Schimmelmannia elegans (Gloiosiphoniaceae, Rhodophyta): South Africa's first introduced seaweed?

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Although there are a number of records of recently introduced marine animals in South African waters, there has never been good evidence of a seaweed introduction. *Schimmelmannia elegans,* a red alga previously only known from Tristan da Cunha and Nightingale Island, is reported for the first time for South Africa. The plants were found growing in the Kelp Tank of the Two Oceans Aquarium in Cape Town. The morphology and reproduction of the specimens are described in detail and agree in all aspects with the original account of *S. elegans*. Several hypotheses on the arrival of this newcomer along the South African coast are discussed: previously overlooked, present as a different life history stage, or recently introduced. Of these, recent introduction seems the most plausible. In this context, the spread and potential ecological significance of an introduced seaweed species are discussed.

INTRODUCTION

One of the main attractions of the Two Oceans public aquarium in the Cape Town Waterfront development is a 6 m deep 'Kelp Tank'. During a survey of the marine benthic algae and associated fauna of this tank by one of us (D.R.-A.), a species that was previously unknown in South Africa was collected. Close examination revealed that the specimens under consideration belonged to the red algal genus *Schimmelmannia* Schousboe *ex* Kützing (Gloiosiphoniaceae, Gigartinales). The latter, at present, contains six species: *S. schousboei* (J. Agardh) J. Agardh (1851) from the north-east Atlantic Ocean and the Mediterranean Sea; *S. bollei* Montagne (1857) from the Cape Verde Islands; *S. frauenfeldii* Grunow (1867) from St Paul Island; *S. elegans* Baardseth (1941) from Tristan da Cunha and Nightingale Island; *S. plumosa* (Setchell) I.A. Abbott (1961) from the North Pacific Ocean (Japan, California); and *S. dawsonii* Acleto (1972) from Peru. Species are mainly distinguished by differences in the overall habit, their mode of branching, and the texture.

Schimmelmannia belongs to Gloiosiphoniaceae, a small red algal family related to the Dumontiaceae and the Weeksiaceae but distinguished from them primarily by the position of the carpogonial branch in relation to the auxiliary cell (Kylin 1930, 1956; Abbott 1968; Lee & Yoo 1979). At present, the Gloiosiphoniaceae contains five genera: *Gloeophycus* I.K. Lee & S.A. Yoo (1979), *Gloiosiphonia* Carmichael *in* Berkeley (1833), *Peleophycus* I.A. Abbott (1984), *Schimmelmannia* Schousboe *ex* Kützing (1849), and *Thuretella* F. Schmitz *in* Schmitz & Hauptfleisch (1897). The placement of a possible sixth genus, *Plagiospora* Kuckuck (1897), in the Gloiosiphoniaceae family was originally proposed by Irvine (1983). The taxonomic affinities of *Plagiospora* remain poorly understood, however, and Maggs (1990) advocated that it might best be placed in its own family in the Gigartinales. As far as

is known, genera of the Gloiosiphoniaceae exhibit a heteromorphic life history, with an erect sexual phase and a crustose tetrasporic phase (West & Hommersand 1981). *Gloiosiphonia* is indeed the only genus in the family for which it has been clearly demonstrated that the life history involves a crustose tetrasporic phase and an erect gametophytic phase (Edelstein 1970; Edelstein & McLachlan 1971). A crustose phase is presumed for the other genera but has never been observed. So as far as *Gloiosiphonia* is concerned, both phases, erect and crustose, are known. For *Gloeophycus, Peleophycus,* and *Thuretella,* tetrasporophytes remain unknown. Chihara (1972) made an attempt to study the life cycle of *S. plumosa*. Germinating carpospores produced a crustose *Hymenoclonium*-like phase (see also, DeCew & West 1982), which, after several months, gave rise to minute erect thalli that were similar in morphology to the gametophytic phase. Unfortunately, the thalli did not become fertile. However, Chihara hypothesized that *Schimmelmannia* is characterized by a life history in which gametophytes are produced directly from a diploid crust. This situation is reported, but not well understood, in several red algae (Hawkes 1990). In the absence of karyological data, it is difficult to interpret Chihara's observations, and additional studies are needed to confirm the direct life cycle in *Schimmelmannia*.

In this paper, we report *S. elegans* for the first time for South Africa. A detailed description of the species is provided because the reproductive anatomy was not described in detail by Baardseth (1941). In addition, initial stages of the development of the presumed tetrasporangial phase were observed in the culture. Finally, the presence of the alga in the harbour of Cape Town is discussed in relation to the hypothesis that it is a recent introduction.

MATERIAL AND METHODS

Specimens were collected in the Kelp Tank of the Two Oceans Aquarium, Cape Town, and transferred directly to the labo-

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ratory. Voucher specimens (leg. O. De Clerck, 03/05/200, ODC 860) are deposited in BOL (Bolus Herbarium, Botany Department, University of Cape Town) and GENT (Herbarium, Biology Department, Ghent University). Fragments of plants were mounted on glass slides in a solution of 1% aniline blue, 3% 1 N HCl, 50% Karo® corn syrup, and 46% water. In order to observe the tetrasporophyte generation, carpospores were inoculated on glass slides and grown at 15°C under cool white light (15–20 μmol m^{-2} s^{-1}; 16:8 h light–dark) in half-strength Provasoli's enriched sea water medium, as described by Bold & Wynne (1978).

RESULTS

Description

Plants grow up to 120 cm tall and are characterized by a soft but not gelatinous texture (Fig. 1). Several axes develop from a crustose holdfast (Fig. 2). The axes are strongly compressed in the middle and apical parts of the thallus, but towards the base they are subterete (Fig. 8). Branching is strictly pinnate in the entire thallus. The pinnae are lanceolate (200–450 μm wide, 2–5 mm long) and are either unbranched or pinnately branched. Branching of the pinnae is mainly restricted to the lower half of the branchlets and often predominantly on the adaxial side, giving the pinnae a secund aspect (Figs 3–7). The initial branching pattern of the pinnae is most easily seen in distal portions of the thallus; in the lower part of the thallus, the branching pattern is somewhat obscured by damaged pinnae, which form adventitious branchlets. The primary axes do not form side axes or branch only once (rarely twice); as a result of damage, an axis may give rise to four or five newly developing axes. The colour is a deep wine-red.

The thallus is uniaxial and has a prominent apical cell, which divides obliquely to form an axial filament (Fig. 9). Each axial cell cuts off five periaxial cells. The first periaxial cell is always formed laterally (switching 180° between successive segments). The second is formed in a lateral position, opposite the first periaxial cell, and the third periaxial cell is formed in a similar position but on the opposite side of the axial cell. The fourth and fifth periaxial cells are formed between the first and second and between the first and third, respectively. The pinnae are invariably formed by the first periaxial cell. The compressed nature of the axes is the result of an unequal development of the periaxial cells, the lateral cells developing more than the transverse ones. The axial filament is only noticeable in the apical parts of the thallus, and is soon obscured by the formation of descending rhizoidal filaments originating from the lower cells of the lateral filaments.

Gametophytic thalli are dioecious. Carpogonial and auxiliary branches are borne on the same supporting cell, which is an accessory cell on the abaxial surface of a lateral periaxial in the ultimate branchlets (Figs 10, 15–17).

Generally, the procarps are borne by the first-formed periaxial cells, which results in a longitudinal series of gonimoblasts alternately to the left and right of an axis. Sometimes a procarp is also formed on any one of the periaxial cells opposite the first-formed periaxial cell. As a rule, however, only a single gonimoblast develops per segment (Fig. 10). The car-

pogonial branch is curved and invariably four cells long. T terminal carpogonium is small and conical. The trichogyne short and strongly constricted at its junction with the car gonium. The hypogynous cell (the cell below the carpogo um) is distinctively larger than any other cell in the car gonial branch. The auxiliary cell branch is four to six ce long and bears a terminal auxiliary cell, which is larger th the other cells. After presumed fertilization, the carpogoni undergoes two transverse divisions. The middle one of resulting three cells fuses directly with the auxiliary cell (F 16). Following this, the enlarged auxiliary cell cuts off a g imoblast initial (Fig. 17). After fertilization, the auxiliary ce swell and become densely protoplasmic. The pit connectic also enlarge considerably. Little change is noted in the ce of the carpogonial branch. The gonimoblast is naked and most all of its cells are converted to carposporangia (12– μm in diameter).

Spermatangia are formed in superficial sori, which co· most of the pinnae. Superficial cells cut off two or three sp matangial mother cells, which cut off two or three spermat gia (2–4 μm in diameter) by oblique septa (Fig. 11). Car spores germinate unidirectionally on cover slips to form ι iseriate prostrate adherent filaments. Germination is chara terized by the formation of a germ tube. The filaments rem; unbranched at first, but later a subapical cell, or a cell at gre er distance below the apex, cuts off two lenticular cells, whi are the initials of lateral filaments (Fig. 12). Lateral filame develop in the same way as the principal filament. We c served that several germinating carpospores could give rise an openly branched web (Fig. 13), which gradually becai pseudoparenchymatous by the production of additional late filaments. After four weeks, the crusts became polystroma (Fig. 14), but then they ceased to grow and eventually di without the production of tetraspores or an erect thallus.
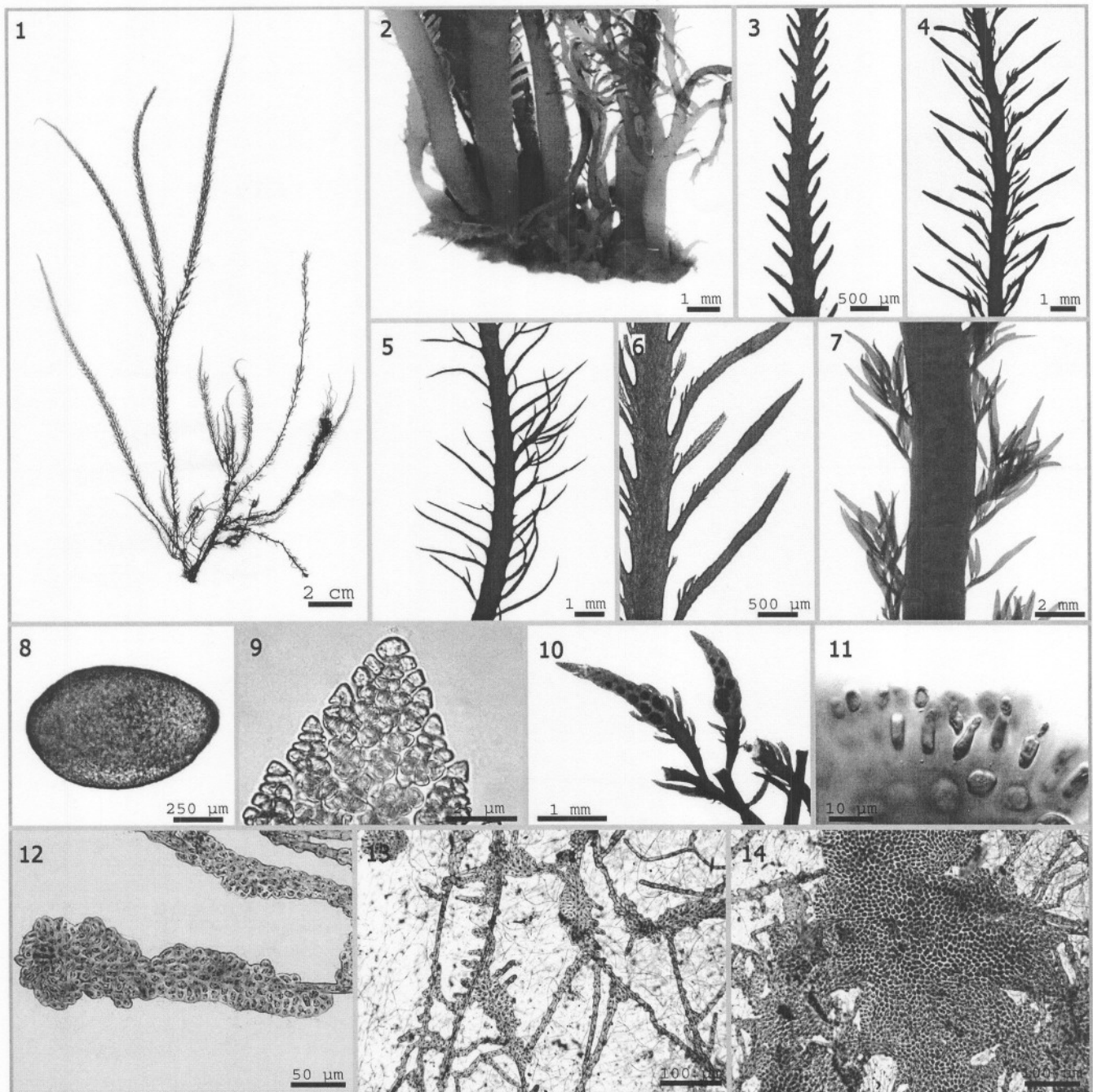
Ecology

The plants only grow at two places in the Kelp Tank of Two Oceans Aquarium in Cape Town, viz. an inlet pipe tl continuously spouts water at great velocity in the tank and a wall next to a plunging device, which generates wave acti in the tank. At both places, *Schimmelmannia* was found gro ing just below the surface. A third group of plants was c served growing outside the aquarium, on a ledge onto whi the outlet from the aquarium is discharged. These plants w growing above the maximum water level in the harbour, l under a constant stream of falling water. They were not ferti and only ≤ 5 cm tall. In contrast, all specimens collected the Kelp Tank were fertile, with each female plant beari hundreds of gonimoblasts.

DISCUSSION

Taxonomy

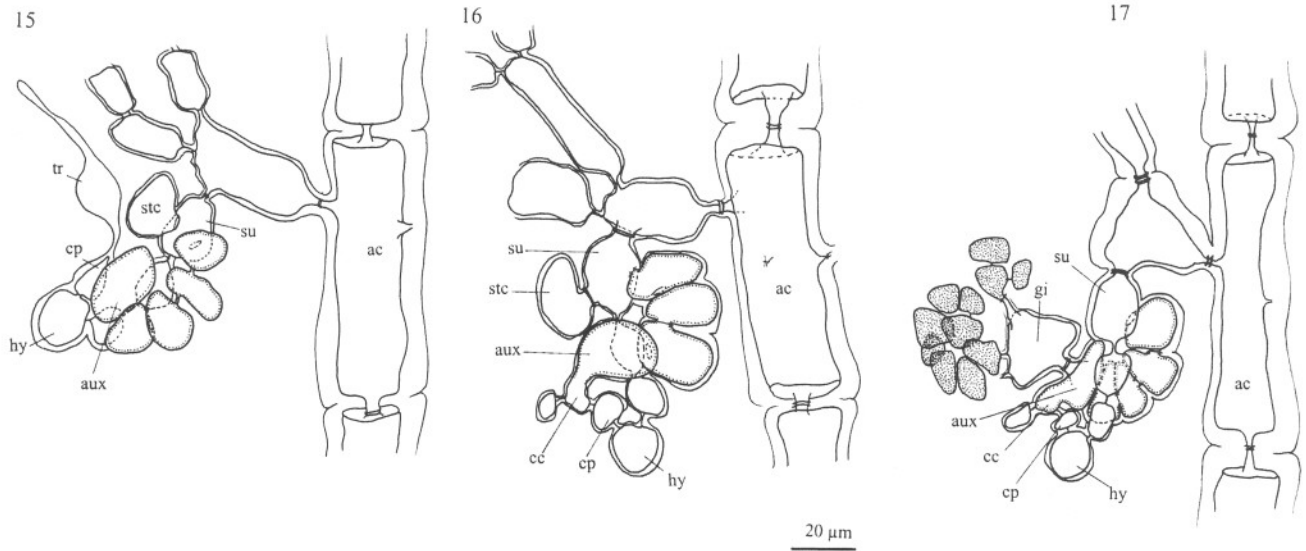A compressed thallus in which the central axis is only clea noticeable in the apical parts of the thallus and an obliqu dividing apical cell are characteristic for the genus *Schi melmannia* and preclude possible confusion with other gen belonging to the Gloiosiphoniaceae (Abbott 1961, 1984; L & Yoo 1979). The combination of a procarp in which t

Figs 1–17. Abbreviations. ac = axial cell; aux = auxiliary cell; cp = carpogonium; cc = connecting cell; hy = hypogynous cell; stc = sterile cell; su = supporting cell; tr = trichogyne.

Figs 1–14. *Schimmelmannia elegans.*

Fig. 1. Habit of a medium-sized specimen collected in the Kelp Tank of the Two Oceans Aquarium (ODC 860).

Fig. 2. Detail of the crustose base giving rise to several erect axes.

Fig. 3. Pinnate branching in the distal parts of the thallus, with the pinnae still unbranched.

Figs 4–7. Branching in the middle and lower parts of thallus, ranging from bipinnate (often secund) to irregular.

Fig. 8. Transverse section of the main axes near the base.

Fig. 9. Detail of an apex.

Fig. 10. Detail of terminal branchlets, each bearing several mature gonimoblasts.

Fig. 11. Detail of spermatangia.

Fig. 12. Young stage in the crustose phase of *S. elegans.*

Fig. 13. Several germinating carpospores coalescing to form an open network.

Fig. 14. Older portions of the crustose phase, which become multilayered.

20 μm

Figs 15–17. Female reproductive structures of *S. elegans.*
  Fig. 15. A mature procarp with a carpogonial branch (four-celled) and auxiliary branch (five-celled) attached to the supporting cell. Note sterile cell attached to the supporting cell.
  Fig. 16. A procarp just after fertilization, showing a connecting cell that has fused with the auxiliary cell. Note the enlarged cells and connections of the auxiliary branch and sterile cell.
  Fig. 17. A young gonimoblast, showing the fusion of the connecting cell with the auxiliary cell, the primary gonimoblast initial, and seve[ral] clusters of carposporangia.

auxiliary cell is in a terminal position and a four- to six-celled auxiliary branch is a another characteristic only found in *Schimmelmannia.* Species of *Schimmelmannia* are distinguished mainly on the basis of the branching pattern, texture, and size of the thallus (Mazza 1913; Baardseth 1941; Acleto 1972). *Schimmelmannia bollei, S. dawsonii,* and *S. plumosa* are characterized by a tri- to quadripinnate thallus. Only *S. elegans* and *S. frauenfeldii* have a bipinnate thallus. According to Baardseth, *S. elegans* differs from *S. frauenfeldii* in its less rigid texture and in the shape of the pinnae. The specimens collected in Cape Town agree extremely well with Baardseth's (1941) account of *S. elegans* and are considered to be conspecific with the alga from Tristan da Cunha.

The reproductive morphology of three species of *Schimmelmannia* has been dealt with in detail: *S. dawsonii* (Acleto 1972), *S. schousboei* (Kylin 1930, as *S. ornata* Schoesboe *ex* Kützing), and *S. plumosa* (Segawa 1938, as *Baylesia plumosa* Setchell; Abbott 1961). The observations on *S. elegans* reported in this paper are largely in agreement with the previous accounts. As in the report on *S. schousboei* by Kylin (1930) and *S. plumosa* by Segawa (1938), a small variation was noticed in the number of cells in the auxiliary branch, which ranges from four to six cells. The number of cells in the carpogonial branch, however, seems to be fixed in *S. elegans,* contrary to *S. plumosa* and *S. schousboei,* where the length varies between four and six cells. According to our observations, the supporting cell often bears a single sterile lateral cell next to the carpogonial and auxiliary branch. So far, a sterile lateral cell on the supporting cell has not been reported in any species of *Schimmelmannia.* Kylin (1930) noticed some variation in the position of the supporting cell, which can be the first or second cell of a filament that is itself borne abaxially on a periaxial cell. In *S. elegans,* the supporting cell is always directly attached to the periaxial cell.

Introduced or overlooked?

So far, *S. elegans* has only been found in the Two Ocea[ns] Aquarium and growing below an outlet pipe where water fr[om] the aquarium is pumped into the harbour. No records exist [of] *S. elegans* on the coast of South Africa. The chance that [the] species has simply been overlooked in the field is small, co[n]sidering its size (up to 120 cm tall) and its ecology. Pla[nts] were found growing at water level in the aquarium, a[nd] Baardseth (1941) reported the species from the intertidal [as] well as the subtidal (to a depth of 10 m). Furthermore, [the] west coast of South Africa, and especially the Cape To[wn] area, has been extensively surveyed (Stegenga *et al.* 199[?] Bolton 1999). Therefore, it can be concluded that the er[ect] gametophytic phase most probably does not occur on [the] shores of South Africa.

There is, however, a possibility that the alga is present alo[ng] the South African coast, but only in the crustose form. Cr[us]tose growth forms have several survival advantages o[ver] erect, fleshy growth forms (such as large reserves of stora[ge] materials and resistance to mechanical damage and grazi[ng]) and are generally considered to be a more resistant pha[se] which enables species to overcome stress periods (Sloc[?] 1980). Furthermore, tetrasporic crusts are able to recy[cle] themselves by means of apomixis (DeCew *et al.* 1982; Gu[?] & West 1984; Maggs 1988), which could explain the abse[nce] of the gametophytic generation for long periods of time. I[t is] unlikely that even this phase is present, however, becau[se] crustose growth forms have received much attention along [the] South African west coast (Anderson & Stegenga 1985; A[n]derson *et al.* 1988; Anderson & Bolton 1990; Stegenga *et* [al.] 1997); for most species with a heteromorphic life cycle, b[oth] phases have been accurately described. It is therefore sign[ifi]cant that the typical crustose growth form of *Schimmelmann[ia]*

as described by Chihara (1972) and in this paper, has not been found in nature along the South African coast.

Chihara (1972) observed a direct life cycle in *Schimmelmannia,* whereby carpospores grow into a crust that gives rise directly to a new gametophyte generation growing on the crust. These observations, however, were not supported by karyological data that would corroborate a direct life cycle. A possibility remains that tetrasporangia (or any other sort of meiosporangia) might have been formed in the crustose growth form and have germinated *in situ.* Such a phenomenon could easily be interpreted as a direct life cycle (Cortel-Breeman 1975). To further complicate the situation, both modes of development, a direct life cycle and *in situ* germination of meiosporangia, can occur in certain species, as has been shown convincingly for *Bonnemaisonia asparagoides* (Woodward) C. Agardh (Cortel-Breeman 1975; Rueness & Åsen 1982). It is clear that a detailed study on the life cycle of *Schimmelmannia,* including karyological data, is needed to clarify this situation. If a direct life cycle is characteristic for *S. elegans* in South Africa, the macroscopic gametophytic phase should be a lot more abundant along the coast and tetrasporic crusts entirely absent. The presence of *Schimmelmannia* as a crust in South Africa, therefore, becomes less likely, but cannot be excluded.

To us, the most probable explanation for the occurrence of *Schimmelmannia* in Cape Town is that it is a recent introduction. There have been a number of well-recorded invasions of marine animals into South African waters, with some of them, notably the European shore crab (*Carcinus maenas*) and the Mediterranean mussel (*Mytilus galloprovincialis*), being ecologically important (Griffiths *et al.* 1992). Contrary to other cold or cool temperate regions (e.g. Australia, Mediterranean Sea, Pacific America), there have been no documented cases of recent seaweed introductions into South Africa. However, some algae that are present along the South African west coast may have been introduced in the recent past, especially *Antithamnionella spirographidis* (Schiffner) Wollaston and *A. ternifolia* (J.D. Hooker & Harvey) Lyle, which are both widespread species on a worldwide scale and are successful exotics in many parts of the world (Maggs & Stegenga 1999); but no historical data exist on the presence of these species along the South African coast. A single specimen of *Bonnemaisonia hamifera* Hariot was found in the drift at Strandfontein by Mary Pocock in 1938 (Stegenga *et al.* 1997). Apparently, this notorious invader, thought to have been introduced from Japan (Maggs & Stegenga 1999), failed to establish a population and has not been found since.

The proposed carrying agents or 'vectors' for seaweeds are many and include ship fouling (*Antithamnionella* Lyle spp.: Maggs & Hommersand 1993), shellfish packaging [*Sargassum muticum* (Yendo) Fensholt: Scagel 1956], oil-rigs (*Laminaria* J.V. Lamouroux spp.: Moss *et al.* 1981), spore dispersal in ballast water (Carlton 1985), anchors, fishing nets, and aquarium escapes [*Caulerpa taxifolia* (Vahl) C. Agardh: Meinesz *et al.* 1993; Meinesz 1999]. All of the organisms in the Two Ocean Aquarium Kelp Tank were collected from local waters. The sea water, however, is pumped into the tank from a submerged inlet in the harbour. The inlet pipe is in the same harbour basin where a number of fishing vessels dock, including some that fish for rock lobster off Tristan da Cunha. Fragments of gametophytes, crusts, or spores may have been

transported to Cape Town in ballast water, discharged into the harbour, and pumped thence into the aquarium system. A SCUBA search, however, revealed no evidence of attached erect or crustose plants within a *c.* 10 m radius of the inlet pipe. It is likely that discharge water from the aquarium has carried spores or plant fragments into the harbour because small plants have become established below the outlet, but at the moment plants are restricted to a ledge in the 'splash' from the outlet, and none occur at or below the water level. The basin into which the outlet pipe discharges is turbid and probably somewhat stagnant, and only macroalgae typical of such habitats (e.g. *Ulva* Linnaeus, *Bryopsis* J.V. Lamouroux) are found there.

The future of *S. elegans* in South Africa

In recent years, there has been an increasing awareness of the occurrence of introduced species around the world (Boudouresque *et al.* 1994; Carlton 1996; Farnham 1997; Jousson *et al.* 2000). Several conditions are required for the successful establishment of a newly arrived alien. Firstly, the dispersal stage must survive transit from one country to another, and the newcomer must establish a viable population; both have been achieved by *S. elegans*. Secondly, the ecological conditions need to be similar to the original habitat. Baardseth (1941) reports that, on Tristan da Cunha, *S. elegans* grows from the low water level to a depth of 10 m and is usually associated with boulders or kelp beds (Baardseth 1941). These habitats are common along the South African west coast. The main factor limiting the geographical distribution of seaweeds is sea water temperature (van den Hoek 1984; Lüning 1990). Annual average sea water temperatures along the South African west coast are 12–13.5°C, and there is a small range between the highest monthly means (13–14.6°C) and the lowest monthly means (11.5–12.5°C) (Bolton & Anderson 1990; Stegenga *et al.* 1997). Temperatures in the nearby False Bay, which is large and enclosed, are warmer, with summer monthly means of 18–19°C and winter monthly means of 12–14°C. Baardseth (1941) reported sea water temperatures for Tristan da Cunha of 12–14°C in winter and 14.8–20°C in summer. Thus, although the temperature tolerances of *S. elegans* have not been studied in culture, it is likely that the species could become established on the west coast of South Africa, especially the False Bay area, with its well-developed kelp vegetation and slightly higher average sea water temperatures. A careful examination of long stretches of the harbour wall, from 0–2 m depth, in several basins in Cape Town harbour failed to locate any *S. elegans*. Furthermore, in all basins adjacent to the Two Oceans Aquarium, the water is turbid and all hard substrata deeper than about 3 m are covered in fine sediment, so that macrophytes are confined to the upper 1–2 m. The fact that *S. elegans* is of extremely limited occurrence in the Kelp Tank, being restricted to areas where water movement is greatest, suggests that it may only grow in relatively high-energy environments, and this may prevent it from spreading out of the harbour. The future success of this species and the resulting impact on native ecosystems will depend on multiple factors (competition with other species, presence of potential grazers, ecological conditions, dispersal mechanisms, etc.) and is, therefore, extremely difficult to predict.

REFERENCES

ABBOTT I.A. 1961. On *Schimmelmannia* from California and Japan. *Pacific Naturalist* 2: 379–386.

ABBOTT I.A. 1968. Studies in some foliose red algae of the Pacific Coast. III. Dumontiaceae, Weeksiaceae, Kallymeniaceae. *Journal of Phycology* 4: 180–198.

ABBOTT I.A. 1984. *Peleophycus multiprocarpium* gen. et sp. nov. (Gloiosiphoniaceae, Rhodophyta). *Pacific Science* 38: 324–332.

ACLETO O.C. 1972. Structure and reproduction of *Schimmelmannia dawsonii* sp. nov. (Rhodophyceae, Cryptonemiales). *Phycologia* 11: 5–9.

AGARDH J.G. 1851. *Species, genera et ordines algarum*, vol. 2, part 1. Gleerup, Lund. 351 pp.

ANDERSON R.J. & BOLTON J.J. 1990. Reproductive morphology and life histories of southern African *Gymnogongrus* species (Rhodophyta, Phyllophoraceae). *British Phycological Journal* 25: 381–390.

ANDERSON R.J. & STEGENGA H. 1985. A crustose tetrasporophyte in the life history of *Nothogenia erinacea* (Turner) Parkinson (Galaxauraceae, Rhodophyta). *Phycologia* 24: 111–118.

ANDERSON R.J., SIMONS R.H. & BOLTON J.J. 1988. *Zeacarpa leiomorpha* (Ralfsiaceae), a new genus and species of crustose marine Phaeophyceae from southern Africa. *Phycologia* 27: 319–326.

BAARDSETH E. 1941. The marine algae of Tristan da Cunha. *Results of the Norwegian Scientific Expedition to Tristan da Cunha (1937–1938)* 9: 1–173.

BERKELEY M.J. 1833. *Gleanings of British algae, being an appendix to the supplement to English Botany*. Sowerby, London. 50 pp.

BOLD H.C. & WYNNE M.J. 1978. *Introduction to the algae – structure and reproduction*. Prentice Hall, New Jersey. 706 pp.

BOLTON J.J. 1999. Seaweed systematics and diversity in South Africa: an historical account. *Transactions of the Royal Society of South Africa* 54: 167–177.

BOLTON J.J. & ANDERSON R.J. 1990. Correlation between intertidal seaweed community composition and sea water temperature patterns on a geographical scale. *Botanica Marina* 33: 447–457.

BOUDOURESQUE C.F., BRIAND F. & NOLAN C. (Eds) 1994. Introduced species in European coastal waters. *Ecosystems Research Reports* 8: 1–111.

CARLTON J.T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanography and Marine Biology Annual Review* 23: 313–371.

CARLTON J.T. 1996. Biological invasions and cryptogenic species. *Ecology* 77: 1653–1655.

CHIHARA M. 1972. Germination of carpospores of *Pikea californica* and *Schimmelmannia plumosa* as found in Japan, with special reference to their life history. *Mémoires de la Société Botanique de France* 1972: 313–322.

CORTEL-BREEMAN A.M. 1975. The life history of *Acrosymphyton purpuriferum* (J. Ag.) Sjöst. (Rhodophyceae, Cryptonemiales). Isolation of tetrasporophytes. With some remarks on the tetrasporophyte of *Bonnemaisonia asparagoides* (Woodw.) C. Ag. (Nemalionales). *Acta Botanica Neerlandica* 24: 111–127.

DECEW T.C. & WEST J.A. 1982. Investigations on the life histories of three *Farlowia* species (Rhodophyta: Cryptonemiales, Dumon aceae) from Pacific North America. *Phycologia* 20: 342–351.

DECEW T.C., WEST J.A. & GANESAN E.K. 1982. The life histories a developmental morphology of two species of *Gloiosiphonia* (R dophyta: Cryptonemiales, Gloiosiphoniaceae) from the Pac Coast of North America. *Phycologia* 20: 415–423.

EDELSTEIN T. 1970. The life history of *Gloiosiphonia capillaris* (H son) Carmichael. *Phycologia* 9: 55–59.

EDELSTEIN T. & MCLACHLAN J. 1971. Further observations on *Gloi iphonia capillaris* (Hudson) Carmichael in culture. *Phycologia* 215–219.

FARNHAM W.F. 1997. Espèces invasives sur les côtes de la Manch de l'Atlantique. In: *Dynamique d'espèces marines invasives: ap cation à l'expansion de* Caulerpa taxifolia *en Méditerranée*, pp. 35. Technique & Documentation, Paris.

GRIFFITHS C.L., HOCKEY P.A.R., ERKOM SCHURINK C. VAN & LE R P.J. 1992. Marine invasive aliens on South African shores: im cations for community structure and trophic functioning. *South rican Journal of Marine Science* 12: 713–722.

GRUNOW A. 1867. Algae. In: *Reise der Österreichischen Fregatte vara um die Erde in den Jahren 1857, 1858, 1859. Botanisc Theil, Erster Band. Sporenpflanzen*, part 1 (Ed. by E. Fenzl), 1–104. K.K. Hof- und Staatsdruckerei, Vienna.

GUIRY M.D. & WEST J.A. 1984. Life history and hybridization stud on *Gigartina stellata* and *Petrocelis cruenta* (Rhodophyta) in North Atlantic. *Journal of Phycology* 19: 474–494.

HAWKES M.W. 1990. Reproductive strategies. In: *Biology of the . algae* (Ed. by K.M. Cole & R.G. Sheath), pp. 455–476. Cambri University Press, Melbourne.

IRVINE L.M. 1983. *Seaweeds of the British Isles, Vol. 1. Rhodoph Part 2A. Cryptonemiales (sensu stricto), Palmariales, Rhodym ales*. British Museum (Natural History), London. 115 pp.

JOUSSON O., PAWLOWSKI J., ZANINETTI L., ZECHMAN F.W., DIN F., GUISEPPE G., WOODFIELD R., MILLAR A. & MEINESZ A. 2000. vasive alga reaches California – the alga has been identified t threatens to smother Californian coastal ecosystems. *Nature* 4 157–158.

KUCKUCK P. 1897. Bemerkungen zur marinen Algenvegetation Helgoland II. *Wissenschaftliche Meeresuntersuchungen (Hel land)*, N.F. 2: 371–400.

KÜTZING F.T. 1849. *Species Algarum*. Brockhaus, Leipzig. 922 pp.

KYLIN H. 1930. Über die Entwicklungsgeschichte der Floride *Lunds Universitets Årsskrift, Ny Földj, Andra Afdelningen* 26, 6: 103.

KYLIN H. 1956. *Die Gattungen der Rhodophyceen*. Gleerups Förl Lund. 673 pp.

LEE I.K. & YOO S.A. 1979. *Gloeophycus koreanum* gen. et sp. n (Rhodophyta, Gloiosiphoniaceae) from Korea. *Phycologia* 18: 3 354.

LÜNING K. 1990. *Seaweeds. Their environment, biogeography, ecophysiology*. J. Wiley, New York. 527 pp.

MAGGS C.A. 1988. Intraspecific life history variability in the Fl deophycidae (Rhodophyta). *Botanica Marina* 31: 465–490.

MAGGS C.A. 1990. Distribution and evolution of non-coralline cr tose red algae in the North Atlantic. In: *Evolutionary biogeogra of the marine algae of the North Atlantic* (Ed. by D.J. Garbary R.G. South), pp. 241–263. NATO ASI series G 22. Springer Verl Berlin.

MAGGS C.A. & HOMMERSAND M.H. 1993. *Seaweeds of the Bri Isles, Vol. 1. Rhodophyta. Part 3A. Ceramiales*. HMSO, Lond 444 pp.

MAGGS C.A. & STEGENGA H. 1999. Red algal exotics on North coasts. *Helgoländer Meeresuntersuchungen* 52: 243–258.

MAZZA A. 1913. Saggio di algologia oceanica. *Nuova Notarisia* 62–74.

MEINESZ A. 1999. *Killer algae. The true tale of a biological invasi* University of Chicago Press, Chicago. 360 pp.

MEINESZ A., DE VAUGELAS J., HESSE B. & MARI X. 1993. Spread the introduced tropical green alga *Caulerpa taxifolia* in north Mediterranean waters. *Journal of Applied Phycology* 5: 141–14

MONTAGNE C. 1857. Huitiéme centurie de plantes cellulaires nouvelles, tant indigènes qu'exotiques. Décades IX et X. *Annales des Sciences Naturelles, Botanique,* series 4, 7: 134–153.

MOSS B.L., TOVEY D. & COURT P. 1981. Kelp as fouling organisms on North Sea platforms. *Botanica Marina* 14: 207–209.

RUENESS J. & ÅSEN P.A. 1982. Field and culture observations on the life history of *Bonnemaisonia asparagoides* (Woodw.) C. Ag. (Rhodophyta) from Norway. *Botanica Marina* 25: 577–587.

SCAGEL R.F. 1956. Introduction of a Japanese alga, *Sargassum muticum,* into the northeast Pacific. *Fisheries Research Papers, Washington Department of Fisheries* 1: 49–59.

SCHMITZ F. & HAUPTFLEISCH P. 1897. Gloiosiphoniaceae. In: *Die natürlichen Pflanzenfamilien,* vol. 1(2) (Ed. by A. Engler & K. Prantl), pp. 505–508. W. Engelmann, Leipzig.

SEGAWA S. 1938. The development of the female reproductive organs in Nagaobane (*Baylesia plumosa* Setchell). *Plants and Animals* 6: 1987–1990.

SLOCUM C.J. 1980. Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. *Journal of Experimental Marine Biology and Ecology* 46: 99–110.

STEGENGA H., BOLTON J.J. & ANDERSON R.J. 1997. Seaweeds of the South African west coast. *Contributions from the Bolus Herbarium* 18: 1–655.

VAN DEN HOEK C. 1984. World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of Rhodophytan genera. *Helgoländer Meeresuntersuchungen* 38: 227–257.

WEST J.A. & HOMMERSAND M.H. 1981. Rhodophyta: life histories. In: *The biology of seaweeds* (Ed. by C.S. Lobban & M.J. Wynne), pp. 133–193. University of California Press, Berkeley.