

Macroalgal diversity associated with rhodolith beds in northern New Zealand

Wendy NELSON^{a,b*}, Roberta D'ARCHINO^a, Kate NEILL^a & Tracy FARR^{a,c}

^a National Institute of Water and Atmospheric Research, Private Bag 14-901, Wellington 6241, New Zealand

^b School of Biological Science, University of Auckland, Private Bag 92-019, Auckland 1142, New Zealand.

^c Royal Society of New Zealand, PO Box 598, Wellington 6140, New Zealand

Abstract – The macroalgal flora associated with rhodolith beds in the Bay of Islands, northeastern North Island, was investigated as part of the first detailed study of subtidal rhodoliths in New Zealand. The rhodolith beds differed in their physical characteristics and in the dominant rhodolith-forming species present, one bed with clear water and predominantly *Lithothamnion crispatum* rhodoliths, and the other bed with turbid water, and *Sporolithon durum* rhodoliths covered by fine sediments. One hundred and three taxa were identified (12 green, 24 brown and 67 red algae), with similar numbers of taxa found in the two seasons sampled. The floral composition at the two beds differed significantly. The flora included range extensions for species previously reported within New Zealand (e.g. *Cutleria multifida*), new records for the New Zealand region (at family, genus and species levels – e.g. Dumontiaceae, *Cutleria*, *Dictyota*, *Peyssonnelia* spp), and new discoveries (e.g. *Halymenia* sp., *Grateloupia* sp., *Tsengia* sp.). Two species with a partially prostrate growth habit, *Caulerpa flexilis* and *Chondracanthus chapmanii*, were present in both beds consolidating rhodoliths and shell debris.

Bay of Islands / *Lithothamnion crispatum* / macroalgal diversity / maerl / New Zealand / rhodoliths / *Sporolithon durum* / subtidal

Résumé – Populations d'algues associées aux bancs de maerl au nord de la Nouvelle-Zélande – Les populations d'algues associées aux bancs de maerl dans la Baie des Îles, au nord-est de l'Île du Nord, furent examinées au cours du premier programme d'étude détaillé sur les bancs de maerl littoraux de Nouvelle-Zélande. Les bancs de maerl étudiés se différençaient à la fois par leurs caractéristiques physiques ainsi que par les espèces dominantes présentes; l'un des sites, en eau claire, était dominé par *Lithothamnion crispatum*, tandis que l'autre, en eau trouble, était dominé par *Sporolithon durum* recouvert de sédiments fins. Cent trois taxons d'algues furent identifiés (12 vertes, 24 brunes, et 67 rouges), avec des chiffres similaires au cours des deux saisons d'échantillonnage. La composition de la flore présentait des différences significatives entre les deux sites. La flore comprenait des espèces déjà répertoriées en Nouvelle-Zélande (ex. *Cutleria multifida*), de nouvelles entrées pour la Nouvelle-Zélande (au niveau de famille, genre, et espèce – ex. Dumontiaceae, *Cutleria*, *Dictyota*, *Peyssonnelia* spp.), et de nouvelles découvertes (ex. *Halymenia* sp., *Grateloupia* sp., *Tsengia* sp.). Deux espèces à forme prostrée, *Caulerpa flexilis* et *Chondracanthus chapmanii*, étaient présentes sur les deux sites et consolidaient les fragments de maerl et de coquille.

Îles de Bay / *Lithothamnion crispatum* / populations de macroalgues / maerl / Nouvelle-Zélande / rhodolithes / *Sporolithon durum* / subtidal

* Corresponding author: wendy.nelson@niwa.co.nz

INTRODUCTION

Rhodoliths occur in localised habitats worldwide, from the tropics to the poles, and from the intertidal zone to depths of over 200 m (Bosence, 1983; Foster, 2001). The rounded, layered or branching thalli of rhodoliths provide very heterogeneous habitats, and collectively the thalli within a rhodolith bed form a fragile, structured biogenic matrix (Foster, 2001; Konar *et al.*, 2006). Rhodoliths are considered to act as ecosystem engineers modifying the physical characteristics of their environment, producing a habitat that can support a high diversity and abundance of marine animals and algae in comparison with surrounding habitats (e.g. Littler *et al.*, 1991; Steller & Foster, 1995; Foster, 2001; Steller *et al.*, 2003; Barberá *et al.*, 2003; Kamenos *et al.*, 2004a, b; Foster *et al.*, 2007; Peña & Bárbara, 2008a, b; Nelson, 2009; Hernández-Kantún *et al.*, 2010; Berlandi *et al.*, 2012).

There are reports, from a number of regions worldwide, of distinct floras associated with rhodolith beds. The crustose phases of a number of heteromorphous species have been reported from rhodolith beds as well as crustose genera such as *Cruoria*, *Hildenbrandia*, *Peyssonnelia*, *Pseudolithoderma*, *Symphyocarpus*, and also prostrate species such as *Gelidiella calicola* Maggs & Guiry (Birkett *et al.*, 1998; Bárbara *et al.*, 2004; Hall-Spencer *et al.*, 2008; Peña & Bárbara, 2010a). Another group of species reported in association with rhodolith beds are gelatinous or fleshy species, for example members of the Acrosymphytaceae, Dumontiaceae, and Kallymeniaceae (Guimaraes & Amado-Filho, 2008, Riul *et al.*, 2009; Hernández-Kantún *et al.*, 2010). In some regions the macroalgal species composition varies seasonally, with indications that both photoperiod and temperature influence the algae present (Bárbara *et al.*, 2004; Peña & Bárbara, 2010b).

Rhodolith beds in New Zealand have remained little explored or documented, both in terms of their location, size, associated flora and fauna. Recent research on the non-geniculate coralline algae of northern and central New Zealand (Harvey *et al.*, 2005; Farr *et al.*, 2009) investigated sites where rhodolith beds had been reported previously as well as clarifying the identity of the rhodolith-forming species in northern New Zealand. This paper documents macroalgae found associated with two rhodolith beds in the Bay of Islands, northeastern North Island, investigated as part of the first detailed field study of subtidal rhodoliths in New Zealand (Nelson *et al.*, 2012).

MATERIALS AND METHODS

Field sites

Rhodolith beds at two locations within the Bay of Islands, northern New Zealand, were selected for this study (Fig. 1). Te Miko Reef (TMR) (35°13'43.80"S, 174°10'55.00"E) lies in the 0.7-1.2 km wide channel between Moturua Island and Motuarohia Island, and is 4 km to the north of Kahuwhera Bay (KWB) (35°15'40.00"S, 174°10'55.00"E), which is situated on the southern side of the larger Manawaora Bay on the mainland (Figs 2 & 3). Field work was carried out in February (late summer) and September (early spring) 2010, temporal sampling of biological and physical data referred to in analyses as seasonal. The water temperature at the study sites ranged from 14.5°C (September) to 21.7°C (February). At each location, sites inside and outside the

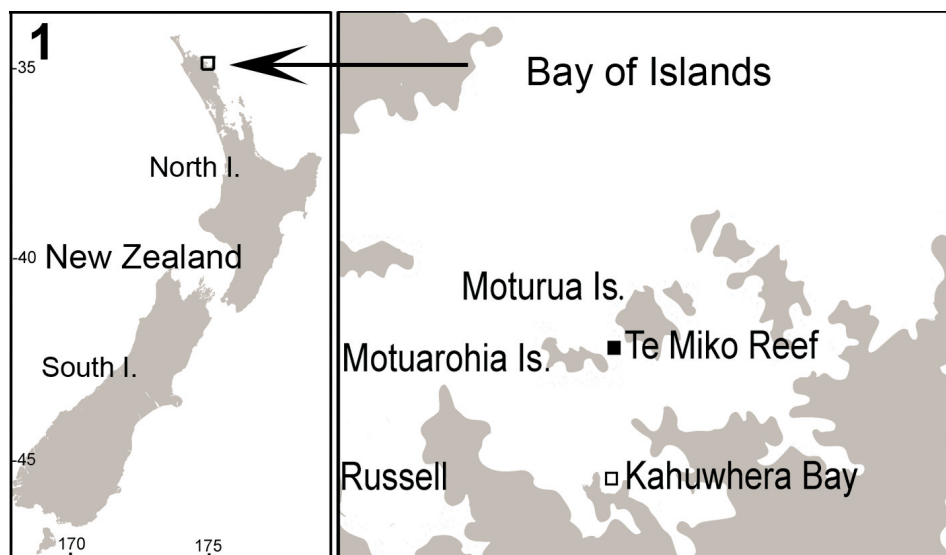


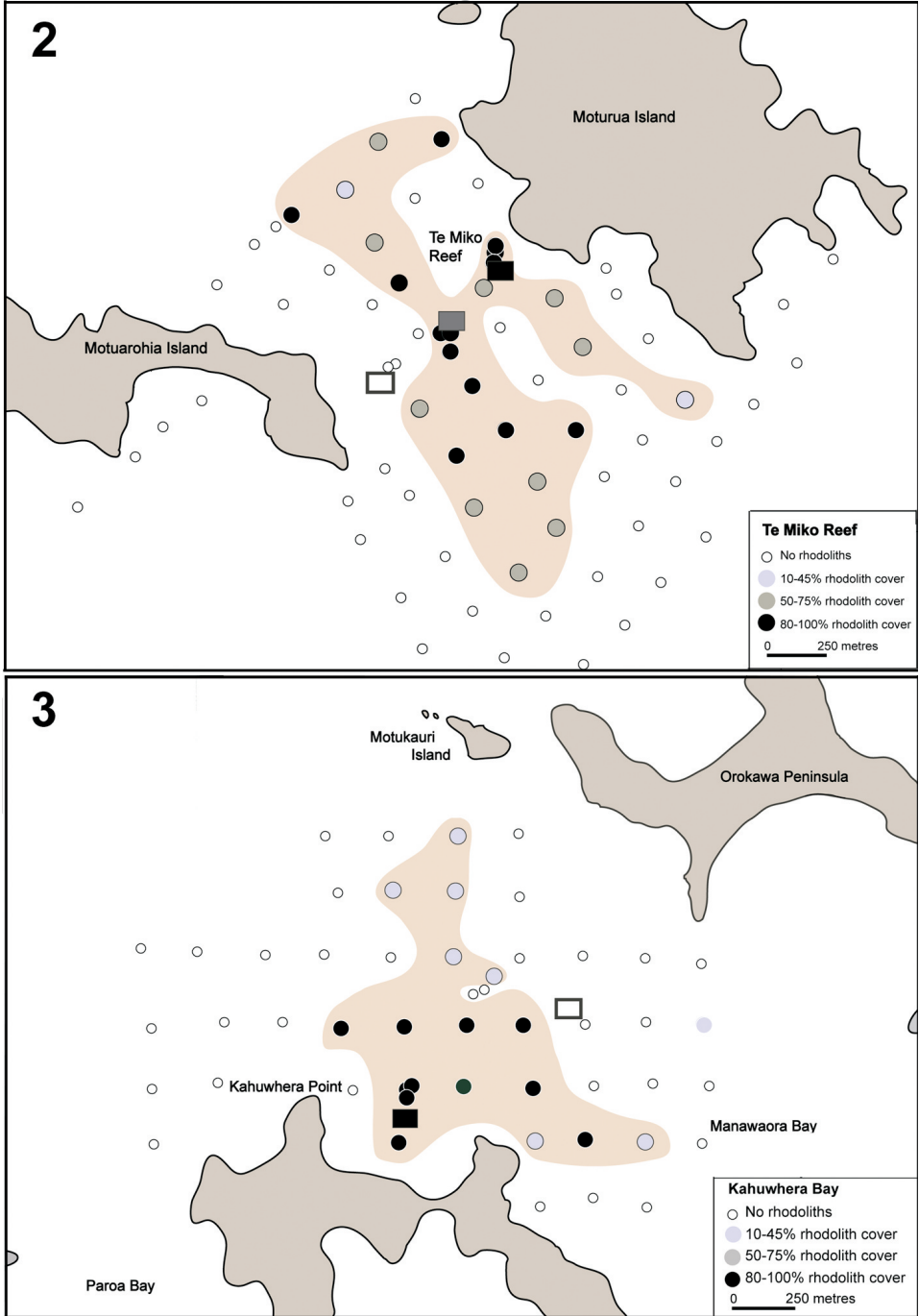
Fig. 1. Map showing the study locations, Te Miko Reef and Kahuwhera Bay, in the Bay of Islands, northern North Island of New Zealand

Table 1. Locations and sites investigated in this study with major rhodolith-forming species, depth and sediment characteristics. (LC = *Lithothamnion crispatum*, SD = *Sporolithon durum*)

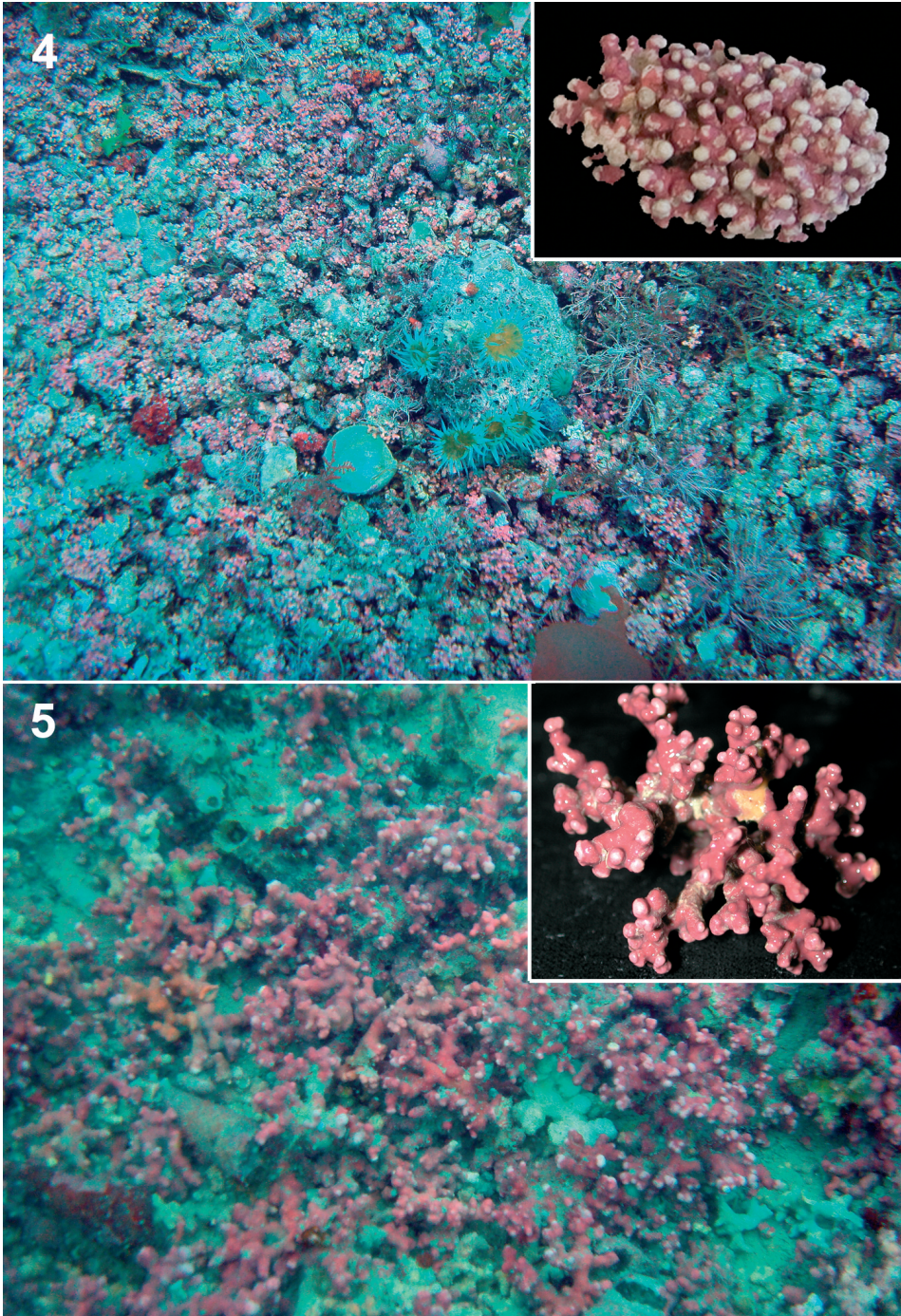
Location	Site	In or out of beds	Rhodoliths	Depth	Gravel (> 2 mm)	Sand (63 μ m – 2 mm)	Mud (< 63 μ m)
Te Miko Reef	TMR	In	LC	7-11	51	47	2
	TMR_B	In	LC & SD	8-11	51	44	4
	TMR_OUT	Out	None		3	94	3
Kahuwhera Bay	KWB	In	SD	5-9	41	19	40
	KWB_OUT	Out	None		23	45	32

rhodolith beds were assessed (two sites at each location, i.e., Te Miko Reef and Te Miko Reef _OUT), and Kahuwhera Bay and Kahuwhera Bay _OUT. At Te Miko Reef an additional site containing mixed rhodolith species was also assessed (Te Miko Reef _B).

The physical characteristics of these sites were documented by Nelson *et al.* (2012), including mapping the beds. The locations and sites studied, the species of rhodolith present, and sediment characteristics are summarised in Table 1. At Te Miko Reef and Te Miko Reef_B viable rhodoliths were clearly visible, sitting on top of the substratum in a more or less single layer over rhodolith- and shell-derived gravel (Fig. 4), in contrast to the partial burial of rhodoliths at Kahuwhera Bay. At Te Miko Reef *Lithothamnion crispatum* Hauck was the rhodolith forming species present, whereas at Te Miko Reef_B rhodoliths of both *L. crispatum* and *Sporolithon durum* (Foslie) R.A.Towns. *et* Woelk. were present. At both the “inside” and “outside” sites at Kahuwhera Bay there were fine sediments suspended in the water column resulting in turbid conditions, with a fine



Figs 2-3. Study sites at Te Miko Reef and Kahuwhera Bay showing the relative density of the rhodoliths within the beds. The rectangles mark the sampling sites: black = in the bed, empty = outside the bed, grey = Te Miko Reef_B.



Figs 4-5. **4.** Te Miko Reef bed with clear water and *Lithothamnion crispatum* rhodoliths (inset). **5.** Kahuwhera Bay with fine sediment covering *Sporolithon durum* rhodoliths (inset)

layer also covering the rhodoliths and associated biota (Fig. 5). All rhodoliths at this site were *Sporolithon durum*. Live rhodoliths were in a more or less single layer overlaying grey to blackened rhodoliths in a darkly coloured rhodolith and sediment sublayer extending to a depth of at least 10 cm, presumably anoxic.

Sampling methods

Sampling was designed to characterise the rhodolith beds at the two locations and to assess biodiversity inside the rhodolith beds and compare this with biodiversity found in sites outside rhodolith beds. As the beds were more or less at single depth, it was not necessary to stratify sampling by depth.

Adapting the methods used in published studies (e.g. Foster *et al.*, 2007; Steller *et al.*, 2003; Steller *et al.*, 2007a, b; Harvey & Bird, 2008) to the conditions at our study sites, we developed a protocol which allowed us to sample macroalgae (data presented in this paper) in addition to invertebrates and fish. Targeted collections of macroalgae (referred to as algal searches) were made by phycologically trained divers over an area of 500 m² in both locations and in adjacent areas outside of the beds. Data from these dives were analysed and interpreted as quantitative observations as they involved the same divers, covering the same area, for dives of equal duration. At each site two 25 m lines were laid out at right angles to the anchor line. On each transect eight 25 × 25 cm quadrats were placed 5 m apart, and all live rhodoliths and associated epifauna and epiflora were collected into plastic bags.

Sample processing

Quadrat samples were tipped out into large plastic containers and then thoroughly sorted. Two rhodolith-forming species were present and these were able to be distinguished by external morphology. All other macroalgae were either fresh-pressed onto herbarium paper or preserved in 4-5% v/v formalin in seawater for subsequent detailed morphological investigations. Some specimens were sub-sampled for molecular analysis with small pieces of tissue removed and dried in silica gel.

Where possible, macroalgae were identified to species level. Some samples that were preserved in the field were examined microscopically with the preparation of permanent slides to examine specific diagnostic anatomical and morphological features. Vouchers of macroalgal collections were retained and representative herbarium specimens were lodged in the Herbarium of the Museum of New Zealand Te Papa Tongarewa.

Molecular sequencing

Molecular sequencing was carried out on a small subset of the collections, particularly for species where current taxonomic knowledge is limited, where only sterile material was available, for novel material, and to add to our existing phylogenetic database and extend our documentation of biodiversity. Target taxa that were sequenced included crustose red and brown algae, species of *Dictyota* and bladed red algae (*Tsengia*, *Grateloupia*, “*Halymenia*”).

DNA was extracted from four coralline algal specimens using a Qiagen Blood and Tissue DNA Extraction Kit with a modified protocol as described in

Broom *et al.* (2008). DNA was extracted from the remaining taxa using the CTAB protocol of Zuccarello & Lokhorst (2005). Extracts were diluted 1:100 with 0.1 × TE buffer, and 3 µl was used in subsequent PCR amplifications. The *psbA* gene was amplified from specimens using standard primers (Yoon *et al.*, 2002). For the red algae, the plastid-encoded large subunit of the ribulose biphosphate carboxylase/oxygenase gene (*rbcL*) was amplified using a set of three primer pairs (F8 and R646, F481 and R1150, F765 and R1381; Wang *et al.*, 2000). DNA was extracted from 6 members of Dictyotales and Cutleriales, and sequence data were obtained from the *psbA* gene (5 specimens), and *psaA* gene (1 specimen) using primers from Yoon *et al.* (2002). Sequence data from the *rbcL* gene (3 specimens) were obtained using primers DJF1 (cta gct tta ttc cga atc ac, J. Sutherland, pers. comm.) and DRL2R (Hwang *et al.*, 2005). Amplified products were checked for correct length, purity and yield on 1% agarose gels stained with ethidium bromide. PCR products were cleaned using ExoSAP-IT (USB, Cleveland, Ohio) or with Exonuclease I/ Alkaline phosphatase digest, and commercially sequenced (Macrogen Inc, Seoul, South Korea, or The Centre for Genomics and Proteomics, The University of Auckland, Auckland, New Zealand). Sequences were compared to sequences held in GenBank using NCBI BLAST (<http://blast.ncbi.nlm.nih.gov/>) and to sequences of New Zealand specimens obtained previously (J. Sutherland, unpublished data) using Geneious V6.1.4, BioMatters Ltd, Auckland.

Data analysis

The overall numbers of algal taxa and the species list are based on all collections, quantitative and qualitative. Further analyses of algal community structure (inside and outside beds) are based on material collected in algal searches. For many algae it is not possible to count the number of individuals, therefore all analyses are on presence/absence data.

Rarity was calculated at several levels for all taxa: i. overall rarity – taxa that only occurred once across all seasons, sites, methods; ii. seasonal rarity – taxa that only occurred once within a season, regardless of site and method; iii. site rarity – taxa that only occurred once at each site (not directly comparable between inside and outside beds).

PRIMER (Clarke & Gorley, 2006; Anderson *et al.*, 2008) was used to assess Bray-Curtis similarities and perform a PERMANOVA (permutational multivariate analysis of variance) to assess differences in community composition between algal searches.

RESULTS

Macroalgae collected in this study are listed in Table 2. Four hundred and nine samples of macroalgae were retained. From these collections 103 distinct taxa (12 green algae, 24 brown algae and 67 red algae) were identified, with 64 identified to species level, 37 to genus and a further two provisionally to order. Seventy-five of these were recorded in February, and seventy in September. The different methods of collection resulted in the following numbers of taxa: algal searches – 85, transects – 28, cores – 8, opportunistic – 43 (includes dredge, scuba, attached to anchor line).

Table 2. Species recorded by site and season. TMR = 1; TMR_B = 2; TMR_Out = 3; KWB = 4; KWB_Out = 5

	Family	Identification	sites	month	
GREEN ALGAE	Caulerpaceae	<i>Caulerpa flexilis</i> J.V. Lamour. ex C.Agardh	1,2,3,4	Feb, Sep	
	Codiaceae	<i>Codium cranwelliae</i> Setch.	2	Feb	
	Codiaceae	<i>Codium fragile</i> ssp. <i>fragile</i> (Suringar) Har.	3,4,5	Feb	
	Codiaceae	<i>Codium gracile</i> (O.C. Schmidt) Dellow	2	Feb	
	Codiaceae	<i>Codium</i> sp.	3	Feb	
	Derbesiaceae	<i>Derbesia novae-zelandiae</i> V.J. Chapm.	2	Feb	
	Cladophoraceae	<i>Chaetomorpha</i> sp.	1	Feb, Sep	
	Cladophoraceae	<i>Cladophora feredayi</i> Harv.	5	Sep	
	Cladophoraceae	<i>Cladophora herpestica</i> (Mont.) Kuetz.	2,5	Feb, Sep	
	Cladophoraceae	<i>Cladophora sericea</i> (Huds.) Kuetz.	4	Sep	
	Cladophoraceae	<i>Cladophora</i> sp.	1,2,3	Feb	
	Ulvaceae	<i>Ulva</i> sp.	1,3,5	Feb, Sep	
	BROWN ALGAE	Dictyotaceae	<i>Dictyota papenfussii</i> Lindauer	2,3	Feb, Sep
		Dictyotaceae	<i>Dictyota</i> sp.1	4	Sep
Dictyotaceae		<i>Dictyota</i> sp.2	1,2,3	Feb, Sep	
Dictyotaceae		<i>Dictyota</i> sp.3	1	Sep	
Dictyotaceae		<i>Dictyota</i> crust	1,2,3	Feb, Sep	
Dictyotaceae		<i>Dictyota</i> sp.	2	Sep	
Dictyotaceae		<i>Distromium skottsbergii</i> Levring	2	Feb	
Dictyotaceae		<i>Zonaria turneriana</i> J. Agardh	1,2	Feb, Sep	
Stypocaulaceae		<i>Halopteris paniculata</i> (Suhr) Prud'homme	2,3	Feb, Sep	
Stypocaulaceae		<i>Halopteris</i> sp.	1,2,3	Feb, Sep	
Sargassaceae		<i>Carpophyllum angustifolium</i> J. Agardh	2,3	Feb, Sep	
Sargassaceae		<i>Carpophyllum flexuosum</i> (Esper) Grev.	4	Feb, Sep	
Sargassaceae		<i>Carpophyllum maschalocarpum</i> (Turner) Grev.	1,2,4	Feb, Sep	
Sargassaceae		<i>Sargassum sinclairii</i> Hook.f. et Harv.	1,2,3,5	Feb, Sep	
Xiphophoraceae		<i>Xiphophora chondrophylla</i> (Turner) Mont. ex Harv.	1,3	Sep	
Sporochnaceae		<i>Carpomitra costata</i> (Stackh.) Batters	2	Feb	
Lessoniaceae		<i>Ecklonia radiata</i> (C. Agardh) J. Agardh	1,2,3,4,5	Feb, Sep	
Cutleriaceae		<i>Cutleria multifida</i> (Turner) Grev.	1,2,4	Feb, Sep	

Table 2. Species recorded by site and season. TMR = 1; TMR_B = 2; TMR_Out = 3; KWB = 4; KWB_Out = 5 (*continued*)

	<i>Family</i>	<i>Identification</i>	<i>sites</i>	<i>month</i>
BROWN ALGAE	Cutleriaceae	<i>Cutleria</i> sp.2	2	Sep
	Scytosiphonaceae	<i>Colpomenia claytoniae</i> S.M. Boo, K.M. Lee, G.Y. Cho et W.A. Nelson	1	Feb
	Scytosiphonaceae	<i>Colpomenia ecuticulata</i> M.J. Parsons	4	Sep
	Scytosiphonaceae	<i>Colpomenia sinuosa</i> (Mertens ex Roth) Derbes et Solier	3,4,5	Feb, Sep
	Scytosiphonaceae	<i>Colpomenia</i> sp.	2,4	Feb, Sep
	Scytosiphonaceae	<i>Hydroclathrus clathratus</i> (C. Agardh) M. Howe	1,2,5	Feb, Sep
	RED ALGAE	Erythrotrichiaceae	<i>Erythrocladia</i> sp.	3
Corallinaceae		<i>Corallina officinalis</i> L.	1,2,3,4,5	Feb, Sep
Corallinaceae		<i>Corallina</i> sp.	1	Sep
Corallinaceae		<i>Jania verrucosa</i> J.V. Lamour.	1	Feb, Sep
Corallinaceae		<i>Jania</i> sp.	2	Sep
Corallinaceae		<i>Lithophyllum pustulatum</i> (J.V. Lamour.) Foslie	1	Feb
Corallinaceae		<i>Pneophyllum fragile</i> Kütz.	1,4	Feb
Hapalidaceae		<i>Lithothamnion crispatum</i> Hauck		
Hapalidaceae		<i>Mesophyllum erubescens</i>	4	Sep
na		non-geniculate coralline	1,2,4,5	Feb, Sep
Sporolithaceae		<i>Sporolithon durum</i> (Foslie) R.A. Towns. et Woelk.		
Liagoraceae		<i>Liagora harveyana</i> Zeh	5	Feb
Scinaiaceae		<i>Scinaia australis</i> (Setch.) Huisman	1,2,3	Feb
Scinaiaceae		<i>Scinaia berggrenii</i> (Levring) Huisman	4,5	Feb, Sep
Scinaiaceae		<i>Scinaia firma</i> Levring	2	Feb
Bonnemaisoniaceae		<i>Asparagopsis armata</i> Harv.	3,4	Feb
Bonnemaisoniaceae		<i>Delisea compressa</i> Levring	3	Feb
Callithamniaceae		<i>Callithamnion colensoi</i> Hook.f et Harv.	2,5	Sep
Callithamniaceae		<i>Callithamnion</i> sp.	3	Sep
Ceramiaceae		<i>Antithamnionella adnata</i> (J. Agardh) N.M. Adams	3	Sep
Ceramiaceae		<i>Ceramium</i> sp.	2	Feb
Ceramiaceae		<i>Pterothamnion confusum</i> (J. Agardh) Athanas.	3	Feb, Sep
Delesseriaceae		<i>Hymenena variolosa</i> (Harv.) Kylin	2,3	Sep
Delesseriaceae	<i>Hymenena</i> sp.	4	Sep	
Delesseriaceae	<i>Laingia</i> sp.	3	Sep	
Delesseriaceae	<i>Schizoseris</i> sp.	2,3,5	Feb, Sep	
Rhodomelaceae	<i>Aphanocladia delicatula</i> (Hook.f. et Harv.) Falkenb.	1	Feb	

Table 2. Species recorded by site and season. TMR = 1; TMR_B = 2; TMR_Out = 3; KWB = 4; KWB_Out = 5 (*continued*)

	<i>Family</i>	<i>Identification</i>	<i>sites</i>	<i>month</i>
	Rhodomelaceae	<i>Chondria</i> sp.	1	Feb
	Rhodomelaceae	<i>Cladhymenia lyallii</i> Harv.	1	Sep
	Rhodomelaceae	<i>Cladhymenia oblongifolia</i> Harv.	1,2,3	Feb
	Rhodomelaceae	<i>Laurencia distichophylla</i> J. Agardh	1,2,5	Feb
	Rhodomelaceae	<i>Laurencia thyrsoifera</i> J. Agardh	1,3,4	Feb, Sep
	Rhodomelaceae	<i>Pleurostichidium falkenbergii</i> Heydrich	1	Sep
	Rhodomelaceae	<i>Vidalia colensoi</i> (Hook.f. et Harv.) J. Agardh	3	Feb, Sep
	Wrangeliaceae	<i>Anotrichium crinitum</i> (Kütz.) Baldock	1	Sep
	Wrangeliaceae	<i>Griffithsia</i> sp.	3	Feb
	Gelidiaceae	<i>Gelidium longipes</i> J. Agardh	5	Sep
	Gelidiaceae	<i>Gelidium</i> sp.	5	Feb
	Gelidiaceae	<i>Pterocladia lucida</i> (Turner) J. Agardh	1,2,3,4	Feb, Sep
	Dumontiaceae	<i>Dudresnaya capricornica</i> Robins et Kraft	4	Feb
	Gigartinaeae	<i>Chondracanthus chapmanii</i> (Hook.f. et Harv.) Fredericq	1,2,3,4,5	Feb, Sep
	Gigartinaeae	" <i>Gigartina</i> " <i>atropurpurea</i> (J. Agardh) J. Agardh	1,2,3,4	Feb, Sep
	Gloiosiphonaceae	<i>Hypnea</i> sp.	1, 3	Feb
	Kallymeniaceae	<i>Psaromenia berggrenii</i> (J. Agardh) D'Archino, W.A. Nelson et Zuccarello	2	Feb
	Phylloporaceae	<i>Stenogramma interruptum</i> (C. Agardh) Mont. ex Harv.	1	Feb
	Peyssonneliaceae	<i>Peyssonnelia boudouresquei</i> Yoneshigue	2,4,5	Feb, Sep
	Peyssonneliaceae	<i>Peyssonnelia</i> sp.	1,3,4,5	Feb, Sep
	Peyssonneliaceae	<i>Peyssonnelia</i> sp.1	1,2,4	Feb, Sep
	Peyssonneliaceae	<i>Peyssonnelia</i> sp.2	1,4	Feb, Sep
	Peyssonneliaceae	<i>Peyssonnelia</i> sp.3	1	Feb
	Peyssonneliaceae	<i>Peyssonnelia</i> sp.4	1	Feb, Sep
	Peyssonneliaceae	<i>Peyssonnelia</i> sp.5	4	Sep
	Peyssonneliaceae	undetermined red crust	1,2	Sep
	Halymeniaceae	<i>Aodes nitidissima</i> J. Agardh	1,2,3,4	Feb
	Halymeniaceae	<i>Grateloupia urvilleana</i> (Mont.) Parkinson	1	Feb
	Halymeniaceae	<i>Grateloupia</i> sp.	1,4	Feb, Sep
	Halymeniaceae	" <i>Halymenia</i> " sp.	1,2,4	Feb
	Tsengiaceae	<i>Tsengia feredayae</i> (Harv.) Womersley et Kraft	2	Feb
	Tsengiaceae	<i>Tsengia</i> sp.	1,2,3,4	Feb, Sep

RED ALGAE

Table 2. Species recorded by site and season. TMR = 1; TMR_B = 2; TMR_Out = 3; KWB = 4; KWB_Out = 5 (*continued*)

	<i>Family</i>	<i>Identification</i>	<i>sites</i>	<i>month</i>
RED ALGAE	Plocamiaceae	<i>Plocamium</i> sp.	1,3	Feb, Sep
	Sarcodiaceae	<i>Sarcodia montagneana</i> (Hook.f. et Harv.) J. Agardh	2,3,4,5	Feb, Sep
	Champiaceae	<i>Champia laingii</i> Lindauer	1,3	Feb, Sep
	Lomentariaceae	<i>Lomentaria umbellata</i> (Hook.f. et Harv.) Yendo	1	Sep
	Lomentariaceae	<i>Lomentaria</i> sp.	1	Sep
	Rhodymeniaceae	<i>Rhodymenia</i> sp.	5	Sep

The data presented here show that more species were recorded in the Te Miko Reef beds than at Kahuwhera Bay (Table 3). In terms of overall rarity, of the 103 taxa considered in this dataset, 39 were only collected on a single occasion. Considering seasonal rarity, in February 32 (of 75) taxa were collected a single time, while in September 30 (of 66) taxa were collected a single time. Comparing sites for rarity, at KWB 16 taxa of 44 total were found on a single occasion, while at TMR 39 taxa of 88 total were found on a single occasion.

The rhodolith beds we studied supported greater floral diversity than the neighbouring areas outside the beds and the composition of species present in the beds and outside the beds also differed. Forty-seven of the taxa recorded were found solely in the rhodolith beds, and 15 taxa were found solely outside the beds.

A PERMANOVA investigating the effects of site and month of sampling on the flora present showed that site was significant ($P(\text{perm}) = 0.007$) whereas month was not ($P(\text{perm}) = 0.06$) (Table 4). However, the species composition of

Table 3. Number of taxa recorded by locations and sites, and seasons

<i>Location</i> <i>Site</i>	<i>Kahuwhera Bay</i>		<i>Total</i>	<i>Te Miko Reef</i>			<i>Total</i>
	<i>KWB</i>	<i>KWB_OUT</i>		<i>TMR</i>	<i>TMR_B</i>	<i>TMR_OUT</i>	
Algae	32	22	44	53	48	42	88
Feb	22	12		35	37	32	
Sep	23	13		33	23	22	

Table 4. PERMANOVA table of results comparing algal search data between sites and months. Monte Carlo test statistics ($P(\text{MC})$) are included to provide for enough possible permutations given the low number of monthly observations (2) per site

<i>Source</i>	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>Unique</i>			
				<i>Pseudo-F</i>	<i>P(perm)</i>	<i>perms</i>	<i>P(MC)</i>
Site	4	13126	381.6	2.3004	0.007	963	0.032
Month	1	4 012.6	4012.6	2.8129	0.06	936	0.088
Res	4	5706	1426.5				
Total	9	22845					

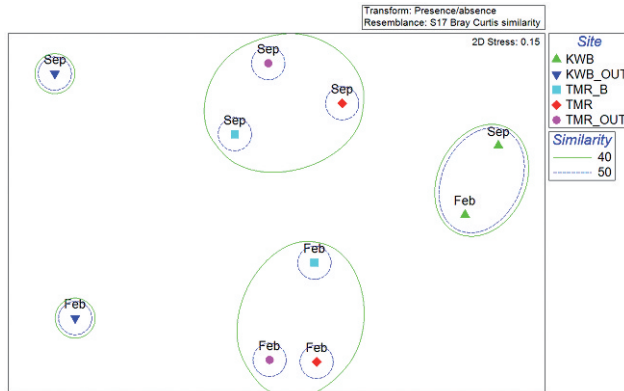


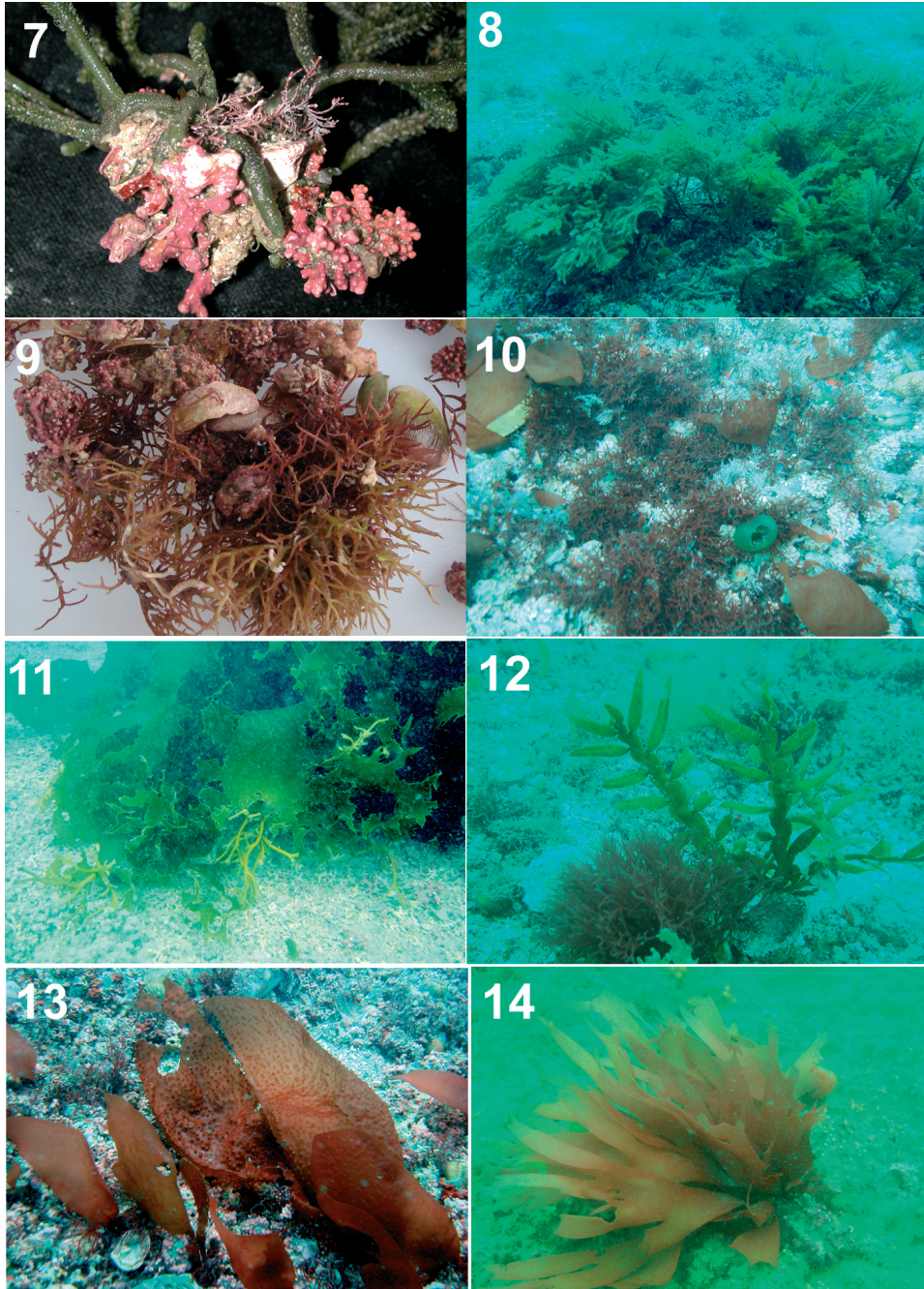
Fig. 6. MDS (multidimensional scaling) diagram of Bray Curtis similarities of algal search data between sites and months. The circles represent similarity profiles (SIMPROF) which test for evidence of structure in an a priori unstructured set of samples and clusters data by 40% similarity (solid line) or 60% similarity (broken line) at 1% significance level. Feb = February, Sep = September.

the flora associated with the two locations differed (Fig. 6). The algal communities at Te Miko Reef clustered by month at a 40% level of similarity, regardless of whether they were from inside or outside the rhodolith beds, however in each month all three Te Miko Reef sites were less than 50% similar. Algae from the bed at Kahuwhera Bay were at least 50% similar between months, whereas at Kahuwhera Bay_OUT the algal communities were less than 40% similar in February and September.

Description of the flora

Structural components of the flora: *Caulerpa flexilis* J.V. Lamour. was a particularly conspicuous part of the flora recorded from all the Te Miko Reef sites and also in the Kahuwhera Bay rhodolith bed. The stoloniferous growth of this species means that it was well anchored in coarse sediment habitats, binding to individual rhodoliths, and forming erect stands c. 15-25 cm high (Figs 7-8). *Chondracanthus chapmanii* (Hook.f. et Harv.) Fredericq (Figs 9-10) was found at all five sites investigated. This species has both creeping as well as upright growth. Where it occurred in rhodolith beds, branches from a single individual were found to be anchored to multiple rhodoliths.

Members of the Laminariales and Fucales were present in the rhodolith beds. Both *Ecklonia radiata* (C. Agardh) J. Agardh (Fig. 11) and *Sargassum sinclairii* Hook.f. et Harv. were common and were collected from four and five of the sites respectively. Three of the four species of *Carpophyllum* that are present in northern New Zealand were recorded in this study with *C. angustifolium* J. Agardh, which is typically found in areas of active water movement, found at Te Miko Reef_B and Te Miko Reef_OUT; *C. flexuosum* (Esper) Grev., which is known to grow more deeply than the other species in the genus and apparently is tolerant of low light conditions, present at Kahuwhera Bay; and *C. maschalocarpum* (Turner) Grev. (Fig. 12), which can be found in a wide array of habitats and exposure conditions on coastal reefs, found at Kahuwhera Bay, Te Miko Reef, and Te Miko Reef_B.



Figs 7-14. **7.** *Caulerpa flexilis* axes and stolons growing around rhodoliths. **8.** *Caulerpa flexilis* canopy in rhodolith bed. **9.** *Chondracanthus chapmanii* with prostrate axes growing around rhodoliths and shell debris. **10.** Patches of *Chondracanthus chapmanii* creeping across rhodolith bed. **11.** *Ecklonia radiata*. **12.** *Carpophyllum maschalocarpum*. **13.** "*Gigartina*" *atropurpurea*. **14.** *Sarcodia montagneana*.

Several species previously recorded as commonly occurring in soft sediment assemblages in the Bay of Islands, were also common in the rhodolith beds sampled in this study, in particular the red algae *Cladhymania oblongifolia* Harv. (both inside and outside the Te Miko Reef sites), "*Gigartina*" *atropurpurea* (J. Agardh) J. Agardh (Fig. 13) (inside and outside the Te Miko Reef sites and inside Kahuwhera Bay), and *Sarcodia montagneana* (Hook.f. et Harv.) J. Agardh (Fig. 14), (inside and outside at the Te Miko Reef and Kahuwhera Bay) (Nelson & D'Archino, 2010). These species provide three dimensional structure and were found attached to both rhodoliths and shell debris.

New records and new taxa

a. Dictyotales. This research revealed the presence of multiple species of the brown algal genus *Dictyota*. Specimens were identified morphologically and with molecular sequence data. Three different sequences were obtained from five specimens. Two of these have not previously been obtained from other New Zealand isolates, while the third sequence is consistent with samples of a species of *Dictyota* (here referred to provisionally as *D. papenfussii*) previously collected from a range of sites in northern New Zealand, including the Cavalli Islands, Stephenson Island and the Okahu Channel. In addition crustose Dictyotales were recorded in the field. (Refer to Table 5 for sequences lodged in GenBank.)

b. *Cutleria* sp. The molecular sequencing results revealed that amongst the crustose brown algae there were two species of *Cutleria* present growing in the heteromorphic "*Aglaozonia*" crustose phase. One of these was confirmed by sequence data to be *Cutleria multifida*, which constitutes a new record for the Bay of Islands. The other species remains unidentified and is different from all sequence data in GenBank. (Refer to Table 5 for sequences lodged in GenBank.)

c. *Dudresnaya*. Two specimens of *Dudresnaya* were collected in Kahuwhera Bay in summer and identified as *Dudresnaya capricornica* Robins & Kraft, a species that is widespread in Australia. This constitutes a new genus and family record for New Zealand. Comparison of material from the rhodolith beds with specimens collected previously, during field work in the north eastern North Island and in the Bay of Islands, revealed that material had been confused with specimens of *Acrosymphyton*. *Dudresnaya capricornica* is usually found in tropical and subtropical seas and is apparently rare and ephemeral in northern New Zealand. A detailed description of specimens collected in New Zealand was presented in D'Archino & Sutherland (2013).

d. Peyssonneliaceae. Peyssonneliaceae crusts were abundant on both beds in summer and winter. The crusts were attached to rhodoliths, or to shell fragments or small pebbles, and ranged in size from very small patches (ca 1-3 mm in diameter) through to larger crusts (ca 2 cm in diameter). The majority of crusts were completely calcified and adhering to the substratum except for one species that had free margins. Although only a proportion of the material collected was identified by sequence data, five distinct species were identified, one of which was identified as *P. boudouresquei* Yoneshigue. This is a new species record for New Zealand. (Refer to Table 5 for sequences lodged in GenBank.)

e. "*Halymenia*". Samples of a foliose red blade were collected at Te Miko Reef in summer and were referred to *Halymenia* on the basis of their vegetative anatomy. However molecular data showed that this taxon represents a distinct genus closely related to *Halymenia abyssicola* Dawson, found in the Gulf of California. Thalli are undivided, up to 60 cm high and 35 cm wide, attached

Table 5. Sequences lodged in GenBank

Specimen number	Identification	Date	Site	Gene(s)	GENBANK
RHO0012	<i>Peyssonnelia</i> sp.3	8/02/2010	TMR	<i>rbcL</i>	KC998951
RHO0225	<i>Peyssonnelia</i> sp.2	8/02/2010	TMR	<i>rbcL</i>	KC998950
RHO0236	Halymeniaceae	9/02/2010	KWB	<i>rbcL</i>	KC998953
RHO0308	<i>Peyssonnelia boudouresquei</i>	9/02/2010	KWB	<i>rbcL</i>	KC998949
RHO0646	<i>Dictyota</i> crust	10/02/2010	TMRB	<i>psbA</i>	KC963409
RHO0671	Halymeniaceae	10/02/2010	TMRB	<i>rbcL</i>	KC998952
RHO0676	<i>Tsengia</i> sp.	10/02/2010	TMRB	<i>rbcL</i>	KC998954
RHO0687	<i>Dictyota</i> sp.2	10/02/2010	TMRB	<i>rbcL, psbA</i>	KC963410, KC963411
RHO2009	<i>Tsengia</i> sp.	19/09/2010	KWB	<i>rbcL</i>	KC998955
RHO2026	<i>Mesophyllum erubescens</i>	19/09/2010	KWB	<i>psbA</i>	KC963418
RHO2028	<i>Cutleria multifida</i>	19/09/2010	KWB	<i>psbA</i>	KC963417
RHO2031	<i>Peyssonnelia boudouresquei</i>	19/09/2010	KWB	<i>rbcL</i>	KC998947
RHO2032	<i>Peyssonnelia</i> sp.1	19/09/2010	KWB	<i>rbcL</i>	KC998958
RHO2033	<i>Peyssonnelia boudouresquei</i>	19/09/2010	KWB,	<i>rbcL</i>	KC998948
RHO2034	<i>Mesophyllum erubescens</i>	19/09/2010	KWB	<i>psbA</i>	KC963419
RHO2077	<i>Dictyota papenfussii</i>	20/09/2010	TMR out	<i>rbcL, psbA</i>	KC963412, KC963413
RHO2099	<i>Lithothamnion crispatum</i>	20/09/2010	TMR	<i>psbA</i>	KC963420
RHO2100	<i>Dictyota papenfussii</i>	21/09/2010	TMRB	<i>rbcL, psbA</i>	KC963414, KC963415
RHO2101	<i>Cutleria</i> sp.	21/09/2010	TMRB	<i>psbA</i>	KC963416
RHO2182	<i>Grateloupia</i> sp.	22/09/2010	KWB	<i>rbcL</i>	KC998957
RHO2185	<i>Grateloupia</i> sp.	22/09/2010	TMR	<i>rbcL</i>	KC998956
RHO2203	<i>Sporolithon durum</i>	21/09/2010	KWB	<i>psbA</i>	KC963421

with a small discoid holdfast, pale pink in the water and becoming darker when dried. The large blades have small holes and were slippery in texture when collected. This taxon was previously collected in Bay of Islands and Northland and will be described in a study on the New Zealand Halymeniales (D'Archino pers. comm.) (Refer to Table 5 for sequences lodged in GenBank as Halymeniales sp1.).

f. *Tsengia*. Two species of *Tsengia* were found in this study. *Tsengia feredayae* (Harv.) Womersley *et* Kraft (fan shaped, dichotomously branched) was collected once on the rhodoliths bed (Te Miko Reef_B). A foliose blade with *Tsengia* vegetative anatomy was found at all Te Miko Reef sites as well as at Kahuwhera Bay. This species differs in *rbcL* sequence data from *T. laingii* (Kylin) Womersley *et* Kraft (type locality southeastern South Island). This represents a new species of *Tsengia* in the New Zealand region.

g. *Grateloupia*. Two species of *Grateloupia* are recorded here. One species is identified as *G. urvilleana* (Mont.) Parkinson, and the second species, distinguished by sequence data, is not currently aligned with species described from the New Zealand region.

Non-indigenous species

Four species recorded from the rhodolith beds are considered to be non-indigenous based on previous analyses of the New Zealand flora; the two species of *Cutleria*; *Hypnea* (only fragmentary material was collected precluding species level identification); and, *Hydroclathrus clathratus* (C.Agardh) M.Howe (considered to be native to the Kermadec Islands but introduced to northern New Zealand).

DISCUSSION

This study was part of the first detailed field investigation of subtidal rhodoliths in New Zealand, examining the structure and physical characteristics of rhodolith beds at two locations and documenting their associated biodiversity, as well as characterising the two rhodolith-forming species, *Lithothamnion crispatum* and *Sporolithon durum*, in terms of their size and shape (Nelson *et al.*, 2012). Rhodoliths in New Zealand have been poorly documented to date and knowledge of the location of beds around the country remains very incomplete. Of the four rhodolith-forming species reported from New Zealand, two species (*Lithothamnion proliferum* and *Lithophyllum* sp.) are known from single specimens, indicating that more targeted collections are required in order to enable the distribution of species to be documented as well as the mapping of rhodolith beds (Farr *et al.*, 2009).

Macroalgae collected during this study included both new records for New Zealand and Northland, but also new discoveries. Crustose brown algae were common on the surface of the rhodoliths. Sequence data and sectioning revealed the presence of both members of the Dictyotales (currently undescribed), as well as the presence of the “*Aglaozonia*” sporophytic (crustose) phase of two species in the genus *Cutleria*. Neither the sporophytic nor gametophytic phase of *C. multifida* has been found previously in the Bay of Islands, with the previous northern record for this species being Whangarei Harbour. In 1980 a collection was made in the Leigh Marine Reserve of a species of *Cutleria* (gametophyte stage), provisionally identified as *C. mollis* Allender et Kraft, a species described from Lord Howe Island (Adams, 1994). This species has not been collected subsequently in northern New Zealand. Further research is required to compare the *Aglaozonia* phase collected during this study with sequence data from *C. mollis*.

The European Atlantic and the Galician rhodolith beds are understood to serve as refuges for crustose phases of heteromorphic species, the crustose phases providing “constant populations during unfavourable seasons” and enabling the later development of gametophytic stages (Birkett *et al.*, 1998; Bárbara *et al.*, 2004; Peña & Bárbara, 2010a). In Galicia Peña & Bárbara (2010a) reported 23 crustose species present in subtidal beds with 8 Ochrophyta and 15 Rhodophyta, including 5 species of *Peyssonnelia*. Our study has revealed a number of *Peyssonnelia* spp. *sensu lato*, increasing the known diversity of this order in New Zealand, and consistent with discoveries in rhodolith beds in other parts of the world. The New Zealand Peyssonneliaceae currently recorded include 5 taxa (Nelson, 2012) although these taxa have not been studied in detail and are still poorly known. No attempt was made to refer the taxa found during this study to species previously reported from New Zealand. As noted by Adams

(1994), names have been used uncritically for one or more of these entities in this region. It is clear that further work and more sampling are required on the New Zealand Peyssonneliaceae, in order to understand these species, their distribution and relationships to other species within the order/family.

Although this study did not specifically examine the relationships between rhodoliths and other species that may play roles in structuring or stabilising the substrata, two of the most common species recorded appear to function in this way. The green alga *Caulerpa flexilis* has previously been recorded from the Bay of Islands in a range of soft sediment habitats, where it was found to stabilise the substrata with its prostrate stem system, anchoring the alga and producing upright branches that provide three dimensional structure for invertebrates and fishes (Nelson & D'Archino, 2010). In rhodolith areas in the northern North Island, including Te Miko Reef, *Caulerpa flexilis* has been observed to grow in rows on the seafloor, often along small ridges, with patches of rhodoliths growing in slight depressions between the clumps or lines of *Caulerpa*. In the rhodolith beds the red alga *Chondracanthus chapmanii* formed extensive patches, effectively consolidating clumps of rhodoliths and shell debris. The kelp *Ecklonia radiata*, typically found as a key species of rocky subtidal reefs in northern New Zealand, was present in the beds. *Ecklonia* plants require a degree of stability to enable their development, indicating that the rhodoliths were not rolling continuously. The holdfast system of *Ecklonia* is hapteral and this is probably more suited to settlement on rhodolith-sized sediments, than a discoidal holdfast, by providing multiple points of contact in contrast to a single discoidal pad.

In other parts of the world creeping algae have been recorded in rhodolith beds, apparently consolidating the beds and reducing movement (e.g. Cabioch, 1969; Maggs & Guiry 1988; Bárbara *et al.*, 2004). Bárbara *et al.* (2004) comment on the role of taxa with spreading or filiform growth, and discuss the role of vegetative propagation with regeneration of thalli from active apices. The type of network formed by *Gelidiella calcicola*, described in European maerl beds (Maggs & Guiry, 1988; Bárbara *et al.*, 2004), is similar to the growth of *Chondracanthus chapmanii* in the New Zealand beds.

Two large red blades belonging to the Halymeniales that were common in February on Te Miko Reef require further attention based on the molecular data obtained to date. The only species of *Halymenia* previously reported from New Zealand has been *Halymenia latifolia* (type locality France). The "*Tsengia*" sp. from the Bay of Islands is not related to specimens of *Tsengia laingii* from the type locality in Brighton, and this newly found species requires further study. The recent discovery and recognition of *Dudresnaya* in northern New Zealand constitutes a new record for New Zealand both for the genus and the family (Dumontiaceae) (D'Archino & Sutherland, 2013).

Peña & Bárbara (2008a) summarised the findings of 24 studies of floras associated with maerl in shallow Atlantic communities, recording the highest number of species in Galicia (226) followed by the British Isles (186) and Brittany (172), and in the Mediterranean, they recorded that Spanish beds also have the highest number of associated species recorded (275) compared with Italy (114), Malta (71), France (60). In eastern Brazil 67 species of fleshy algae were found associated with subtidal rhodolith beds at 10, 15 and 20 m depth (Riul *et al.*, 2009), 109 species in south eastern Brazil (Amado-Filho *et al.*, 2007), and Pascelli *et al.* (2013) reported 44 species, lower diversity and abundance than found at more northern sites. Macroalgae collected during this study (103 taxa) compare with a total flora of ca 421 spp. recorded from habitats in north eastern New Zealand

(herbarium Museum of New Zealand Te Papa Tongarewa, Nelson *et al.*, submitted). The diversity found within the beds we studied is comparable to that reported from studies of single beds (e.g. Barberá *et al.*, 2003; Amado-Filho *et al.*, 2007; Riul *et al.*, 2009), however, given the very modest collection effort that has been possible to date in New Zealand rhodolith beds, it is most unlikely that we have fully sampled the flora found in these beds. Collections from late summer and late winter/early spring provide a snapshot of macroalgal diversity within the beds, but it is important to recognise that sampling only occurred on two occasions in contrast to the research effort that has been applied in other regions (e.g. Peña & Bárbara (2008a) undertook 911 surveys in sampling 60 Galician beds using both dredge and scuba). Our study did not provide the scope for a closer examination of patchiness in terms of substrata, shelter /exposure to water motion within the rhodolith beds, and how such features may have an impact on the associated flora.

In this study, similar numbers of species were found in February and September, although the composition of the algal communities differed significantly by site. A slightly higher proportion of taxa were collected once in February (47%) than in September (41%). Although our study had a temporal component, we were not able to fully explore seasonal responses within the beds. More intra-annual (seasonal) and inter-annual sampling is required to get a fuller picture and to address hypotheses about rarity and richness in these assemblages. In three shallow subtidal Galician beds the highest species richness and total percentage cover were recorded in spring and summer, and the lowest in autumn and winter, and a similar pattern was reported by Pascelli *et al.* (2013) in southern Brazil. In contrast, in the Gulf of California Steller *et al.* (2003) reported the highest macroalgal richness in winter with 36 species present compared with only 6-7 species in summer, and attributed this to high water temperatures, potential anoxic conditions and thermal stratification in the summer having a deleterious impact on the flora.

There were significant differences between the beds sited in relatively close proximity (approximately 4 km apart), in terms of physical characteristics such as water motion and sediment characteristics, as well as their floral composition. The Te Miko Reef rhodolith bed had attributes typical of beds described elsewhere, in an area of consistent directional water movement, apparently not so strong as to damage the rhodoliths or dislodge and transport them to unfavourable habitats or out of the euphotic zone, in addition to high water clarity, and a conspicuous associated flora and macrofauna on the surface of the bed. The Kahuwhera Bay bed, however, could be considered to be atypical of the majority of rhodolith habitats reported in the literature. Visibility was much lower than at Te Miko Reef and the seafloor was covered in a coating of fine sediments with a substantial proportion of the rhodoliths buried. Sediment is usually regarded as being deleterious for rhodolith growth and health although there are some published reports of rhodoliths from areas of fine sediments in other parts of the world (e.g. Perry, 2005; Wilson *et al.*, 2011). The key issue for rhodolith survival and health appears to be the amount of sediment transport and mobilisation that occurs and also the amount of water motion – that is, whether there is sufficient water motion to prevent burial and to enable adequate photosynthesis to proceed. Burial can result from sedimentation and also from disturbance resulting from water motion and storm events. Swales *et al.* (2010) found that sedimentation rates in the Bay of Islands, and in particular in the Te Rawhiti Reach, have increased markedly over the past century associated with land use changes and deforestation. It is not clear if the bed at Kahuwhera Bay is

threatened by this increasing sedimentation and the risk of burial or whether the conditions in the bed are well within the thresholds for survival of *Sporolithon* (and the associated biota). Further research on the functioning of the system and on productivity of the rhodoliths would be required to determine the health and state of the beds. Interestingly, the species present subtidally and able to withstand sediment cover at Kahuwhera Bay, *Sporolithon durum*, is also the species found at Te Miko Reef in the brightly lit subtidal bed, and also reported growing in the intertidal zone at Whangaparaoa Peninsula exposed to bright light conditions and with little sediment present (Basso *et al.*, 2009). Given the substantial physical and biological differences between these beds, it is premature to generalise about rhodoliths in New Zealand and how rhodoliths may respond to stressors.

The rhodolith beds that we have focused on are in the coastal zone. It is not known how the diversity and species composition of these beds in the Bay of Islands will compare with subtidal beds elsewhere in New Zealand (e.g., Kapiti Island, Marlborough Sounds, Fiordland, Foveaux Strait), or with intertidal beds (e.g. Basso *et al.*, 2009). Internationally rhodolith beds are generally regarded as fragile habitats that harbour high biodiversity, and there is a strong consensus about the need to protect these habitats as well as the need for information on the distribution and attributes of the beds in order to manage both the specific habitats and species effectively.

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REFERENCES

- ADAMS N.M., 1994 — *Seaweeds of New Zealand. An illustrated guide*. Christchurch, Canterbury University Press, 360 p.
- AMADO-FILHO G.M., MANEVELDT G., MANSO R.C.C., MARINS-ROSA B.V., PACHECO M.R. & GUIMARÃES S.M.P.B., 2007 — Structure of rhodolith beds from 4 to 55 meters deep along the southern coast of Espírito Santo State, Brazil. *Ciencias Marinas* 33: 399-410.
- ANDERSON M.J., GORLEY R.N. & CLARKE K.R. 2008 — PERMANOVA + for PRIMER: guide to Software and Statistical Methods. PRIMER-e: Plymouth, UK.
- BÁRBARA I., CREMADES J. & VEIGA A.J., 2004 — A floristic study of a maerl and gravel subtidal bed in the Arousa ría (Galicia, Spain). *Botánica Complutensis* 28: 35-46.
- BARBERÁ C., BORDEHORE C., BORG J.A., GLÉMAREC M., GRALL J., HALL-SPENCER J.M., DE LA HUZ CH., LANFRANCO E., LASTRA M., MOORE P.G., MORA J., PITA M.E., RAMOS-ESPLA A.A., RIZZO M., SANCHEZ-MATA A., SEVA A., SCHEMBRI P.J. & VALLE C., 2003 — Conservation and management of northeast Atlantic and Mediterranean maerl beds. *Aquatic conservation: marine and freshwater ecosystems* 13: S65-76.
- BASSO D., NALIN R. & NELSON C.S., 2009 — Shallow-water *Sporolithon* rhodoliths from North Island (New Zealand). *Palaios* 24: 92-103.
- BERLANDI M.R., FIGUEIREDO M.A. DE O. & PAIVA P.C., 2012 — Rhodolith morphology and the diversity of polychaetes off the southeastern Brazilian coast. *Journal of coastal research* 28: 280-287.

- BIRKETT D.A., MAGGS C.A. & DRING M.J., 1998 — An overview of dynamics and sensitivity characteristics for conservation management of marine SACs. Maerl Biotopes V. Scottish Association for Marine Science, UK Marine SACs Project, 117 p.
- BOSENCE D.W.J., 1983 — The occurrence and ecology of recent rhodoliths. In: Peryt T. (ed.) *Coated Grains*. Berlin, Springer Verlag, pp. 225-242.
- BROOM J.E.S., HART D.R., FARR T.J., NELSON W.A., NEILL K.F., HARVEY A.H. & WOELKERLING W.J., 2008 — Utility of *psbA* and *nSSU* for phylogenetic reconstruction in the Corallinales based on New Zealand taxa. *Molecular phylogenetics & evolution* 46: 958-973.
- CABIOCH J., 1969 — Les fonds de maerl de la baie de Morlaix et leur peuplement végétal. *Cahiers de biologie marine* 10: 139-162.
- CLARKE K.R. & GORLEY R.N., 2006 — PRIMER v6: User manual/tutorial. PRIMER-E Ltd, 190 p.
- D'ARCHINO R. & SUTHERLAND J.E., 2013 — First record of the genus *Dudresnaya* (Dumontiaceae, Rhodophyta) in New Zealand waters. *Phycological research* (in press).
- FARR T., BROOM J., HART D., NEILL K. & NELSON W., 2009 — Common coralline algae of northern New Zealand: an identification guide. *NIWA information series* 70, 249 p.
- FOSTER M.S., 2001 — Rhodoliths: between rocks and soft places. *Journal of phycology* 37: 659-667.
- FOSTER M.S., MCCONNICO L.M., LUNDSTEN L., WADSWORTH T., KIMBALL T., BROOKS L.B., MEDINA-LÓPEZ M., RIOSMENA-RODRÍGUEZ R., HERNÁNDEZ-CARMONA G., VÁSQUEZ-ELIZONDO R.M., JOHNSON S. & STELLER D.L., 2007 — Diversity and natural history of a *Lithothamnion muelleri* – *Sargassum horridum* community in the Gulf of California. *Ciencias marinas* 33: 367-384.
- GUIMARAES S. & AMADO-FILHO G.M., 2008 — Deep-water gelatinous rhodophytes from southern Espírito Santo State, Brazil. *Botanica marina* 51: 378-387.
- HALL-SPENCER J., KELLY J. & MAGGS C.A., 2008 — Assessment of maerl beds in the OSPAR area and the development of a monitoring program. (Department of Environment, Heritage and Local Government: Ireland).
- HARVEY A.S., WOELKERLING W.J., FARR T.J., NEILL K.F. & NELSON W.A., 2005 — Coralline algae of central New Zealand: An identification guide to common “crustose” species. *NIWA information series* 57, 145 p.
- HARVEY A.S. & BIRD F.L., 2008 — Community structure of a rhodolith bed from cold temperate waters (southern Australia). *Australian journal of botany* 56: 437-450.
- HERNÁNDEZ-KANTÚN J., RIOSMENA-RODRÍGUEZ R., LÓPEZ-VIVAS J.M. & PACHECO-RUIZ I., 2010 — Range extension for *Kallymenia* spp. (Kallymeniaceae: Rhodophyta) associated with rhodolith beds, new records from the Gulf of California, Mexico. *Marine biodiversity records* 3: e84, 1-5.
- HWANG I.-K., KIM H.S. & LEE W.J., 2005 — Polymorphism in the brown alga *Dictyota dichotoma* (Dictyotales, Phaeophyceae) from Korea. *Marine biology* 147: 999-1015.
- KAMENOS N.A., MOORE P.G. & HALL-SPENCER J.M., 2004a — Small-scale distribution of juvenile gadoids in shallow inshore waters; what role does maerl play? *ICES Journal of marine science* 61: 422-429.
- KAMENOS N.A., MOORE P.G. & HALL-SPENCER J.M., 2004b — Nursery-area function of maerl grounds for juvenile queen scallops *Aequipecten opercularis* and other invertebrates. *Marine ecology progress series* 274: 183-189.
- KONAR B., RIOSMENA-RODRÍGUEZ R. & IKEN K., 2006 — Rhodolith bed: a newly discovered habitat in the North Pacific Ocean. *Botanica marina* 49: 355-359.
- LITTLER M.M., LITTLER D. & HANISAK M.D., 1991 — Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. *Journal of experimental marine biology and ecology* 150: 163-182.
- MAGGS C.A. & GUIRY M.D., 1988 “1987” — *Gelidiella calcicola* sp. nov. (Rhodophyta) from the British Isles and northern France. *British phycological journal* 22: 417-434.
- NELSON W.A., 2009 — Calcified macroalgae - critical to coastal ecosystems and vulnerable to change: A review. *Marine and freshwater research* 60: 787-801.
- NELSON W. & D'ARCHINO R., 2010 — Bay of Islands OS20/20 survey report. Chapter 12: Attached benthic macroalgae [pdf]. In: *Bay of Islands OS20/20 survey report*, 31 p. ftp://ftp.niwa.co.nz/os2020/boi/Final_chapters/Chapter_12_Macroalgae.pdf
- NELSON W.A., 2012 — Phylum Rhodophyta: red algae. In: Gordon D.P. (ed.) *New Zealand Inventory of Biodiversity. Volume Three. Kingdoms Bacteria, Protozoa, Chromista, Plantae, Fungi*. Christchurch, Canterbury University Press, pp. 327-346.
- NELSON W.A., NEILL K., FARR T., BARR N., D'ARCHINO R., MILLER S. & STEWART R., 2012 — Rhodolith beds in northern New Zealand: characterisation of associated biodiversity and vulnerability to environmental stressors. *New Zealand aquatic environment and biodiversity report*. 99, 106 p.

- NELSON W.A., DALEN J. & NEILL K.F. (in prep) Insights from natural history collections: analysing the New Zealand macroalgal flora using herbarium data.
- PASCELLI C., RIUL P., RIOSMENA-RODRIGUEZ R., SCHERNER F., NUNES M., HALL-SPENCER J.M., OLIVEIRA, E.C.DE & HORTA P., 2013 — Seasonal and depth driven changes in rhodolith bed structure and associated macroalgae off Arvoredo island (southeastern Brazil). *Aquatic Botany* (in press).
- PEÑA V. & BÁRBARA I., 2008a — Maerl community in the north-western Iberian Peninsula: a review of floristic studies and long term changes. *Aquatic Conservation: Marine and freshwater ecosystems* 18: 339-366.
- PEÑA V. & BÁRBARA I., 2008b — Biological importance of an Atlantic European maerl bed off Benecia Island (northwest Iberian Peninsula). *Botanica marina* 51: 493-505.
- PEÑA V. & BÁRBARA I., 2010a — New records of crustose seaweeds associated with subtidal maerl beds and gravel bottoms in Galicia (NW Spain). *Botanica marina* 53: 41-61.
- PEÑA V. & BÁRBARA I., 2010b — Seasonal patterns in the maerl community of shallow European Atlantic beds and their use as a baseline for monitoring studies. *European journal of phycology* 45: 327-342.
- PERRY C.T., 2005 — Structure and development of detrital reef deposits in turbid nearshore environments, Inhaca Islands, Mozambique. *Marine geology* 214: 143-161.
- RIUL P., LACOUTH P., PAGLIOSA P.R., CHRISTOFFERSEN M.L. & HORTA P.A., 2009 — Rhodolith beds at the easternmost extreme of South America: community structure of an endangered environment. *Aquatic botany* 90: 315-320.
- STELLER D.L. & FOSTER M.S., 1995 — Environmental factors influencing distribution and morphology of rhodoliths on Bahía Concepción, B.C.S., México. *Journal of experimental marine biology and ecology* 194: 201-212.
- STELLER D.L., RIOSMENA-RODRÍGUEZ R., FOSTER M.S. & ROBERTS C.A., 2003 — Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. *Aquatic conservation: marine and freshwater ecosystems* 13: S5-20.
- STELLER D.L., HERNÁNDEZ-AYÓN J.M., RIOSMENA-RODRÍGUEZ R. & CABELLO-PASINI A., 2007a — Effect of temperature on photosynthesis, growth and calcification rates of the free-living coralline alga *Lithophyllum margaritae*. *Ciencias marinas* 33: 441-456.
- STELLER D.L., RIOSMENA-RODRÍGUEZ R. & FOSTER M.S., 2007b — Sampling and monitoring rhodolith beds: rhodolith distribution and taxonomy, biodiversity and long-term sampling. In: Rigby P.R., Iken K. & Shirayama Y. (Eds), *Sampling biodiversity in coastal communities: NaGISA protocols for seagrass and macroalgal habitats*. Singapore, Ridge Books (NUS press), pp. 93-97.
- SWALES A., OVENDEN R., WADHWA S. & RENDLE D., 2010 — Bay of Islands OS20/20 survey report. Chapter 4: Recent sedimentation rates (over the last 100-150 years [pdf]. In: *Bay of Islands OS20/20 survey report*, 48 p. ftp://ftp.niwa.co.nz/os2020/boi/Final_chapters/Chapter_04_Recent_sedimentation.pdf
- WANG H.W., KAWAGUCHI S., HORIGUCHI T. & MASUDA M., 2000 — Reinstatement of *Grateloupia catenata* (Rhodophyta, Halymeniaceae) on the basis of morphology and *rbcl* sequences. *Phycologia* 39: 228-237.
- WILSON B., BLAKE S., RYAN D. & HACKER J., 2011 — Reconnaissance of species-rich coral reefs in a muddy, macro-tidal, enclosed embayment, Talbot Bay, Kimberley, Western Australia. *Journal of the royal society of Western Australia* 94: 251-265.
- YOON H.S., HACKETT J. & BHATTACHARYA D., 2002 — A single origin of the peridinin- and fucoxanthin- containing plastids in dinoflagellates through tertiary endosymbiosis. *Proceedings of the national academy of sciences USA* 99: 11724-11729.
- ZUCCARELLO G.C. & LOKHORST G., 2005 — Molecular phylogeny of the genus *Tribonema* (Xanthophyceae) using *rbcl* gene sequence data: monophyly of morphologically simple algal species. *Phycologia* 44: 384-392.

