CHANGES IN THE SEAWEED FLORA OF THE NETHERLANDS

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Abstract

Recent investigations of the SW Netherlands coastal waters have revealed the arrival of nearly 30 species of multicellular benthic algae since the publication of a comprehensive flora in 1983. This is a considerable speeding up of the gradual process of flora enrichment that appears to be going on in this century. Among these new introductions there are six regarded as aliens. Loss of species during the same period seems to be limited to a few species, none of which were ever common. The most important factor underlying these changes is probably the execution of the 'Delta Hydrotechnical Works', which has created a variety of new habitats and caused considerable improvement of the water quality in the tidal Oosterschelde and the stagnant Grevelingen.

Introduction

Historical documentation of the Netherlands' seaweed flora is incomplete. Major publications are those of Van den Bosch (1853), Van Goor (1923), Den Hartog (1959), Nienhuis (1980) and Stegenga & Mol (1983a). Some of these publications deal exclusively or mainly with only a part of the Dutch coast, e.g. the Wadden Sea or the SW Netherlands' 'Delta Area', and they usually cover the observations over relatively short periods of time. A recent checklist (Stegenga et al. 1997) gives a compilation of 229 species that were found growing on our coast at one time or another. As will be shown, this number is about double that of ca. 75 years ago, and the increase has not been a gradual process. Our paper will focus on the developments in the SW Netherlands, with occasional remarks on the Wadden Sea area.

Material and methods

Development of species richness has been determined from a survey of

the literature, combined with the results of a recent (and still current) reinvestigation of the SW Netherlands algal flora. A check of the existing historical collections (mainly in the Rijksherbarium (L), aimed at a more detailed description of the development of individual species and floristic composition, is in progress, but since this is time-consuming work the final results are foreseeen only in about three years from now. Unless indicated otherwise, the nomenclature for all species mentioned is as in Stegenga et al (1997).

Results

Changes in the marine environment

The marine coastal environment of the Netherlands, including the artificial "rocky shores", is for a large part man-made. Earlier this century great changes took place in the north: in 1932 the completion of the "Afsluitdijk" (= Barrage) cut off the Zuiderzee from tidal influence, leaving it to develop into a freshwater lake, with to the north of the dam the tidal Waddenzee. In the SW Netherlands various dams were constructed in the course of ca. 35 years after the disastrous flood of 1953. For location and a brief characterization of the various waters that resulted, see fig. 1 and Stegenga et al. (1997); in general, a more strict separation of marine and freshwater environments has diminished the estuarine character of the SW Netherlands.

Species numbers

Numbers of species are difficult to compare between the various publications as systematic groups have been revised taxonomically at various times. For instance, the number of recognized *Enteromorpha* species in our country rose from 7 (Den Hartog 1959) to 17 (Koeman 1985), although it can be assumed that the increase had little to do with newly introduced species. Other more or less monographic studies have also contributed to the presently recognized species number of 229, e.g. Prud'homme van Reine (1982), Stegenga & Mol (1980).

In Table I we show approximate numbers of species at various times during the last 150 years, as can be distilled from the most important publications. There is a good deal of reinterpretation involved here: for instance, in Van den Bosch (1853) it is not always immediately clear which species are truly autochthonous; Den Hartog (1959) mentions a total of 174 species known to him, probably an accumulation of his own and previous observations - careful examination of his publication yields a number of 120; in Nienhuis' (1975) list of 173 species there are

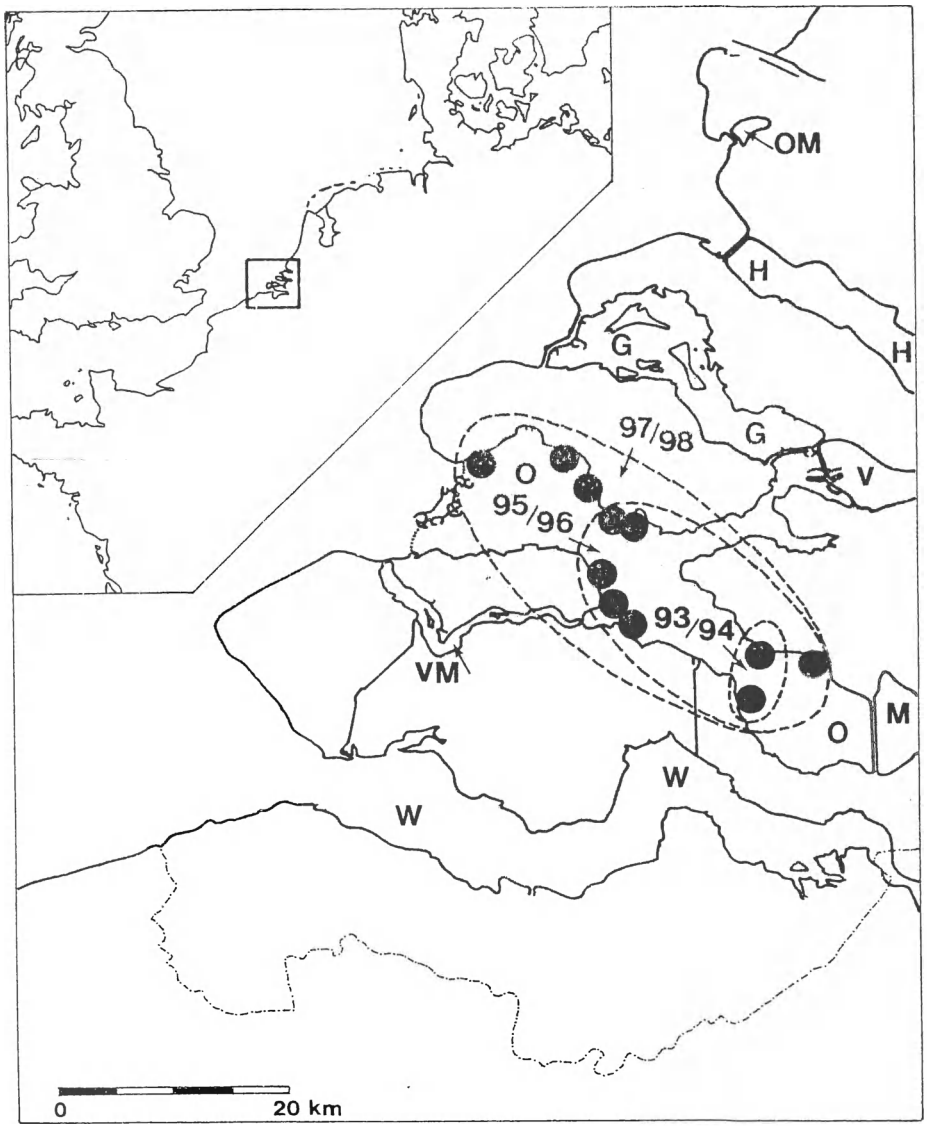

Fig 1

Fig. 1. The SW Netherlands coastal area, with waters mentioned in the text: G = Grevelingen; H = Haringvliet; M = Markiezaatsmeer; O = Oosterschelde; OM = Oostvoornse Meer; V = Volkerak; VM = Veerse Meer; W = Westerschelde. Also shown is the expansion of the alien rhodophyte *Polysiphonia senticulosa* (black dots), established in 1993 - by spring 1998 this species was a co-dominant in the algal vegetations where the first collections were made.

several that were identified only down to genus and especially the green algae comprised a number of freshwater species. Our own "actual" numbers are collections from the period 1993-1998.

Table I. Numbers of marine algal species in the Netherlands, according to major publications (multicellular green, brown and red algae).

Source	Total for Netherlands		SW Netherlands
	actual	cumulative	actual
v.d. Bosch 1853		45*)	45*)
van Goor 1923	106	106	45*)
den Hartog 1959	120	174	100
Nienhuis 1975	130	?	130
Stegenga & Mol 1983a	?	173	?
recent 1998	174	229	170

*) as reinterpreted by Van Goor (1923)

Despite the uncertainties that surround the reinterpretation of the historical sources, we can safely conclude that there has been a considerable rise in species number, especially in the SW Netherlands, and especially in the last fifteen years. A list of additions for this latter period is given in table II.

Floristic composition of algal vegetations

Phytosociology of algal vegetations has not developed to the same degree as that of higher plants. However, for the Netherlands we are fortunate to have the study of Den Hartog (1959), which gives a clear picture of structure and composition of the epilithic algal vegetations both in the N and SW Netherlands for the period 1952-1955(-1958). Even without having to go into details of methodology, we can easily make comparisons between Den Hartog's sample plots and present-day algal communities, and the way they are related to such factors as exposure and position in the tidal zone. It soon became clear that the greatest changes have taken place in the sublittoral fringe (and below, but algal vegetations do not extend deep down, either for lack of suitable substrate or because of the quickly diminishing light quantity). In the intertidal, the only quantitatively significant additions since Den Hartog (1959) have been *Gelidium pusillum* and the commonly

associated *Chaetomorpha mediterranea*, which are now abundant in some localities along the Oosterschelde; Den Hartog (l.c.) mentioned the first as one of the species that (on the continent) did not penetrate further north than the Strait of Dover. Decreased abundance has been observed for *Pelvetia canaliculata* and *Polysiphonia lanosa* (presently known from a single locality). Observed great reduction in cover of the common fucoids (mainly *Ascophyllum nodosum* and *Fucus serratus*) (Van Berchum & Meijer 1997) has not been monitored long enough to conclude to their definite decline, as long as long-term cyclic events are incompletely understood.

Table II. Species of seaweeds established in the SW Netherlands since 1983; list does not cover additions resulting from purely taxonomic decisions.

Cladophora hutchinsiae	Stictyosiphon soriferus
Ulvella lens	Striaria attenuata *)
Botrytella reinboldii	Colpomenia peregrina
Feldmannia globifera	Hildenbrandia crouanii
Herponema solitarium	Choreocolax polysiphoniae
Hincksia fuscata	Grateloupia doryphora
Hincksia hincksiae	Lomentaria clavellosa
Hincksia intermedia	Ceramium cimbricum
Kuetzingiella battersii	Ceramium shuttleworthianum
Elachista sp.	Seirospora interrupta
Leptonematella fasciculata	Spermothamnion repens
Leathesia verruculiformis	'Dasysiphonia sp.'
Myriactula 'rivulariae'	Polysiphonia devoniensis
Microspongium globosum	Polysiphonia senticulosa

*) reintroduction, previously found ca. 1845

In the sublittoral fringe, *Laminaria saccharina* is one of the species that have declined in the Oosterschelde since the completion of the storm-surge barrier. This can be ascribed to the higher summer maximum temperature, often over 20°C, considered the upper lethal temperature for this species (Wiencke et al. 1994); however, it must be remembered that *L. saccharina* was not always a common alga before this time: Den Hartog (1959) mentions it as an extremely rare species in the SW Netherlands, describing the "Laminarietum" formation only from the N

Netherlands. Rather extensive *Laminaria* growth in the Oosterschelde is reported by Nienhuis (1980), De Kluyver (1986), and has been repeatedly observed by ourselves before 1983. Other species in decline appear to be *Sphacelaria plumigera* and *Halidrys siliquosa*, both not found in recent years.
These few disappearances seem insignificant, but the change in composition of lower intertidal and sublittoral fringe algal vegetations is more dramatic. The community described by Den Hartog (1959) under the name "Codieto-Hypoglossetum" has been replaced by a vegetation with the dominant *Sargassum muticum*, and often large numbers of other 'aliens' like *Antithamnionella spirographidis*, *Polysiphonia harveyi* and *Polysiphonia senticulosa*, while the here previously unknown *Lomentaria clavellosa, Ceramium cimbricum* and *Halurus flosculosus* are common in these vegetations; *Bryopsis plumosa, B. hypnoides, Dictyota dichotoma* and *Cystoclonium purpureum* are often co-dominant and far more prominent than described by Den Hartog (l.c.). Species present in large numbers then and now are a.o. *Ulva spp., Chondrus crispus, Ceramium nodulosum, Polysiphonia fucoides* and *P. stricta*. However, the original 'characteristic' species have not completely disappeared: *Codium fragile*, now infrequent in the tidal Oosterschelde, has become very abundant in Lake Grevelingen (see below) and *Hypoglossum hypoglossoides* can still be found in reasonable numbers in many places along the Oosterschelde coast. Similar changes appear to have taken place in the "Polysiphonieto-Chaetomorphetum", which in a recognizable form is now mainly found on the more exposed North Sea coast.

Special environments - the Lakes
The "Delta Hydrotechnical Works" created a number of lakes cut off from tidal influence (fig. 1). Some, like Haringvliet, Volkerak and Markiezaatsmeer are no longer in the marine realm. But others are in the range of meso-haline to euhaline waters: Oostvoornse Meer (10 promille salinity), Veerse Meer (13-16 promille, with seasonal fluctuation) and Grevelingen (ca. 30 promille). In the case of the latter two this salinity level is artificially maintained through annual or more frequent exchange of water. The algal flora's of these lakes are very different in species richness and floristic composition:
Oostvoornse Meer has a recorded number of only 10 species of multicellular algae, among which a *Spirogyra sp.* A massive development of *Gracilaria gracilis* in summer is the most striking aspect

of this flora.
Veerse Meer, with about 25 species of seaweeds, is eutrophic and shows mass development of *Ulva spp.* and *Chaetomorpha linum*, but also the otherwise rare *Dasya baillouviana* is common in summer.
In Grevelingen, largest of the lakes (108 km²), we have registered 89 species since 1993 - curious enough a similar number is known for the period 1964-1970, prior to the closure and thus concerning a tidal sea-arm. It needs little explanation that, as species richness appears to be stable (if not always, in the intervening period salinity has temporarily been lower and species number accordingly decreased), floristic composition has changed considerably. This involved disappearance of tidal zone species (*Fucus spp., Ascophyllum*) and massive development of some invader species (*Codium fragile, Colpomenia peregrina, Sargassum muticum, Polysiphonia harveyi*). Other (temporarily) common to abundant species are *Ulva spp., Chaetomorpha aerea (in wash zone), Cladophora spp., Bryopsis spp.*, various *Ectocarpaceae*, *Leathesia difformis* and *Punctaria latifolia*. *Striaria attenuata* was re-established here after an absence from the Netherlands of almost 150 years (Otten & Prud'homme van Reine 1992). Extensive meadows of *Zostera marina* L., developed in the 1970's in shallow soft-substrate areas (Critchley et al. 1987), were reduced to a few hectares in recent times. Finally, it may be remarked that a few of the previously high intertidal/supralittoral species survive in the spray/splash zone of the now stagnant water: *Ulothrix spp., Blidingia minima, Prasiola stipitata, Porphyra umbilicalis*, and (very locally) even *Fucus spiralis*.

The aliens
Over a dozen species in the Dutch marine flora (about 6%) presumably have arrived from distant shores (if only indirectly: several were earlier known from other W European localities). The year of arrival is approximately known for most of them (Table III), but only in a few cases has the expansion within the Netherlands been documented, e.g. for *Sargassum muticum* (Critchley et al. 1987) and *Polysiphonia senticulosa* (fig. 1).
It is noteworthy that three of the introduced browns are small epi/endophytes, almost wholly restricted to a single host: *Sargassum muticum*. It seems that *Elachista sp.* and *Leathesia verruculiformis* have arrived in Europe over 20 years later than the host, *Myriactula sp.* was present in drifting *Sargassum* in 1980. These epi/endophytes are among the species that are more or less exclusively found in Lake Grevelingen

Table III. Invader species on the Dutch coast, with approximately the year of introduction or first observation.

Codium fragile (1900)
Colpomenia peregrina (1989)
Botrytella sp. ? (1919)
Elachista sp. (1993)
Leathesia verruculiformis (1994)
Myriactula sp. (1983) *)
Sargassum muticum (1980)
Grateloupia doryphora (1994)
Anotrichium furcellatum (1968)
Antithamnionella spirographidis (1974)
Dasya baillouviana (1951)
'Dasysiphonia sp.' (1994)
Polysiphonia harveyi (1960?)
Polysiphonia senticulosa (1993)

*) Earlier identified as *M. rivulariae*; however, the diameter of the paraphyses is up to 15-25 μm, considerably smaller than *M. rivulariae* (according to Fletcher (1987) up to 25-43 μm).

far less frequently in tidal waters, although *Sargassum* may be abundant there.

Discussion

An earlier rapid increase in species numbers appears to have happened in the 1950's: Koster (1950) and Den Hartog (1953, 1954) reported between the two of them 15 species new to the Netherlands. As not much systematic research on seaweeds had been done since Van Goor (1923), these species could have been introduced gradually or overlooked in the intervening period, and some (e.g. *Giraudia sphacelarioides, Desmarestia viridis, Ahnfeltia plicata*) have not been collected again in more recent times. Unfortunately the existing collections in L reflect the discontinuity in observations.

While it is clear that species numbers have risen and that floristic composition has changed, we can ask ourselves whether the developments are going in any specific direction and whether they

indicate one or more underlying factors as the most important. For instance, a gradual rise in temperature would be expected to affect the R/P quotient. For the Netherlands this has always had a low value and even with the new introductions there is no new trend discernible. R/P has varied between 1.10 (Den Hartog 1959, Nienhuis 1975) and 1.24 (Van Goor 1923) and presently stands at 1.18 (actual data).
Looking at the Dutch seaweed flora in a N Atlantic context shows that the composition is rather special. The proportion of species that our flora has in common with the NW Atlantic is ca. 72%, a much higher figure than that for the temperate W European flora as a whole (ca. 43% - data derived from South & Tittley 1986). No doubt this reflects the necessarily eurythermic nature of species that can survive the great annual temperature fluctuations in the southern North Sea. Here, the latest arrivals seem to indicate a somewhat different trend: 55% are exclusively European (i.e. non-American), 45% are amphi-Atlantic (based on the 20 species in Table II that are non-alien introductions). A similar analysis of 20 species that were first observed between 1950 and 1983 (Koster 1952, Den Hartog 1953, 1954, Stegenga & Mol 1983b) showed that only one species (= 5%) was exclusively European, while 19 species were amphi-Atlantic. Not surprisingly, the majority of the exclusively European species have a distribution area to the south of our country. Many of those that were recently established still have a very limited distribution in our country and low abundance. This is in stark contrast with the alien species, which often have become abundant in a short time; their success can be explained as most likely their provenance is the NW Pacific where large annual temperature fluctuations occur.
We conclude that, although several of the recent additions to the SW Netherlands algal flora may be the result of a somewhat milder climate, the majority reflect the improvement of environment, especially the higher salinity in Oosterschelde and the clearer water both in Oosterschelde and Grevelingen.

Prospects for further development
Further development of the SW Netherlands algal flora will mainly depend on two factors: climate and human activities. The first, although probably influenced by man, is certainly not under our control. If a considerable rise in atmospheric temperature should materialize, then the coastal waters of the southern North Sea will follow suit. We believe that especially a higher winter minimum temperature will allow several

W European species to establish themselves. At the same time, higher summer maxima will almost certainly cause the definite disappearance of the still present Laminariales (*Laminaria, Chorda*) and negatively affect some of the dominant Fucales.
In the SW Netherlands, human activities determine to a large extent such important environmental parameters as type of substratum, wave exposure, salinity, eutrophication and even tidal regime. There may develop conflicts of interest between various sections of society. Evidently, our ever-active "Rijkswaterstaat" (= Directorate-General of Public Works and Water Management) will not sit back and watch things happen. But demands from the recreational sector may well be different from those of Fisheries (including an important shellfish industry) or Nature Conservation. From the point of view of a phycologist the present situation, with a variety of water types, allows an almost optimum development of algal biodiversity within the boundaries set by climatic factors. Should the SW Netherlands coastal environment be returned to a more estuarine character, then this will probably cause reduction in species number: what is good for birds is not always good for seaweeds.

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