgrass, *Zostera marina*. In: E.K. Duursma (ed.). Progr.Rep. 1979 Inst.for Hydrobiol.Res. 19-21.
NIENHUIS, P.H., in press. Attached *Sargassum muticum* found in the S.W.-Netherlands.Aquat.Bot.
PERKINS, H.F., 1903. The development of *Gonionema murbachi*. Proc.Acad.Nat.Sci.Philadelphia 54:750-90.
PICARD, J., 1955. Nouvelles recherches sur les Hydroméduses des herbiers méditerraneens de Posidonies. Rec.Trav.Stat.Mar.Endoume 15:59-71.
RUGH, R., 1929. Egg-laying habits of *Gonionemus murbachi* in relation to light. Biol.Bull.Woods Hole 57.
RUSSELL, F.S., 1953. The medusae of the British Isles. Cambridge Univ.Press.
SPOEL, S. v.d. and A.C. PIERROT-BULTS, eds., 1979. Zoogeography and diversity of plankton. Bunge Scient.Publ., Utrecht.
TAMBS-LYCHE, H., 1964. *Gonionemus vertens* L. Agassiz (Limnomedusae) - a zoogeographical puzzle. Sarsia 15:1-8.
TEISSIER, G., 1932. Existence de *Gonionemus murbachi* sur les côtes de Bretagne. Trav.Stat.Biol.Roscoff 10:115-16.
TEISSER, G., 1950. Note sur quelques Hydrozoaires de Roscoff. Arch.Zool.Exp.Gén. 87(1):1-10.
TODD, E.S., A. KIER and A.W. EBELING, 1966. *Gonionemus vertens* L. Agassiz (Hydrozoa: Limnomedusae) in southern California. Bull.So.Calif.Acad.Sci. 65(4): 205-210.
UCHIDA, T., 1929. Studies on Japanese Hydromedusae 3. Olindiadae. Annot.Zool.Japon. 12:351-71.
WERNER, B., 1950a. Die Meduse *Gonionemus murbachi* Mayer im Sylter Wattenmeer. Zool.Jahrb. (Systematik) 78:471-505.
WERNER, B., 1950b. Weitere Beobachtungen über *Gonionemus murbachi* Mayer im Sylter Wattenmeer und ihre Entwicklungsgeschichte. Verhandl.deutscher Zool.Mainz, 1949, 138-151.