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Checklist of marine benthic green algae (Chlorophyta) on Hainan, a subtropical island off the coast of China: comparisons between the 1930s and 1990–2009 reveal environmental changes

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Abstract

A complete checklist of intertidal to shallow subtidal marine green seaweeds (Chlorophyta) growing on the subtropical island of Hainan (China) is presented here for the first time. It covers data from extensive recent (1990–2009) and historical (1933–1935) collections, and additional published records from various time periods. Data were analyzed by time period. We postulate that environmental changes on Hainan Island documented since the 1980s (e.g., degradation of coral reefs, development of tourism and mariculture farms) are reflected in the green algal species complement and in the dominance or absence of specific algal groups during different time periods. In total, 105 green algal taxa were recorded, including 37 new to Hainan Island, and 18 new records for China. There was a clearly evident change in floristic composition between early and recent collections. In the 1930s, there was a dominance of Caulerpaceae, Codiaceae and Cladophoraceae. By 1990/1992, the numbers of Ulvaceae had increased 1.6-fold and numbers of Cladophoraceae 1.7-fold. Both families contain many opportunistic species that prefer nutrient-enriched or degraded environments. At the same time, species richness of Codiaceae, Caulerpaceae and Udotaceae, families with complex thallus structures, decreased considerably. The floristic differences between the 1990/1992 and 2008/2009 collections were minor.

Keywords: checklist; Chlorophyta; floristic changes; Hainan; new records.

Introduction

Hainan Island is located in the South China Sea on the subtropical northern periphery of the Indo-Pacific Ocean. Coral reefs occupying shallow subtidal areas between 3 and 10 m depths are the major habitat off Hainan Island. Seagrass beds, estuaries and mangrove swamps are present to a lesser degree. Seaweeds occur in all habitats but with highest species richness on coral reefs (Zhang et al. 2006).

The coral reefs of Hainan Island are among the most prominent fringing reefs of China. Their species diversity is generally declining. The highest biodiversity was recorded between the 1950s and 1960s (Gurianova 1959), with dramatic decreases in the following 20 years (Hutchings and Wu 1987, Zou et al. 2004, Zhang et al. 2006). Almost 80% of the fringing reefs along the coastline of Hainan Island have been damaged by human activities, including dynamite fishing, which poses a major threat to this valuable habitat (Hutchings and Wu 1987, Fiege et al. 1994, Hodgson and Yau 1997, Tadashi et al. 2008). Increasing tourist numbers, the building of hotels directly on the beach and the aquaculture industries (pearl shell culture and *Eucheuma* cultivation) have endangered the coastal marine fauna and flora since the 1990s. Additional impacts are abalone farms that adversely affect coral reefs due to increased sediment loads, pollution from land and required coastal building constructions (Zhang et al. 2004).

Biodiversity changes in seagrass communities and coral reefs off Hainan have been studied recently (Zhao et al. 2008), but changes in seaweed biodiversity have not been reported so far. It is well known that seaweeds are good indicators of environmental change and degradation; green algae in particular have been used to detect eutrophication (Lapointe et al. 2005a). Increased concentrations of dissolved inorganic and organic nitrogen and phosphorus in seawater lead to increases in the production of green seaweeds, to green algal blooms of filamentous and thin blade-like forms, spatial dominance of these algae and, in part, to the appearance of new species (e.g., Lapointe et al. 1997, 2005a,b,c, Malta and Verschuure 1997, Diaz-Pulido and McCook 2002, Gartner et al. 2002, McClanahan et al. 2006, Sfriso and Curiel 2007, Titlyanov et al. 2008). Some green seaweed species, such as *Ulva compressa*, *Ulva lactuca*, *Ulva prolifera*, *Cladophora laetevirens*, *Cladophora liniformis*, *Chaetomorpha linum* and *Caulerpa prolifera*, are known sewage indicator species (Burrows 1971, Barile 2004). We postulate that environmental changes off Hainan Island documented since the 1980s may be reflected in green algal species composition and in the dominance/absence of specific groups during different time periods. We therefore compiled a comprehensive checklist of all marine green seaweeds off Hainan Island and nearby islets by taking into consideration the following: comparable early collections of Tseng and coworkers in the 1930s and between 1953 and 1957, all other published records and our own recent collections from 1990/1992 and 2008/2009. Subsequently, we analyzed the qualitative changes in floristic composition that have taken place.

Materials and methods

Study area and algal collections

Hainan island (18°10′–20°9′ N, 108°37′–111°1′ E) is characterized by an annual mean sea surface temperature (SST) of 26°C (1970–2002), with an average seasonal range of 12.1°C (Sun et al. 2005). The annual SST maximum (30.8°C) and minimum (18.7°C) usually occur in July and January, respectively. Mean sea surface salinity (SSS) in the South China Sea fluctuates between 33.3 and 34.0. However, SSS is strongly seasonal off Hainan Island, decreasing to a mean value of 26.5 due to freshwater runoff and rain during the summer wet season (Levitus and Boyer 1994). The mean tidal range is mostly less than 1.5 m (Zhang et al. 1996).

The three major algal collections off the island of Hainan and all subsequent publications were considered for this investigation. All collection sites are shown in Figure 1. The first seaweed sampling program on Hainan Island was performed by Tseng and colleagues in June 1933, March, April, May, June 1934 and in December 1935. Collection sites are indicated with their old locality names (Figure 1B) according to Tseng (1936, 1938). Many publications were based on these collections (Tseng 1935, 1936, 1938, Tseng et al. 1983, Tseng and Gilbert 1942), which covered 78% of taxa representative of the early time period listed in Table 1. Between 1953 and 1957, small collections were performed, and these were published by Tseng and Chang (1962) and Tseng et al. (1962). A few green seaweed records for Hainan are mentioned in Zhu and Liu (1980), Tseng et al. (1983) and Liu (2008) without precise times of collection. Nevertheless, we assumed that all data were representative for a time without considerable development of tourist facilities (summarized under the period 1933–1935 in Table 1) as data from the extensive 1990/1992 collection have not yet been published (B. Xia, personal communication).

Half a century later, another major sampling campaign in the intertidal and infralittoral fringe was conducted within the framework of two German-Chinese expeditions from October to December 1990 and from March to April 1992 (Figure 1A). For details see Titlyanova et al. (2011). Sets of herbarium sheets have been deposited in BRM and the Institute of Oceanology in Qingdao. A third intertidal and shallow subtidal survey (3–5 m depth) was performed in October 2008 and April 2009 in the Sanya area only (Luhuitou, Dadonghai, Xiaodonghai, Figure 1A). Herbarium material of these expeditions has been deposited at the A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences.

In 1990/1992, the intertidal/infralittoral reef flat was characterized by moving blocks of dead corals; sometimes stones

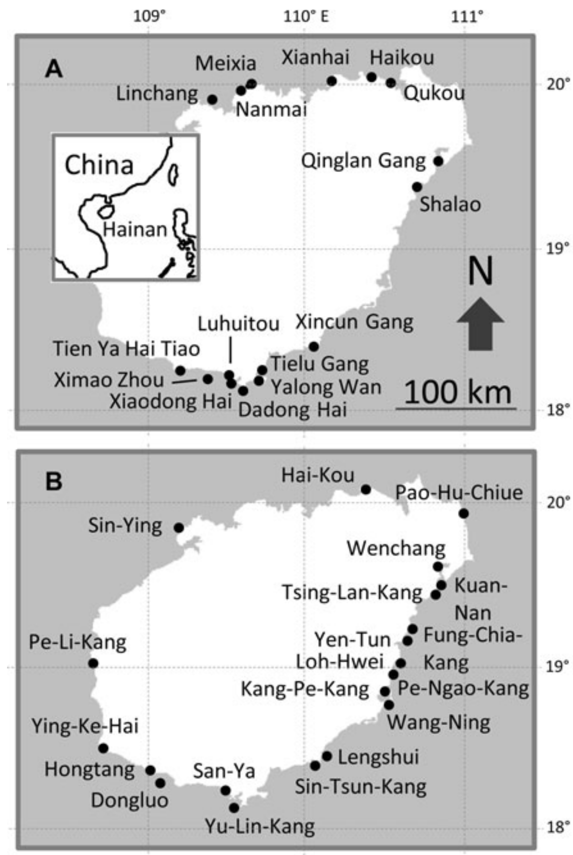

Figure 1 Hainan Island (South China Sea, China) (18°10′–20°9′ N, 108°37′–111°1′ E).
(A) Collection sites during the 1990/1992 and 2008/2009 expeditions. (B) Collection sites of Tseng and coworkers in 1933–1935 with old spellings of names (after Tseng 1936).

or boulders were interspersed with sandy areas in Dadonghai, Linchang, Luhuitou, Xiaodonghai, and Yalong Bay. Sandy beaches with interspersed dead coral blocks were present at Xinhai. Poorly developed mangrove areas with extensive mudflats and seagrass fields were present at Qukou and Qinglangang. Near Haikou, algae were collected in fishponds with variable salinity. The *Eucheuma* farm in Shalao was characterized by a sandy bay with an offshore reef flat composed of mostly dead corals. The offshore island Ximaozhou was the only place where the amount of living corals increased with depth in the shallow subtidal, and was generally species-rich. The low water mark, however, was characterized by dead coral blocks. At Meixia in the north of the island, extensive stony intertidal areas with offshore reef flats mostly comprising dead corals were dominant. An extensive reef flat with many living corals above or between dead corals was located at Nanmai, a few hundred meters west of Meixia (all habitat descriptions: I. Bartsch personal observations). In 2008/2009, Luhuitou and Dadonghai were characterized by damaged coral reefs (projective cover of live corals approximately 30% to ≤5%, respectively), whereas Xiaodonghai was characterized by dead coral reefs and seagrass beds (I. Titlyanov and T. Titlyanova personal observations).

Table 1 Checklist of species (including varieties and forms) of benthic marine green algae (Chlorophyta) for Hainan Island (China).

Chlorophyta species	1933–1935	November/ December 1990	March/ April 1992	October 2008	April 2009	References
Chlorococcales						
Chlorochytriaceae						
[1]*Chlorochytrium cohnii* Wright**	–	++	++	++	–	Titlyanova et al. (2011)
Ulotrichales						
Ulotrichaceae						
Ulothrix implexa (Kützing) Kützing*	–	–	–	–	++	This paper
Gomontiaceae						
Monostroma nitidum Wittrock	++[2]	–	++	–	–	Tseng and Chang (1962)
Ulvales						
Ulvellaceae						
[1]*Acrochaete geniculata* (N.L. Gardner) O'Kelly**	–	++	++	–	++	Titlyanova et al. (2011)
[1]*Acrochaete leptochaete* (Huber) R. Nielsen*	–	++	–	–	++	Titlyanova et al. (2011)
[1]*Acrochaete viridis* (Reinke) R. Nielsen**	–	++	++	–	++	Titlyanova et al. (2011)
Pringsheimiella scutata (Reinke) Marchewianka**	–	++	++	–	–	Titlyanova et al. (2011)
Ulvella lens P.L. Crouan *et* H.M. Crouan	++	–	–	–	++	Tseng (1938)
[3]Ulvaceae						
Ulva chaetomorphoides (Börgesen) Hayden, Blomster, Maggs, P.C. Silva, M.J. Stanhope *et* J.R. Waaland**	–	++	–	–	–	Titlyanova et al. (2011)
Ulva clathrata (Roth) C. Agardh	++[2]	++	–	++	++	Tseng et al. (1962), as *Enteromorpha clathrata*
Ulva compressa Linnaeus*	–	++	++	–	++	Titlyanova et al. (2011)
Ulva conglobata Kjellman	++	++	++	++	++	Tseng (1936)
[4]*Ulva flexuosa* Wulfen	++	++	++	–	++	Tseng (1938), as *Enteromorpha flexuosa*
Ulva intestinalis Linnaeus*	–	–	++	–	++	Titlyanova et al. (2011)
Ulva kylinii (Bliding) Hayden, Blomster, Maggs, P.C. Silva, M.J. Stanhope *et* J.R. Waaland*	–	++	++	–	–	Titlyanova et al. (2011)
Ulva lactuca Linnaeus	++	–	++	–	++	Tseng (1935)
Ulva linza Linnaeus	++[2]	–	–	–	–	Tseng et al. (1962) as *Enteromorpha linza*
Ulva pertusa Kjellman*	–	–	++	–	–	Titlyanova et al. (2011)
Ulva prolifera O.F. Müller	++	–	–	++	++	Tseng (1938), as *Enteromorpha prolifera*
Ulva ralfsii (Harvey) Le Jolis**	–	++	++	++	–	Titlyanova et al. (2011)
Cladophorales						
Cladophoraceae						
Chaetomorpha antennina (Bory de Saint-Vincent) Kützing	++	–	–	–	–	Tseng (1936)
Chaetomorpha brachygona Harvey	++	–	–	–	–	Tseng (1936)
Chaetomorpha gracilis Kützing	++	–	–	++	–	Tseng (1936)
Chaetomorpha javanica Kützing**	–	–	++	–	–	Titlyanova et al. (2011)
Chaetomorpha ligustica (Kützing) Kützing*	–	–	–	++	–	This paper
Chaetomorpha linum (O.F. Müller) Kützing	++	–	++	–	++	Tseng (1936), as *Chaetomorpha crassa*
Chaetomorpha minima F.S. Collins *et* Hervey**	–	++	++	–	–	Titlyanova et al. (2011)
Chaetomorpha spiralis Okamura	++	–	–	–	–	Tseng (1936), as *Cladophora torta*
[5]*Cladophora albida* (Nees) Kützing**	–	++	–	–	–	Titlyanova et al. (2011)
[6]*Cladophora aokii* Yamada	++	–	–	–	–	Tseng (1936)
Cladophora catenata (Linnaeus) Kützing	++	–	++	–	–	Tseng (1936), as *Chaetomorpha fuliginosa*
[7]*Cladophora coelothrix* Kützing**	–	++	–	–	–	Titlyanova et al. (2011)

(*Table 1 continued*)

Chlorophyta species	1933–1935	November/ December 1990	March/ April 1992	October 2008	April 2009	References
Cladophora flexuosa (O.F. Müller) Kützing	du	++	++	–	–	Zhu and Liu (1980)
Cladophora herpestica (Montagne) Kützing*	–	++	++	–	–	Titlyanova et al. (2011)
Cladophora horii Hoek *et* M. Chihara**	–	++	–	–	++	Titlyanova et al. (2011)
Cladophora laetevirens (Dillwyn) Kützing**	–	++	–	–	++	Titlyanova et al. (2011)
[7]*Cladophora patentiramea* (Montagne) Kützing*	–	++	–	–	–	Titlyanova et al. (2011)
Cladophora perpusilla Skottsberg *et* Levring in Levring**	–	++	–	–	–	Titlyanova et al. (2011)
[6]*Cladophora prolifera* (Roth) Kützing	du	++	–	–	–	Tseng et al. (1983), as *Cladophora rugulosa*
Cladophora sibogae Reinbold*	–	–	++	–	–	Titlyanova et al. (2011)
Cladophora socialis Kützing*	–	++	++	++	–	Titlyanova et al. (2011)
Cladophora vagabunda (Linnaeus) Hoek*	–	–	++	++	–	Titlyanova et al. (2011)
Rhizoclonium grande Børgesen	++	++	–	++	–	Tseng (1936)
[8]*Rhizoclonium riparium* (Roth) Harvey*	–	++	++	++	++	Titlyanova et al. (2011)
[8]*Rhizoclonium riparium* var. *implexum* (Dillwyn) Rosenvinge	++	–	–	++	–	Tseng (1936), as *Rhizoclonium kochianum*
Anadyomenaceae						
Anadyomene wrightii Harvey ex J.E. Gray	++	++	++	++	++	Tseng (1938)
Microdictyon japonicum Setchell	++	–	–	–	–	Tseng (1936), as drift
Siphonocladales						
Boodleaceae						
[9]*Boodlea composita* (Harvey) F. Brand	++	++	++	–	++	Tseng (1936)
[10]*Cladophoropsis fasciculatus* (Kjellman) Wille	++	–	–	–	–	Tseng (1938), as *Cladophoropsis fasciculata*
[10]*Cladophoropsis sundanensis* Reinbold	++	–	++	++	++	Tseng (1936)
[9]*Phyllodictyon anastomosans* (Harvey) Kraft *et* M.J. Wynne*	–	++	++	++	++	Tseng et al.(1983), as *Struvea anostomosans*
Struvea enomotoi Chihara	du	–	–	–	–	Liu (2008)
Siphonocladaceae						
Boergesenia forbesii (Harvey) Feldmann	++	++	++	–	–	Tseng (1936), as *Valonia forbesii*
Dictyosphaeria cavernosa (Forsskål) Børgesen	++	++	++	++	++	Tseng (1936)
Dictyosphaeria intermedia Weber-van Bosse	++	–	–	–	–	Tseng and Chang (1962)
Dictyosphaeria versluysii Weber-van Bosse	++	++	++	++	–	Tseng and Chang (1962)
Valoniaceae						
[11]*Valonia aegagropila* C. Agardh	++	++	++	++	–	Tseng (1936)
[11]*Valonia utricularis* (Roth) C. Agardh*	–	++	–	++	–	Titlyanova et al. (2011)
Valonia ventricosa J. Agardh*	–	++	–	++	++	Titlyanova et al. (2011)
Valoniopsis pachynema (G. Martens) Børgesen	++	++	++	–	–	Tseng (1936)
Dasycladales						
Dasycladaceae						
Bornetella oligospora Solms-Laubach*	–	++	++	–	++	This paper
Bornetella sphaerica (Zanardini) Solms-Laubach	du	++	++	–	++	Tseng et al. (1983)
Neomeris annulata Dickie	++	++	++	–	++	Tseng (1936)
Polyphysaceae						
Acetabularia caliculus J.V. Lamouroux in Quoy *et* Gaimard	++	–	++	–	–	Tseng (1936)

(*Table 1 continued*)

Chlorophyta species	1933–1935	November/ December 1990	March/ April 1992	October 2008	April 2009	References
Parvocaulis clavatus (Yamada) S. Berger, U. Fettweiss, S.GlS. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitzky *et* G.C. Zuccarello*	–	–	–	++	++	This paper
Parvocaulis exiguus (Solms-Laubach) S. Berger, U. Fettweiss, S.GlS. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitzky *et* G.C. Zuccarello*	–	–	–	–	++	This paper
Parvocaulis parvulus (Solms-Laubach) S. Berger, U. Fettweiss, S.GlS. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitzky *et* G.C. Zuccarello	++	++	++	++	–	Tseng (1936), as *Acetabularia moebii*
Parvocaulis pusillus (M. Howe) S. Berger, U. Fettweiss, S.GlS. Berger, U. Fettweiss, S. Gleissberg, L.B. Liddle, U. Richter, H. Sawitzky *et* G.C. Zuccarello	++	–	–	++	–	Tseng (1936), as *Acetabularia pusilla*
Bryopsidales						
Bryopsidaceae						
Bryopsis australis Sonder**	–	–	++	++	–	Titlyanova et al. (2011)
Bryopsis pennata J.V. Lamouroux**	–	++	–	++	++	Titlyanova et al. (2011)
Pseudobryopsis hainanensis C.K. Tseng	++	++	–	–	–	Tseng (1936)
[12]Caulerpaceae						
Caulerpa brachypus f. *parvifolia* (Harvey) A.B. Cribb	++	–	–	–	–	Tseng (1936), as *Caulerpa parvifolia*
Caulerpa cupressoides (West) C. Agardh	++	–	–	–	–	Tseng (1936)
Caulerpa nummularia Harvey ex J. Agardh	du	–	–	–	–	Tseng et al. (1983)
Caulerpa peltata J.V. Lamouroux	++	–	++	++	–	Tseng (1936)
Caulerpa racemosa (Forsskål) J. Agardh	++	++	++	++	–	Tseng (1936), as *Caulerpa racemosa* var. *clavifera*
Caulerpa racemosa var. *occidentalis* (J. Agardh) Børgesen	++	–	–	–	–	Tseng (1936)
Caulerpa serrulata (Forsskål) J. Agardh	++	++	++	++	++	Tseng (1936)
Caulerpa serrulata f. *lata* (Weber-van Bosse) C.K. Tseng	++	–	–	–	–	Tseng (1936), as *Caulerpa serrulata* var. *typica* f. *lata*
Caulerpa sertularioides (S.G. Gmelin) M.A. Howe	++	–	–	–	–	Tseng (1936)
Caulerpa sertularioides f. *longiseta* (Bory de Saint-Vincent) Svedelius	du	–	–	–	–	Tseng et al. (1983)
Caulerpa taxifolia (M. Vahl) C. Agardh	++	++	–	–	–	Tseng (1936)
Caulerpa verticillata J. Agardh	++	–	–	–	–	Tseng (1936)
Caulerpella ambigua (Okamura) Prud'Homme van Reine *et* Lokhorst**	–	–	++	–	++	Titlyanova et al. (2011)
Udoteaceae						
Avrainvillea erecta (Berkeley) A. Gepp *et* E.S. Gepp	++	++	–	–	–	Tseng (1938)
Avrainvillea lacerata Harvey ex J. Agardh	++	++	–	–	–	Tseng (1938)
Chlorodesmis caespitosa J. Agardh	++	–	–	–	–	Tseng (1936), as *Rhipidodesmis caespitosa*

(*Table 1 continued*)

Chlorophyta species	1933–1935	November/ December 1990	March/ April 1992	October 2008	April 2009	References
Chlorodesmis hildebrandtii A. Gepp *et* E.S. Gepp	++	–	–	–	–	Tseng (1936)
Chlorodesmis sinensis C.K. Tseng *et* M.L. Dong	du	++	++	–	–	Liu (2008)
Penicillus sibogae A. Gepp *et* E.S. Gepp**	–	–	–	++	++	This paper
Rhipidosiphon javensis Montagne	++	++	–	++	++	Tseng (1936), as *Udotea javensis*
Udotea flabellum (J. Ellis *et* Solander) M.A. Howe	++	–	–	–	–	Tseng (1936)
Udotea fragilifolia C.K. Tseng *et* M.L. Dong	du	–	–	–	–	Liu (2008)
[13]Codiaceae						
Codium arabicum Kützing	++	–	++	–	–	Tseng (1936)
[14]*Codium bartlettii* C.K. Tseng *et* W.J. Gilbert	++	–	–	–	–	Tseng and Gilbert (1942)
Codium decorticatum (Woodward) M.A. Howe	++	–	–	–	–	Tseng and Gilbert (1942)
[15]*Codium geppiorum* O.C. Schmidt	++	–	–	–	–	Tseng (1938), as *Codium geppei*
Codium intricatum Okamura	++	–	–	–	–	Tseng (1936)
Codium papillatum C.K. Tseng *et* W.J. Gilbert	++	–	–	–	–	Tseng and Gilbert (1942)
Codium papillatum var. *hainanense* C.K. Tseng in C.K. Tseng *et* W.J. Gilbert	++	–	–	–	–	Tseng and Gilbert (1942)
Codium repens P.L. Crouan *et* H.M. Crouan in Vickers	++	–	++	–	–	Tseng (1936)
[16]*Halimeda incrassata* (J. Ellis) J.V. Lamouroux	du	–	–	–	–	Tseng et al. (1983)
[16]*Halimeda macroloba* Decaisne	++	–	–	++	–	Tseng (1936)
Halimeda opuntia (Linnaeus) J.V. Lamouroux	du	++	–	–	–	Tseng et al. (1983), as *Halimeda opuntia* f. *triloba*
Derbesiaceae						
Pedobesia ryukyuensis (Yamada *et* T. Tanaka) Kobara *et* Chihara**	–	–	++	–	–	Titlyanova et al. (2011)

–, species not recorded; ++, species recorded; du, collection year unknown; *new record for Hainan island; **new record for China. References: first record for Hainan Island. Systematics follows Guiry and Guiry (2011). Collections 2008 and 2009 only cover Sanya area. [1]The species concept in the genera *Chlorochytrium* and *Acrochaete* is rather unstable (e.g., Nielsen et al. 2007, Guiry and Guiry 2011). [2]Collection year between 1953 and 1957. [3]Species circumscriptions in the genus *Ulva* have been found extremely unreliable based on morphological characteristics. *Ulva* from tropical and subtropical regions are largely unique and probably separated from temperate and boreal species, thereby requiring new taxon names (e.g., Kraft et al. 2010, O'Kelly et al. 2010). [4]Hayden et al. (2003) mention that *Ulva flexuosa* is very close to *Ulva lingulata.* [5]Tropical records of *Cladophora albida* probably belong to *C. montagneana* (van den Hoek 1982). [6]*Cladophora aokii* closely resembles juvenile specimens of *C. prolifera* and both are also very closely related (Leliaert et al. 2007). Thus, both might have been confused. [7]Sequence data have shown that the tropical *Cladophora coelothrix* is unrelated to the European clade (Leliaert et al. 2007) and probably represents a different species. An available name is *C. patentiramea* which is morphologically indistinguishable (F. Leliaert personal communication). [8]*Rhizoclonium riparium* var. *implexum* is currently regarded as a taxonomic synonym of *R. implexum* (Dillwyn) Kützing, but see also taxonomic notes in Guiry and Guiry (2011) for discussion of synonymy with *R. riparium.* [9]*Boodlea composita* and *Phyllodictyon anastomosans* are morphological forms within the plastic *Boodlea* species complex, which consists of at least 13 species (Leliaert and Coppejans 2007, Leliaert et al. 2009). [10]*Cladophoropsis* is also part of the *Boodlea* complex. Although Leliaert and Coppejans (2006) regard *C. sundanensis* Reinbold as the earliest name for a entity that includes *C. fasciculatus* (Kjellman) Wille, the latter has priority (M.J. Wynne personal communication, 23 May 2007, in Guiry and Guiry 2011). [11]See Silva et al. (1996) for misidentifications. [12]Morphological variability in *Caulerpa* species is high and partially obscure species identity. Molecular evidence supports the taxonomic entity of *C. serrulata*, *C. cupressoides*, *C. sertularioides*, *C. racemosa*, and *C. taxifolia* (Famà et al. 2002, de Senerpont Domis et al. 2003, Yeh and Chen 2004), whereas some varieties of *C. racemosa* possibly belong to other species (Yeh and Chen 2004). [13]See Verbruggen et al. (2007) for discussion of disagreement between morphological and molecular species concept in the genus *Codium.* [14]*Codium bartlettii* represents a morphological form within one of the cryptic species of *Codium latum* (Verbruggen et al. 2007). [15]The morphospecies *Codium geppiorum* represents several cryptic species (Verbruggen et al. 2007). [16]Although several cryptic species have been proposed in the genus *Halimeda*, a modified morphological species concept applies well (Verbruggen et al. 2005a).

Material in the 1990–2009 collections was identified using monographic publications, floristic studies and systematic articles by Abbott and Huisman (2004), Børgesen (1940, 1948), Dawes and Mathieson (2008), Dawson (1954, 1956), Dong and Tseng (1985), Durairatnam (1961), Egerod (1952), Leliaert and Coppejans (2003), Littler and Littler (2000), Pham (1969), Reyes (1976), Taylor (1960), Trono (1968), Tseng (1936, 1938), Tseng et al. (1983), Tseng and Dong (1978), Vinogradova (1979), Womersley (1984), Wynne (1993), Yamada (1934), and Yamada and Tanaka (1938). Detailed descriptions of new records for Hainan and China from the 1990/1992 collections are given in Titlyanova et al. (2011).

Floristic analysis

All available data on green seaweeds (Chlorophyta) for Hainan island (excluding Xisha Island, which belongs to Hainan Province) were compiled and integrated into a common checklist allocating all published records to either historical (1933–1935) or recent time periods (1990, 1992, 2008, 2009) (Table 1). The systematic order of species and binomial authorities follow AlgaeBase (Guiry and Guiry 2011). Synonyms are not given. New records for Hainan and China that were collected in either 1990/1992 or 2008/2009 are marked with one or two asterisks, respectively (Table 1).

Relative change was analyzed by comparing the floristic composition during the different time periods. First, the collections of 1933–1935 and 1990/1992 were compared as both included (1) all available habitats (coral reefs, mangrove swamps, sandy habitats, and seagrass beds), (2) only intertidal to shallow subtidal locations (Tseng 1936), (3) all coasts (Figure 1), (4) at least two seasons (spring to summer and autumn to winter), and (5) were performed to assess the general species richness of the island. Therefore, we assumed that during these two surveys most available species were recorded, giving a representative overview of the green algal species richness during both time periods. Second, detailed collections performed at Sanya Bay in 1990/1992 and 2008/2009 (Luhuitou, Dadonghai, Xiaodonghai) were compared to analyze local change that took place during a phase of rapid tourist development (Zhang et al. 2006).

To analyze relative floristic similarity among different time periods, data were also visualized in a two-dimensional non-metric multidimensional scale (n-MDS) ordination plot, with time periods as samples and species as variables. (Primer Version 6.0; presence/absence data; Bray-Curtis similarity). Additionally, a cluster analysis was performed on the same dataset (group average with Bray-Curtis similarities). Resulting maximum percentage similarity lines were overlaid on the n-MDS plot.

Results

A total of 105 taxa of green algae were collected and identified in the intertidal and upper subtidal zones off Hainan Island between 1935 and 2009 (Table 1). Bryopsidales (33 species and 4 varieties/forms; 35% of total taxon number) and Cladophorales (26 species and 1 variety; 25% of the total) were the dominant elements in the Hainan green algal flora. In these orders, most species belonged to the Cladophoraceae (24 species and 1 variety or 23%). Ten species and three varieties/forms (12%) belonged to the Caulerpaceae, and 10 species and one variety (10%) to the Codiaceae. The order Ulvales comprised 17 species (16%). Other families were present with one to eight species (1–8%).

New records for green algae off Hainan and China

Taking into account the whole literature on the floristic composition of Hainan through the present, many new species were recorded for Hainan and China during the expeditions in 1990/1992 and 2008/2009. In total, 37 new records were documented for Hainan Island, 18 species among them were new to China (Table 1, Titlyanova et al. 2011). There were 10 new records in the genus *Cladophora* (*C. albida*, *C. coelothrix*, *C. herpestica*, *C. horii*, *C. laetevirens*, *C. patentiramea*, *C. perpusilla*, *C. sibogae*, *C. socialis*, *C. vagabunda*), six in the genus *Ulva* (*U. chaetomorphoides*, *U. compressa*, *U. intestinalis*, *U. kylinii*, *U. pertusa*, *U. ralfsii*), three in the genus *Acrochaete* (*A. geniculata*, *A. leptochaete*, *A. viridis*), three in the genus *Chaetomorpha* (*C. javanica*, *C. ligustica*, *C. minima*), two in the genus *Valonia* (*V. utricularis*, *V. ventricosa*), two in the genus *Bryopsis* (*B. australis*, *B. pennata*), two in the genus *Parvocaulis* (*P. clavatus*, *P. exiguus*). Additionally, new records for *Bornetella oligospora*, *Caulerpella ambigua*, *Chlorochytrium cohnii*, *Pedobesia ryukyuensis*, *Penicillus sibogae*, *Phyllodictyon anastomosans*, *Pringsheimiella scutata*, *Rhizoclonium riparium*, and *Ulothrix implexa* were documented.

Recent losses of green algal taxa

Twenty-four species and four varieties/forms that had been collected in the period 1933–1960 were not encountered during the expeditions of 1990/1992 and 2008/2009. Figure 2 summarizes the changes in species richness within orders and families. In detail, the taxa previously present, but not found in later surveys included five species of Cladophoraceae (*Chaetomorpha antennina*, *C. brachygona*, *C. gracilis*, *C. spiralis*, *Cladophora aokii*), eight taxa of Caulerpaceae (*Caulerpa brachypus* f. *parvifolia*, *C. cupressoides*, *C. nummularia*, *C. racemosa* var. *occidentalis*, *C. serrulata* f. *lata*, *C. sertularioides*, *C. sertularioides* f. *longiseta*, *C. verticillata*), seven taxa of Codiaceae (*Codium bartlettii*, *C. decorticatum*, *C. geppiorum*, *C. intricatum*, *C. papillatum*, *C. papillatum* var. *hainanense*, *Halimeda incrassata*), four species of Udoteaceae (*Chlorodesmis caespitosa*, *C. hildebrandtii*, *Udotea flabellatum*, *U. fragilifolia*) and four species in other families (*Dictyosphaeria intermedia*, *Microdictyon japonicum*, *Struvea enomotoi*, *Ulva linza*).

During the expedition in 2008/2009, five species that had been recorded for Sanya Bay in 1990/1992 were not encountered again: *Boergesenia forbesii*, *Chaetomorpha minima*, *Cladophora perpusilla*, *Ulva kylinii*, and *Valoniopsis pachynema*.

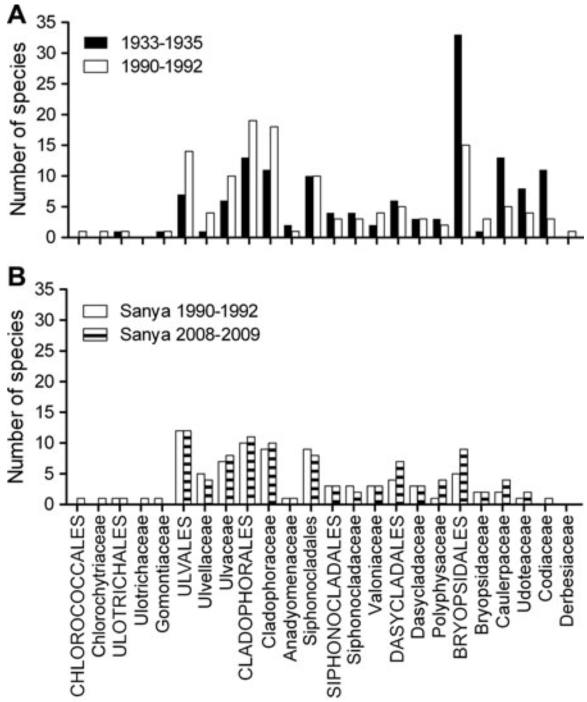

Figure 2 Numbers of green seaweed species for Hainan Island recorded during different collection periods by order and family.
(A) Comparison of species recorded in the periods 1933–1935 (including other times periods, see Table 1), and 1990–1992. (B) Comparison of species recorded in Sanya Bay (Dadonghai, Xiaodonghai and Luhuitou, see Figure 1) in 1990–1992 and 2008–2009.

Changes in green algal species composition between 1933–1935 and 1990–2009

The relative floristic similarities among the early time period 1933–1935, winter 1990, spring 1992, autumn 2008, and spring 2009 (Table 1) are shown in a two-dimensional n-MDS plot (Figure 3). It was evident that floristic composition had changed over time. The overlay of the MDS plot with the cluster dendogram similarity lines indicate the respective maximum boundary values for discrimination of clusters. The maximum relative similarity of all samples (time periods) was only 37% (Figure 3). The 1933–1935 cluster was least similar to all others. The collections from 1990, 1992, 2008 and 2009 had a maximal floristic similarity of 45%. The three collections from 1990, 1992 and 2009 had a maximum similarity of 50% and were more similar to each other than to all other samples (Figure 3). To assess which floristic components were responsible for the observed variation, change in species composition was analyzed in more detail.

During the early collection period, 68 taxa of green algae were identified. These were 48 species and five varieties/forms that were found between 1933 and 1935, five additional species were found around 1960 and nine more species and one variety are undated records listed in Zhu and Liu (1980, one species), Tseng et al. (1983, six species, one variety) and Liu (2008, two species). These taxa were probably present before increased tourism development (Table 1). Within these earlier collections, there was a clear dominance of Bryopsidales, which made up nearly 50% of all recorded taxa (Table 1, Figure 2A). Within this order, the Caulerpaceae comprised most taxa (nine species and three varieties/forms, or 18% of all green algal taxa recorded for the respective time period), followed by the Codiaceae (10 species plus one variety or 16%) and Udoteaceae (eight species or 12%). The second richest order was the Cladophorales, with a clear dominance of Cladophoraceae (11 species or 16%). All other green algal families were represented by only one to six taxa. Representatives of the Ulotrichaceae and Derbesiaceae were not recorded in the marine flora of Hainan between 1933 and 1935. The genera *Caulerpa* (nine species and three varieties/

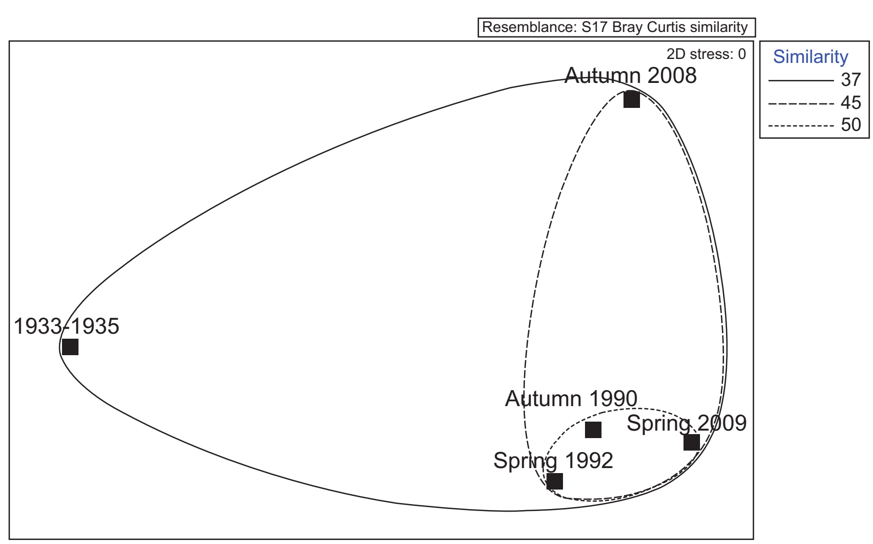

Figure 3 Two-dimensional non-metric multidimensional scaling ordination (n-MDS) of floristic similarities of the green algae of Hainan Island for different time periods (see Table 1).
The low stress value indicates no distortion in the compression of the multidimensional data into two dimensions. The groups indicated derive from a parallel cluster analysis showing the respective maximum similarity boundary values. Similarity values shown in the key are percentages.

forms), *Codium* (seven species and one variety), *Ulva* (six species), and *Chaetomorpha* (five species) contributed the most species (Table 1).

In the time period 1990/1992, 66 taxa were recorded, a richness value similar to that of 1933/1935. In contrast to the early time period, the highest species numbers were not members of the order Bryopsidales but of the Cladophorales (Figure 2A). Most species were recorded in the Cladophoraceae (18 species; 27%) and in the Ulvaceae with 10 species or 15% (Table 1). This is a nearly 100% increase in species richness in the Cladophoraceae and a 50% increase in Ulvaceae since 1935. In contrast, the number of Caulerpaceae decreased by 59% from 12 taxa in the period 1933–1935 to five taxa in 1990/1992, and the number of Udoteaceae decreased by 50% from eight species to four species between 1933–1935 and 1990/1992 (Figure 2A). Other families were represented by one to four species only and did not follow any trend between the two time periods. In 1990/1992, the genera *Cladophora* (13 species) and *Ulva* (11 species) dominated the material collected.

Species composition of green algae in the region of Sanya between 1990/1992 and 2008/2009

As the expeditions in 2008/2009 focused only on collections near Sanya city (Xiaodonghai, Dadonghai, Luhuitou, see Figure 1A), the green algal floristic composition of this region is considered separately here. A total of 59 taxa amounting to 56% of all taxa in the present checklist were collected near Sanya city in 1990/1992 and 2008/2009. This total included members of all families found off Hainan except the Gomontiaceae and Derbesiaceae. Especially striking was the reduced species richness within the order Bryopsidales in this area, with only 5 of 11 genera and 11 of 38 species being present. Furthermore, the genera *Microdictyon*, *Phyllodictyon* [*Struvea*] and *Parvocaulis* [*Acetabularia*] were not recorded at all near Sanya city. In total, 47% of all species found near Sanya city belonged to the Cladophorales (15 species) and Ulvales (13 species), with a dominance of Cladophoraceae (14 species) and Ulvaceae (nine species). Other families comprised only one to five species. The highest species richness was in the genus *Ulva* (9), followed by four species of *Cladophora* and three of *Chaetomorpha*. The remaining genera comprised only one to three species. In 1990/1992, a total of 41 species of green algae was recorded in the Sanya region. Similarly, in 2008–2009 the total number of green algal species at these sites was 48. Common to both time periods were 29 species representing only 49% of all species recorded for the Sanya region. At a higher taxonomic level, however, the differences between the two collections in 1990/1992 and 2008/2009 were minor (Figure 2B).

Discussion

The present checklist of marine green algae is the first complete compilation for the intertidal and shallow subtidal habitats off the island of Hainan. We recorded 105 taxa of marine green algae (94 species and 11 varieties/forms) collected over 75 years between 1933 and 2009. The green algal species richness of Hainan is comparable to other subtropical western Pacific islands, such as neighboring Taiwan Island or the Fiji islands, where 117 and 136 species of green algae have been documented, respectively (http://web.ntm.gov.tw/seaweeds/english/f/f3_list.asp, Lewis and Norris 1987, South and Skelton 2003). In other similarly located islands, such as the Dampier Archipelago in Western Australia, only 54 green algal species have been recorded (Huisman and Borowitzka 2003).

As this checklist of green algae is based on substantial collections before and after extensive coastal use and fisheries, tourist development and coral bleaching events (Zhang et al. 2006), it may show trends of long-term responses to human impact on Hainan Island. The collections of 1935–1937 and 1990/1992 were comparable in their extent, geographic coverage, seasonal sampling, and habitats sampled. Although only qualitative data are available, the extensive nature of the collections allows a comparison of species richness and its changes. In both collections, approximately 70 taxa of green algae were recorded, but the floristic similarity value (38%) was low (Figure 3). This was mainly due to shifts in the species composition of three algal orders, namely the Bryopsidales, the Cladophorales, and the Ulvales (Figure 2A). The early collections were very rich in Caulerpaceae and Codiaceae, whereas these families were only poorly represented in 1990/1992. Instead, during 1990/1992 the collection was dominated by Cladophoraceae, Ulvellaceae and Ulvaceae, with 10 new records of *Cladophora*, and six new records of *Ulva*. Furthermore, nine *Caulerpa* species and six *Codium* species recorded by Tseng and coworkers in the 1930s have not been encountered since.

This obvious difference in algal composition among the collections may have different root causes. The possibility of inadequate sampling during both time periods cannot be ruled out. Furthermore, it can be expected that different taxonomic skills of collectors and identifiers as well as a different focus of research may have added to the observed difference. By contrast, floristic changes may be a result of environmental changes on Hainan.

The coastal ecosystems of Hainan Island were not subject to large anthropogenic stress in the 1930s, although coral reefs, mangroves, and seagrass meadows of Hainan Island were already being exploited at that time, e.g., by fishing and gathering of molluscs and edible algae (Gurianova 1959). During the second half of the 20th century, the reef ecosystems were subjected to destructive dynamite fishing (Zhao et al. 2008). Since 1980, intensive development of pond maricultures (mostly shrimps and fish) on shallow coastal platforms has resulted in increased pollution by mariculture waste products (Zhang et al. 2004, 2006, Zhao et al. 2008). From 1988 onwards, Hainan Island was established as the largest special economic zone in China. Tourism increased and urbanization strongly spread over the entire island, especially in Sanya Bay, which became an international holiday resort (Huang et al. 2003, Gu and Wall 2007), thus increasing pressure on the coral reef ecosystem. During the 1990/1992 survey, reef degradation and sediment load were already considerable (Fiege et al. 1994, I. Bartsch personal observation). Intertidal and shallow subtidal habitats were mostly characterized by dead or partially dead coral substratum (Titlyanova et al. 2011). These environmental changes probably had diverse consequences:

i. Occupation of new substratum space by opportunistic benthic algae, with a dominance of green seaweeds, especially of the genera *Ulva*, *Cladophora*, and *Chaetomorpha* has been reported for coral reef ecosystems (e.g., Lapointe et al. 1997, Diaz-Pulido and McCook 2002, Titlyanov and Titlyanova 2008, Titlyanov et al. 2008). The observed increase in Ulvaceae (genus *Ulva*) and Cladophoraceae (genus *Cladophora* and *Chaetomorpha*) between 1935 and 1990/1992 and the coverage of dead coral substratum by luxuriously growing *Ulva* species in 2008/2009 point to this process.

ii. Degradation of coral reefs (e.g., by coral bleaching) may also change the overall structure of algal communities, with the appearance of new dominant species, especially of fine, filamentous, or branched algae such as *Ceramium*, *Centroceras*, or *Cladophora* (Diaz-Pulido and McCook 2002, Birrell et al. 2008, Titlyanov et al. 2008). The new occurrence of species from 1990 onwards may also thus be a reflection of reef destruction. Most new records belong to fine filamentous or epiphytic forms with a high surface to volume ratio: *Acrochaete* spp. are epiphytes and endophytes, *Ulva* spp. have tube-like and filamentous forms, *Cladophora* spp. are fine filamentous, *Rhizoclonium* and *Chaetomorpha* spp. are filamentous, *Phyllodictyon* spp. have a netlike blade, *Valonia* is coenocytic, coarse and sac-like, *Bryopsis* spp. is bushy and filamentous, and *Caulerpella* and *Pedobesia* spp. are also fine and filamentous.

iii. Overall structural changes during environmental degradation are often characterized by a concomitant decline in growth rates of frondose marine plants with a low surface to volume ratio (e.g., Morand and Briand 1996, Diaz-Pulido and McCook 2002, Morand and Merceron 2004, Lapointe et al. 2005a,b, Titlyanov et al. 2008). Diverse *Caulerpa* and *Codium* species, which have a more complex frond organization, disappeared after 1935. This may indicate a special susceptibility of these species to coral reef, seagrass bed, and mangrove degradation that has taken place on Hainan. The possibility of intensive intertidal gathering of edible *Caulerpa* species by local people might have added to the observed decrease in species richness.

Increased nutrient loads are not detrimental to *Caulerpa* but, on the contrary, may be favorable. Two species that were present in the 1930s but not encountered from 1990 onwards (*Caulerpa brachypus* f. *parvifolia* and *Caulerpa sertularioides*) are invasive bloom-forming species on other coral reefs subjected to high nutrient loads (Fernandez and Cortés 2004, Lapointe et al. 2005b, Lapointe and Bedford 2010, Smith et al. 2010). By contrast, there is experimental evidence that *Codium edule* from Taiwan overgrows living but not dead corals in nutrient enriched situations (Liu et al. 2009), indicating that coral reef destruction may not only affect corals but also algae.

After 1990/1992, increased urbanization on Hainan caused problems with domestic sewage, agricultural wastes, and industrial discharges resulting in a rapid increase of heavy metals in Sanya Bay (Yang et al. 2004). Nutrient levels vary seasonally on Luhuitou and Xiaodonghai reefs (Sanya Bay). Dissolved inorganic nitrogen (DIN) ranges between 0.84 and 3.93 μM, and orthophosphate levels range between 0.13 and 0.17 μM (Titlyanov et al. 2011). These data suggest that during most of the year, seawater is highly enriched with dissolved nitrogen and phosphorus in contrast to other tropical reefs. Seawater around oceanic atolls, e.g., the Great Barrier Reef (Australia) contains only 0.05 μM of total oxidized nitrogen (TON, NO_3^-+NO_2^-) and 0.08 μM of soluble reactive phosphorus (SRP) (Furnas et al. 1997). In Tikehau Atoll (French Polynesia), seawater contents of TON and SRP range between 0.03–0.06 μM and 0.10–0.11 μM, respectively (Charpy-Roubaud and Charpy 1994, Charpy et al. 1998). These comparisons show that DIN and dissolved inorganic phosphorus of seawater in Sanya Bay were much elevated (5- to 7-fold and doubled, respectively) compared to concentrations in clear waters of oceanic atolls and reefs (Titlyanov et al. 2011). However, analyses of the molar C:N ratio in the tissue of macroalgae inhabiting Luhuitou reef showed that they were nitrogen limited despite the high DIN concentration in seawater. This may explain why the floristic composition of the green algae in the Sanya region between 1990/1992 and 2008/2009 during times of ongoing pollution only show variability at the species level but not at a higher taxonomic level (Figure 2B). The four new species records for Hainan during the period 2008–2009 (*Ulothrix implexa*, *Chaetomorpha ligustica*, *Cladophora socialis*, and *Penicillus sibogae*) all inhabit the Asian-Pacific region and are probably common and not indicative of environmental change. Generally, however, it may be possible that both the floristic composition and the abundances of species have changed within the time period in question. This can only be substantiated with regular and quantitative monitoring programs – an action that might be reasonable in future.

Finally, it should be noted that our merely floristic data and results should be interpreted with care as morphology-based species delimitation and identification in several green macroalgal groups has been found to be contentious. Several cases of incorrect taxon delineation and cryptic species diversity have been disclosed by application of molecular markers. Species identification by morphological characters is extremely difficult in *Ulva* (e.g., Kraft et al. 2010, O'Kelly et al. 2010). In this genus, most if not all of the morphological characters that have been used in the past to identify and characterize species have been falsified, and only molecular markers seem to be able to correctly delimitate species. Similarly, in *Valonia*, convergence of the limited number of diagnostic characters (branching pattern, cell dimensions, and organization of tenacular cells) leads to unclear species boundaries

(Leliaert et al. 2007). Species within the genera *Boodlea*, *Phyllodictyon*, and *Cladophoropsis* have been found to represent growth forms within the *Boodlea* species complex, which includes at least 13 highly plastic species (Leliaert et al. 2009). Other examples of problematic morphology-based species circumscriptions are found in *Codium* (Verbruggen et al. 2007), *Caulerpa* (Famà et al. 2002, de Senerpont Domis et al. 2003, Yeh and Chen 2004), and *Halimeda* (Verbruggen et al. 2005b). In the latter genus, however, a modified morphology-based approach using many anatomical features could again relate molecular with morphological and anatomical characters for species delimitation (Verbruggen et al. 2005a). In the genera *Chlorochytrium* and *Acrochaete*, several species have been newly recorded for China; both genera comprise minute epiphytic or endophytic forms and the species concept is still highly unstable (e.g., Nielsen et al. 2007, Guiry and Guiry 2011). It is possible that during earlier studies on Hainan, these epiphytes were not under investigation and may thereby have been overlooked. Nonetheless, although possible species misidentifications and taxonomic difficulties on the species level may have biased our results, they clearly highlight a general trend in change of species composition. As the observed change also became visible on the functional form level, we are therefore confident that our main conclusion, namely that environmental changes at Hainan Island since the 1980s are reflected in green seaweed species composition, generally holds.

Conclusion

Analysis of the floristic composition of the marine green algae of Hainan Island during different time periods revealed that considerable changes took place between 1933 and 1990/1992. There was an increase in filamentous, tubular, and fine blade-like green algae and a displacement of fleshy algae with a low surface to volume ratio, probably as a consequence of reef degradation and other environmental changes. Increased urban and aquaculture waste products in the Sanya region during the past 19 years, however, resulted in less obvious changes in species composition and functional groups of green algae.

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