Review article

History, current status and future of marine macroalgal research in New Zealand: Taxonomy, ecology, physiology and human uses

Catriona L. Hurd,1* Wendy A. Nelson,2 Ruth Falshaw3 and Kate F. Neill2

¹Department of Botany, University of Otago, PO Box 56, Dunedin, ²National Institute of Water and Atmospheric Research, Private Bag 14-901, Kilbirnie and ³Industrial Research Limited, PO Box 31-310, Lower Hutt, New Zealand

SUMMARY

New Zealand has a rich and diverse macroalgal flora that has been studied since James Cook's first voyage to New Zealand in 1769. The New Zealand region ranges from cool temperate seas at southerly latitudes to subtropical waters in the north. Here we review the history of phycological research in New Zealand since 1900, and the current status of research in taxonomy, ecology, physiology and seaweed uses including aquaculture and seaweed extracts. Some 770 species of seaweed are known to New Zealand, of which 22 are alien. Few taxa have received monographic treatment and many remain to be described. Polysaccharides have been identified from over 80 New Zealand seaweeds and many of these compounds have commercial potential. In addition to urgent taxonomic work, future research should include a national program of longterm (> 5 years) monitoring of macroalgal communities, rates of growth and primary production, and the contribution of seaweed-based production to coastal food webs.

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Key words: aquaculture, chemistry, human uses, intertidal and subtidal ecology, macroalgae, New Zealand, physiology, seaweed, taxonomy.

INTRODUCTION

The marine macroalgal flora in New Zealand is rich and diverse, with a high degree of endemism. These algae are part of globally unique coastal ecosystems ranging from cool temperate seas in the south to subtropical waters in the north. Here we assess the status of research on New Zealand seaweeds, identify gaps in our knowledge that hinder phycological progress, and make recommendations for future research. This review is split into four major sections: (i) systematics and biogeography; (ii) ecology (species assemblages and top-down processes controlling macroalgal communities); (iii) physiology and physiological ecology (environmental control or bottom up-processes); and (iv) seaweed uses including aquaculture and seaweed extracts. At the end of each major section we make recommendations for future study. We have referred mainly to published literature but recognize that there is a wealth of information in the form of unpublished theses and reports. The locations referred to in the text are indicated on Figure 1.

SYSTEMATICS AND BIOGEOGRAPHY

Historical perspective

The New Zealand macroalgal flora has received relatively little detailed taxonomic attention. Prior to Adams (1994), the only complete illustrated treatments of macroalgae from New Zealand (both the sub-antarctic islands and mainland New Zealand) were by Harvey and Hooker (1845) and Harvey (1855). An overview of the history of marine botany in New Zealand from the time of Cook's first voyage to New Zealand in 1769 is given by Adams (1994). The contributions of V. W. Lindauer were particularly significant during the mid-twentieth century (Cassie 1971; Cassie Cooper 1995). The Algae Nova-Zelandicae Exsiccatae distributed by Lindauer between 1939 and 1953 has served as a reference set of New Zealand algae in both national and international institutions, with 38 of the 350 sheets having some level of type status (Nelson & Phillips 1996).

Early collections of New Zealand algae are housed in a number of European herbaria, particularly the Agardh Herbarium in Lund, Trinity College, Dublin and the Natural History Museum, London. Locating and documenting the type material of New Zealand taxa remains an issue (e.g. Nelson *et al.* 1998; Nelson & Phillips 2001).

* To whom correspondence should be addressed. Email: catriona.hurd@botany.otago.ac.nz Communicating editor: J. West. Received 8 July 2003; accepted 3 October 2003. Fig. 1. Map of New Zealand showing locations mentioned in the text. 1, Leigh, incorporating Goat Island Marine Reserve; 2, Dunedin, incorporating Port Chalmers and Otago Harbor.



In the first of a series of flora treatments 'Marine Algae of New Zealand', Chapman (1956) treated the Myxophyceae (Cyanobacteria) and the Chlorophyceae. He recognized 92 endemic species in a flora of 161 green algae, including many new entities (species, subspecies, varieties, forms and ecads), a number of which subsequent authors have had difficulty recognizing. The underlying problems in the systematics of New Zealand green algae were highlighted by Adams (1994) in her treatment of the seaweed flora. The most speciose genera are also the ones with the most serious taxonomic problems (e.g. *Enteromorpha, Ulva, Monostroma, Cladophora, Bryopsis, Chaetomorpha*). The Phaeophyceae, published as the second part of the 'Marine Algae of New Zealand' series, served as an excellent foundation document and reference text for the brown seaweeds (Lindauer *et al.* 1961). Following the publication of Adams (1994) there have been three endemic brown algae described from the New Zealand region: *Zonaria aureomarginata* (Phillips & Nelson 1998), *Landsburgia ilicifolia* (Nelson 1999a) and *Marginariella parsonsii* (Nelson 1999b). Recently, *Giraudyopsis stellifera* was recorded from collections made at Stewart Island (Broom *et al.* 1999b): this is the first record of a macrophytic chrysophyte from the New Zealand region.

	Red	Green	Brown
Genera	210	42†	80
Species	483	134	153
Endemic genera	6	1	7
Endemic species	180	37	48
Estimated no. undescribed species	75	?	13
Alien species	11	1	10
	Antithamnionella ternifolia Champia affinis Chondria harveyana Griffithsia crassiuscula Polysiphonia brodiaei Polysiphonia constricta Polysiphonia harveyii Polysiphonia senticulosa Polysiphonia sertularioides Polysiphonia subtilissima Solieriaceae sp. indet.	Codium fragile ssp. tomentosoides	Asperococcus bullosus Chnoospora minima Colpomenia durvillaei Cutleria multifida Dictyota furcellata Hydroclathrus clathratus Punctaria latifolia Sargassum verruculosum Striaria attenuata Undaria pinnatifida

 Table 1.
 Total number of genera and species of marine macroalgae currently known in New Zealand, and the proportion of the marine macroalgal flora that are endemic and alien

[†]Numbers of genera and species for the green algae likely to be overestimated.

Chapman and coworkers published four parts in the Marine Algae of New Zealand series dealing with sections of the red algal flora (Chapman 1969; Chapman & Dromgoole 1970; Chapman & Parkinson 1974; Chapman 1979). A fifth volume was intended to be published to cover the Ceramiales. As noted by Parsons (1985a, 1985b), many of the genera covered in Chapman's treatments require extensive revision as the volumes were essentially compilations from widely scattered literature and contained little original research.

Treatments of New Zealand red algae published after Adams (1994) include work on *Porphyra* (Nelson 1993; Broom *et al.* 1999a, 2002; Nelson *et al.* 2001), *Pyrophyllon* and *Chlidophyllon* (Nelson *et al.* 2003), *Curdiea* (Nelson & Knight 1997; Nelson *et al.* 1999), *Pleurostichidium, Adamsiella* (formerly *Lenormandia*) (Phillips 2000, 2002), *Abroteia* and *Nancythalia* (Millar & Nelson 2002), *Gelidium* (Nelson & Farr 2003). Systematic studies carried out in Australia have also contributed to knowledge about New Zealand red algae (e.g. Guiry & Womersley 1993; Johansen & Womersley 1994; Womersley 1994, 1996, 1998, 2003).

Recent studies have employed not only traditional morphological and anatomical approaches to algal taxonomy, including culture techniques (e.g. Knight & Nelson 1999), but also have used molecular sequence data to develop phylogenetic hypotheses as well as to inform understanding of species boundaries (e.g. Fredericq & Ramirez 1996; Broom *et al.* 1999a; Candia *et al.* 1999; Broom *et al.* 2002). Chemotaxonomy has been useful in several taxonomic groups, such as *Curdiea* (Falshaw *et al.* 1998), *Gelidium* (Nelson *et al.* 1994) and *Gracilaria* (Wilcox *et al.* 2001).

Diversity

Table 1 summarizes the numbers of genera and species currently recognized within New Zealand, including the numbers of alien species. These figures should be used with the utmost caution: in the absence of modern systematic studies it is not clear how the current estimates of species numbers reflect the actual biodiversity of New Zealand macroalgae. In genera where research is currently underway (e.g. *Porphyra, Bangia, Gelidium*) it is clear that there are many undescribed species that require study and circumscription.

Although the Phaeophyceae are the best known group in New Zealand, there is no doubt there are more species to be discovered. In the past 15 years new species belonging to some of the largest and most conspicuous genera have been discovered and described, for example, two species of *Lessonia*, and one each of *Marginariella*, *Landsburgia and Zonaria*.

Significant features of distribution/ biogeography

Laing (1895, 1927) was the first person to attempt an analysis of the biogeography of the New Zealand seaweed flora. As a step to understanding distribution of macroalgae in the New Zealand region, over the past 30 years a series of accounts have been published, providing vouchered lists of species and summarizing available information for portions of the New Zealand region (Adams 1972; Adams *et al.* 1974; South & Adams 1976; Nelson & Adams 1984; Parsons & Fenwick 1984; Adams & Nelson 1985; Hay *et al.* 1985; Nelson & Adams 1987; Nelson *et al.* 1991; Nelson *et al.* 1992; Neale & Nelson 1998; Nelson *et al.* 2002). In a three tiered analysis of the macroalgal flora, Nelson (1994) discussed the distribution of 100 large brown algae within the New Zealand archipelago as well as examining the distribution patterns found in southern hemisphere Laminariales. The most serious limiting factor in a comprehensive analysis of the flora and its relationships is the level of systematic knowledge, a point that has been made repeatedly (Parsons 1985a, 1985b; Nelson 1994, in press a, in press b, in press c; Adams 1994).

The antiquity of the red algae, and the diversity of evolutionary histories represented among these orders and families, presents a very complex setting in which to develop hypotheses about biogeographic relationships. In addition, the poor state of knowledge and the critical lack of monographic studies of most red algal taxa in New Zealand places a severe constraint on biogeographic analyses of the flora. Hommersand (1986) hypothesized about the timing of distribution events that link the floras of the West Cape region of South Africa with Tasmania, South Australia and New Zealand. Using evidence from rbcL sequence analyses and morphological studies, Hommersand et al. (1999) considered there is support for the origin of the Gigartinaceae being in the Pacific Ocean along the eastern and southern edge of Gondwana, with a later distribution along the Pacific coast of South and North America. As a result of recent phylogenetic analyses of New Zealand Bangia, a southern origin for Porphyra and Bangia has been postulated (Broom et al. 2004). Entwisle and Huisman (1998) observed that phylogenetic hypotheses are an integral part of good systematics and cautioned that phycologists should be extremely circumspect in proposing biogeographic hypotheses.

Alien species

Of the 22 adventive species of seaweed currently recognized in New Zealand (Table 1) 11 species are red algae (Nelson 1999c; McIvor et al. 2001; Nelson et al. 2004). None of these are considered to pose a serious risk to native flora or fauna. In some cases they are locally abundant but restricted in their distribution (e.g. Chondria harveyana). Only one green marine macroalga has been reported as a naturalized alien in New Zealand waters - Codium fragile ssp. tomentosoides. The impact and risk presented by this species is far from clear (Nelson 1999c); although it has been suggested that it has become widespread in northeastern North Island (Trowbridge 1995), there are very few specimens in collections or vouchered records to substantiate its spread. The aquarium seaweed Caulerpa taxifolia has been introduced into New Zealand in the past, but was not the same strain that has been invasive in the Mediterranean, and to date it appears to be have been restricted to growth within aquaria in New Zealand (Nelson & Broom 2002).

Ten of the 22 adventive macroalgae recognized in New Zealand belong to the Phaeophyceae (Nelson 1999c; Nelson *et al.* 2004). Of these species, eight appear to pose little or no risk to the native flora, apparently not reproducing rapidly nor spreading far from their points of introduction. The impact of *Colpomenia durvillaei* is less clear. This is a seasonal species, and disappears for some months. In late winter/early spring this species has been observed to form dense populations (e.g. Mahia, East Cape, Wellington) and appears to dominate substrata in a broad intertidal band.

The Asian kelp *Undaria pinnatifida* is clearly the most serious algal pest species to have established in New Zealand. It combines a very high reproductive output with a tolerance of a wide range of growing conditions, enabling it to function as a very successful 'weed' species. From its initial introduction and recognition in Wellington Harbor in 1987, it has spread over the past 13 years to have been recorded from the Coromandel Peninsula, Gisborne, Napier, Wellington, Picton and the Marlborough Sounds, Kaikoura, Lyttelton, Timaru, Oamaru, Port Chalmers, Bluff and Stewart Island (Hay & Luckens 1987; Hay 1990a; Forrest *et al.* 2000).

Gaps in knowledge and scope for future research

There is a critical need for monographic studies of genera and families of New Zealand red algae, with serious shortfalls in virtually all families. The non-geniculate coralline algae are poorly known in New Zealand. Given the ubiquity of this group throughout low intertidal and subtidal shores and their apparent ecological significance, implicated in the settlement and development of invertebrates such as paua (*Haliotis* spp.), it is important to understand their distribution and diversity (regional and ecological).

Studies on the Gigartinaceae over recent years have resulted in amended generic concepts with many species previously placed in Gigartina being moved to the genera Chondracanthus, Sarcothalia, Mazzaella and Chondrus (Fredericq et al. 1996; Hommersand et al. 1993, 1994, 1999). These studies have included some representatives of New Zealand taxa. However, the results from this work do not yet allow the placement of all New Zealand members of the Gigartinaceae into clearly defined genera. There is an urgent need to resolve both generic and species concepts for the 23 taxa currently recognized in this family, given the diversity of the family throughout New Zealand, as well as the commercial interest in these carrageenophytes. At present the lack of systematic, biological and ecological information is a serious bottleneck to the development of the economic potential of these algae.

Research on the genera Porphyra and Bangia has uncovered unexpected diversity within the New Zealand region (Broom et al. 1999a; Farr et al. 2001, 2003; Nelson et al. 2001, 2004). Given the cultural significance of Porphyra to Maori and its use internationally as a food crop, there is a need to gain a fuller understanding of these taxa. Research is currently underway on endophytic brown algae with culture studies, ultrastructural investigations and molecular sequencing, and a number of new taxa will be recognized as a result of this work (S. Heesch, unpubl. data, 2002). The crustose brown algae in New Zealand have received very little attention, as have the morphologically simple filamentous species. It will be necessary for research on these algae to include a variety of approaches including studying the growth of species in culture. Although the Fucales are conspicuous elements of the coastal flora, there remain taxonomic problems to be addressed with a number of members of this order. The systematics of almost all green algae in New Zealand require attention. Parsons (1985b) considered that once the green algae are revised fewer species will be recognized in New Zealand, although there are also unrecorded species and new species that will require description.

Although collections have now been made throughout the New Zealand botanical region there remain areas of coastline that are largely unexplored because of access difficulties, and the seasonal coverage of collections for many of the offshore islands, including the Chatham Islands, is very poor.

ECOLOGY

Ecological studies of New Zealand seaweeds began in the early 20th century. Over the next 40–50 years a large number of descriptive intertidal studies were carried out, predominantly in the northeastern region of the North Island. These studies were largely qualitative, focusing on the relative abundance and distribution of individual species, or species assemblages. From the 1960s onwards, algal populations and communities began to be described in terms of density or percentage cover, but only later did studies involving experimental ecology appear in the literature.

Algal abundance and distribution

The locations of studies providing quantitative descriptions of algal abundance around New Zealand are given in Table 2. Qualitative studies are listed below. Generalized descriptions of the intertidal ecology of the New Zealand coastline are provided by Oliver (1923), Moore (1961) and Knox (1960, 1963). In specific localities, many authors have described the intertidal algal zonation patterns and/or estimated abundance. In the North Island, these include Northland (Bergquist 1960a), the Hauraki Gulf (Chapman 1950; Dellow 1950a; Carnahan 1952; Trevarthen 1953; Chambers 1955; Dellow 1955; Bergquist 1960b; Dromgoole 1964) and Piha (Beveridge & Chapman 1950). Studies have also been conducted at the Poor Knights Islands (Cranwell & Moore 1938), and the Coromandel Peninsula (Dellow 1950b; Turnbull 1950). In the South Island descriptions of intertidal ecology are provided for localities in Banks Peninsula (Knox 1953), Otago (Batham 1956, 1958) and Fiordland (Batham 1965).

Patterns of macroalgal distribution and abundance have also been qualitatively described in relation to wave exposure (Silvester 1963; Beever *et al.* 1971; Grace & Puch 1977; Creese & Ballantine 1986) and rock type (Silvester 1963). Generalized descriptions of algal zonation in various habitat types are provided by Ayling (1974a, 1974b, 1975a, 1975b). Brief descriptions of aspects of autecology are available for *Pterocladia lucida* and *Pterocladiella capillacea* (previously *Pterocladia*) (Moore 1944a, 1944b), *Codium* spp. (Dellow 1953), *Lessonia tholiformis* (Hay 1989), and the adventive kelp *Undaria pinnatifida* (Hay & Luckens 1987).

Descriptive studies of subtidal algae are less common, but include reports by Bergquist (1960b), Grace (1966, 1972, 1983), Grace and Grace (1976), Grace and Puch (1977) and Grace and Whitten (1974) for localities in the northeast of the North Island.

Reproductive ecology and population dynamics

The abundance and distribution of algal assemblages cannot be understood without first gaining a knowledge of the life histories and dynamics of the species involved (Schiel 1990). Spore release, spore dispersal, successful recruitment, reproduction and survival are all critical stages in the establishment and maintenance of algal populations. However, these factors, particularly spore release and dispersal, have been little quantified for New Zealand seaweeds.

Aspects of the timing and scale of fertility and recruitment are best known for members of the Phaeophyceae: *Durvillaea* sp. (Hay & South 1979), *Ecklonia radiata* (Novaczek 1984), *E. radiata, Landsburgia quercifolia, Sargassum sinclairii* and *Carpophyllum* spp. (Schiel 1988), *Xiphophora gladiata* (Gillanders & Brown 1994), *Pseudolithoderma* sp. (Williamson & Creese 1996) and *Carpophyllum flexuosum* (Cole *et al.* 2001). For the Rhodophyta, seasonal abundance has been quantified for *Porphyra 'columbina'* (Brown *et al.* 1990), and for each life-history phase of *Gracilaria chilensis* (as *G. sordida*) (Nelson 1989; Pickering *et al.* 1990). There have been no such studies for the green macroalgae in New Zealand.

Longevity, survivorship and mortality have been quantified for only four species: *Durvillaea antarctica* (Hay 1979b), *Sargassum sinclairii, Carpophyllum maschalocarpum* (Schiel 1985) and *C. flexuosum* (Cole *et al.*

 Table 2.
 A summary of studies reporting quantitative macroalgal abundance at various locations in New Zealand

Reference	Location	Species/assemblage	Measure of abundance	Factors considered
Andrew & Choat (1982) Andrew & Choat (1985) Andrew & MacDiarmid (1991)	Leigh, Northeastern NZ Leigh, Northeastern NZ Leigh, Northeastern NZ	Macroscopic browns Ecklonia radiata Ecklonia radiata Carpophyllum maschalocarpum C. angustifolium	Density/2 m ² Density/m ² Density/m ²	Time, grazing Site Site
Ayling (1981)	Leigh, Northeastern NZ	Ephemeral algae Coralline turf	% cover	Site, time, grazing
Babcock <i>et al.</i> (1999) Choat & Ayling (1987) Choat & Schiel (1982)	Northeastern NZ Northeastern NZ Three Kings Northeastern NZ (× 4) Owhiro Bay, Wellington	Ecklonia radiata Ecklonia radiata Large brown algae Ecklonia radiata Lessonia variegata Carpophyllum angustifolium C. flexuosum C. maschalocarpum C. plumosum Landsburgia quercifolia Sargassum johnsonii S. sinclairii	Density/m ² Density/m ² Density/m ²	Site, habitat, time Exposure Depth, site
Coates (1998) Cole <i>et al.</i> (2001) Davidson & Chadderton (1994)	Otago Peninsula Northeastern NZ Nelson region	S. sinclarin Sargassum sp. Combined algae Carpophyllum flexuosum Carpophyllum maschalocarpum Ecklonia radiata Coralline algae Foliose red algae	% cover Density/m ² Density/m ²	Country, exposure Site, exposure, depth Site, substrate
Gillanders & Brown (1994) Hay (1994) Hay & South (1979) Hay & Villouta (1993)	Otago Various Kaikoura, Otago Wellington, Timaru,	Other brown algae Xiphophora gladiata Durvillaea antarctica Durvillaea antarctica Undaria pinnatifida	Density/m ² Density/m ² Density/m ² Density/m ²	Time Wave force Time, clearance Site, time, depth
Hayward (1971)	Oamaru Northwestern NZ	Apophlaea sinclairii Carpophyllum maschalocarpum Microdictyon mutabile Porphyra columbina Splachnidium rugosum Xiphophora chondrophylla Encrusting calcareous	% cover	Shore height, wave action
Kotua-Dickson (1984)	Northeastern NZ	Small red algae Carpophyllum flexuosum C. maschalocarpum C. plumosum Ecklonia radiata	Density/m ² % cover	Depth, exposure, site
Menge <i>et al</i> . (1999)	South Island east coast $(\times 2)$ South Island west coast $(\times 2)$	Coralline crust Corallina officinalis Foliose reds	% cover	Coast, site, shore height
Nelson (1989)	Wellington (\times 2)	Gracilaria sordida	Density/m ²	Time, reproductive state
Novaczek (1984) Paine (1971)	Northeastern NZ Northwestern NZ	(= Cimerists) Ecklonia radiata Coralline algae Gigartina alveata Pachymenia lusoria Ralfsia verrucosa Ulva sp. Durvillaea antarctica Other algal species	Density/m ² Proportion cover	Site, depth <i>Stichaster</i> removal

Reference	Location	Species/assemblage	Measure of abundance	Factors considered
Pickering et al. (1990)	Southland	Gracilaria sordida	Density/m ²	Time, reproductive state
Raffaelli (1979)	Northeastern NZ	(= <i>chilensis</i>) Algal diversity index	Presence/absence in	Site, shore height, grazing
Saies (1973)	Otago Peninsula Northeastern NZ	Apophlaea sinclairii Carpophyllum angustifolium Codium adhaerens Gelidium pusillum Gigartina alveata Laurencia sp. Melanthalia abscissa Nemastoma oligarthra Splachnidium rugosum	% cover (kite diagrams)	Site, shore height
Saies <i>et al</i> . (1972)	Northeastern NZ	Ulva lactuca Xiphophora chondrophylla Coralline paint Apophlaea sinclairii Bostrychia sp. Carpophyllum angustifolium Lomentaria sp. Pterocladia capillacea Ulva lactuca Xiphophora chondrophylla Coralline paint	% cover (kite diagrams)	Site, shore height
Schiel (1982)	Northeastern NZ	Coralline turf Ecklonia radiata Carpophyllum angustifolium C. maschalocarpum C. plumosum Cystophora torulosa Landsburgia quercifolia	Density/m ²	Depth, echinoids
Schiel <i>et al</i> . (1986)	Kermadec Islands	Sargassum sinclairii Foliose and filamentous algae	% cover	Depth
Schiel <i>et al.</i> (1995)	Chatham Islands	Encrusting red algae Carpophyllum flexuosum C. maschalocarpum C. plumosum Landsburgia spp. Lessonia tholiformis Macrocystis pyrifera Xiphophora gladiata Laminarians Fucaleans	% cover Density/m ²	Site, depth
Schiel & Hickford (2001)	Kaikoura	Understorey algae Carpophyllum maschalocarpum	% cover	Site, coast, depth
	Banks Peninsula Fiordland	Caulerpa brownii Ecklonia radiata Landsburgia quercifolia Lessonia variegata Macrocystis pyrifera Marginariella spp. Sargassum sinclairii Coralline flat Mixed algae Algal groups Xiphophora gladiata Cystophora congesta Carpophyllum flexuosum Lessonia sp. Ecklonia radiata	Density/m ² % cover Density/m ²	Site, depth

Table 2. Continued

Reference	Location	Species/assemblage	Measure of abundance	Factors considered
Schiel & Hickford (2001)	Chatham Islands	Carpophyllum flexuosum C. maschalocarpum C. plumosum Landsburgia spp. Lessonia tholiformis Macrocystis pyrifera Xiphophora gladiata Fucaleans Laminarians	% cover Density/m²	Site, depth
Schiel & Taylor (1999)	Kaikoura coast (× 2)	Hormosira banksii Coralline turf Encrusting corallines Other algae	% cover	Site, season, trampling
Shears & Babcock (2002)	Northeastern NZ	Coralline turf Crustose corallines <i>Carpophyllum flexuosum</i> <i>Ecklonia radiata</i> <i>Halopteris virgata</i> Small seasonal brown algae	% cover	Site, time, urchin removal
Shears & Babcock (2003)	Northeastern NZ	Ecklonia radiata	Density/m ²	Depth, time
		<i>Carpophyllum</i> spp. Turfing algae Mixed algae Kelp forest	% cover	Reserve status, time
South & Hay (1979)	Auckland Kaikoura (× 3) Westland Otago Stewart island	Durvillaea antarctica	Density/m ²	Site, wave action
Starling (1968) Staveley Parker (1976)	Northeastern NZ Northeastern NZ	Various Apophlaea sinclairii Carpophyllum angustifolium Hormosira banksii Melanthalia abscissa Splachnidium rugosum Ulva lactuca Xiphophora chondrophylla Coralline paint Coralline turf	% cover (scale only) % cover/no. individuals (kite diagrams)	Site Site, shore height
Trowbridge (1995)	Northeastern NZ	Corallina Hormosira banksii	% cover	-
Williamson & Creese (1996)	Northeastern NZ	Pseudolithoderma sp.	% cover	Site, substrate, colonization

2001). In northeastern New Zealand mass mortality within *Ecklonia radiata* populations has been documented on several occasions (e.g. Cole & Babcock 1996). Viral pathogens (Easton *et al.* 1997) and amphipod grazing (Haggitt & Babcock 2003) have been implicated in these dieback events.

Population and community ecology

Algal habitats for marine invertebrates and fish Macroalgae play an important role in structuring the marine environment for other organisms and influence these organisms at various stages of their lifecycles. The larvae of the common New Zealand sea urchin (*Evechinus chloroticus*) settle on coralline algae in preference to other substrata such as oyster shells, rock or plastic (Lamare & Barker 2001) and their survival rates are greater on coralline flats than in deep (> 15 m) reefs or dense *Ecklonia radiata* beds occurring between 8 and 12 m (Andrew & Choat 1985). Larvae of the green-shell mussel *Perna canaliculus* also settle on macroalgae in preference to rock, and settle in higher numbers on algae with filamentous and branched morphologies (e.g. species of *Champia, Gigartina, Laurencia* and *Corallina*) than on broad-bladed species such as *Ulva, Durvillaea, Pachymenia* and *Aeodes* (Paine 1971).

Experimental work involving the addition and removal of macroalgae indicates that recruitment of juveniles of the carnivorous temperate reef fish *Noto-labrus celidotus* (as *Pseudolabrus celidotus*) in north-eastern New Zealand (Leigh) is greatly enhanced in the presence of macroalgae (predominantly *Ecklonia radiata* and *Carpophyllum* spp.) (Jones 1984). Furthermore, juvenile and adult *N. celidotus* are more abundant in dense compared to sparse macroalgal beds (Choat & Ayling 1987).

The presence or absence of macroalgae influences where adult fish live on temperate reefs and in what numbers (see Jones 1988 for a review on the ecology of rocky reef fish in northeastern New Zealand). Herbivorous fish abundance is generally greater in fucalean and laminarian-dominated shallows (0-5 m depth), than in either coralline flats (5–10 m depth) or kelp (Ecklonia radiata) forests at >10 m depth (Jones 1988; Meekan & Choat 1997; Cole 2001). Macroalgae also influence the composition of fish assemblages. In areas of northern New Zealand that are dominated by large brown algae, small algalpicking and plankton-feeding fish dominate with fewer large benthic-feeding fish present. On coralline flats the situation is reversed, with large benthicfeeding fish being more prevalent (Choat & Ayling 1987). Furthermore, a negative correlation has been found between algal density and numbers of large (> 150 mm) carnivorous reef fish in contrast to the positive correlation observed for the smaller Notolabrus celidotus (Choat & Ayling 1987).

Attached macroalgae and off-shore drift algae are also habitats for animals. The composition and size of mobile epifauna vary among species of attached seaweed (Taylor 1998a) and are influenced by algal morphology (Taylor & Cole 1994). Seaweed density may also influence the dispersal of epifauna (Taylor 1998b). Offshore, drift algae provide habitat to fish and invertebrates, both of which are more abundant around drift algae than in adjacent open water (Kingsford & Choat 1985; Kingsford 1992). It is postulated that drift algae are an important means of movement for presettlement fish, and may therefore influence recruitment of fish that inhabit nearshore areas as adults (Kingsford 1992).

Algae-algae interactions

The role of interspecific interactions in the maintenance and establishment of algal communities has received little attention in New Zealand. The exceptions are experiments in which the canopies of *Ecklonia radiata*, *Carpophyllum maschalocarpum* and *C. angustifolium* were removed, and the subsequent recruitment of these three species and of *Landsburgia quercifolia* were recorded (summarized by Schiel 1988, 1990). The species, level and order of succession varied according to the frequency and season of removal, but in most cases recruitment was substantially greater in cleared areas than under intact canopies (Schiel 1988). There have been only two studies on intraspecific competition between New Zealand seaweeds: *Ecklonia radiata, Sargassum sinclairii* and *Carpophyllum maschalocarpum* (Schiel & Choat 1980; Schiel 1985). Schiel and Choat (1980) were the first to suggest that seaweed populations do not follow the –3/2 self-thinning law that applies to terrestrial plants, although this finding is not the case for all seaweed communities (e.g. Cousens & Hutchings 1983; Scrosati & Servière-Zaragoza 2000, and references therein).

Algae–echinoid interactions

The distribution and abundance of the New Zealand sea urchin (Evechinus chloroticus, Maori name, kina) in relation to stands of large brown algae has been well documented, particularly in northern New Zealand (see review in Andrew 1988). In this region there is a characteristic subtidal pattern with fucalean species of Carpophyllum, Sargassum and Landsburgia forming dense stands in the shallow subtidal (approximately 0-7 m) and coralline flats at ~8 m and below (e.g. Ayling 1981; Choat & Schiel 1982; Schiel 1982; Andrew 1988; Schiel 1990). Coralline flats are E. chloroticusdominated areas with up to 100% cover of encrusting or turfing coralline algae. These areas are generally free of large brown algae, giving rise to the inappropriate terms 'barrens' or 'barren grounds' (see Choat & Schiel 1982; Schiel & Foster 1986). Below 10 m where E. chloroticus densities are lower, large stands of laminarian algae occur, principally Ecklonia radiata. This kelp often exhibits a bimodal distribution, occurring in higher densities in the 0-7 m zone and below 8-10 m, with mixed laminarian/fucalean stands at ~3-6 m (Choat & Schiel 1982).

The role of sea urchin species in maintaining coralline flats is well documented. In northeastern New Zealand experimental removal or exclusions of adult Evechinus chloroticus from coralline flats resulted in increased densities of large brown algae (Ecklonia radiata, Sargassum sinclairii and species of Carpophyl*lum*) (Andrew & Choat 1982; Andrew & MacDiarmid 1991; Shears & Babcock 2002), of ephemeral and coralline turf algae (Ayling 1981; Shears & Babcock 2002), and of small brown and red algae of the genera Halopteris, Dictyota, Colpomenia, Asparagopsis and Champia (Shears & Babcock 2002). In Fiordland, two years of *E. chloroticus* removal in a range of habitats and depths led to significant increases in the density of kelps, crustose, turfing and herbaceous algae (Villouta et al. 2001). There is some debate regarding the role of urchin dietary preferences in determining the persistence of algal species at local scales (Schiel 1982; Schiel 1990; Cole & Haggitt 2001).

In regions of New Zealand close to, or south of, Cook Strait the above-mentioned subtidal pattern is not characteristic (Schiel 1990). At Owhiro Bay in Wellington, for example, Evechinus chloroticus are not common and the 5-10 m depth range, instead of being dominated by corallines, contains mixed stands of laminarian and fucalean algae (Choat & Schiel 1982). At Kaikoura, Banks Peninsula, the Chatham Islands and Fiordland, extensive coralline flats are not characteristic but corallines do occur in small (< 25 m²) patches (Schiel et al. 1995; Schiel & Hickford 2001), or in larger areas in localized parts of Fiordland (e.g. Villouta et al. 2001). In those areas where coralline flats are not common, Schiel and Hickford (2001) suggest that interactions between algae become more important in the regulation of community structure; however, predation by E. chloroticus may also be important (see earlier section).

Parallels have been drawn between the trophic cascades in the Northern hemisphere and the New Zealand situation (see Andrew 1988; Babcock et al. 1999, and authors therein). In the Northern Hemisphere subtidal community structures are controlled by a three-tiered trophic cascade in which the sea urchin populations that control macroalgal communities are themselves controlled by carnivores such as sea otters (northwest Pacific), lobsters (north Atlantic) or fish (Mediterranean) (see Schiel 1990). In New Zealand, predation by fish has not been considered to exert sufficient pressure to control the impact of urchin grazing on macroalgae, and a simpler two-tiered trophic cascade between Evechinus chloroticus and macroalgae has been suggested (Andrew 1988; Schiel 1990; Babcock et al. 1999, and authors therein). However, more recent studies in northeastern New Zealand comparing animal and macroalgal communities within no-take marine reserves and adjacent non-reserved areas provide indications of a three-tiered cascade between predatory fish (predominantly Pagrus auratus) and spiny lobsters (Jasus edwardsii), sea urchins and macroalgae (Cole & Keuskamp 1998; Babcock et al. 1999; Shears & Babcock 2002, 2003). Furthermore, macroalgal abundance within the marine reserves has increased as a consequence of increased predation on urchins (Shears & Babcock 2003). This finding indicates that over-fishing of predatory fish has resulted in a simpler ecosystem structure.

Algae–mollusc interactions

The distribution and abundance of macroalgae and various molluscan grazers has been quantified for various parts of the country. These include areas around Dunedin (Raffaelli 1979), three tidal zones at sites on the east and west coasts of the South Island (Menge *et al.* 1999), areas of the Chatham Islands (Schiel *et al.* 1995; Schiel & Hickford 2001), Abel Tasman (Davidson & Chadderton 1994), Kaikoura, Banks Peninsula, Fiordland (Schiel & Hickford 2001)

and one site in Wellington (Choat & Schiel 1982). In northern and northeastern New Zealand the density of various gastropods and large brown algae have also been quantified in a number of studies (Ayling 1981; Andrew & Choat 1982, 1985; Choat & Schiel 1982; Choat & Andrew 1986; Creese 1988; Andrew & Mac-Diarmid 1991).

Interactions between molluscan grazers and macroalgae have been reviewed by Creese (1988). Molluscan grazing appears to exert a lesser influence on subtidal community structure than urchin grazing, but is still an important process affecting smaller macroalgal species. Molluscan grazers suppress algal growth (Watts 1977 in Creese 1988; Ayling 1981; Menge et al. 1999), limit the upper distributions of some algal species (Hay 1979a; Edwards 1982 in Creese 1988), and their feeding methods and preferences influence algal community structure (e.g. Luckens 1974; Raffaelli 1979; Choat & Andrew 1986). There is evidence that urchins and gastropods can benefit from coexistence (Andrew & Choat 1982; Choat & Andrew 1986), and that their co-occurrence enhances their effect on coralline flats (Ayling 1981; Choat & Andrew 1986). In intertidal situations the strength of grazer impacts on macroalgae is significantly influenced by their level on the shore (Raffaelli 1979).

Algae-herbivorous fish interactions

Nutritional ecologists determine why fish choose particular algae as food by examining relationships among the algal diet, feeding structures and digestive physiology of fish (Choat & Clements 1998). In New Zealand, work has focused on the determination of fish diets (Russell 1983), feeding rates (Choat & Clements 1993) and the nutritional quality of the seaweed eaten by marine herbivorous fishes, not only by measurements of gross algal components such as protein and energy (e.g. Lamare & Wing 2001), but also by the interplay between the components of the algae and the ability of the fish to access, digest and assimilate these algal components (Zemke-White & Clements 1999; Zemke-White *et al.* 1999b, 2000, 2002; Moran & Clements 2002).

Human impacts

Studies on the impact of humans on macroalgae in New Zealand have been limited to the effects of marine reserve protection, trampling by humans and harvesting. In 1975, New Zealand was among the first countries in the world to establish a marine reserve. In this no-take reserve at Goat Island, Leigh, where predatory fish and the spiny lobster *Jasus edwardsii* are not removed from ecosystems, algal abundances have increased as a consequence of increased predation on echinoid grazers (see above; Babcock *et al.* 1999; Shears & Babcock 2002, 2003). Intertidal beds of *Hormosira banksii* are sensitive to trampling by humans and canopy recovery time is dependent on the season in which trampling occurred (Schiel & Taylor 1999). Intertidal coralline turfs are less sensitive to trampling, but turf height and turf dry weight declines with higher levels of trampling intensity (Brown & Taylor 1999).

Macroalgae are not intensively harvested in New Zealand (see Seaweed uses below). While a number of studies have assessed the impact of harvest methods and timing from natural populations on subsequent harvest yield (Hay & South 1979; Nelson & Conroy 1989; Nelson et al. 1990; Schiel & Nelson 1990, and others therein; Gerring et al. 2001) few have considered the effects of harvesting on surrounding communities, nor have the effects of large-scale removal of beach cast algae been assessed. Porphyra harvest is considered to have negligible ecological impacts due to the high shore position of this group (Schiel & Nelson 1990). Complete removal of the dominant mid/low intertidal Durvillaea antarctica is likely to promote significant changes in community structure (see Paine 1971), more so if harvesting was carried out during summer when D. antarctica does not produce gametes for recolonization (Hay & South 1979; Schiel & Nelson 1990; Hay 1994). The importance of Ecklonia radiata to marine communities is well documented and the phenology of this species indicates that the ecological consequences of harvesting could be significant (Schiel 1988; Schiel & Nelson 1990, and authors therein). The ecological impacts of harvesting other macroalgae of economic potential (e.g. Macrocystis, Pterocladia, Gracilaria, Gigartina and Undaria) are little known. Gerring et al. (2001) report that removal of Pterocladia lucida had no significant effect, at the scale they tested, on the abundance of large brown algae or large grazers.

Gaps in knowledge and scope for future research

There are two clear biases in the ecological work on New Zealand macroalgae published to date. The first is geographic with a large majority of the descriptive and experimental ecological work being on macroalgae from northeastern New Zealand. This bias is due to the strong ecological focus of researchers at the University of Auckland's Leigh Marine Laboratory over the past 50 years and is currently being addressed on the East Coast of the South Island by the University of Canterbury's Marine Ecology Research Group (e.g. Schiel & Hickford 2001), and in Fiordland by the Department of Marine Sciences, University of Otago.

The second bias is taxonomic; the majority of work published to date assesses the role of laminarian and fucalean algae in structuring nearshore communities, with far fewer studies investigating the ecology of red seaweeds, and virtually none examining green seaweeds. This bias is partially due to identification issues, with large brown seaweeds being easier to find and to identify. There are many identification and taxonomic problems with New Zealand red and green seaweeds; these are therefore less likely to be chosen as study subjects.

There have been no true demographic studies on New Zealand seaweeds (sensu Lobban & Harrison 1994) and there are relatively few phenological studies. Seasonal studies of intertidal or subtidal communities are lacking, with many studies being snapshots in time. It has recently been noted that the density of Sargassum johnsonii and Ecklonia radiata at the Three Kings Islands has varied substantially over the past 30 years (Zemke-White & Clements, unpubl. data, 2003). In 1979 and 2002, E. radiata was absent but this species was dominant in 1993; a similar trend was observed for S. johnsonii. These decadal changes in macroalgal populations are thought to be related to El Niño events, and they strongly influence the diet of the herbivorous fish Odax cyanoallix. This finding highlights the importance of long-term monitoring of macroalgal communities.

PHYSIOLOGICAL ECOLOGY AND PHYSIOLOGY

Marine macroalgae contribute around 35% of coastal primary production worldwide (Charpy-Roubaud & Sournia 1990). In temperate waters, the seasonal patterns of subtidal seaweed growth, and hence production, is either controlled directly, or modulated, by light and seawater nitrogen concentrations (Kain 1989). Environmental factors such as salinity and water motion influence subtidal seaweed production on a local scale. For intertidal seaweeds, stresses resulting from fluctuating temperature, salinity, light, UV and nutrient availability also affect growth and production rates. Seasonal patterns of growth rate have been studied for only a few New Zealand taxa: Porphyra 'columbina' (Brown et al. 1990), Gracilaria chilensis (Pickering et al. 1990), Macrocystis pyrifera (Kain 1982; de Nys et al. 1990, 1991; Nyman et al. 1990; Nyman et al. 1993; Brown et al. 1997), Undaria pinnatifida (Stuart et al. 1999; Dean & Hurd pers. obs. 2003) and Durvillaea spp. (Hay 1994 and references therein).

Growth rates

Growth, erosion and production rates of seaweeds measured in conjunction with their carbon, nitrogen and phosphorus content allow estimation of their contribution to the coastal food webs and to nutrient recycling. New Zealand research has focused on two members of the Order Laminariales, *Macrocystis pyrifera* and

Species	Reference	Location	%C	%N	C:N
Intertidal					
Scytothamnus australis	Phillips & Hurd (2003)	Otago	32–37	1.2-1.8	22–30
Xiphophora gladiata	Phillips & Hurd (2003),	Otago	30–36	1.2-2.2	18–28
	Gillanders & Brown (1994)	-			
Stictosiphonia arbuscula	Phillips & Hurd (2003)	Otago	27–35	2.8–5	8–15
Apophlaea Iyallii	Phillips & Hurd (2003)	Otago	35–40	2–2.8	17–23
Porphyra 'columbina'	Brown <i>et al.</i> (1990)	Stewart Island and Otago	28–33	1–5	7.4-71
Subtidal		_			
Undaria pinnatifida	Dean & Hurd (pers. obs. 2003)	Otago Harbor	19–35	1.5-2.9	12–23
Macrocystis pyrifera	Brown <i>et al</i> . (1997)	Otago Harbor, Otago	22–31	0.9–3.0	9.5–38 : 1

Each study followed %C, %N on a seasonal basis. The ranges are maximum and minimum of average values.

Undaria pinnatifida, both from Otago Harbor, Dunedin. Growth and primary production rates of these populations are within the ranges of those reported for these species in other geographic regions (e.g. Wheeler & Srivastava 1984; Yoshikawa et al. 2001). Undaria pinnatifida in Otago Harbor exhibits a seasonal growth cycle of a winter annual (Dean & Hurd pers. obs. 2003) with maximum growth rates during winter, which decline in spring with the onset of sporophyll formation (Dean & Hurd pers. obs. 2003). For M. pyrifera the seasonal pattern of blade relative growth rate (RGR) in Otago Harbor varies between years. Blade RGR during 1986–1987 were similar year-round except for summer when lower rates were recorded, leading Brown et al. (1997) to conclude that this pattern represented Nlimited growth similar to that of *M. pyrifera* in California. However, our ongoing work on a nearby M. pyrifera population indicates that between 1998 and 2000, blade RGR was light-limited during winter and Nlimited from mid-summer, a pattern consistent with M. pyrifera from British Columbia, Canada (Wheeler & Srivastava 1984) and the Falkland Islands (van Tussenbroeck 1989). The high intra-annual variation seen in growth rates of *M. pyrifera* illustrate the importance of long-term (> 1 year) monitoring to gain a thorough understanding of seasonal patterns.

Durvillaea spp. are ecologically dominant in the intertidal and shallow subtidal of the South Island and west coast of the North Island (Hay 1979b; Hay 1994). Standing stocks of *Durvillaea* at >100 kg/m² are higher than any other intertidal seaweed community (Hay 1994) and, although not measured directly, this genus must make a very important contribution to the coastal food chain and nutrient recycling.

Patterns of growth and reproduction, population density and chemical composition of *Porphyra* 'columbina' gametophytes, and the factors controlling sporophyte growth, have been investigated (Brown 1987; Frazer *et al.* 1988; Friedlander *et al.* 1989; Brown *et al.* 1990; Aitken *et al.* 1991; Frazer & Brown 1995). Unfortunately, our improved understanding of the taxonomic status of *Porphyra* means that the *Porphyra* collected for these studies could be one of more than

seven species that occur on southern coasts. Furthermore, '*Porphyra subtumens*' studied by Friedlander *et al.* 1989) and Aitken *et al.* (1991) has been moved from the order Bangiales and placed in a new genus in the Erythropeltidales, *Pyrophyllon subtumens* (Nelson *et al.* 2003).

Relative growth rates of *Gracilaria chilensis* (as *G. sordida*) at Mokomoko Inlet, Bluff, varied between sites and for the different strains used. Overall, RGR ranged from -7 (i.e. tissue loss) to +5% day⁻¹, rates that were considered typical of *Gracilaria* species (Pickering *et al.* 1990).

Nitrogen status and acquisition

Nitrogen is considered the nutrient most likely to limit seaweed growth in temperate coastal waters worldwide and is the best studied aspect of New Zealand seaweed physiological ecology. Inorganic nitrogen in New Zealand coastal surface waters varies seasonally and this variation is due to changes in nitrate rather than ammonium, which remains relatively constant year round (0.5-2 µmol/L, Gillanders & Brown 1994; Brown et al. 1997; Rees et al. unpubl. data 2003). Nitrate in New Zealand nearshore waters exhibits the typical pattern of temperate coastal waters with concentrations being maximal in winter (5-12 µmol/L) and minimal in summer (0.3–0.5 μ mol/L) (Hay 1990b; Brown et al. 1990, 1997; Gillanders & Brown 1994; Phillips & Hurd 2003). In Otago, this seasonal pattern of inorganic nitrogen in seawater is generally reflected in the total tissue nitrogen content of seaweeds, which are typically minimal during summer/early autumn and maximal during winter (Table 3). Seasonal patterns of nitrogen-limited growth can be implied from the ratio of tissue carbon (C) and nitrogen (N) (C:N), with higher ratios indicating greater N-limitation. For the Order Laminariales, 10-15 indicates N-sufficiency, 16-20 indicates mild N-limitation while values >25 indicate severe N-limitation (Sjøtun et al. 1996). For Undaria pinnatifida and Macrocystis pyrifera from Otago Harbor, the maximum C:N ratio is rarely >20, indicating only mild N-limitation in summer (Table 3).

The potential for nitrogen limitation for intertidal seaweeds is considered greater than for subtidal seaweeds because seaweeds are removed from their nitrogen source during low tide (e.g. Lobban & Harrison 1994; Phillips & Hurd 2003). Furthermore, species growing higher up the intertidal zone are usually considered more nutrient-limited than low-shore species. Consistent with the latter hypothesis, high shore populations of Porphyra had greater C:N ratios than low shore populations (Brown et al. 1990), although the extremely high C:N ratios reported in this case of >70 are probably indicative of a senescing population rather than severe nitrogen limitation. In contrast, high and low shore populations of Stictosiphonia arbuscula, which grows at the same high shore position as Porphyra sp., had similar C:N ratios of 7-15 and showed little evidence of nitrogen-limited growth year round (Phillips & Hurd 2003). For four species of intertidal seaweed (Stictosiphonia arbuscula, Apophlaea Iyallii, Scytothamnus australis and Xiphophora gladiata) nitrogen content was correlated with height above low water, a trend that is opposite to Northern hemisphere intertidal communities (Phillips & Hurd 2003).

The source of nitrogen available to intertidal seaweeds varies seasonally, with the inorganic source ammonium being the preferred in winter, while nitrate and ammonium are both equally important during summer. The contribution of the organic nitrogen source, urea, is negligible during winter but provides up to 33% of nitrogen to intertidal seaweeds during summer (Phillips & Hurd 2003). Rates of ammonium uptake by northeastern New Zealand seaweeds are lower than Northern Hemisphere seaweeds, for example, >3 times lower than seaweeds from the Baltic (Taylor et al. 1998; Taylor & Rees 1999). Ammonium is not considered an important nitrogen storage pool because it may be toxic at high concentrations, but for intertidal seaweeds from Otago, ammonium pools were up to three-fold greater than those of nitrate (Phillips & Hurd 2003). Ammonium excreted by sessile or mobile marine invertebrates contributes an important Nsource to intertidal (Williamson & Rees 1994) and subtidal (Taylor & Rees 1998) seaweeds and mobile epifauna might contribute up to 79% of the nitrogen budget of the subtidal fucalean seaweed, Carpohyllum plumosum.

The direct effect of nitrogen on seaweed growth rate has been investigated for only one species, *Gracilaria chilensis*, for which growth rates increased with increased nitrogen flux (Pickering *et al.* 1993). In areas where nitrogen is not limiting (due to nitrogen inputs from farming, land run-off and sewage), phosphate is the nutrient that most likely becomes limiting to seaweeds (e.g. Lobban & Harrison 1994). There are no published studies on phosphate uptake by New Zealand seaweeds.

Light, salinity and temperature

The few studies on the photosynthetic physiology of New Zealand seaweeds indicate that rates are within the ranges of Northern hemisphere seaweeds (Taylor et al. 1999). Rates of photosynthesis under saturating light have been determined for Cystophora torulosa, Xiphophora chondrophylla, Melanthalia abscissa, Osmundaria colensoi, Pterocladia capillacea, Zonaria turneriana, Corallina officinalis, Ulva sp. and Enteromorphra sp. (Taylor et al. 1999). Photosynthesis versus irradiance curves have been determined for only the adventive seaweed Undaria pinnatifida (Dean & Hurd pers. obs. 2003). The influences of pH and inorganic carbon concentration on photosynthesis have been examined for Carpophyllum maschalocarpum and C. flexuosum (Dromgoole 1978a), the effect of oxygen concentration on photosynthesis was tested for four Carpophyllum species, Sargassum sinclarii, E. radiata, Scytothamnus australis and Codium fragile (Dromgoole 1978b), and photosynthesis under fluctuating light was determined for Carpophyllum maschalocarpum, E. radiata and Hormosira banksii (Dromgoole 1987, 1988). Neither the effects of salinity nor temperature on physiology, growth or production rates of New Zealand seaweeds have been examined.

Water motion

Wave-swept shores are typical of much of New Zealand's coastline and research has focused on how seaweeds are adapted to withstand the large forces associated with breaking waves. Durvillaea spp. grow an order of magnitude larger than any other seaweed inhabiting wave-exposed intertidal sites and can withstand wave forces of 300 N (Stevens et al. 2002). Biomechanical testing has demonstrated that Durvillaea stipes are extremely elastic and extensible compared to other seaweeds (Harder et al. 2000). The forces imparted by breaking waves may be shared by populations of *D. antarctica*, thereby reducing the loading on individuals (Stevens et al. 2004). Zygotes of D. antarctica attach to the rock substratum more rapidly than those of Hormosira banksii and Cystophora torulosa, and greater wave-forces are required to dislodge D. antarctica zygotes (Taylor & Schiel 2003).

In some wave-sheltered, current-dominated estuaries that have become nutrient enriched, drift populations of *Ulva lactuca* can reach nuisance levels. Hawes and Smith (1995) estimated that currents of 0.4–1.2 m s⁻¹ were sufficient to impart the breaking force of 0.7–0.93 N required to detach *U. lactuca*.

Stress physiology

The abilities of intertidal seaweeds to withstand the stresses associated with emersion is related to their

vertical position on the shore. Dromgoole (1980) was among the first internationally to demonstrate that evaporation rates of water from seaweeds in air were not related to their shore position and thus most intertidal seaweeds have physiological rather than morphological mechanisms to tolerate the severe stress imposed by their environment. The ability of New Zealand seaweeds to recover metabolic processes following desiccation and freezing increases with increasing shore height (Brown 1987; Frazer *et al.* 1988), a pattern typical of intertidal seaweeds from temperate regions worldwide. The rate of regeneration of antioxidant pools is a key mechanism of stress tolerance of the high intertidal seaweed *Stictosiphonia arbuscula* (Burritt *et al.* 2002).

Gaps in knowledge and scope for future research

There are no published studies on production rates of New Zealand seaweeds or macroalgal communities and thus we know little of their contribution to coastal food webs or nutrient cycling. The six species for which there are estimates of growth (Macrocystis pyrifera, Undaria pinnatifida, Durvillaea antarctica, Gracilaria chilensis and Porphyra 'columbina') were examined largely because of their commercial potential rather than ecological function. If we are to understand the contribution of macroalgae to coastal primary production in New Zealand, ecologically dominant members of the Order Fucales and the Rhodophyta should be targeted and techniques for estimating their growth and/or production rates in situ developed. For example, an underwater metabolism chamber could be used to measure photosynthetic and production rates of individual seaweeds or communities, and determine the effects of nutrient additions on production (Longstaff et al. 2002). Finally, to further understand the functioning of coastal ecosystems, the fate of seaweed production should be traced through the coastal food webs. This can be achieved using carbon and nitrogen stable isotopes (e.g. Herman et al. 2000; Kaehler et al. 2000).

SEAWEED USES

The major uses of seaweeds throughout the world are both direct (e.g. as human foods, animal fodder or as fertilizer) and indirect (as raw materials from which certain components can be extracted) (Chapman 1970). The outbreak of World War II and the requirement to find local supplies of seaweeds for various uses fuelled the work of L. B. Moore at Botany Division, Department of Scientific and Industrial Research (D.S.I.R). She focused particularly on the agar-bearing genera *Pterocladia* and *Gelidium*, and the kelp *Macrocystis*, as well as being involved in a

supplements and cosmetics. In the absence of substantial scientific data, the Ministry of Fisheries has taken a conservative approach to wild harvesting of seaweeds and since 1971, fishing permits have been required for the removal of attached seaweeds from specified areas (Luxton & Courtney 1987). This approach was extended by the introduction of a moratorium on the issue of new permits in 1988 (Zemke-White et al. 1999a). The moratorium on the collection of attached seaweeds remains in place with the enactment of the 1996 Fisheries Act. In addition, a permit is now also required for the collection of unattached, free-floating (but not beach-cast) red seaweeds. Only beach-cast red seaweed can be taken for commercial purposes without a fishing permit, as a result of the long-established, and continuing, use of red seaweeds for the production of agar.

ucts from New Zealand seaweeds, such as dietary

Direct uses

In New Zealand, Maori consume species of *Porphyra* (karengo), *Gigartina* (rehia) and *Durvillaea* (known most commonly as rimurapa) (Riley 1988), and Crowe (1997) has described 15 species of New Zealand seaweeds as edible. Considerable research was undertaken in the 1990s into the aquaculture of the adventive Japanese brown seaweed, *Undaria pinnatifida* (known as wakame), for food use (Zemke-White *et al.* 1999a). Although results of seeding and field trails were positive, this research has not progressed further due to concerns over the spread of an invasive, foreign species when its impact on the native New Zealand flora is not known.

Sheep in New Zealand have been reported to graze *Cystophora, Sargassum* and *Hormosira* and chopped seaweed has been used as a supplemental cattle feed (Chapman 1970).

Indirect uses

Fertilizer extracts

Various New Zealand and overseas companies produce concentrated seaweed extracts for use as fertilizers, and some use New Zealand seaweed raw materials. However, a number of seaweed-based products have been shown to be ineffective by New Zealand scientists (Feyter *et al.* 1989).

Small organic molecules

A number of low molecular weight natural products have been extracted from New Zealand seaweeds. Four natural products, including a novel hydroazulenoid ditepene, have been found in Glossophora kunthii (de Nys et al. 1993). A crude methanol extract from Rhodophyllis membranacea was found to have antifungal activity, which was linked to the presence of several polyhalogenated indoles in the extract (Brennan & Erickson 1978). A wide range of natural products has been extracted from both Laurencia thyrsifera (Blunt et al. 1978a, 1981, 1984a) and Laurencia sp. cf. L. gracilis (König & Wright 1994). Distinctly different compounds have been found in morphologically similar samples of Laurencia distichophylla from Northland (Blunt et al. 1984b) and Plocamium cartilagineum from Kaikoura (Blunt et al. 1978b, 1985; Bates et al. 1979). These results may have taxonomic significance. Glombitza and coworkers have isolated numerous natural products from a range of New Zealand seaweeds, including Cystophora retroflexa and Carpophyllum angustifolium (e.g. Sailler & Glombitza 1999; Glombitza & Schmidt 1999). Knöss and Glombitza (1993) also isolated phenolsulfatase activity in four of six New Zealand seaweeds screened. The amino acid, gigartinine, has been shown to serve as a chemotaxonomic marker to distinguish two species of Gracilaria with very similar morphologies (Wilcox et al. 2001).

Polysaccharides

Agar production (mainly from Pterocladia lucida but also Pterocladiella capillacea) started during the Second World War when supplies of Japanese agar ceased (Moore 1944a, 1944b). Agar produced from attached plants is generally of higher and more uniform quality than that from beach-cast material and, in 1983, 31% of the seaweed used for agar production was from attached plants (collected under permit by divers using snorkels) (Luxton & Courtney 1987). By 2001, the proportion of attached seaweed used had declined to 15%. Various harvesting strategies for attached P. lucida have been assessed on a small scale by Gerring et al. (2001). This study concluded that harvesting of attached plants from this species could be sustainable, if managed proactively, but that further research on a larger scale was required. Tissue and cell culture of Pterocladia lucida and Pterocladiella capillacea have also been attempted (Liu & Gordon 1987). The structure of commercial Pterocladia agar has been studied by Brasch et al. (1981a, 1984a) and enhanced growth of macroalgal cells on commercial Pterocladia agar has been reported (Polne-Fuller et al. 1993).

Gracilaria chilensis is another red seaweed growing in New Zealand that has commercial potential for agar production. The effects of various conditions on the growth and agar content of this species (as *G. sordida*) have been investigated in culture (Christeller & Laing 1989; Laing *et al.* 1989; Pickering *et al.* 1993) and in the wild (Pickering *et al.* 1990). Recently, the biosynthesis of agar polysaccharides in *Gracilaria chilensis* have been studied extensively (Hemmingson *et al.* 1996a, 1996b; Hemmingson & Furneaux 1997, 2001).

Carrageenans are another group of industrially useful polysaccharides that are obtained from certain red algae. Prior to 1939, the major commercial use of New Zealand seaweed was the production of seameal custard using carrageenan from Gigartina species (Miller 1999). Both the gelling and non-gelling carrageenan contents of various New Zealand Gigartina species have been studied (Pickmere et al. 1973, 1975; Parsons et al. 1977). Recently, the commercial potential of the carrageenans from Gigartina atropurpurea has been assessed in two dairy applications (Falshaw et al. 2003). Small-scale field trials have indicated the potential of this species for aquaculture or sustainable wild harvest for carrageenan production (McNeill et al. 2003) but more research work is required to confirm this.

The other major seaweed polysaccharide currently used industrially is alginate, obtained from certain brown algae. Moore (1942b) speculated that Macrocystis pyrifera harvested for fertilizer (Rapson et al. 1942) could also be used for production of alginate. More recently, the alginate content of various New Zealand brown algae has been determined. An alginate content of 20–35% for *M. pyrifera* is within the range of other brown algae (McKee et al. 1992) while at 40-60%, Durvillaea spp. have the highest alginate content of any seaweed (Hay & South 1979; South 1979; South & Hay 1979; Kelly & Brown 2000). Hay (1979b) investigated the ecology of Durvillaea spp. and proposed a commercial harvesting strategy. The effect of harvesting and the historical exploitation of Durvillaea spp. for alginate production have also been reviewed by Hay (1994).

Considerable research effort has been directed at determining the potentially novel structures of polysaccharides from the many macroalgae found in New Zealand. The types of polysaccharide characterized to date are shown in Table 4 (see individual references for specific structural details). The determination of polysaccharide structures has led to the development of new analytical techniques, such as formolysis (Brasch et al. 1984b), reductive hydrolysis (Stevenson & Furneaux 1991), partial reductive hydrolysis (Falshaw & Furneaux 1995a) and two-dimensional nuclear magnetic resonance spectroscopy (Falshaw et al. 1996). Unusual polysaccharide structures have also been shown to have taxonomic significance (e.g. Nelson et al. 1994, 1999; Hemmingson & Nelson 2002) and, in some cases, unusual properties. For example, unusually high melting temperatures of agar gels are related to particular patterns of natural methyl-ether

Table 4.	Publications detailing structura	I analysis of polysaccharides	from New Z	ealand macroalgae
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Family	Species name used in reference	Current name (if different)	Polysaccharide type	Reference
Reds				
Rangiaceae	Porphyra cinnamomea		Galactan	Hemmingson & Nelson (2002)
Bangiaceae	Porphyra coleana		Galactan	Hemmingson & Nelson (2002)
Bangiaceae	Porphyra rakiura		Galactan	Hemmingson & Nelson (2002)
Bangiaceae	Porphyra virididentata		Galactan	Hemmingson & Nelson (2002)
Bangiaceae	Porphyra columbina	Species identity uncertain	Galactan	Brasch et al (1981a) (1981b)
Daligiaceae	Γοιρηγία columbina	Species identity uncertain	Galactali	(1984b)
Caulacanthaceae	Trematocarpus acicularis		Complex galactan	Miller (2002b)
Ceramiaceae	Ceramium rubrum		Xylo-galactan	Miller & Blunt (2002)
Ceramiaceae	Euptilota formosissima			Miller & Furneaux (1997)
Champiaceae	Champia novae zealandiae		Complex galactan	Miller <i>et al</i> . (1996)
Delesseriaceae	Myriogramme denticulata		Complex galactan	Miller (2001b)
Erythrotrichiaceae	Porphyra cameronii	Pyrophyllon cameronii	Xylo-galactan	Hemmingson & Nelson (2002)
Erythrotrichiaceae	Porphyra kaspar	Chlidophyllon kaspar	Xylo-galactan	Hemmingson & Nelson (2002)
Erythrotrichiaceae	Porphyra subtumens	Pyrophyllon subtumens	Xylo-galactan	Hemmingson & Nelson (2002)
Faucheaceae	Cenacrum subsutum		Carrageenan?	Adams <i>et al</i> . (1988)
Gelidiaceae	Gelidum allanii		Agar	Nelson <i>et al</i> . (1994)
Gelidiaceae	Gelidium caulacantheum		Agar	Miller & Furneaux (1982);
				Nelson <i>et al</i> . (1994)
Gelidiaceae	Gelidium pusillum	Capreolia implexa	Agar	Miller & Furneaux (1982)
Gelidiaceae	Pterocladia pinnata, P. capillacea	Pterocladiella capillacea	Agar	Miller & Furneaux (1982);
				² Nelson <i>et al</i> . (1994)
Gelidiaceae	Pterocladia lucida		Agar	Miller & Furneaux (1982);
				Stevenson & Furneaux (1991)
Gigartinaceae	Gigartina decipiens		Carrageenan	Falshaw & Furneaux (1994)
Gigartinaceae	Gigartina clavifera		Carrageenan	Falshaw & Furneaux (1995b)
Gigartinaceae	Gigartina alveata		Carrageenan	Falshaw & Furneaux (1995b)
Gigartinaceae	Gigartina lanceata	Sarcothalia lanceata	Carrageenan	Falshaw & Furneaux (1998)
Gigartinaceae	Gigartina chapmanii	Chondracanthus chapmanii	Carrageenan	Falshaw & Furneaux (1998)
Gigartinaceae	Gigartina atropurpurea	,	Carrageenan	Lawson et al. (1973);
0	0 1 1		0	Penman & Rees (1973)
				Falshaw et al. (2003)
Gigartinaceae	Iridea lanceolata		Carrageenan	Adams et al. (1988)
Gigartinaceae	Iridea sp.		Carrageenan	Adams et al. (1988)
Gracilariaceae	Gracilaria sordida	Gracilaria chilensis	Agar	Stevenson & Furneaux (1991)
Gracilariaceae	Gracilaria truncata		Agar	Furneaux <i>et al.</i> (1990)
Gracilariaceae	Gracilaria secundata f.	Gracilaria chilensis	Agar	Miller & Furneaux (1987a)
	pseudoflagellifera		0	
Gracilariaceae	Gracilaria secundata f. secundata	G. secundata	Agar	Miller & Furneaux (1987b)
Gracilariaceae	Gracilaria secundata f. compacta	G. chilensis	Agar	Miller & Furneaux (1987b)
Gracilariaceae	Gracilaria secundata f.	G. chilensis	Agar	Miller & Furneaux (1987b)
	pseudoflagellifera			
Gracilariaceae	Gracilaria secundata	Uncertain	Agar	Brasch et al. (1981a), (1983),
				(1984a)
Gracilariaceae	Melanthalia abscissa		Complex xylo-galactar	nFurneaux <i>et al</i> . (1990)
Gracilariaceae	Curdiea coriacea		Agar	Furneaux <i>et al</i> . (1990);
				Falshaw <i>et al</i> . (1998)
Gracilariaceae	Curdiea flabellata		Agar	Furneaux <i>et al</i> . (1990);
				Falshaw <i>et al</i> . (1998)
Gracilariaceae	Curdiea codioides		Agar	Falshaw <i>et al</i> . (1998)
Gracilariaceae	Curdiea sp. nov. (3 Kings)	Curdiea balthazar	Agar	Falshaw <i>et al</i> . (1998)
Gracilariaceae	Curdiea balthazar		Agar	Nelson <i>et al</i> . (1999)
Halymeniaceae	'Kallymenia berggrenii'†	Cryptonemia sp.	Complex galactan	Miller & Furneaux (1996)
Halymeniaceae	Pachymenia Iusoria		Complex galactan	Miller <i>et al</i> . (1995);
				Miller <i>et al</i> . (1997)
Halymeniaceae	Pachymenia laciniata		Complex galactan	Miller <i>et al</i> . (1997)
Halymeniaceae	Pachymenia crassa		Complex galactan	Miller <i>et al</i> . (1997)
Hildenbrandiaceae	Apophlaea Iyallii		Complex galacto-	Watt <i>et al.</i> (2002)
			glucunono-xylo-glycar	1
Nemastomaceae	Nemastoma laciniata		Carrageenan	Adams <i>et al.</i> (1988)
Palmariaceae	Leptosarca simplex	Palmaria decipiens	Xylan	Adams <i>et al.</i> (1988)
Phyllophoraceae	Ahnfeltia torulosa	Gymnogongrus torulosus	Carrageenan	Furneaux & Miller (1985)
Phyllophoraceae	<i>Ahnfeltia</i> sp.	?	Carrageenan	Furneaux & Miller (1985)
Phyllophoraceae	Stenogramme interrupta	Stenogramme sp. nov.	Starch, carrageenan	Furneaux & Miller (1985);
				Miller (1998)
Phyllophoraceae	Gymnogongrus nodiferus	Gymnogongrus furcatus	Carrageenan	Furneaux & Miller (1985)

 Table 4.
 Continued

Family	Species name used in reference	Current name (if different)	Polysaccharide type	Reference
Phyllophoraceae Phyllophoraceae Phyllophoraceae Plocamiaceae Rhodomelaceae Rhodomelaceae Rhodomelaceae Rhodomelaceae Rhodomelaceae	Gymnogongrus humilis Gymnogongrus 'vermicularis' Gymnogongrus sp. Plocamium costatum Lenormandia chauvinii Lenormandia angustifolia Bryocladia ericoides Vidalia colensoi Laurencia thyrsifera Dasyclonium incisum Chondria macrocarpa	Gymnogongrus furcatus Plocamium cirrhosum Adamsiella chauvinii Adamsiella angustifolia Osmundaria colensoi	Carrageenan Carrageenan Carrageenan Complex galactan Agaroid Agaroid Agaroid Complex xylo- galactan Agaroid Complex xylo- galactan	Furneaux & Miller (1985) Furneaux & Miller (1985) Furneaux & Miller (1985) Falshaw <i>et al.</i> (1999) Miller <i>et al.</i> (1993b) Miller <i>et al.</i> (1993b) Miller <i>et al.</i> (1993b) Miller <i>et al.</i> (1993b) Miller <i>et al.</i> (1993a) Furneaux & Stevenson (1990); Miller & Blunt (2002)
Rhodomelaceae Rhodomelaceae Rhodomelaceae Rhodomelaceae Rhodomelaceae Rhodomelaceae	Streblocladia glomerulata Polysiphonia strictissima Polysiphonia abscissoides Cladhymenia oblongifolia Lophurella caespitosa Lophurella hookeriana	lumana ladia abandriasia	Agaroid Agaroid Complex galactan Agaroid Agaroid	Miller & Furneaux (1997) Miller & Furneaux (1997) Miller & Furneaux (1997) Miller & Blunt (2000) Miller (2002a) Miller (2002a)
Browns Alariaceae Chordariaceae Chordariaceae	Hymenociadia sanguinea Ecklonia radiata Papenfussiella lutea Myriogloia intestinalis	Hymenociaala chonaricola	Alginate Alginate Alginate Alginate	Miller (2001a) Miller (1996) Miller (1996) Miller (1996); Miller & Blunt (2003)
Cystoseiraceae Cystoseiraceae	Cystophora torulosa Cystophora retroflexa		Alginate Alginate	Miller (1996) Panikkar & Brasch (1996);
Durvilleaceae	Durvillaea antarctica		Alginate	Panikkar & Brasch (1997) Miller (1996); Panikkar & Brasch (1996); Panikkar & Brasch (1997);
Durvilleaceae	Durvillaea willana		Alginate	Kelly & Brown (2000) Panikkar & Brasch (1996); Panikkar & Brasch (1997); Kelly & Brown (2000)
Fucaceae Hormosiraceae	Xiphophora chondrophylla Hormosira banksii		Alginate Alginate	Miller (1996) Miller (1996); Panikkar & Brasch (1996); Panikkar & Brasch (1997)
Lessoniaceae Lessoniaceae	Lessonia variegata Macrocystis pyrifera		Alginate Alginate	Miller (1996) McKee <i>et al.</i> (1992); Panikkar & Brasch (1996); Panikkar & Brasch (1997)
Sargassaceae Scytosiphonaceae Seirococcaceae	Carpophyllum maschalocarpum Scytosiphon lomentaria Marginariella boryana		Alginate Alginate Alginate	Miller (1996) Miller (1996) Panikkar & Brasch (1996); Panikkar & Brasch (1997)
Splachnidaceae Greens Cladophoraceae	Splachnidium rugosum Chaetomorpha coliformis		Alginate Cellulose	Miller (1996); Miller & Blunt (2003) Newman (1999)

[†]This name was incorrectly applied to the specimen analyzed.

substitution in agars from certain *Curdiea* species (Furneaux *et al.* 1990; Falshaw *et al.* 1998). Despite the extensive research already undertaken in this area, there remain many species of New Zealand macroalgae that have yet to be examined for polysaccharide content and structure. As science in New Zealand becomes more commercially driven, the challenge for researchers will be to produce commercial quantities of useful algae.

RECOMMENDATIONS FOR FUTURE RESEARCH

The taxonomic status of many New Zealand seaweeds requires serious attention. Such knowledge is essential to assess macroalgal biodiversity, as well as the impacts of introduced species, pollution or aquaculture on macroalgal communities. The process of cataloguing New Zealand's marine flora requires that researchers are

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trained in both traditional and modern (e.g. molecular phylogenetics) taxonomic techniques. In order for researchers and managers of coastal marine ecosystems to make informed decisions, long-term monitoring (minimum of 5-10 years) of temporal changes in macroalgal-dominated communities is required. A national monitoring programme using standard monitoring methodologies could easily be established for a range of coastal ecosystems around New Zealand where research institutions and/or field laboratories are conveniently based: Leigh, Cook Strait, Canterbury, Otago, Stewart Island and Fiordland. A similar programme to assess the production rates of dominant intertidal and subtidal macroalgal species and/or communities could be established, along with studies on the fate of macroalgal production in the coastal food web. The expansion of the New Zealand seaweed industry will be dependent on access to suitable resources. The longterm effects of seaweed removal on marine communities will need to be investigated if wild harvest is to be a sustainable option. Information on reproduction and growth requirements of specific species will be required if aquaculture or wild harvest are to be viable options. To make best use of funding for macroalgal research, and to prevent duplication of research, we recommend enhanced collaborations between research institutions.

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