Sea-grass communities: structure, distribution and classification

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Abstract

Aims: In the marine biological literature sea-grass beds are generally regarded as being more or less similarly structured, and typically indicated as the sea-grass ecosystem. This assumption regarding their structure is discussed and rejected, as regarded on a worldwide scale sea-grass beds show considerable variation in many qualities to be elucidated in this paper. **Study area**: Sea-grass beds of the world. **Methods**: A combination of the formation approach and the phytosociological approach is applied, using genera (instead of species) and some structural vegetation characteristics as variables. The study of sea-grass beds with the two mentioned approaches is elucidated, and the history of their application for the classification is outlined. **Results**: Six well-defined classes of sea-grass communities are recognised on a global scale (top-down). The classification of the sea-grass communities is presented in the form of an identification key. The descriptions are based on floristic composition, physical structure (stratification, rooting system), relation to the substrate (soft substrate or rock), and degree of permanence (from annual presence to millennia). **Conclusions**: The assumption that sea-grass communities may be considered as more or less similarly structured ecosystems is an unjustified simplification, as the world's sea-grass beds show, apart from differences in the species composition, considerable variations in their structure, persistence and performance. They have been accepted as a 'formation' in its own right. Sea-grass communities are well distinguished from all other plant communities, and show only occasionally some overlap with communities of brackish and continental salt waters. Descriptions of sea-grass communities are generally based on the dominant angiosperm component, and thus present in fact only taxo- or merocoenoses. Consequently, they may show considerable regional variations, and even within the same area, if the algal flora, the fauna and environmental parameters, such as exposition to wave action, salinity, and substrate are being considered. The importance of the proposed classification is that comparisons of sea-grass communities can be made at the right level, and that generalisations should be considered in a more critical manner.

Keywords: Climax species; community architecture; deductive approach; formation; frame community; inductive approach; rhizome-root system.

Nomenclature: Den Hartog & Kuo (2006, Appendix pp. 22–23).

Abbreviations: ICPN = International Code of Phytosociological Nomenclature

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Introduction

Sea-grass beds are a conspicuous feature along many coasts all over the world, and they have been studied by both biologists and marine scientists for a long time. Given this diversity of researchers, sea-grass beds have been studied from many different points of view, depending on the aims and the interest of the researchers. Marine biologists, working with sea-grass beds, have described in various degrees of detail all kinds of ecological aspects of these communities, such as biomass evolution, primary production, respiration, nutrient cycling, oxygen and carbon household, food chains and food webs, effects of currents and storms, floristic and faunistic composition, microbial processes, etc. Usually, these studies are restricted to one topic. Nevertheless, they have shown that many sea-grass beds are very rich communities with a high degree of organisation and a high species diversity,

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but they have also shown that this does not hold always true (McRoy & Helfferich 1977; Larkum et al. 1989; Kuo et al. 1996; Larkum et al. 2006; Ruiz et al. 2015). Usually these researchers do not arrive at generalisations in the form of a vegetation classification, because that is not the purpose of their research. Nevertheless, among these studies are many excellent descriptions of communities, e.g. that of the *Posidonia oceanica* association of the Mediterranean (Mazzella et al. 1986), those of the *Phyllospadix scouleri* association and the *Phyllospadix torreyi* association of the Californian shores (Steward & Myers 1980), that of the deep-water association of *Halophila decipiens* in St Croix (Josselyn et al. 1986), and that of the *Halophila baillonii* beds in Belize (Short et al. 2006). If more general conclusions are presented one usually refers, perhaps unconsciously, to 'the sea-grass system'. This is, however, an unfounded simplification, as the structural diversity of the sea-grass communities is considerable. One needs only to compare the beds of the giant sea-grass *Zostera caulescens* of Japan (Aioi et al. 1998) with those of the tiny *Halophila* species of the tropical and subtropical seas to show the dissimilarity.

The formation approach

The first investigator who distinguished the sea-grass beds as a special plant formation was Warming (1895) in his book, "Plantesamfund. Grundtræk af den økologiske Plantegeografi". He attempted to describe and define the main plant formations of the world, and in his opinion the aquatic halophyte communities were of sufficient importance to give them the status of a plant formation in the sense of Grisebach (1872) and Drude (1889), i.e. a vegetation type characterised by species having the same physiognomy and the same life forms, but generally belonging to very different taxa (species, genera or even families). Warming (1895, pp. 126–127) named it the "Enalidernes Samfundsklasse". In the German edition of his work (Warming 1896, p. 148), this unit was called the "Enaliden-Vereinsklasse", and in the English edition (Warming 1909, edited by Groome and Balfour, p. 177) "Enhalid-formations". In the 3rd German edition (Graebner & Warming 1918, p. 392), the same unit is called "Formation der Seegräser (Enhaliden)". It has to be realised that in the original concept of this formation not only the true sea-grass communities were included, but also the communities of eurysaline aquatic plants who are characteristic for poikilosaline habitats, such as brackish waters and continental salt waters.

The difference between the sea-grasses and the eurysaline aquatic plants is that the sea-grasses are restricted in their distribution to the marine environment, where the dominant salt is sodium chloride (NaCl), but that the eurysaline taxa can occur in all kinds of environments with a high content of electrolytes, thus not only in waters

with a high content of chlorine, but also in waters where sulphates, hydrocarbonates and similar anions dominate. Most of them are also able to stand large fluctuations in the concentration of the various salts. As a consequence, they are not limited to coastal areas, but can occur in all kinds of continental salt waters and even fresh water, up to 4,800 m altitude. Along the sea coast, they belong mainly to the genera *Ruppia*, *Zannichellia* and *Stuckenia* (formerly *Potamogeton* subgenus *Coleogeton*), which at present are regarded as belonging to a separate formation (Formation of aquatic plant communities of shallow poikilosaline coastal and continental waters; Den Hartog 2003). Warming's original concept of the sea-grass formation is without doubt based on observations in the Baltic Sea, where as a result of low salinity sea-grass beds and beds of brackish-water plants often form mosaics or even occur mixed. When regarded on a global scale this is, however, an aberrant situation caused by the very special hydrological conditions in that particular sea. Børgesen (1898, 1905) was the first researcher to apply the concept "Havgræsformationen" (= sea-grass formation) in the strict sense, thus only to the totality of communities of true marine angiosperms (including fully correctly the rhizophytic macroalgae growing with the sea-grasses). He based himself on the work of Kjellman (1878), who elaborated the formation approach for the communities in the marine environment and has been followed by most phycologists that studied marine vegetation.

Later, the Enhalid formation has also been recorded by Rübel (1930, p. 300), and classified together with the "Limnaën formation" (which comprised the pleustonic and rhizophytic fresh-water plant communities), and the formations of the Limnonereids and Halonereids of rocky bottoms, into the formation class *Submersiherbosa*, comprising all submerged plant growth. Rübel did not give a definition of his Enhalid formation, but mentioned only the names of some of the associations within the formation, viz. *Zosteretum marinae*, *Zosteretum nanae* (= *Zosteretum noltei*), *Thalassietum testudini*, *Posidonietum*. Phillip (1936) used the term "enalid plant association" to describe some sea-grass communities with *Zostera marina* and *Zostera noltei* (*Zostera nana* in his text) in the Humber estuary, Great Britain. (In his paper Phillip mentions only *Zostera marina* and *Ruppia rostellata*. His illustration of the leaf apex of the latter shows doubtless that not a *Ruppia* but *Zostera noltei* is the second species.) The guidelines for the recognition of associations and formations were not very strict, as appears from the work of Schimper (1935), who recognised a formation of the small sea-grasses (Formation der Zwergseegräser) with two associations, and in the sublittoral "ausgedehnte Wiesen des gewöhnlichen Seegrases *Zostera marina*".

The phytosociological approach

The treatment of the sea-grass communities in the phytosociological literature is generally very limited. The phytosociology is focussed on the floristically defined plant communities, i.e. assemblages of species occurring in a certain space at a certain time. In contrast to the deductive phytogeographical approach, as used by Warming (1895), the general phyto-sociological procedure is to start with the description of the smallest communities, the associations, and to unite these into higher units – alliances, orders and classes – based on floristic similarities and differences, thus an inductive procedure. It is the aim of this science to study the structure, the functioning, and the dynamic and historic aspects of these plant communities, as well as to elaborate a system for their classification. This approach was initiated in the 1920s by Braun-Blanquet (1921, 1928), who advocated his "pflanzensoziologisches System auf floristischer Grundlage", later indicated as the "hierarchical system of syntaxa", the Braun-Blanquet system, or the Zürich-Montpellier system, in which the floristic composition of the vegetation is considered the 'only valid criterion' for classification. This made it a unifactoral system with all the disadvantages of such a system. Regrettably, up to the eighties of the 20th century the phytosociological literature has been dominated by the aspect of the classification of plant communities, and other aims have remained generally underdeveloped. Phytosociologists are basically terrestrial ecologists, and the sea-grass communities are in the periphery of their interest. Nevertheless, they have to be incorporated within the system of syntaxa for the sake of completeness, as this system is often presented as the ultimate 'natural' vegetation classification system.

Regrettably, usually without any thorough research, phytosociologists came to far reaching generalisations, where sea-grass communities are involved. In their view, the sea-grass communities were regarded as 'primitive' (Fukarek 1964) or 'very lowly organised' (Tüxen 1974). This idea probably arose from the fact that many sea-grass communities contain only one angiosperm species and have generally a quite uniform physiognomy, and from the fiction that these aquatic communities consist only of pioneering species, and finally will develop into terrestrial communities. Such succession schemes have indeed been published, but without any evidence (Chapman 1959, 1960, 1974; Chapman & Ronaldson 1958; Burrows 1990). This preoccupation and lack in profoundness is a pity, as it is my view that phytosociological generalisations, which are usually expressed in the form of a classification scheme, can be very useful for the comparison of sea-grass communities with their counterparts in other areas of the world, and as an important step towards the understanding of the structure of these communities. The generalisations, however, must be based on critical observations and careful analysis of data according to well-defined criteria.

The disadvantage of the inductive approach in phytosociology, however, is that many investigators have built up classifications in often rather restricted areas in which local differences are stressed, instead of the more general patterns. In the case of the sea-grass communities, most phytosociologists working in coastal areas would have only one or two associations in their area of study, and, therefore, are not able to appreciate the large degree of diversity these communities express worldwide. The deductive approach of plant geography, that works top-down, gives a more general perspective, but is quite useless when applied on a local scale. The phytosociological classification of sea-grass communities has seriously suffered from the situation that researchers who generally had never worked with these communities did find it necessary to incorporate them in their papers for reasons of completeness, but generally without consulting existing literature. In the case of the sea-grass communities it is very obvious indeed, that many phytosociologists did hardly or not at all take notice of the works of researchers of related science branches. This lack of interest in related research has been signalized as a general phenomenon and has been criticised most strongly by Caspers (1980) in his review of Oberdorfer's (1977) "Süddeutsche Pflanzengesellschaften".

Further, one has to realise as well that phytosociological descriptions based on angiosperms present only part of the communities, as algae, fauna and microorganisms play a very important part in sea-grass beds; their presence is much more obvious in these communities than in most terrestrial communities. It has to be understood that the sea-grass communities, as presented in the phytosociological system, are no more than taxo- or merocoenoses defined by the dominant growth form. Sea-grass communities are typical "frame communities", i.e. the dominant species does provide a number of niches and in this way determines to a large extent the possibilities for the accompanying algae and animal species. Each species whose life cycle fits within the pattern exhibited by the dominant can in principle be found in the sea-grass community. A species of which only a part of the life cycle fits within this pattern can only occur, if in the immediate surroundings environments are available which satisfy its requirements for the rest of its life cycle. This provides an explanation for the fact that small beds in a varied environmental setting are generally much richer in species than extensive beds that are homogeneous for miles.

History of the phytosociological approach in relation to sea-grass communities

Braun-Blanquet was the first researcher of this branch of plant ecology to take sea-grass beds into account, and he even established a higher syntaxon. In his "Aperçu des

groupements végétaux supérieurs du Bas-Languedoc" (Braun-Blanquet 1931), he produced a tabulated survey in which he classified an "Association de *Posidonia* et *Cymodocea*" in the *Posidonion*. At the same time he proposed a *Ruppion maritimae* in order to accommodate an "Association à *Ruppia* et *Zannichellia pedicellata* Sous-association à *Zostera nana*". These two alliances were placed, together with some associations of fresh-water plants within the order *Potametalia*. From this it is obvious, that Braun-Blanquet accommodated all water-plant communities in one order, without bothering about the guiding principle of his own system, and in this respect his system did not show any advance above the earlier systems of Warming (1895) and Rübel (1930). He did not give any information about the exact contents of the two newly recognised alliances, and in the case of the *Posidonion* he refrained even from mentioning the names of the species. Nevertheless, this subdivision has had as a consequence that later several authors classified the *Zostera* communities within the *Ruppion* alliance. A further step towards the development of a hierarchy was the erection of the order *Zosteretalia* by Béguinot (1941), comprising the associations of marine and brackish waters, which he described from the lagoon of Venice. Béguinot did not give any further details of the order *Zosteretalia*, and that led to a lot of irrelevant discussion about its contents, regrettably not based on research but on opinions (Braun-Blanquet & Tüxen 1943, 1952; Tüxen & Oberdorfer 1958).

Pignatti (1953) was the first phytosociologist who recognized that the communities of the marine angiosperms differed floristically as well as ecologically completely from the fresh-water communities, and that their classification within the *Potametea* was not in accordance with the floristic principle. For this reason, he founded a separate class *Zosteretea*. This class was, however, not clearly defined. According to Pignatti (personal communication), he intended the class to contain all sea-grass communities. So the *Zosteretea* in the sense of Pignatti would coincide with the sea-grass formation in the sense of Børgesen (1898). Fortunately, in later phytosociological studies the name *Zosteretea* has mainly been used in a restricted way to comprise the communities characterized by *Zostera* species. Borhidi (1991) used the class *Zosteretea* Chapman 1974 as the unit containing all sea-grass syntaxa occurring in the West Indies, and particularly Cuba, in fact following the original concept of Pignatti (1953), in spite of the total absence of representatives of the genus *Zostera* in the whole area.

Knapp (1964, 1965, 1968) was the first phytosociologist who understood that the tropical sea-grass communities had to be classified in separate syntaxa, as they had no species in common with the temperate communities, but here ends also his merit for the sea-grass sociology. Among the many papers he has published on higher syntaxa from various areas of the world, there are only three in which sea-grass communities are mentioned, but extremely poorly described. In 1964 he has coined the order *Thalassio-Cymodoceetalia manatorum* for the coast of Central America. Further, he distinguished in the Indian Ocean the class *Halophilo-Cymodoceetea* (Knapp 1968), with the orders *Thalassio-Halophiletalia ovatae* Knapp 1965 for Sri Lanka and *Halophilo-Cymodoceetalia* Knapp 1968 for the Red Sea. In all cases he refrained from defining these units, but only mentioned the names of some species and recorded that these occur in salt water along the coast. I consider these names as *nomina nuda*.

Sea-grass community classification at a global scale

In preparing the monograph "Sea-grasses of the World" (Den Hartog 1970), I obtained a rather detailed image of the geographical distribution of all sea-grass taxa, and also collected many data of their co-occurrences and communities. This data set, collected from herbarium labels, published papers and reports, and my own field experience, offered the possibility to distinguish between various types of sea-grass communities, a topic that held my interest for a very long time. My general thought has been, that if there was one set of communities that could be easily classified at a global scale it must be sea-grass communities, because they hardly show any overlap with other aquatic communities. In 1971, I presented a first attempt towards a general classification of sea-grass communities of the world within the existing Braun-Blanquet system in order to start a discussion to the Royal Botanical Society of The Netherlands, of which only the abstract was published (Den Hartog 1972). During the International Seagrass Workshop, Leiden, The Netherlands, 22–26 October 1973, a review paper was distributed dealing with structure, function and classification of sea-grass communities (Den Hartog 1973); in this paper the higher syntaxa were outlined on a global scale. The full text was published four years later (Den Hartog 1977). Preceding this publication an overview of the consequences of this classification for the European sea-grass communities was presented during a Colloque Phytosociologique in Lille in 1975 (Den Hartog 1976). These reviews were presented before the first edition of the Code of Phytosociological Nomenclature (Barkman et al. 1976) was available. Later on I published a new fully updated paper on the global classification of sea-grass communities (Den Hartog 2003), recognising 6 classes. In the present paper, I will outline this classification again, be it with a number of alterations and additions, mainly concerning nomenclature. My approach is in fact quite new: a combination of both the formation approach and the phytosociological approach, but the latter not on the species level, but rather on the level of the genera. In my

opinion, it leads to a simple system, but it is not fully in accordance with the present-day rules of phytosociological nomenclature. In principle, the nomenclature follows the 3rd edition of the International Code of Phytosociological Nomenclature (ICPN; Weber et al. 2000), except for some cases where the strict application of the rules leads to absurdities (ICPN, art. 2, 3g, 7).

To arrive at this classification of the higher units, the following criteria have been applied consciously; they have been presented more extensively in several other papers (Den Hartog 1973, 1979, 1982, 1983; Den Hartog & Van der Velde 1988; Den Hartog & Phillips 2001):

1. Floristic composition of the communities at the generic level.
2. Geographical distribution of the sea-grass genera.
3. Nature of the substratum, i.e. soft substrates such as sand and mud versus hard substrates such as rock or coral.
4. The general above-ground structure of the communities, i.e. the architecture. Particular attention has been given to the way the leaves develop, e.g. whether they arise in bundles from extremely short vertical shoots close to the substratum (monopodial branching), or whether they develop upright lignified but leafy stems (sympodial branching). This architecture is extremely important for the accompanying organisms; in well-developed beds of the first category the shoots are generally densely packed, while in the beds with the sympodially branching rhizomes with upright stems there is much more space under the leaf canopy.
5. The general below-ground structure of the communities can show quite different patterns. Rhizomes of the *Zosteraceae* (except for *Heterozostera*) generally grow in a horizontal direction, and have no possibility to grow vertically; if the forming of a rhizome mat in such communities occurs, it means that new plants have developed overgrowing the rhizomes of the original plants; this happens frequently when sedimentation exceeds erosion (Blois et al. 1961). In several other genera, the vertical short shoots have the capacity to form horizontal branches which function as rhizomes; in this way they can keep pace with sedimentation and are not dependent for survival on new offspring. Some genera show some very slow vertical growth. These processes are essential for the stability of sea-grass beds. Another point to be mentioned here is the depth of penetration of the roots, the number of roots per node, the degree of branching, and the degree of anchoring of the roots in the substratum. Some sea-grasses root very superficially, others penetrate to a depth of more than a metre in the substrate.
6. Age of the rhizome-root system, its annual performance, and its longevity. Some of the sea-grass communities are generally annual, e.g. those dominated by *Halophila* species, but there are also communities which can maintain themselves for centuries, e.g. the

Thalassodendretum ciliatae, or even millennia, e.g. the *Posidonietum oceanicae*.
7. The potential number of epiphyte communities on the sea-grass plants.
8. Place in the coastal zonation.

Outline of the classification of sea-grass communities

Although the formation as a unit has no formal status in the hierarchical system of syntaxa, it is used here for the practical reason to group the classes of sea-grass communities, independent of their degree of organisation. The term 'sea-grass formation', with equivalents in German (Seegras), Dutch (zeegras), and Danish (Havgræs), proposed originally by Warming (1895), and applied in the sense of Børgesen (1898), is preferred for the totality of the sea-grass communities. The difference with the brackish-water communities has been explained above. Superfluous names in the literature covering more or less the same concept of 'sea-grass formation' are:

– *Halobenthalia* Chapman 1959, which has been discussed extensively by Den Hartog (2003). In this concept the brackish-water communities are included as well.
– *Zosterea* De Bolós 1968, which is less appropriate, as it has a semantic affinity with the temperate genus *Zostera*, making it unsuitable for use in the tropics. In fact, for the same reason, there is among the sea-grasses not one genus name suitable for the characterisation of this formation.

The sea-grass formation is characterized by the dominance of sea-grasses, an ecological group (Kuo & Den Hartog 2000) consisting of 12 genera of angiosperms, belonging to four plant families, of which three (*Zosteraceae* with three genera, *Posidoniaceae* with one genus, and *Cymodoceaceae* with five genera) are exclusively marine in their occurrence, and the fourth family, *Hydrocharitaceae*, is represented by three exclusively marine genera (of which two have the status of a subfamily). The complete generative cycle of all sea-grasses takes place when fully submerged, with the exception of the genus *Enhalus* having hydrophilous surface pollination. Apart from sea-grasses, rhizophytic algae may play a part in some of these communities. Most of the sea-grass species are stenohaline, i.e. sensitive to changes in salinity, but some have a greater tolerance to fluctuations in the salinity, and, therefore, can live in the intertidal belt and can penetrate to some extent into estuaries. Consequently, in these habitats sometimes interference with representatives of the 'Formation of the aquatic plant communities of shallow poikilosaline coastal and continental waters' occurs. In great contrast to the aquatic angiosperms of brackish and fresh water, many sea-grasses can grow at considerable depths, down to more than 50 m, the deep-

est record being 91 m for *Halophila engelmanni* in the Gulf of Mexico (Taylor 1928). Fresh-water angiosperms rarely go further down than 10 m.

Within the formation, six groups of sea-grass communities can be distinguished at the class level. I have conceived a key to these classes, but have not incorporated deviations as a consequence of aberrant hydrographical conditions, or minor local circumstances. These would have made the key too complicate. For the same reason, I have not included the alliances.

Key to the classes and orders of sea-grass communities

1a. Sea-grass beds on soft bottoms
2a. *Zostera* communities in temperate waters of the northern and southern hemisphere . . . . Class 1 ***Zosteretea***
3b. Beds of large *Zostera* species (subgen. *Zostera*) in the sublittoral of the northern hemisphere . .   Order 1A ***Zosteretalia***
3a. Beds of small *Zostera* species (subgen. *Zosterella*) in the intertidal belt, but in the absence of the large *Zostera* species they may occupy also the upper sublittoral belt . . . .   Order 1B ***Nanozosteretalia***
2b. Communities dominated by *Thalassia*, *Cymodocea*, *Syringodium*, *Halodule*, *Halophila* and *Enhalus* in the tropics and subtropics . . . . Class 2 ***Halodulo-Thalassietea***
4a. Beds mainly consisting of *Halodule* and/or *Halophila* species in the intertidal belt and down to considerable depths in the absence of *Thalassia* and *Syringodium* . . . . Order 2A ***Haloduletalia***
4b. Beds dominated mainly by *Thalassia* in the upper sublittoral . . . . Order 2B ***Thalassietalia***
1b. Beds on rock and other hard substrata
5a. Communities consisting of species without upright lignified stems in the sublittoral
6a. Communities dominated by *Phyllospadix* in the temperate northern Pacific in the intertidal belt and the upper sublittoral . . . . Class 3 ***Phyllospadicetea***
6b. Sublittoral *Posidonia* communities with a very thick rhizome-root layer, and a densely packed leaf carpet . . . . Class 4 ***Posidonietea***
5b. Communities consisting mainly of species with upright lignified stems, forming a thick rhizome-root layer, but between the leaf canopy and the substrate much open space
7a. Communities mainly consisting of *Amphibolis* in temperate Australia . . . . . . Class 5 ***Thalassodendro-Amphiboletea***
7b. Communities mainly consisting of *Thalassodendron ciliata* in the tropical Indo-West Pacific . . . . Class 6 ***Thalassodendretea ciliatae***

Class 1 *Zosteretea* Pignatti 1953

Nomenclature history: Emended by Den Hartog & Segal (1964); later synonym *Coeno-Zostereta* Michaelis, Ohba & R. Tüxen 1971

Sea-grass communities, characterised by the dominance of *Zostera* species, on sandy and muddy bottoms, extending from the lower part of the intertidal belt downward to considerable depths (3–30 m, depending on the degree of transparency of the water), in marine and polyhaline coastal waters of temperate seas of the northern and southern hemisphere. These communities stabilise the bottom and protect it from erosion; the capacity to raise the bottom by fixing the sediment and catching floating material is rather restricted, as the rhizomes of the *Zostera* species are not able to grow in vertical direction; the vertical shoots are not able to produce horizontal side-shoots to keep pace with sedimentation (Blois et al. 1961). Most of the sublittoral stands are perennial, and may develop a rhizome mat, up to 10 cm thick. In the beds consisting of annual and biennial populations, occurring mainly in the intertidal belt, the bottom becomes only temporarily raised during the active growth season, but after the autumnal die-off the bottom is levelled off by erosion. Epiphytic algae are restricted to the leaves; the living rhizomes are devoid of epiphytes. The *Zostera* communities show considerable differences in organisation. The communities occurring in the intertidal belt are considerably poorer in accompanying species and less complex than the communities in the permanently submerged sublittoral beds. For this reason, I have distinguished two orders, the *Zosteretalia* and the *Nanozosteretalia* (Den Hartog 2003), i.e. a division of the class that only could be established by a global study of these communities.

Order 1A *Zosteretalia* Béguinot 1941

Nomenclature history: The emendation of the *Zosteretalia* by Ohba & Sugawara (1981) relates to the division of the order into two alliances. My emendation (Den Hartog 2003) is more radical, because the order has been split into two separate orders, each with one alliance.

This order is characterised by communities dominated by species of *Zostera* subgen. *Zostera*, and is distributed in the sublittoral of temperate seas of the northern hemisphere, and locally extends into the Arctic Ocean. With the exception of *Zostera marina*, the species of this subgenus show hardly any overlap in their distribution. I have recognized only one alliance to accommodate the various associations, because they are from a structural point of view quite similar.

Alliance 1A1 *Zosterion* Christiansen 1934

Nomenclature history: As apart from the *Zosteretum marinae* three other associations, based on other *Zostera* species, have been described in this alliance, I have, in spite of the

rules of the ICPN, deleted the specific epithet from the alliance name, as maintaining it could only lead to confusion.

The *Zosteretum marinae* (Fig. 1) is the most widely distributed association within this alliance. It shows a great deal of local and regional variation with respect to accompanying algae and fauna, depending on salinity, substrate, exposition to currents and wave action, and the nature of the adjacent communities. The first extensive description of this association has been made by Van Goor (1921, 1923). Although this association generally occurs on soft bottoms, in several places it inhabits also areas where the bottom consists of a mixture of sand, gravel, stones and shells. The above-ground community becomes in that case a mixed stand with *Zostera marina*, rooting in the bottom, and many epilithic algal species being fixed to the hard substrata, shaping their own associations. Quite recently, it appeared that the invasive, epilithic brown alga, *Sargassum muticum*, is able to replace the sea-grass in these mixed beds. As a consequence of its large size and very dense growth, it shadows the sea-grass out (Den Hartog 1997).

The other associations occur only in the northern Pacific, and have been described by Ohba & Miyata (2007). The *Zosteretum asiaticae* is distributed from northern Japan to California, the *Zosteretum caespitosae* and the *Zosteretum caulescentis* are restricted in their distribution to northern Japan and some adjacent areas.

Fig. 1. A sublittoral bed of *Zostera marina*, extending from 1.5 to 6–7 m depth in the Gullmar Fjord along the Swedish west coast. The photo was taken on 14 July 2014 in the upper part of the bed. On hard substrates in the front, the algae *Fucus vesiculosus* and *Chondrus crispus* can be recognized. Photo by courtesy of Mrs. Dr. B. van Tussenbroek.

Order 1B *Nanozosteretalia* Den Hartog 2003

This order is characterised by communities dominated by species of *Zostera* subgen. *Zosterella*, recently also considered to be a separate genus *Nanozostera* (Tomlinson & Posłuzny 2001). It is distributed in temperate seas of the northern and southern hemisphere. Some of its communities extend into the tropics, e.g. the *Zosteretum capensis* occurs also in Kenia and Tanzania, and the *Zosteretum capricorni* reaches even New Guinea The communities occur mainly in the intertidal belt, but in regions where no other sea-grasses occur they may extend into the sublittoral; there they may develop a considerably different habit. The areas of the species of this subgenus do not overlap, or show only very marginal coexistences, e.g. in South Australia, where *Zostera muelleri* and *Zostera mucronata* may meet. Within this order, only one alliance has been recognized, as the various communities are structurally very similar.

Alliance 1B1 *Nanozosterion* Den Hartog 2003

Nomenclature history: Invalid synonyms are Formation der Zwergseegräser Schimper 1935 and the *Zosterion noltii-japonicae (Zosterellion)* Ohba & Sugawara 1981. Although the latter name has been conceived strictly according to the ICPN, it is invalid, because the name connects two species which never have been found together in a natural environment. It shows exactly why I object to unnessecary use of species names, when coining the name of a new higher syntaxon. It can never have been the intention of the ICPN to lead to the composition of irrational names of syntaxa. As shown in the former paragraph, Ohba & Sugawara (1981) mention *Zosterellion* within parentheses, without any clear reason. This name cannot be used for naming an alliance or other syntaxon of the *Zosteretea*. In the taxonomy of sea-grasses it has only been used at the level of section and subgenus. Ascherson founded already in 1868 the section *Zostera* sect. *Zosterella*, it was raised by Ostenfeld in 1918 to the subgenus level. Small (1907) described the genus *Zosterella* for two species of *Heteranthera* of the family *Pontederiaceae*, blocking its use in the *Zosteraceae*.

In this alliance, several associations may be distinguished; these associations exclude each other geographically, but are very similar in structure. Best known is the *Zosteretum noltei* in western Europe and the Mediterranean. This association is, however, very variable, and consists of a set of very different fauna communities with the only similarity that they are dominated by *Zostera noltei*. For example, in the southern North Sea and along the Channel occur at least 3 communities in the intertidal belt, respectively on mud, on detritus-rich fine sand, and on practically pure sand (Den Hartog 1983). The patterns of the beds may also be very different as a consequence of hydrodynamic factors, varying from the leopard-skin pattern and the stripey zigzag pattern to a pattern in which the sea-grass is arranged in a large number of equidistant parallel lines (Chassé 1962; Den Hartog 1973). In the Mediterranean, the *Zostera noltei* association occurs

submerged in shallow water in sites that are protected from currents and heavy wave action. Similar beds are formed by all species of *Zostera* subgen. *Zosterella.*

Class 2 *Halodulo-Thalassietea* Den Hartog 1976

Nomenclature history: I consider the *Halophilo-Cymodo-ceetea* Knapp 1968 as a nomen nudum (see above). The name has been used quite recently by Ohba & Miyata (2007) for the tropical sea-grass communities of southern Japan. The name *Halodulo wrightii-Thalassietea testudinum* Rivas-Martínez et al. 1999 is superfluous, as it covers only the communities of the West Indies. The addition of the species epithets has made the name only suitable for use in the West Indies; this means a geographical restriction of the usefulness of the original name, what explicitly has not been the intention when it was published in 1976.

Sea-grass communities on sand, mud, and coral rubble, in marine and polyhaline coastal waters of tropical seas, characterised by representatives of the genera *Halodule*, *Halophila*, *Thalassia*, *Cymodocea*, *Syringodium* and *Enhalus*; locally extending into subtropical waters.

This class is more or less the tropical counterpart of the *Zosteretea*. This similarity appears also from the fact that it can also be split on the ground of basic structural differences into two orders, the *Haloduletalia* which structurally resemble the *Nanozosteretalia* and the *Thalassietalia* which show some structural similarity with the *Zosteretalia*. In contrast to the *Zostera* species the vertical shoots of *Halodule*, *Cymodocea* and *Thalassia* are able to produce horizontal side shoots, and in this way can keep pace with sedimentation. Epiphytic algae are restricted to the leaves; the living rhizomes are free of epiphytes.

Order 2A *Haloduletalia* Den Hartog 1977

Nomenclature history: *Halophilo-Cymodoceetalia* Knapp 1968, nomen nudum. This name has been used recently by Ohba & Miyata (2007) for some tropical sea-grass communities of southern Japan.

Sea-grass communities on sandy and muddy sediment bottoms, in marine and polyhaline waters, extending from the mid-tide level down to depths of more than 50 m. The characteristic genera are *Halodule* and *Halophila*. In the littoral belt, they are usually more or less permanent. In the upper sublittoral and around low-water mark they are on most occasions only temporary pioneer stages which can be succeeded by communities of the *Thalassietalia*; they are only permanent in localities where due to environmental or geographic circumstances the coarser species of the latter order are absent. In deep water, *Halophila* species form permanent communities. Apart from stabilising the bottom the *Halodule* species are even able to raise it, but they rarely do so. The stabilising function of most *Halophila* species is limited. Two vicarious alliances can be distinguished, which are identical in structure, but differ in species composition. They

have only two species in common: *Halodule wrightii* which is widely distributed in the tropical Atlantic Ocean and locally in the western part of the Indian Ocean, and the sublittoral *Halophila decipiens* which has a pantropical distribution.

Alliance 2A1 *Halodulion uninervis* Den Hartog 2003

Nomenclature history: The name *Halodulion indo-pacificum* Den Hartog 1977 has been replaced in order to comply with the ICPN rules. Ohba & Miyata (2007) distinguished two alliances within the concept of the *Halodulion uninervis*, viz. *Halodulion* with two associations (*Haloduletum tridentati* and *Haloduletum uninervis*), and *Halophilion ovatae* (probably *Halophilion ovalis* is meant, as the species *Halophila ovata* has nowhere been mentioned in their text) with 4 associations (*Halophiletum ovalis*, *Halophiletum majoris*, *Halophiletum nipponicae* and *Halophiletum nipponicae notoensis*).

This alliance is widely distributed in the Indian Ocean and the tropical western Pacific and it is characterised by *Halodule uninervis*, *Halodule pinifolia* (only in the Gulf of Bengal and the western Pacific), *Halophila ovalis* and *Halophila minor*. Various *Halophila* species are characteristic for communities in extreme environments, such as creeks in mangrove swamps (*Halophila beccarii*) or on sandy patches in deep-water coral reef habitats (*Halophila capricorni*, *Halophila tricostata*). Several *Halophila* species with relatively small areas of distribution occur in more than one community. Although Ohba & Miyata (2007) present a slightly different classification within the *Halodulion uninervis*, their figure 3 shows that the general zonation pattern in tropical Japan hardly differs from the zonation in eastern Africa and Australia.

Alliance 2A2 *Halodulion wrightii* Den Hartog prov.

Nomenclature history: The name *Halodulion atlanto-pacificum* Den Hartog 1977 is contrary to the nomenclature rules. The newly proposed name has the disadvantage that *Halodule wrightii* occurs mainly in the Caribbean, a part of the Gulf of Mexico and along the West coast of Africa, and often is confused with *Halodule beaudettei*. Although *Halodule wrightii* has been generally recorded as occurring along the coast of the United States of America, I have so far not seen a single specimen from there. There are very few records of *Halodule* species along the coast of South America, and about their ecological performance is hardly anything known. More data are required before a definitive name of the alliance can be proposed.

The alliance is widely distributed in the western Atlantic, from North Carolina as far south as the state of São Paulo in Brazil. Along the African Atlantic coast it has been found in Mauritania, Senegal, the Cap Verdian Islands, and Angola; more localities are expected to be found. Further, some stands of *Halodule beaudettei* and *Halophila baillonis* have been found along the Pacific coast of Central America. The alliance has several characteristic

species: *Halodule wrightii*, *Halodule beaudettei* and *Halodule emarginata*, but none of these occurs over the whole area of the alliance's distribution. *Halophila* species occur as well, but form usually monospecific communities; moreover they are quite rare.

Borhidi & Del-Risco (Borhidi et al. 1983) described from Cuba a *Halodulo-Ruppietum maritimae*, which they accommodate into the alliance *Ruppion maritimae*. The latter alliance has not yet been critically studied in North America, but it is very unlikely that *Ruppia maritima* is involved.

Order 2B *Thalassietalia* Den Hartog 1976

Nomenclature history: The names *Thalassio-Cymodoceetalia manatorum* Knapp 1964, nomen nudum, and *Thalassio-Syringodietalia filiformis* (Knapp) Borhidi & Del-Risco in Borhidi et al. 1979 cover only the communities of the *Thalassietalia* in the Caribbean and the Gulf of Mexico, and coincide with the alliance *Syringodio-Thalassion* Borhidi 1979 (in Borhidi et al. 1979). From the species mentioned for this order it is clear that Borhidi has included in his concept also communities which I consider to fit in the *Halodulion wrightii*. *Thalassio-Halophiletalia ovatae* Knapp 1965 was described for the coast of Sri Lanka; Knapp does not give any detail, except for mentioning five species; it is considered here as a nomen nudum. In the *Halophilo-Cymodoceetalia* Knapp 1968, nomen nudum, a number of species is mentioned known to occur in the Red Sea, but further without any details. From the species mentioned one can clearly deduct that this order is a mixture of the three orders presently known to occur in the Red Sea, but that is not a valid description of an order.

Tropical and subtropical sea-grass communities around low-water mark and in the sublittoral, down to a depth of 10–12 m, composed of species of the genera *Thalassia*, *Syringodium*, *Cymodocea* and *Enhalus*. Further, it is a very common phenomenon that *Halodule* and *Halophila* species can occur in considerable quantities in these terminal communities of the sublittoral succession. Their occurrence very probably depends on frequent disturbances, such as damage by storms, the formation of sand mounts by callianassid crustaceans and other burrowing infauna, grazing by marine mammals and water-birds, human activity such as fishing and boating, etc. So a terminal stage is generally littered with small-scale degeneration and regeneration stages, the typical characters of a dynamic equilibrium. Further, apart from the sea-grasses, representatives of various genera of rhizophytic green algae such as *Halimeda*, *Caulerpa*, *Penicillus* and *Avrainvillea* play an important part in these communities. Epiphytic algae are mainly restricted to the leaf-blades; the rhizomes are generally free of algal growth.

This order consists of three vicarious alliances, which are structurally and ecologically very similar, although they have no species in common.

Alliance 2B1 *Cymodoceo-Thalassion hemprichii* Den Hartog 1977

Nomenclature history: The *Cymodoceion rotundatae-serrulatae* Ohba & Miyata 2007 fits seamless in the *Cymodoceo-Thalassion hemprichii*.

This alliance is widely distributed in the Indo-West Pacific, and characterized by *Thalassia hemprichii*, *Cymodocea rotundata*, *Cymodocea serrulata*, *Syringodium isoetifolium* and *Enhalus acoroides*. *Thalassia hemprichii* is usually the dominant species; the other species are interspersed, but here and there can come also to dominance, forming mosaics with *Thalassia*. Particularly the patches of *Cymodocea serrulata* move, as a consequence of horizontal growth of the rhizomes, within the *Thalassia* mats up to 7 m a year. (Brouns 1987). Due to the proliferation of the rhizome, the extension of the *Cymodocea serrulata* patch makes the impression of a front. The other species in the *Thalassia* mat move also around in the course of time. In fact the only association of the alliance, the *Cymodoceo-Thalassietum hemprichii*, is a community always in motion.

Alliance 2B2 *Cymodoceion nodosae* Den Hartog 1976

This alliance is restricted to the Mediterranean and the Atlantic coast from southern Portugal to Senegal, as well as the Canary Islands. It is characterised by *Cymodocea nodosa* and the green alga *Caulerpa prolifera*. I kept this alliance apart from the *Cymodoceo-Thalassion hemprichii*, because of its paucity in participating taxa, and its fully separate geographical distribution. It has not one angiospermous genus in common with the *Syringodio-Thalassion testudinum*. For this reason, I strongly disagree with Rivas-Martinez et al. (2001) who placed this alliance in the synonymy of the *Syringodio-Thalassion testudinum*. If they did not want to accept the alliance *Cymodoceion nodosae* as an independent syntaxon, incorporation within the *Cymodoceo-Thalassion hemprichii* would have been more logical.

Alliance 2B3 *Syringodio-Thalassion testudinum* Borhidi 1979

Nomenclature history: The name *Thalassion caraibicum* Den Hartog 1977 has been replaced in order to comply with ICPN rules.

This alliance occurs only in the Caribbean and the Gulf of Mexico, and extends slightly along the eastern coast of Florida. It is characterized by *Thalassia testudinum* and *Syringodium filiforme*. The first species in particular is the dominant in most of the sea-grass beds of the area (Fig. 2). The phytogeographer Ciferri (1936), who presented a general outline of the vegetation of the West Indian island Santo Domingo (Hispaniola), was the first to record the "associazione *Thalassia-Cymodocea*"; however, without further data. The first real description of this community is given by Lot-Huelgueras (1968a,

Fig. 2. Bed of *Thalassia testudinum* along the coast of Aku-mal, north of Tulum, Yucatan, Mexico. Here and there leaves of *Syringodium filiforme* can be found interspersed between the *Thalassia.* Photo by courtesy of Mrs. Dr. B. van Tussen-broek.

1968b) as "ceibadales" of *Thalassia testudinum*, i.e. the *Thalassietum testudinum*, along the coast of Mexico. The *Syringodio-Thalassietum testudinum* (Ciferri 1936) Borhidi in Borhidi et al. 1983 is a later synonym.

Class 3 *Phyllospadicetea* Den Hartog 1977
Sea-grass communities on wave-exposed rocky shores along the temperate northern Pacific, dominated by re-presentatives of the genus *Phyllospadix*.

Order 3A *Phyllospadicetalia* Den Hartog 1977
The genus *Phyllospadix* consists of 5 (or perhaps 6) spe-cies of which two are limited to the north temperate coast of Asia, and the three other ones to the coast of North America. Each species occupies its own ecological niche and thus each one forms its own association. Even in coastal stretches where more than one species occurs, their associations do not mix, but show spatial segrega-tion. In North America the epiphytic algae are restricted to the leaves of the *Phyllospadix* plants, and appear to be the same as the ones on exposed *Zostera* leaves. The epi-lithic algae on the substrate are the same ones that grow also outside the *Phyllospadix* stands. Because of the struc-tural similarity of these associations, I have recognised only one alliance (Fig. 3).

Alliance 3A1 *Phyllospadicion* Den Hartog 1977
The associations described so far need further study. Par-ticularly the undergrowth of algae is little known, and very probably shows great differences from area to area. The *Phyllospadicetum iwatensis* in China occurs in eulit-toral pools, but can also form closed stands around low-water mark. On Hokkaido, Japan, I found the associa-

tion in the form of large patches near low-water mark, interspersed between large groups of very large Lami-nariales (not identified). In North America, the *Phyllo-spadix* species form belts, the *Phyllospadicetum torreyi* occupies the lower eulittoral and the upper sublittoral, the *Phyllospadicetum scouleri* the middle eulittoral; the *Phyllospadicetum serrulatus* is confined to eulittoral pools. The communities of *Phyllospadix torreyi* and *Phyllospadix scouleri* have been described by Steward & Myers (1980) for the southern coast of California, with much attention for the algae growing on the rocky sub-stratum. Particularly the coralline algae form a dense mat in which the spiny *Phyllospadix* seeds become entangled and develop into a vegetation of densely growing robust plants. These catch much sand and in this way out-com-pete the algae. When the sand layer becomes thicker, the sea-grass starts withering, because the photosynthetic surface becomes partly buried, and this leads finally to the death of the sea-grass and the sand will be washed away. Consequently, the rocky substrate becomes clean again and the coralline algae re-establish themselves. This cyclic succession has been described several times (Gibbs 1902; Turner 1983).

Class 4 *Posidonietea* Den Hartog 1976
Communities on sandy and rocky substrates in the sub-littoral, down to at least 40 m depth, mainly composed of species of the genus *Posidonia*, which are able to raise the bottom considerably by vertical but very slow growth. The dominant species are characterised by extreme lon-gevity, and because of this the communities appear to be very stable in the course of time. They may last for cen-

Fig. 3. Bed of *Phyllospadix torreyi* in the lower eulittoral belt along the west coast of Whidbey Island (Washington, U.S.A.) in August 2012. The *Phyllospadix* beds form mosaics with vegetation dominated by large brown algae, mainly *Nereo-cystis lutkeana* and *Alaria marginata*. The first mentioned species is clearly shown in the foreground of the photo.

turies and even several millennia. The biotic differentiation is considerably higher than in the classes 1–3. They are characterized by separate epiphyte communities on the leaves, and on the rhizomes; the epiphytic community of the rhizomes shows some similarity with sciaphilous rocky shore communities.

Order 4A *Posidonietalia* Den Hartog 1976
Within the order three alliances can be recognized on floristic, structural and geographical grounds.

Alliance 4A1 *Posidonion oceanicae* Braun-Blanquet 1931, pro parte
Nomenclature history: Braun-Blanquet (1931) included the *Cymodocea nodosa* stands in this alliance; in the present study, these are considered to represent an alliance in its own right, the *Cymodoceion nodosae*, within the *Thalassietea*.

The *Posidonion oceanicae* comprises the often very uniform extensive beds of *Posidonia oceanica* in the Mediterranean, first described as an association by Funk (1927). These communities are very long-lived. The vertical growth of the *Posidonia* rhizomes is at most a few milli-

Fig. 4. Summer aspect of the climax association of *Posidonia oceanica* occurring at 6 m depth in Águilas (Murcia region, southeastern Spain). The mat of *Posidonia* on the left side has been raised 1.5-2 m and is at least 2000-3000 years old. The platform on the right side shows also *Posidonia*, but is considerably younger; the age is estimated to be at least 1.5 centuries. The triangle at the base of the photo is an accumulation of old decaying leaves of *Posidonia*. The structures left at the base present some dead *Posidonia* rhizomes colonized by photophilous algae, mainly *Jania rubens* and *Padina pavonia*. Photo by courtesy of Dr. J.M. Ruiz Fernandez.

metres in a year, but the sediment deposits fixed by the dead parts of the rhizomes can be up to 12 m thick (Boudouresque et al. 1994). The continuity of the rhizomes from the base to the top of these formations has also been demonstrated. The upper 40 cm of the formation contains the living rhizome branches. This means that well-developed *Posidonia* beds may have an uninterrupted history of at least to 6,000–7,000 years (Pérez et al. 2016, see their figs. 4 and 5) and can be considered a climax community, i.e. the structurally most differentiated community that can develop and maintain itself under the existing circumstances. The height of the leaf canopy may be about 1 m (Fig. 4).

Although the beds may seem very uniform, there are considerable differences in species diversity between the stands in the upper sublittoral and the deeper stands, mainly due to the differences in illumination, water movement, and exposure to erosion, material transportation and deposition of sand and silt. The papers on the mediterranean *Posidonia* community by Mazzella et al. (1986) and Pérez et al. (2016) are classical examples of good community descriptions.

Alliance 4A2 *Posidonion australis* Den Hartog 2003
This alliance comprises the *Posidonia australis* association, the *Posidonia sinuosa* association and the *Posidonia angustifolia* association, all confined in their geographical distribution to the temperate coasts of Australia.

The *Posidonietum australis* forms extensive beds in the sublittoral of relatively sheltered waters, where they are subjected to sedimentation. According to Cambridge and Kuo (1979), the *Posidonietum australis* usually does not occur deeper than 15 m. Its leaf canopy may reach ca 80 cm in height, and is continuous. The thickness of the rhizome mat is at most 10 cm. This association has a distribution from Shark Bay, Western Australia to Sydney, New South Wales.

The *Posidonietum sinuosae* also forms large meadows in the sublittoral in waters that are exposed to a moderate swell. They occupy areas where sand has been deposited on the bedrock. When the sand layer is not thicker than 50 cm, *Posidonia sinuosa* comes to dominance. It does not occur deeper than 15 m (Cambridge & Kuo 1979). According to Cambridge and Kuo (1979) the beds of *Posidonia sinuosa* often consist of linear rows, up to 50 cm wide, parallel to the prevailing direction of water movement. In areas where the bedrock has a thicker cover of fine sand with cobbles, *Posidonia angustifolia* is the dominant species. This association always has a continuous cover, and descends down to a depth of 35 m. According to Shepherd & Womersley (1981), the height of the canopy of both species amounts to ca. 1 m. There are no records of the thickness of the rhizome mat in these associations. *Posidonia sinuosa* often forms a marginal belt along the edge of *Posidonia australis* beds, probably indicating the reduced sedimentation near the margins of

Fig. 5. A community of fruiting *Posidonia australis* in 2–4 m deep water south of Fremantle, Western Australia. Photo taken by Mrs. L. Rivers, by courtesy of Prof. Dr. J. Kuo.

these beds (Fig. 5). The *Posidonietum sinuosae* as well as the *Posidonietum angustifoliae* are distributed from the west coast of Australia to South Australia. Further research on the thickness of the root-rhizome layer of these communities is recommended.

Alliance 4A3 **Posidonion coriaceae** Den Hartog 2003
This alliance is characteristic for the *Posidonia* communities in very turbulent waters, growing unprotected on sandy substrate in the open ocean, mainly in the southwestern part of Western Australia and South Australia. The roots of the participating species are very long, a necessity for sufficient anchoring of the plants in this rough environment. There are 5 characteristic species, all belonging to the genus *Posidonia*: *P. coriacea*, *P. robertsoniae*, *P. denhartogii*, *P. kirkmanii* and *P. ostenfeldii*. All these species are characterised by very long, thick tough leaves; their growing points are usually deeply buried in the substrate (Kuo & Cambridge, 1984). They do not form true meadows, but clumps and patches of a few decimetres diameter to groups of several m². The largest beds can be formed by *P. coriacea*. The ecological differences between the species depend on the degree of roughness of the environment. *P. ostenfeldii* probably thrives under the most adverse conditions, while *P. coriacea* and *P. robertsoniae* can occur also in relatively sheltered circumstances. The *P. ostenfeldii* community, described by Shepherd & Womersley (1981) from South Australia, no doubt refers to a stand of *P. coriacea*. For reports on the dynamics of this environment one is referred to Kirkman (1985) and Kirkman & Kuo (1990). I may add that J. Kuo and myself visited Middleton beach near Albany (W. Australia), a beach exposed to the open ocean, 5 days after a very heavy gale in September 2014. The damage to the sea-grass bed was obvious, as blocks of sand with a

surface area of up to 10 m² and up to 1 m thick, kept together by sea-grass rhizomes, were washed ashore. The aboveground vegetation on these blocks, consisting of 4 *Posidonia* species (*P. ostenfeldii*, *P. denhartogii*, *P. coriacea* and *P. robertsoniae*), had at most a coverage of 10–20%. This shows that the photosynthetic biomass in this extremely exposed environment is quantitatively much less than the biomass in the substratum.

Class 5 **Thalassodendro-Amphiboletea** Den Hartog 1977
In its original version the tropical and temperate communities, consisting of coarse sea-grasses with lignified, leafy stems of the genera *Amphibolis* and *Thalassodendron*, have been taken together as one class. This class was divided into the tropical order *Thalassodendretalia* and the temperate order *Amphiboletalia*. As these orders have, with the exception of the similarity of the growth form, very little in common I have raised the tropical order to class level (Den Hartog 2003).

The *Thalassodendro-Amphiboletea* are confined to the temperate coasts of Australia, occurring on sand and sand-covered rocks, characterized by the dominance of species with upright, lignified leafy stems of the genera *Amphibolis* and the finer *Heterozostera*. *Thalassodendron pachyrhizum* also belongs within this category, but has a very restricted distribution. Usually these species are very permanent, but it is also known that they can colonise very rapidly suitable areas that become available as a result of erosion. The rhizome mats are 5–20 cm thick in well-established stands, and very well fixed into sandy substrate; if sand is covering rock, the roots cling to the rock. On the leaves and the rhizomes, different epiphyte communities can be found, and in *Amphibolis* and *Thalassodendron* stands a third epiphyte community can develop on the upright stems. The canopy height is rather variable depending on the depth, but also the age of the community; it may reach a height of ca. 1 m.

Order 5A **Amphiboletalia** Den Hartog 1977

Alliance 5A1 **Amphibolion antarcticae** Den Hartog 1977
The characteristic species of this alliance, *Amphibolis antarctica*, *Amphibolis griffithii*, *Thalassodendron pachyrhizum*, and *Heterozostera nigricaulis* (recently described by Kuo 2005) can occur in mixed and monospecific communities, from low-water mark down to at least 35 m depth. The beds of *Amphibolis* and *Heterozostera* often show mosaics with groups of *Posidonia* species (Fig. 6). The communities belonging to this alliance are distributed along the whole south-coast of Australia and along the west-coast up to Shark Bay. The beds of *Heterozostera chilensis* found along the coast of Chile need further study, but considering the morphological structure of this sea-grass, they most likely should be classified within the *Amphiboletalia* as an alliance of its own.

Fig. 6. A bed of *Heterozostera nigricaulis* with here and there some solitary plants of *Posidonia australis* in 2–4 m deep water south of Fremantle, Western Australia. Photo taken by Mrs. L. Rivers, by courtesy of Prof. Dr. J. Kuo.

Class 6 Thalassodendretea ciliatae Den Hartog 2003
[*Halophilo-Cymodoceetea* Knapp 1968, pro minore parte]

Seagrass communities composed of dense monospecific stands of *Thalassodendron ciliatum*, on sand, sand-covered rock and on coral reefs, going down to a depth of at least 30 m. They form a climax vegetation of high stability on the outer side of reefs. Within the lagoons they occupy the most exposed sites. According to Brouns (1985), who studied the association in the Banda Sea, In-
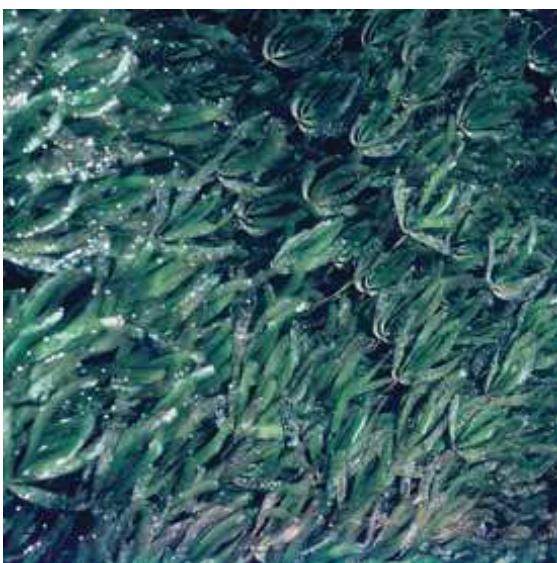
Fig. 7. Climax association of *Thalassodendron ciliatum* along the most southern part of the Sinai coast of the Bay of Aqaba between Nabq and Na'ama, directly opposite the island in the Strait of Tiran, August 1978.

donesia, the rhizome mat can be up to 70 cm thick; on coral reefs, living and dead rhizomes can hardly be visually distinguished and appear to be fully integrated in the substrate. The canopy can be up to 1 m high. It consists of the lignified upright stems with a dense carpet of leaves atop. Three communities of epiphytic algae can be recognized, viz. a community of heliophilous algae on the leaves, a community of shade-tolerant algae on the stems, and at the base a community rather similar to that of the sublittoral rocky shore. The vegetation of this class is difficult to approach and needs further study. It is widely distributed in the Indian Ocean and less common in the tropical western Pacific Ocean with only one association.

Order 6A *Thalassodendretalia ciliatae* Den Hartog 1977

Alliance 6A1 *Thalassodendrion ciliatae* Den Hartog 1977

One association, the *Thalassodendretum ciliatae* has been described by Lipkin (1977, 1988) from the outer reefs of the Red Sea (Fig. 7).

Formation of the aquatic plant communities of shallow poikilosaline brackish and continental waters

In addition to the six classes of the sea-grass formation, there is only one truly marine association, characterised by *Ruppia* aff. *tuberosa* and *Lepilaena marina*, that does not fit within the concept of the sea-grass formation. It can be placed without any difficulty in the class *Ruppietea*, up to now the only class of the formation of the aquatic plant communities of shallow poikilosaline coastal and continental waters (Den Hartog 2003). There are only six genera that form this ecological group: *Ruppia*, *Stuckenia*, *Zannichellia*, *Lepilaena*, *Althenia* and *Pseudalthenia*.

The similarities between the sea-grasses and the eurysaline aquatic plants are that taxa of both categories are able to live permanently in the marine environment. Some of the sea-grass genera occur only in undiluted seawater, e.g. *Posidonia, Thalassodendron, Amphibolis, Syringodium, Thalassia,* some are more euryhaline and can penetrate estuaries and the intertidal belt, where the salinity may fluctuate due to freshwater input by rivers or by rain during low tide, e.g. *Zostera, Phyllospadix, Halodule,* and *Halophila*. In *Halophila* there are strictly marine species, but also typically estuarine species, e.g. *Halophila beccarii*. The true sea-grasses can tolerate only relatively small fluctuations in salinity.

The fundamental difference between the sea-grasses and the eurysaline aquatic plants was outlined in the Introduction. The sea-grasses are restricted in their distribution to the marine environment, where the dominant salt is NaCl, but the eurysaline taxa can occur in all kinds

of environments with a high content of electrolytes, such as chlorine, sulphates, hydrocarbonates, etc. Most of them are also able to stand large fluctuations in the concentration of the various salts. As a consequence, they are not limited to the coastal area. Taxa of the eurysaline group occur generally in sheltered marine waters, where sea-grass is absent, or in brackish lagoons where the annual salinity fluctuations are considerable. Some species of *Ruppia* may occur sometimes in the intertidal belt, but if sea-grasses penetrate such areas they will disappear within a few years by lack of competitive power. In the case of strong coastal pollution, sea-grass may disappear, and *Ruppia* may take over, e.g. after the oil spill along the coast of Louisiana (personal communication by A. Thorhaug). This is a bad omen, an indication of degradation of the substrate.

A recently recognised new species, *Ruppia mexicana*, inhabits both marine and brackish as well as fresh-water sites, even crater lakes at an altitude of more than 2,300 m (Den Hartog et al. 2016). In Europe, *Ruppia* species can occur also at considerable heights, e.g. *Ruppia maritima* in the Alsace, France (personal communication by L. Triest), and *Ruppia drepanensis* in Spain (in Herbarium of Firenze).

From recent morphological taxonomic and molecular-genetic research, it is apparent the genus *Ruppia* needs a worldwide revision. The name *Ruppia maritima* was traditionally used, but generally incorrectly. There occur at least 4 species in Europe, 5 in North America, and at least 5 in Australia (Jacobs & Brock 1982). A very recent study in China yielded 3 species (S. Yu & Den Hartog 2014), but not *R. maritima*, the only species recorded in the Flora of China (Guo et al. 2010).

For the genus *Zannichellia* that, with the exception of one species, does not occur under marine conditions, a similar situation has been established. In contrast to the treatment in the Flora Europaea (Dandy 1980), in which the genus has been treated as a monospecific one, there occur in Europe alone at least 6 well-defined species (Talavera et al. 1986). The consequences for the phytosociological classification I am uncertain about at this moment, but I anticipate they will be profound.

A plea for a similar approach for the classification of fresh-water plant communities

For the classification of the sea-grass communities 8 criteria were used consciously in order to arrive at a relatively simple system. A similar approach is recommended for the classification of the fresh-water plant communities. Except for the *Lemnetea* and the *Charetea,* practically all other aquatic communities are classified within the *Potametea*, a kind of reservoir without any organisation. It contains plants with floating leaves (nymphaeids,

all over the world, Van der Velde, 1980), completely submerged plants such as the parvopotamids, magnopotamids, myriophyllids, ceratophyllids (worldwide), the combination of *Batrachium* and *Callitriche* species (in many places in Europe). It must be possible to bring some order to this vegetation class by taking into account life- and growth forms, life cycles, architecture, rhizome-root systems, longevity, etc. Now, as a consequence of the deductive approach (bottom-up) has every area, where phytosociological work has been performed, its own system, with its own higher syntaxa. In my opinion this is an undesirable situation, a relict of the past. Den Hartog & Segal (1964) did a first, at that time premature, attempt to split up the *Potametea*. Wiegleb (1981) is also of the opinion this class is very heterogeneous. The break-up of the *Potametea* needs to take place orderly, based on sufficient research.

I want to indicate as an example one study where the establishment of higher syntaxa has been performed in an irresponsible way. Ohba & Sugawara (1981) erected for the 6 Japanese representatives of the family *Podostemaceae*, belonging to 2 genera, 6 monospecific associations, which were taken together in one alliance. Subsequently they founded the order *Podostemonetalia* and the class *Podostemonetea*. This is incomprehensible, because the family *Podostemaceae* contains, according to Cook (1990), worldwide 47 genera with 268 species; moreover the African *Hydrostachydaceae* with only one genus with 22 species occupies the same kind of biotopes. This ecological group is qua size and the spectrum of life-forms extremely diverse, and a serious study should certainly show that there are quite a number of orders and classes to be distinguished. My own experience with *Podostemaceae* is very limited. I found in Queensland and Papua New Guinea the species *Torrenticola queenslandica* in a dense community of bryophytes, showing the possibility that at least some vegetation with *Podostemaceae* could be classified within aquatic syntaxa dominated by bryophytes.

A final remark

The sea-grass communities are heavily threatened practically everywhere in the world. Therefore, I want to conclude this paper with a plea for the unconditional protection of sea-grass beds. They have a crucial function as a nursery environment for numerous organisms, also for those who as mature individuals live in completely different environments. During the long period I have studied sea-grass beds, many of them have disappeared completely, mostly as a result of human activities: (1) eutrophication, (2) coastal development (new dams, new ports, industrial complexes, dredging), (3) purposeful destruction to make place for the culture of oysters, mussels, fish, and other edible creatures, (4) tourist industry

(marinas, harbours for yachts, and all kinds of facilities to attract tourists), and (5) oil spills, and drilling and mining accidents. Natural causes may sometimes also play a role. For some still unknown reason(s), natural recovery does not seem to happen, or perhaps very rarely. One can only guess how the sea-grass beds came into existence in the past and which natural factors played a key role in that process. Nowadays only a few species are successful and extend their area rapidly, because they have managed to pass an ecological barrier, and are thus adventives in the new areas they colonize. *Halophila stipulacea*, originally confined to the western Indian Ocean, has passed the Suez Canal and is now well established in the eastern Mediterranean, slowly progressing in western direction. Recently, it has been also discovered in the Caribbean, where it is likely to become a pest (B. van Tussenbroek, personal communication). How it arrived there is a matter of speculation. It is absolutely unclear, why this species is so successful in the Mediterranean and the Caribbean, while it did not extend its area in the Indo-West Pacific. Another sea-grass, *Zostera japonica*, colonized in the last century the intertidal belt of a long coastal area from British Columbia to California. Probably, it arrived there accidentally with imported oysters. In this case, the sea-grass settled in an empty niche, which along similar shores in Europe, East Asia, South Africa and Australia is occupied by other members of *Zostera* subgen. *Zosterella*. This is the main reason that I bring this to the front. Attempts to help nature to recover with transplants of sea-grass often fail; in the case of *Posidonia oceanica*, this is self-evident, but transplants of the much simpler structured *Zostera* or *Thalassia* beds disappear also within a relatively short time. Very recently, Van Katwijk et al. (2016) published a global analysis of 1,786 sea-grass bed restoration projects, showing that large-scale planting generally is the most effective, but also very expensive. Even more recently it has been discovered that marine *Phytophthora* species, found on both sides of the Atlantic Ocean, appear to be responsible for the fact that a large percentage of seeds of *Zostera marina* are unable to germinate (Govers et al. 2016). Further research on the fungal occurrence and its effect on *Zostera*, but also on other sea-grasses, is recommended.

Acknowledgements

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