

## GLOBAL ECOLOGY OF THE GIANT KELP *MACROCYSTIS*: FROM ECOTYPES TO ECOSYSTEMS

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**Abstract** The giant kelp *Macrocystis* is the world's largest benthic organism and most widely distributed kelp taxon, serving as the foundation for diverse and energy-rich habitats that are of great ecological and economical importance. Although the basic and applied literature on *Macrocystis* is extensive and multinational, studies of large *Macrocystis* forests in the northeastern Pacific have received the greatest attention. This review synthesises the existing *Macrocystis* literature into a more global perspective. During the last 20 yr, the primary literature has shifted from descriptive and experimental studies of local *Macrocystis* distribution, abundance and population and community structure (e.g., competition and herbivory) to comprehensive investigations of *Macrocystis* life history, dispersal, recruitment, physiology and broad-scale variability in population and community processes. Ample evidence now suggests that the genus is monospecific. Due to its highly variable physiology and life history, *Macrocystis* occupies a wide variety of environments (intertidal to 60+ m, boreal to warm temperate) and sporophytes take on a variety of morphological forms. *Macrocystis* sporophytes are highly responsive to environmental variability, resulting in differential population dynamics and effects of *Macrocystis* on its local environment. Within the large subtidal giant kelp forests of southern California, *Macrocystis* sporophytes live long, form extensive surface canopies that shade the substratum and dampen currents, and produce and retain copious amounts of reproductive propagules. The majority of subtidal *Macrocystis* populations worldwide, however, are small, narrow, fringing forests that are productive and modify environmental resources (e.g., light), yet are more dynamic than their large southern California counterparts with local recruitment probably resulting from remote propagule production. When intertidal, *Macrocystis* populations exhibit vegetative propagation. Growth of high-latitude *Macrocystis* sporophytes is seasonal, coincident with temporal variability in insolation, whereas growth at low latitudes tracks more episodic variability in nutrient delivery. Although *Macrocystis* habitat and energy provision varies with such ecotypic variability in morphology and productivity, the few available studies indicate that *Macrocystis*-associated communities are universally diverse and productive. Furthermore, temporal and spatial variability in the structure and dynamics of these systems appears to be driven by processes that regulate *Macrocystis* distribution, abundance and productivity, rather than the consumptive processes that make some other kelp systems vulnerable to overexploitation. This global synthesis suggests that the great plasticity in *Macrocystis* form and function is a key determinant of the great global ecological success of *Macrocystis*.

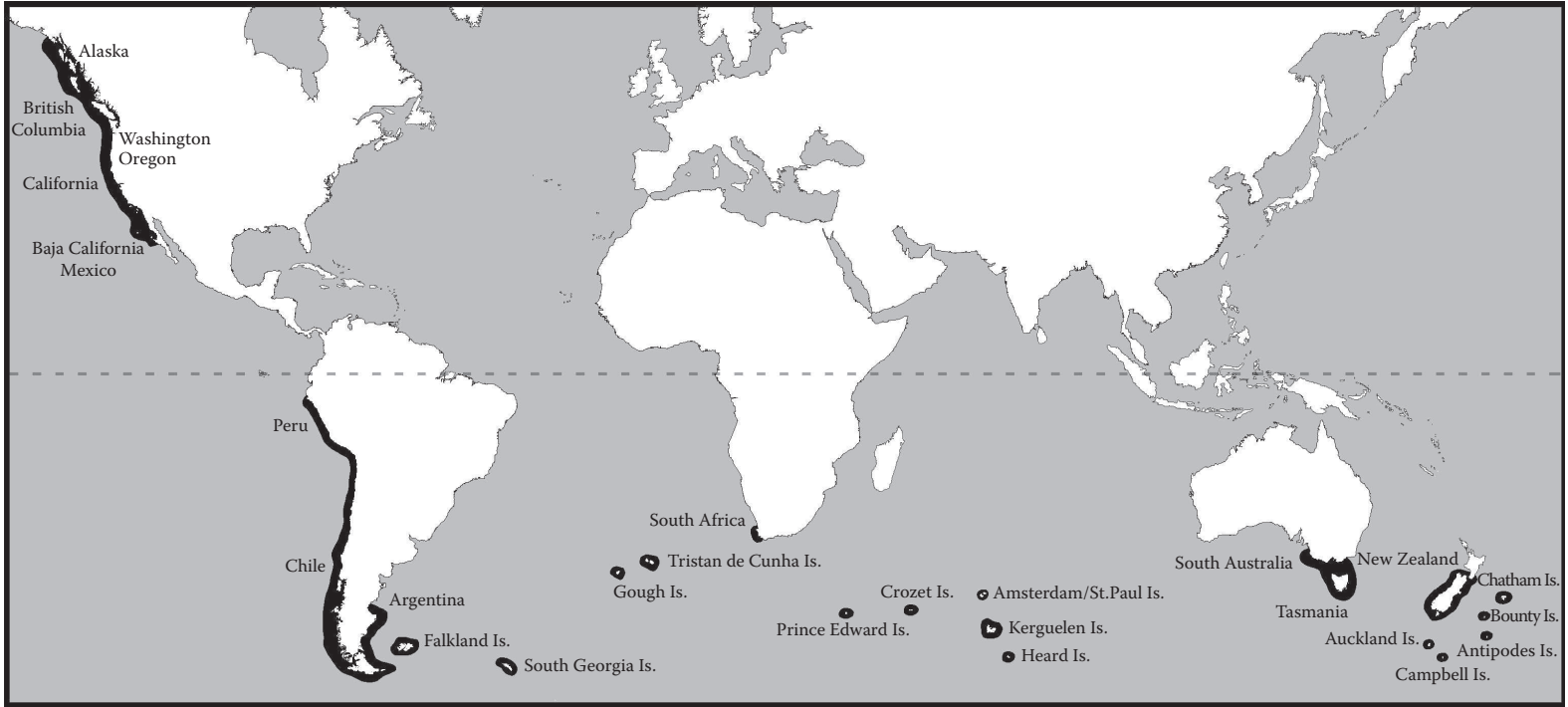
## Introduction

Kelp beds and forests represent some of the most conspicuous and well-studied marine habitats. As might be expected, these diverse and productive systems derive most of their habitat structure and available energy (fixed carbon) from the kelps, a relatively diverse order of large brown algae (Laminariales, Phaeophyceae; ~100 species). Kelps and their associated communities are conspicuous features of temperate coasts worldwide (Lüning 1990), including all of the continents except Antarctica (Moe & Silva 1977), and the proximity of such species-rich marine systems to large coastal human populations has subsequently resulted in substantial extractive and non-extractive industries (e.g., Leet et al. 2001). It is therefore not surprising that the basic and applied scientific literature on kelps is extensive.

Our present understanding of the ecology of kelp taxa is not uniform, as the giant kelp *Macrocystis* has received the greatest attention. *Macrocystis* is the most widely distributed kelp genus in the world, forming dense forests in both the Northern and Southern hemispheres (Figure 1). The floating canopies of *Macrocystis* adult sporophytes also have great structural complexity and high rates of primary productivity (Mann 1973, Towle & Pearse 1973, Jackson 1977, North 1994). Furthermore, although *Macrocystis* primary production can fuel secondary productivity through direct grazing, most fixed carbon probably enters the food web through detrital pathways or is exported from the system (e.g., Gerard 1976, Pearse & Hines 1976, Castilla & Moreno 1982, Castilla 1985, Inglis 1989, Harrold et al. 1998, Graham 2004). In some regions, such habitat and energy provision can support from 40 to over 275 common species (Beckley & Branch 1992, Vásquez et al. 2001, Graham 2004).

Venerated by Darwin (1839), the ecological importance of *Macrocystis* has long been recognised. The genus, however, did not receive thorough ecological attention until the 1960s when various *Macrocystis* research programmes began in California, and later in British Columbia, Chile, México, and elsewhere. Since that time, several books and reviews and hundreds of research papers have appeared in both the primary and secondary literature, primarily emphasising the physical and biotic factors that regulate *Macrocystis* distribution and abundance, recruitment, reproductive strategies and the structure and organisation of *Macrocystis* communities (see reviews by North & Hubbs 1968, North 1971, 1994, Dayton 1985a, Foster & Schiel 1985, North et al. 1986, Vásquez & Buschmann 1997).

This review synthesises this rich literature into a global perspective of *Macrocystis* ecology and such a review is timely for three reasons. First, the last review of *Macrocystis* ecology was done by North (1994) and thoroughly covered the literature until 1990, yet there has been significant progress on many aspects of *Macrocystis* ecology since that time. Second, during the last 15–20 yr the general focus of *Macrocystis* research (and that of kelps in general) has shifted from descriptive and experimental studies of local *Macrocystis* distribution, abundance and population and community structure (e.g., competition and herbivory) to comprehensive investigations of *Macrocystis* life history, dispersal, recruitment, physiology and broad-scale variability in population and community processes. Finally, previous reviews of *Macrocystis* ecology have been from an inherently regional perspective (e.g., California or Chile) and there is currently no truly global synthesis. This last aspect is of great concern because it effectively partitions kelp forest researchers into provincial programmes and limits cross-fertilisation of ideas. Such a limitation is compounded by the great worldwide scientific and economic importance of this genus, the acclimatisation of *Macrocystis* to regional environments, and the recent finding that gene flow occurs among the most geographically distant regions over ecological timescales (Coyer et al. 2001). Therefore, the goal here is not to review the existing *Macrocystis* literature in its entirety, but rather to (1) focus on progress made during the last 15 yr, (2) discuss the achievements of *Macrocystis* research programmes worldwide and (3) identify deficiencies in the understanding of *Macrocystis* ecology that warrant future investigation.



**Figure 1** Global distribution of the giant kelp *Macrocystis*. Locations are given for distinct *Macrocystis* mainland and island populations determined directly from citations herein.

In particular, it is now recognised that great variability exists in *Macrocystis* morphology, physiology, population dynamics and community interactions at the global scale and it is considered that such ecotypic variability is key to understanding the role of *Macrocystis* in kelp systems worldwide.

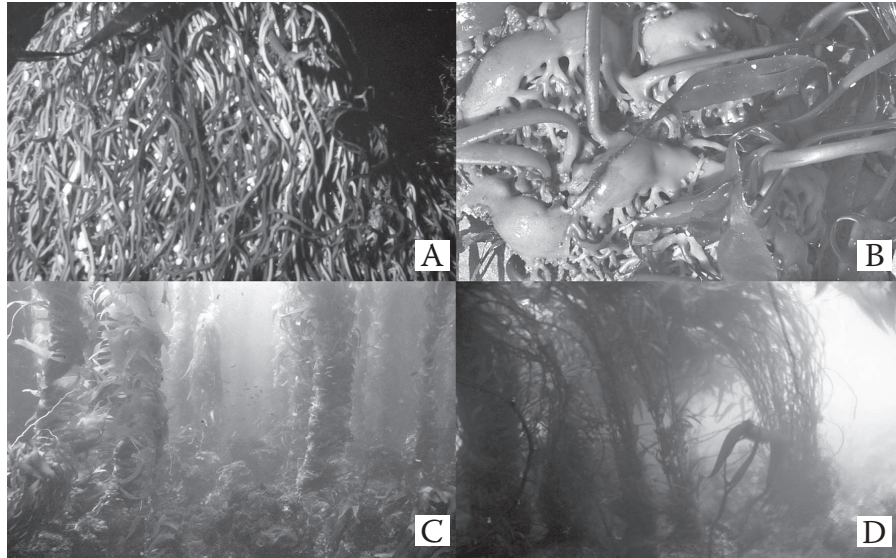
### Organismal biology of *Macrocystis*

Most of the biological processes that ultimately prove to be important in regulating the dynamics and structure of *Macrocystis* populations and communities (e.g., morphological complexity, photosynthesis, growth, reproductive output, gene flow) operate primarily at the scale of individual organisms. The standard means of studying *Macrocystis* organismal biology continues to be through laboratory studies. Clearly, laboratory studies allow researchers to address various processes under controlled environmental conditions, but in many cases the reliance on laboratory studies has been due to technical limitations in collecting organismal data *in situ*. Various technological advances since the 1960s (most occurring in the last two decades), however, have resulted in a surge of studies of *Macrocystis* evolutionary history, distribution, life history, growth, productivity and reproduction.

#### *Evolutionary history*

The order Laminariales has traditionally included five families (Chordaceae, Pseudochordaceae, Alariaceae, Laminariaceae, Lessoniaceae) but various ultrastructural and molecular data suggest that subordinal classification (i.e., families, genera, and species) is in need of significant revision (Druehl et al. 1997, Yoon et al. 2001, Lane et al. 2006). For example, the Chordaceae and Pseudochordaceae should not be included in the Laminariales (Saunders & Druehl 1992, 1993, Druehl et al. 1997) and a new family has been proposed (Costariaceae; Lane et al. 2006). The order is presumed to have originated in the northeast Pacific (Estes & Steinberg 1988, Lüning 1990) and molecular studies have estimated the date of origin to be between 15 and 35 million yr ago (Saunders & Druehl 1992). Within the order, the genus *Macrocystis* was formerly assigned to the family Lessoniaceae (including *Lessonia*, *Lessoniopsis*, *Dictyoneurum*, *Dictyoneuroopsis*, *Nereocystis*, *Postelsia* and *Pelagophycus*; Setchell & Gardner 1925), which was considered paraphyletic to the Laminariaceae (Druehl et al. 1997, Yoon et al. 2001). Recent molecular studies, however, have found that *Lessonia*, *Lessoniopsis*, *Dictyoneurum* and *Dictyoneuroopsis* are actually in phylogenetic clades that do not include *Macrocystis*, and that *Macrocystis*, *Nereocystis*, *Postelsia* and *Pelagophycus* group together in a derived clade that is nested well within the Laminariaceae (Lane et al. 2006), with *Pelagophycus porra* being the most closely related taxon to *Macrocystis*.

Species classification within the genus *Macrocystis* was originally based on blade morphology yielding over 17 species (see review by North (1971)). Blade morphology was then considered a plastic trait strongly affected by environmental conditions and subsequently all 17 *Macrocystis* species were synonymised with *Macrocystis pyrifera* (Hooker 1847). *Macrocystis* species were later described based on holdfast morphology ultimately leading to the current recognition of three species: *M. pyrifera* (conical holdfast; Figure 2A), *M. integrifolia* (rhizomatous holdfast; Figure 2B), and *M. angustifolia* (mounding rhizomatous holdfast) (Howe 1914, Setchell 1932, Womersley 1954, Neushul 1971). The fourth currently recognised species, *M. laevis*, was described by Hay (1986), again based on blade morphology (*M. laevis* has smooth fleshy blades and a *M. pyrifera*-type conical holdfast). Four lines of evidence, however, suggest that this current classification of *Macrocystis* is also in need of revision: (1) *M. pyrifera*, *M. integrifolia* and *M. angustifolia* are interfertile (Lewis et al. 1986, Lewis & Neushul 1994; interfertility with *M. laevis* has not been



**Figure 2** *Macrocyctis* holdfast morphologies and sporophyte spacing. (A) Holdfast of *pyriferiform* sporophyte from La Jolla, southern California. (Published with permission of Scott Rumsey.) (B) Holdfast of *integrifolium* sporophyte from Huasco, northern Chile. (Photograph by Michael Graham.) (C) Vertical structure of *pyriferiform* population from San Clemente Island (15 m depth), southern California; note average sporophyte spacing is 3–7 m. (Published with permission of Enric Sala.) (D) Vertical structure of *angustifolium* population from Soberanes Point (3 m depth), central California; note average sporophyte spacing is 10–50 cm. (Published with permission of Aurora Alifano.)

tested); (2) intermediate morphologies have been observed in the field (Setchell 1932, Neushul 1959, Womersley 1987, Brostoff 1988); (3) in addition to blade morphology (Hurd et al. 1997), holdfast morphology is phenotypically plastic (Setchell 1932, M.H. Graham, unpublished data); and most importantly, (4) patterns of genetic relatedness among all four species are not in concordance with current morphological classification (Coyer et al. 2001). This evidence strongly supports the recognition of the genus *Macrocyctis* as a single morphologically plastic species, with global populations linked by non-trivial gene flow. For the purpose of this review, therefore, the four currently recognised species are referred to simply as giant kelp, *Macrocyctis*.

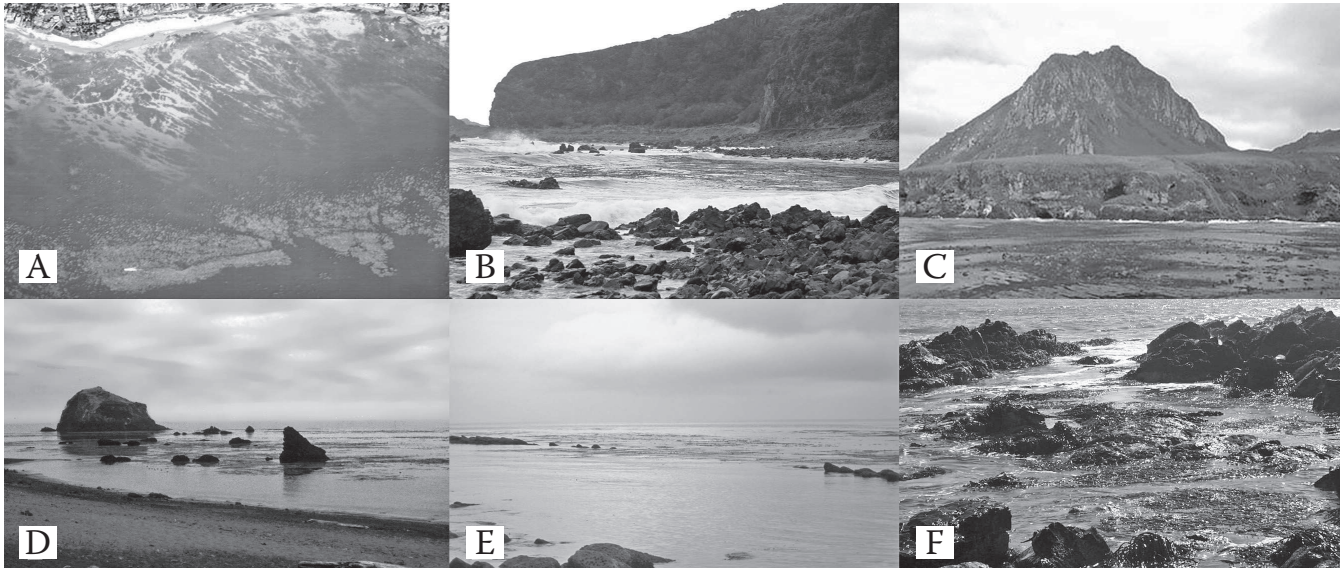
Biogeographic studies of extant kelp in the north Pacific suggest that the bi-hemispheric (antitropical) global distribution of *Macrocyctis* developed as the genus arose in the Northern Hemisphere and subsequently colonised the Southern Hemisphere (North 1971, Nicholson 1978, Estes & Steinberg 1988, Lüning 1990, Lindberg 1991). Alternatively, North (1971) and Chin et al. (1991) proposed a Southern Hemisphere origin of the genus, the latter via vicariant processes that have been questioned (Lindberg 1991). Recently, Coyer et al. (2001) studied the global phylogeography of *Macrocyctis* using recombinant DNA internal transcribed spacer (ITS1 and ITS2) regions. In addition to suggesting that the morphological species description of *M. pyriferiform*, *M. integrifolium*, *M. angustifolium* and *M. laevis* has no systematic support, Coyer et al. (2001) described a well-resolved phylogeographic pattern in which Southern Hemisphere *Macrocyctis* populations nested within Northern Hemisphere populations, linked by *Macrocyctis* populations on the Baja California Peninsula, Mexico. This pattern, and the greater genetic diversity among *Macrocyctis* populations in the Northern Hemisphere (within-region sequence divergences 1.7% and 1.2% for ITS1 and ITS2, respectively) relative to their Southern Hemisphere counterparts (within-region sequence

divergences 0.8% and 0.6% for ITS1 and ITS2, respectively), supports a northern origin of the genus with subsequent range expansion to include the Southern Hemisphere (Coyer et al. 2001); Coyer et al. (2001) suggested that gene flow across the equator may have occurred as recently as 10,000 yr ago.

Despite such progress, however, many questions remain regarding the evolutionary history of *Macrocystis*. Most importantly, how can this single, globally distributed species maintain gene flow throughout its range, yet at a regional scale exhibit relatively high geographic uniformity in such seemingly important characters as blade and holdfast morphology (i.e., ecotypes or forms)? The data of Coyer et al. (2001) suggest that simple founder effects may have resulted in the unique morphologies of the *laevis* form at the Prince Edward Islands (including Marion Island) and *angustifolia* form in Australia. The smooth-bladed *laevis* form has been found occasionally at the Falkland Islands (van Tüssenbroek 1989a) and a recent description from Chiloé Island, Chile (Aguilar-Rosas et al. 2003), is probably a misidentification of sporophylls as vegetative blades (Gutierrez et al. 2006). Still, despite the apparently high gene flow and morphological plasticity, the distinct forms with distinct ecologies can dominate different habitats often adjacent to each other (e.g., *integrifolia* form in shallow water vs. *pyrifera* form in deep water). The identification of which *Macrocystis* form is present within a region will aid in the understanding of the region's ecology (see 'Population' section, p. 54). In this context, it is hypothesised that the great plasticity in *Macrocystis* form and function may, in fact, be an adaptive trait resulting in its great global ecological success. Studies testing this hypothesis will require a better understanding of the nature of *Macrocystis* morphological plasticity, including biomechanics, structural biochemistry and quantitative genetics studies of genes regulating *Macrocystis* form.

### Distribution

*Macrocystis* distributional patterns have been well described (especially in the Northern Hemisphere) due primarily to the large stature of *Macrocystis* sporophytes and ability to sense their surface canopies remotely from aircraft or satellites (Jensen et al. 1980, Hernández-Carmona et al. 1989a,b, 1991, Augenstein et al. 1991, Belsher and Mouchot 1992, Deysher 1993, North et al. 1993, Donnellan 2004). *Macrocystis* typically grows on rocky substrata between the low intertidal and ~25 m depth (Figure 3; Rigg 1913, Crandall 1915, Baardseth 1941, Papenfuss 1942, Scagel 1947, Guiler 1952, 1960, Cribb 1954, Chamberlain 1965, Neushul 1971, Foster & Schiel 1985, Westermeier & Möller 1990, van Tüssenbroek 1993, Schiel et al. 1995, Graham 1997, Spalding et al. 2003, Vega et al. 2005) and is distributed in the northeast Pacific from Alaska to México, along the west and southeast coasts of South America from Perú to Argentina, in isolated regions of South Africa, Australia and New Zealand and around most of the sub-Antarctic islands to 60°S (Figure 1; Crandall 1915, Baardseth 1941, Cribb 1954, Papenfuss 1964, Chamberlain 1965, Neushul 1971, Hay 1986, Stegenga et al. 1997). In unique circumstances, sexually reproducing populations can exist in deep water (50–60 m; Neushul 1971 (Argentina), Perissinotto & McQuaid 1992 (Prince Edward Islands)), in sandy habitats (Neushul 1971) and unattached populations that reproduce vegetatively can exist in the water column (North 1971) or shallow basins (Moore 1943, Gerard & Kirkmann 1984, van Tüssenbroek 1989b). High latitudinal limits appear to be set by increased wave action (Foster & Schiel 1985, Graham 1997) and decreased insolation (Arnold & Manley 1985, Jackson 1987), whereas low latitudinal limits appear to be set by low nutrients associated with warmer (non-upwelling) waters (Ladah et al. 1999, Hernández-Carmona et al. 2000, 2001, Edwards 2004) or competition with warm-tolerant species (e.g., *Eisenia arborea* on the Baja California Peninsula, Mexico; Edwards & Hernández-Carmona 2005). The upper shallow limits of *Macrocystis* populations are ultimately regulated by the increased desiccation and high ultraviolet and/or photosynthetically active radiation (PAR) of the intertidal zone (Graham 1996, Huovinen et al. 2000, Swanson & Druehl 2000),



**Figure 3** Photographs of various *Macrocytis* populations. (A) Infrared aerial canopy photo of subtidal *pyrifera*-form population at La Jolla, southern California. (Published with permission of Larry Deysher/Ocean Imaging.) (B) Shallow subtidal *pyrifera*-form population at Mar Brava, central Chile. (Photograph by Michael Graham.) (C) Subtidal *pyrifera*-form population at Nightingale Island near Tristan da Cunha Island, South Atlantic Ocean. (Published with permission of Juanita Brock.) (D) Intertidal *integrifolia*-form population at Van Damme State Park, northern California. (Photograph by Michael Graham.) (E) Intertidal *integrifolia*-form population at Strait of Juan de Fuca, Washington. (Photograph by Michael Graham.) (F) Intertidal *integrifolia*-form population at Huasco, northern Chile. (Photograph by Michael Graham.)

although wave activity, grazing and competition with other macroalgae in shallow subtidal areas can also be important (Santelices & Ojeda 1984a, Foster & Schiel 1992, Graham 1997). At local scales, decreased availability of light and rocky substratum, and occasionally sea urchin grazing, appear to set the lower off-shore limits of *Macrocystis* populations (Pearse & Hines 1979, Lüning 1990, Spalding et al. 2003, Vega et al. 2005). Finally, within these upper and lower limits, the lateral distribution of *Macrocystis* populations typically corresponds with abrupt changes in bathymetry or substratum composition (e.g., sand channels or harbour mouths; North & Hubbs 1968, Dayton et al. 1992, Kinlan et al. 2005).

There is an interesting pattern within the global distribution of *Macrocystis* whereby different regions may have large *Macrocystis* populations of one morphological form or another (Neushul 1971, Womersley 1987). For example, the *integrifolia* and *angustifolia* forms of *Macrocystis* are generally found in shallow waters (low intertidal zone to 10 m depth), whereas the *pyrifera* form is generally found in intermediate-to-deep waters (4–70 m depth) (Table 1). In the Northern Hemisphere, the *integrifolia* form is most commonly observed at higher latitudes north of San Francisco Bay with scattered populations found as far south as southern California (Abbott & Hollenberg 1976, M.H. Graham, personal observations), whereas the *pyrifera* form is most common at lower latitudes south of San Francisco Bay with scattered populations found as far north as southeast Alaska (Gabrielson et al. 2000). In South America, the *integrifolia* and *pyrifera* forms also appear to occupy shallow and deep habitats, respectively (Howe 1914, Neushul 1971). Latitudinally, however, the Southern Hemisphere *Macrocystis* distribution is opposite that of the Northern Hemisphere: the *integrifolia* form is generally found at lower latitudes, restricted to Perú México, and northern Chile (Howe 1914, Neushul 1971), whereas the *pyrifera* form dominates the higher latitudes of central and southern Chile (and Argentina; Barrales & Lobban 1975), but can also be found far north in Perú (Howe 1914, Neushul 1971). The *pyrifera* form also appears to be

**Table 1** Maximum depths of worldwide populations of *Macrocystis* ecotypes

<i>Macrocystis</i> form	Location	Depth (m)	Reference
<i>angustifolia</i>	South Australia	6	Womersley 1954
	South Africa	8	Isaac 1937
<i>integrifolia</i>	British Columbia	10	Druehl 1978
	Northern Chile	8, 14	Neushul 1971, Vega et al. 2005
	Perú	20	Juhl-Noodt 1958*
<i>pyrifera</i>	Southern Chile	10	Dayton et al. 1973
	Tasmania	15	Cribb 1954
	New Zealand	16	Hay 1990
	St. Paul/Amsterdam Is.	20	Delépine 1966*
	Crozet Is.	25	Delépine 1966*
	Falkland Is.	25	Powell 1981
	South Georgia Is.	25	Skottsberg 1941
	Southern California	30	Neushul & Haxo 1963
	Central California	30	Spalding et al. 2003
	Tristan da Cunha Is.	30	Baardseth 1941
	Baja California	40	North 1971
	Perú	40	Juhl-Noodt 1958*
	Southern Argentina	55	Neushul 1971
Kerguelen Is.	40	Grua 1964*	
Gough Is.	55	Chamberlain 1965	
<i>laevis</i>	Prince Edward Is.	68	Perissinotto & McQuaid 1992

\* Depths interpreted by Perissinotto & McQuaid (1992).

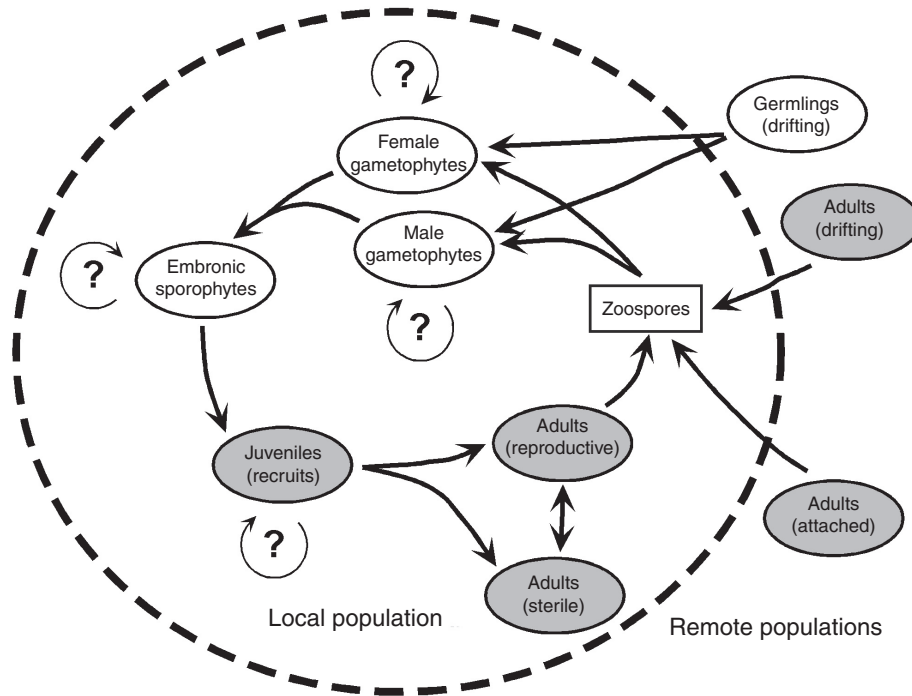


most common where *Macrocystis* is found elsewhere in the Southern Hemisphere (e.g., Tasmania, New Zealand, various sub-Antarctic islands), except in South Australia and South Africa where the *angustifolia* form is common (Cribb 1954, Womersley 1954, 1987, Hay 1986, Stegenga et al. 1997). Jackson's (1987) analyses suggested that high latitude *Macrocystis* sporophytes would be light limited in subtidal waters, forcing a shift in distribution to shallower water above 53° latitude. This may explain the Northern Hemisphere distributional pattern, but cannot explain why shallow-water *Macrocystis* is the most common form in northern Chile. Furthermore, exceptions to these patterns clearly exist. For example, *pyrifera*-form individuals can be found in the intertidal zone (e.g., Guiler 1952, 1960 (Tasmania), Chamberlain 1965 (Gough Island), Westermeier and Möller 1990 (southern Chile), van Tüssenbroek 1993 (Falkland Islands)), sometimes even side by side with *integrifolia*-form individuals (M.H. Graham, personal observations in California; J.A. Vásquez, personal observations in northern Chile). Intermediate morphologies similar to the *angustifolia* form of South Australia-South Africa can also be observed at intermediate depths (2–6 m) between adjacent *pyrifera*-form and *integrifolia*-form populations in central California (M.H. Graham, personal observations). Still, these global distribution patterns support the general consideration of the *integrifolia* and *angustifolia* forms as having more shallow-water affinities than the *pyrifera* form.

Another interesting global distributional pattern is the apparent restriction of large *Macrocystis* forests (>1 km<sup>2</sup>) to the southwest coast of North America (Point Conception in southern California to Punta Eugenia in Baja California, Mexico; Hernández-Carmona et al. 1991, North et al. 1993), although *Macrocystis* forests on most of the sub-Antarctic islands have not been explored. The southwest coast of North America has broad shallow-sloping subtidal rocky platforms to support wide *Macrocystis* populations (up to 1 km width), whereas the regions north to Alaska and south to Patagonia have steep shores and typically support very narrow *Macrocystis* populations (<100 m width); in some cases, narrow *Macrocystis* populations can fringe entire islands in the Pacific Northwest (Scagel 1947), southern Chile (Santelices & Ojeda 1984b) and many sub-Antarctic islands (e.g., Crandall 1915, Cribb 1954, van Tüssenbroek 1993). Thus, several key unanswered questions remain: (1) does the geological restriction of *Macrocystis* to small forests outside southern California affect the ecology of these systems (see 'Population' section, p. 54), (2) why are the shallow-water forms found poleward in the Northern Hemisphere and equatorward in the Southern Hemisphere, (3) does the recruitment of *Macrocystis* individuals to different depths or regions determine their ultimate morphological form or (4) does variability in *Macrocystis* morphological form determine the depth or region in which sporophyte recruitment and survival will be successful?

### *Life history*

As with all kelps, *Macrocystis* exhibits a biphasic life cycle in which the generations alternate (Sauvageau 1915), and the general life history is well understood (Figure 4; see review by North (1994)). Macroscopic sporophytes attach to substrata by a holdfast consisting of a mass of branched and tactile haptera. Dichotomously branched stipes arise from the holdfast and are topped by apical meristems that split off laminae (blades) as they grow to the surface; gas-filled pneumatocysts join laminae to the stipes and buoy them. The resulting fronds consisting of stipes, laminae and pneumatocysts can form extensive surface canopies and represent the bulk of photosynthetic biomass (North 1994). Other, shorter stipes give rise to profusely and dichotomously branched specialised laminae near the base of the sporophyte (sporophylls) that bear sporangia aggregated in sori (Neushul 1963); occasionally sori are observed on laminae in the canopy (A.H. Buschmann, personal observations in southern Chile) and sporophylls can bear pneumatocysts (Neushul 1963). Each sporangium contains 32 haploid biflagellate pyriform zoospores produced through meiosis and subsequent mitoses (Fritsch 1945). Haplogenic sex determination apparently results in a 1:1 male-to-female zoospore sex ratio (Fritsch 1945, Reed 1990, North 1994), although the two



**Figure 4** *Macrocystis* life cycle depicting various life-history stages important in regulating local *Macrocystis* population dynamics. Ovals represent benthic stages and rectangles represent pelagic stages; white stages are microscopic and shaded stages are macroscopic. Circular arrows represent potential for retention within particular stages for unknown durations.

sexes cannot be distinguished easily at the zoospore stage (Druehl et al. 1989). Zoospores (~6–8  $\mu\text{m}$  length) are released into the water column where they disperse via currents until they reach suitable substrata where they settle, germinate and develop into microscopic male or female gametophytes. As gametophytes mature, the females extrude oogonia (eggs) accompanied by the pheromone lamoxirene (Maier et al. 1987, 2001). Upon sensing the pheromone, male gametophytes release biflagellate non-photosynthetic antherozoids (sperm) that track the pheromone to the extruded egg. Subsequent fertilisation gives rise to microscopic diploid sporophytes, which ultimately grow to macroscopic (adult) size and complete the life cycle.

Although these steps necessary for *Macrocystis* to progress through its life cycle are straightforward, specific resources are necessary for gametogenesis, fertilisation, and growth of microscopic stages. As a result, variability in environmental factors can greatly affect *Macrocystis* recruitment success and completion of its life cycle. The experiments of Lüning & Neushul (1978) clearly identified light quality and quantity as important in regulating female gametogenesis in *Macrocystis*, and kelps in general. Deysher & Dean (1984, 1986a) quantified gross light (PAR), temperature and nutrient (nitrate) requirements of *Macrocystis* gametogenesis and fertilisation, with embryonic sporophyte formation limited to PAR above  $0.4 \mu\text{M}$  photons ( $\mu\text{Einstein}$ )  $\text{m}^{-2} \text{s}^{-1}$ , temperatures from 11 to 19°C and nitrate concentrations of  $>1 \mu\text{M}$ . Such critical irradiance, temperature and nutrient thresholds were further supported by field experiments (Deysher & Dean 1986b). Although these studies did not provide data amenable to the development of probability density functions for predicting *Macrocystis* recruitment success as a function of variable environmental conditions, the research was vital to the development of the concept of temporal ‘recruitment windows’, during

which environmental factors exceeded minimum levels for successful gametogenesis and fertilisation. Deysher & Dean (1986a) also found that the growth of embryonic sporophytes to macroscopic size was inhibited at low PAR and nitrate concentrations, but these PAR levels were higher than the threshold for gametogenesis and fertilisation. This suggests that the growth of embryonic sporophytes to macroscopic size may be a stronger bottleneck in the *Macrocystis* life history than gametogenesis and fertilisation. The photosynthesis studies of Fain & Murray (1982) similarly identified differences in physiology between *Macrocystis* gametophytes and embryonic sporophytes.

The process leading to *Macrocystis* recruitment from gametophytes can thus be divided into two functionally different stages: (1) sporophyte production (gametogenesis and fertilisation, with relatively lower light requirements) and (2) growth of sporophytes to macroscopic size (with relatively higher light requirements). It follows that the timing and success of *Macrocystis* recruitment will depend on both the duration of each stage and whether such durations can be extended to allow for delayed recruitment (Figure 4) similar to the concept of seed banks for terrestrial plants (Hoffmann & Santelices 1991).

Laboratory and field studies indicate that the sporophyte production stage is relatively short (1–2 months) and rigid in its duration, suggesting limited potential for delayed *Macrocystis* recruitment via gametophytes. In California, female *Macrocystis* gametophytes appear to have an initial competency period of 7–10 days prior to gametogenesis (North 1987) and lose fertility after ~30 days (Deysher & Dean 1984, Kinlan et al. 2003), whereas in Chile, laboratory culture studies under ample light and nutrient conditions suggest that *Macrocystis* female gametophytes may remain fertile for up to 75 days (Muñoz et al. 2004). However, *Macrocystis* gametophytes can apparently survive indefinitely under ‘unnatural’ artificial light-quality conditions (i.e., red light only; Lüning & Neushul 1978). In California, unfertilised female gametophytes older than ~30 days have limited potential for fertilisation (Deysher & Dean 1986b) and thus recruitment, which was supported by the laboratory studies of Kinlan et al. (2003). As indicated by Kinlan et al. (2003), however, the necessary studies have not been done to determine whether this lack of fertilisation success is due to senescence of female gametophytes or of their male counterparts. Also, it has been demonstrated that zoospore swimming ability is correlated with germination success (Amsler & Neushul 1990) and a similar mechanism may affect fertilisation of oogonia by antherozoids. The demonstration of a shorter life-span (period of fertility) for *Macrocystis* male gametophytes relative to females would suggest the potential for cross-fertilisation among different zoospore settlements via perennial females.

Another well-known aspect of sporophyte production is the minimum density of settled zoospores necessary for recruitment. Specifically, the reliance of kelps on the presence of lamoxirene as a trigger for antherozoid release (Maier et al. 1987, 2001) and the dilution of this sexual pheromone over short distances from the oogonia inherently require sufficient zoospore settlement densities (and survivorship to maturation) to ensure that males and females are close enough for fertilisation to be successful. Such ‘critical settlement densities’ were demonstrated in a series of laboratory and field experiments by Reed and his colleagues (Reed 1990, Reed et al. 1991). Specifically, Reed et al. (1991) identified 1 settled zoospore  $\text{mm}^{-2}$  (vs. 0.1 or 10 settled zoospores  $\text{mm}^{-2}$ ) as the minimum *Macrocystis* (and *Pterygophora*) zoospore settlement density above which fertilisation and sporophyte production could be expected. These experiments focused on recruitment from single zoospore settlement cohorts and cross-fertilisation among different zoospore settlements may result in fertilisation even if cohort settlement densities are  $<1$  settled zoospore  $\text{mm}^{-2}$ . It has recently been demonstrated that *Macrocystis* sporophytes can be produced from unfertilised gametes through apogamy (Druehl et al. 2005). Although the frequency of parthenogenic sporophyte production in the field has not been tested, parthenogenesis may obviate the need for  $>1$  settled zoospore to yield an adult sporophyte. Reed (1990) also demonstrated that species-dependent female maturation rates combined with species-independent pheromone activity might

result in chemically mediated competition among microscopic stages of kelp species, although this was only suggested for *Macrocystis* and *Pterygophora* in southern California. In addition to producing valuable life-history data, these studies clearly demonstrated the utility of combining laboratory and field experiments of kelp recruitment and resulted in a surge in studies of the ecology of kelp microscopic stages.

Nevertheless, several key issues regarding the *Macrocystis* life history remain to be resolved. Most importantly, *Macrocystis* microscopic life-history stages have not been observed in the field. Microphotometric techniques have recently been developed for identifying *Macrocystis* zoospores based on species-specific zoospore absorption spectra (Graham 1999, Graham & Mitchell 1999). Subsequent determination of *Macrocystis* zoospore concentrations from *in situ* plankton samples led to direct studies of *Macrocystis* zoospore planktonic processes (e.g., Graham 2003). However, upon settlement, *Macrocystis* zoospores germinate into gametophytes of variable cell number and pigment concentration, negating the use of microphotometric techniques for studying post-settlement processes (Graham 2000). Fluorescently labelled monoclonal antibodies have been developed for distinguishing between *Macrocystis* and *Pterygophora* gametophytes based on cell surface antigens (Hempel et al. 1989, Eardley et al. 1990). However, the effectiveness of these tags diminishes when applied to field samples, in which kelp cells are universally coated with bacteria (D.C. Reed, personal communication). Additionally, although Kinlan et al. (2003) observed plasticity in growth of laboratory-cultured *Macrocystis* embryonic sporophytes under realistic environmental conditions (light and nutrients), and thus the potential for arrested development in this stage, their experiments provided no evidence of arrested development of gametophytes. This study demonstrated (1) that delayed recruitment of *Macrocystis* post-settlement stages is possible and (2) the general lack of understanding of the physiological processes that regulate the growth, maturation and senescence of *Macrocystis* microscopic stages. For example, it is considered that kelp female gametophytes living under adequate environmental conditions will have only one or very few cells, one oogonium per gametophyte, and become reproductive in the shortest period possible (e.g., Lüning & Neushul 1978, Kain 1979). In the absence of light and nutrients, female gametophytes are typically sterile and multicellular (e.g., Lüning & Neushul 1978, Kain 1979, Hoffmann & Santelices 1982, Hoffmann et al. 1984, Avila et al. 1985, Reed et al. 1991), suggesting a trade-off or antagonistic relationship between gametophyte growth and fertility. In some Chilean populations, however, female *Macrocystis* gametophytes grown under standard laboratory conditions (1) were multicellular, (2) produced multiple viable oogonia per gametophyte, (3) often resulted in numerous sporophytes per gametophyte and (4) took longer to mature than Californian populations (Muñoz et al. 2004). These results must be validated by additional laboratory and field studies but they did demonstrate the highly plastic physiology of *Macrocystis* life-history stages. Our lack of understanding of variability in the biology of *Macrocystis* microscopic stages, especially at the global level, is an important constraint on future progress in *Macrocystis* population dynamics (see 'Population' section, p. 54).

### *Growth, productivity and reproduction*

Recruitment processes are the main determinant of when and where *Macrocystis* sporophytes might occur, yet it is the survival and growth of established sporophytes that constrain sporophyte size, self-thinning, population cycles and the primary productivity and canopy structure that ultimately provide energy and habitat for *Macrocystis* communities.

The maximum age of *Macrocystis* sporophytes is unknown. Individual fronds generally senesce after 6–8 months (North 1994) although van Tüssenbroek (1989c) observed maximum frond survival of 1 yr and *Macrocystis* sporophytes can produce new fronds from apical meristems (frond initials) retained above the holdfasts near the sporophylls (Lobban 1978a,b, van Tüssenbroek 1989c, North

1994). As such, the sporophytes may survive as long as they remain attached to the substratum and environmental conditions are adequate for growth. In some regions of central California and Argentina, most *Macrocystis* sporophytes die within a year due to high wave activity (Barrales & Lobban 1975, Graham et al. 1997), whereas in southern California, sporophytes can live up to 4–7 yr (Rosenthal et al. 1974, Dayton et al. 1984, 1999), a life-span that coincides with the periodicity of the El Niño Southern Oscillation (ENSO); in southern Chile, the life-span of *Macrocystis* sporophytes often exceeds 2 yr (Santelices & Ojeda 1984b, Westermeier & Möller 1990). Interestingly, the only *Macrocystis* populations known to recruit and senesce on an annual cycle occur in the protected waters around 42°S in Chilean fjords (Buschmann et al. 2004a). The life-span of vegetatively reproducing *Macrocystis* sporophytes (e.g., *angustifolia* and *integrifolia* forms) has never been determined in the field, although *integrifolia*-form sporophytes have been shown to survive very high levels of rhizome fragmentation (Druehl & Kemp 1982, Graham 1996) and cultivated sporophytes can live 2–3 yr (Druehl & Wheeler 1986). In any case, the life-span of *Macrocystis* sporophytes appears to be far less than that of other perennial kelp genera (Reed et al. 1996, Schiel & Foster 2006), for example, *Pterygophora* and *Eisenia*, which can live for 10+ yr (Dayton et al. 1984).

The relatively high turnover of *Macrocystis* sporophytes is probably due to their massive size (up to 400 fronds per *pyrifera*-form sporophyte; North 1994) and the almost strict reliance of sporophyte growth and productivity on the biomass of the surface canopy (Reed 1987, North 1994, Graham 2002). Shallow-water *Macrocystis* sporophytes typically have lower frond numbers than deeper sporophytes (North 1994). Numerous studies have demonstrated high *Macrocystis* frond productivity rates with estimates of 2–15 g fixed carbon m<sup>-2</sup> day<sup>-1</sup> in the Northern Hemisphere (reviewed by North 1994), and values that vary between 7 and 11 g C m<sup>-2</sup> day<sup>-1</sup> in the southern Indian Ocean (Attwood et al. 1991). Delille et al. (2000) also observed a significant ‘draw-down’ of pCO<sub>2</sub> when off-shore water entered a dense *Macrocystis* bed at the Kerguelen Islands, suggesting that the productivity of *Macrocystis* fronds was high enough to decrease inorganic carbon concentrations in the water column. Furthermore, Schmitz & Lobban (1976) determined that *Macrocystis* sporophytes can translocate photosynthates from production sources in the surface canopy to energy sinks (meristems, holdfasts, sporophylls) at rates of 55 to 570 mm h<sup>-1</sup>; the canopy typically represents the greatest contribution to total sporophyte biomass (Nyman et al. 1993, North 1994). Such high rates of productivity and translocation appear to be necessary to maintain sporophyte growth in the face of high metabolic demands (Jackson 1987) because, unlike other perennial kelp genera (e.g., *Pterygophora*), *Macrocystis* sporophytes have very limited nutrient and photosynthate storage capabilities (2 wk; Gerard 1982, Brown et al. 1997). The subsequent reliance on the surface canopy, and the vulnerability of surface canopy fronds to both physical and biological disturbance, results in considerable spatial and temporal variability in *Macrocystis* productivity potential, size structure and overall health.

The linkage between *Macrocystis* sporophyte growth, productivity and biomass therefore results in a plastic response of sporophyte condition to temporal and spatial variability in resource availability (Kain 1982, Reed et al. 1996). The low storage capabilities are clearly disadvantageous during periods of suboptimal environmental conditions, such as occur seasonally in southern California (Zimmerman & Kremer 1986) and the inland waters of southern Chile (Buschmann et al. 2004a). Again, other perennial kelp genera either possess greater storage capabilities or exhibit seasonally offset periods of growth and photosynthesis in order to weather periods of low resource availability (e.g., light or nutrients; Chapman & Craigie 1977, Gerard & Mann 1979, Dunton & Jodwalis 1988, Dunton 1990). At high latitudes, like British Columbia, southeast Alaska, and the Kerguelen and Falkland Islands, *Macrocystis* sporophyte growth follows distinctly seasonal patterns in insolation, with frond elongation ranging from 2 to 4.7 cm day<sup>-1</sup> during the summer maximum (Lobban 1978b, Asensi et al. 1981, Druehl & Wheeler 1986, Wheeler & Druehl 1986, Jackson

1987, van Tüssenbroek 1989d). At lower latitudes, like California, distinct seasonal growth patterns due to variability in insolation were not apparent (North 1971, Wheeler & North 1981, Jackson 1987, Gonzalez-Fragoso et al. 1991, Hernández-Carmona 1996). Instead, Zimmerman & Kremer (1986) described seasonal frond growth rates that corresponded with variability in ambient nutrient concentrations (nitrate), in which frond growth was maximised during winter-spring (12–14 cm day<sup>-1</sup>; upwelling periods) and minimised during summer-fall (6–10 cm day<sup>-1</sup>; non-upwelling periods). In New Zealand, minimum *Macrocystis* frond growth rates also occurred during summer, but were relatively high throughout the remainder of the year (Brown et al. 1997), whereas in northern Chile frond growth rates of 5–10 cm day<sup>-1</sup> were observed with no seasonal variability (Vega et al. 2005). In many regions, light and nutrients can be present well above limiting levels throughout the year (e.g., central California or central Chile) thereby permitting continuously high *Macrocystis* sporophyte productivity (Jackson 1987).

The reliance of *Macrocystis* sporophyte growth and productivity on the biomass and health of the canopy also helps to explain much of the sensitivity of *Macrocystis* to ENSOs, relative to that of other kelp genera (Dayton et al. 1999). There is a strong inverse relationship between water column nitrate concentrations and water temperature (Zimmerman & Robertson 1985, Tegner et al. 1996, 1997, Dayton et al. 1999, Hernández-Carmona et al. 2001). Kelp growth becomes nutrient limited below approximately 1  $\mu$ M nitrate, which typically occurs in southern California when water temperatures rise above 16°C (Jackson 1977, Zimmerman & Robertson 1985, Dayton et al. 1999); the same threshold appears to occur around 18°C in Baja California, Mexico (Hernández-Carmona et al. 2001). During ENSOs, depression of the thermocline shuts down nutrient replenishment via coastal upwelling and decreases the propagation of nutrients via internal waves (Jackson 1977, Zimmerman & Robertson 1985, Tegner et al. 1996, 1997). Due to its limited nutrient storage capabilities, *Macrocystis* canopy biomass begins to deteriorate when tissue nitrogen drops below 1.1% dry weight (Gerard 1982). When frond losses exceed frond initiation, the biomass necessary to sustain meristems is lost and the sporophytes die. Sporophyte mortality was 100% in many *Macrocystis* forests in southern and Baja California following the 1983 and 1997 ENSOs (Dayton et al. 1984, 1992, 1999, Tegner & Dayton 1987, Dayton & Tegner 1989, Hernández-Carmona et al. 1991, Ladah et al. 1999, Edwards 2004), although sporophytes may find refuge in deep water (Ladah & Zertuche-Gonzalez 2004) or within the benthic boundary layer (Schroeter et al. 1995). Finally, during ENSOs, regulatory control over growth of juvenile *Macrocystis* sporophytes shifts from light inhibition under *Macrocystis* surface canopies (Dean & Jacobsen 1984) to nutrient limitation (Dean & Jacobsen 1986).

Extensive plasticity in sporophyte growth is by no means restricted to *Macrocystis* adults. Due to the high temporal variability in sporophyte growth potential and the striking differences in biomass among small and large *Macrocystis* sporophytes, the transition among different size classes can also be delayed in time similar to the arrested development described above for embryonic sporophytes. Santelices & Ojeda (1984a) and Graham et al. (1997) observed that *Macrocystis* juveniles could survive for many months under adult canopies, growing rapidly to adult size when adult densities decreased and light became available. Presumably, light levels under the canopy were adequate to meet the metabolic demands of the juveniles, but inadequate to sustain growth (Dean & Jacobsen 1984). It is unknown, however, how long juveniles or subadults can survive such conditions. Another important feature of *Macrocystis* growth potential is that frond initiation is indeterminate because sporophytes can tolerate sublethal biomass loss (loss of fronds) as long as meristems are present and abiotic conditions are conducive to survival (North 1994). Subsequently, sporophyte age is decoupled from sporophyte size, which can be advantageous for both young and old individuals, but disadvantageous to researchers trying to use size as a proxy of age (Santelices & Ojeda 1984b). Graham (1997) found that large *Macrocystis* sporophytes living in the surf zone suffered greater mortality due to wave action than those that survived sublethal loss

of canopy biomass, which presumably decreased overall sporophyte drag and the likelihood of detachment by waves. Finally, it has been demonstrated that the response of *Macrocystis* juvenile growth to variable nutrient concentrations is under genotypic control (Kopczak et al. 1991), resulting in broad latitudinal variability in sporophyte growth and recruitment potential. Again, it is interesting that such genotypic variation can occur in spite of non-trivial gene flow among *Macrocystis* populations (Coyer et al. 2001).

The reliance of sporophyte growth on surface canopy biomass also constrains reproductive output. Unlike most other kelp genera, *Macrocystis* sporophyll and sorus production can occur continuously given adequate translocation of photosynthates from the surface canopy (Neushul 1963, McPeak 1981, Reed 1987, Dayton et al. 1999, Graham 2002, Buschmann et al. 2006). The number of sporophylls per fertile *Macrocystis* sporophyte varies from 1 to 100+ (Lobban 1978a, Reed 1987, Reed et al. 1997, Buschmann et al. 2004a, 2006), although sporophyll growth rates have yet to be determined. In *Macrocystis*, two processes lead to turnover of reproductive material: growth of sporophylls and production of sori on the sporophylls (Neushul 1963). Both processes decrease in magnitude following either natural or experimental loss of canopy biomass (Reed 1987, Graham 2002), although the cessation of sorus production appears to be more sensitive than sporophyll growth to biomass loss and can result in complete sporophyte sterility within 9 days of disturbance to the canopy (Graham 2002).

It is unknown whether sublethal biomass loss also affects the quantity or quality of zoospores in sori or the timing of their ultimate release into the water column. Due to the continuous reliance of *Macrocystis* reproduction on canopy biomass, however, variability in environmental factors can also greatly affect reproductive output. Reed et al. (1996) demonstrated that nitrogen content of *Macrocystis* zoospores varied as a function of *in situ* water temperature (and presumably water column nutrient concentrations) and nitrogen content of adults, whereas the nitrogen content of *Pterygophora* zoospores remained relatively constant. Reed et al. (1996) argued that the ability of *Macrocystis* sporophytes to respond to favourable environmental conditions allowed them to be reproductively successful despite their relatively short life-span. Again, such plasticity in reproductive timing can be adaptive, especially given the apparently low cost of reproduction in kelps (DeWreede & Klinger 1988, Pfister 1992). For example, *Macrocystis* sporophytes living in wave-exposed locations in southern Chile reproduce year-round and produce high numbers of sporophylls, whereas *Macrocystis* sporophytes living in nearby wave-protected populations are annuals, have increased zoospore production per sorus area and are fertile for only a few months, presumably to ensure successful zoospore settlement and fertilisation prior to the disappearance of adult plants every autumn (Buschmann et al. 2004a, 2006).

Overall, *Macrocystis* sporophyte growth, productivity and reproduction are very responsive to variability in environmental conditions. This response differs from that of most known kelps and other algae (see review by Santelices 1990) and is probably essential to the success of *Macrocystis* as a competitive dominant throughout much of its global distribution. What remains to be determined, however, is how this variable physiology is expressed among the different morphological forms of *Macrocystis* and across the variety of habitats in which *Macrocystis* populations are present. For example, the *integrifolia* and *pyrifera* forms inhabit low intertidal and deeper subtidal environments, respectively, which differ strikingly in factors known to regulate *Macrocystis* growth, productivity and reproduction (e.g., water motion, water quality and light availability). Consequently, it is expected that these two forms will respond differently to environmental perturbations (e.g., van Tüssenbroek 1989c,e), with potentially significant consequences at the population and community levels. This scenario is further complicated by the vegetative growth capabilities of the *integrifolia* form, absent in the *pyrifera* form, because the relative contribution of vegetative growth to sexual reproduction in maintaining *integrifolia*-form giant kelp populations is unknown. Furthermore, kelp physiological studies presently focus on measurements of physiological processes for

specific structures (e.g., photosynthesis, growth, or nutrient uptake of excised laminae), and few have integrated these processes across entire sporophyte thalli (but see the translocation studies of Schmitz & Lobban (1976)). For example, translocation elements (sieve tubes and trumpet hyphae) run through the rhizomes of *integrifolia*-form sporophytes, which may spread over greater lengths of substratum than *pyrifera*-form holdfasts, potentially providing a physiological connectivity among fronds over the scale of metres. This limitation has inhibited the development of realistic carbon and nitrogen budgets for kelps and thus constrained our understanding of the physiology of entire sporophytes. This limitation is critical because it is at the level of individual sporophytes, not individual laminae, that mortality, growth and reproduction have consequences for population biology.

### Population biology of *Macrocystis*

Most of the work on *Macrocystis* population dynamics prior to 1990 focused on processes regulating seasonal-to-annual variability in adult sporophyte mortality (see review by North 1994), including competition (Reed & Foster 1984, Santelices & Ojeda 1984a), herbivory (Harris et al. 1984, Ebeling et al. 1985, Harrold & Reed 1985) and physical disturbance (Rosenthal et al. 1974, Dayton et al. 1984). Stimulated by the research of Reed and his colleagues (Reed 1990, Reed et al. 1988, 1991, 1992, 1996, 1997, 2004), a more population-based approach to *Macrocystis* biology and ecology has recently emerged in which studies have shifted to focus on reproduction, dispersal and recruitment and the consequences of these processes to the persistence of *Macrocystis* populations. Subsequently researchers have developed a more integrated view of *Macrocystis* population dynamics that unites variability in mortality agents with recruitment processes to provide a better understanding of local and global differences in *Macrocystis* population cycles.

#### *Stage- and size-specific mortality*

*Macrocystis* populations do not exhibit unbounded growth (Dayton 1985a, Foster & Schiel 1985, North 1994). Although *Macrocystis* populations are probably never at equilibrium, *Macrocystis* populations often reach an apparent maximum in abundance or biomass per unit area (carrying capacity) that is determined by the availability of environmental resources (e.g., space, light and nutrients; Nisbet & Bence 1989, Burgman & Gerard 1990, Graham et al. 1997, Tegner et al. 1997). Furthermore, it has been well established that a variety of density-dependent and density-independent processes result in stage- and size-specific sporophyte mortality (reviewed by Schiel & Foster 2006) and retain *Macrocystis* at a population level below carrying capacity and initiate population cycling.

Due to their large size and high drag, *Macrocystis* adult sporophytes are extremely vulnerable to removal by high water motion, and wave-induced sporophyte loss is considered the primary factor resulting in *Macrocystis* mortality (Foster 1982, Dayton et al. 1984, Seymour et al. 1989, Schiel et al. 1995, Graham 1997, Graham et al. 1997, Edwards 2004). The probability of a sporophyte being removed from the substratum by passing or breaking waves increases when the force (drag) experienced by the sporophyte due to water motion (related to both water velocity and the cross-sectional area of the sporophyte exposed to the flow; Seymour et al. 1989, Utter & Denny 1996) exceeds the attachment strength of the sporophyte holdfast (for whole sporophyte mortalities) or the breaking strength of individual fronds (for sublethal frond mortality; Utter & Denny 1996). High seasonal and year-to-year variability in wave intensity and sporophyte biomass therefore results in highly variable sporophyte mortality throughout the year. For example, in California, most sporophyte mortalities occur during the first large fall-winter storms (Zobell 1971, Gerard 1976, Graham et al. 1997), when adult biomass is high following long periods of low wave activity (spring to fall). It appears that sporophytes that survive these storms, but shed fronds and canopy



biomass, decrease their overall drag and increase the probability of surviving subsequent and often more severe storms (Graham et al. 1997). On the Chatham Islands, *Macrocystis* populations are only found at protected sites (Schiel et al. 1995) and never attain large sporophyte or population sizes. In southern California, uprooted sporophytes are often observed entangled with attached sporophytes, further increasing the attached sporophytes' drag and probability of detachment (Rosenthal et al. 1974, Dayton et al. 1984) and resulting in a 'snowball effect' that can clear large swaths in the local population (Dayton et al. 1984). Such massive entanglements, however, appear to be rare in central California (Graham 1997), possibly due to more rapid transport of detached sporophytes out of and away from the local population. Increased sporophyte biomass, therefore, simultaneously increases both *Macrocystis* growth and reproductive potential (described in the Organismal biology section) and the probability of wave-induced mortality. This trade-off between fitness and survival is probably viable because of the temporal and spatial unpredictability in wave intensity experienced throughout the alga's global distribution and its ability to survive and quickly recover from sublethal loss of biomass. Exceptions are the wave-protected annual *Macrocystis* populations in southern Chile in which there seems to be no trade-off between reproductive output and survival (Buschmann et al. 2006). In this case, synchronous growth, reproduction and senescence occur in the near absence of water motion.

Despite the high temporal variability in wave-induced mortality, *Macrocystis* sporophytes exhibit distinct spatial patterns in survivorship. Wave-induced mortality of all size classes of adult sporophytes increases with both increasing wave exposure (Foster & Schiel 1985, Graham et al. 1997) and decreasing depth (Seymour et al. 1989, van Tüssenbroek 1989c, Dayton et al. 1992, Graham 1997). These patterns are primarily due to spatial variability in water motion because wave activity increases toward shallow water, the tips of rocky headlands and regions of high storm production (e.g., the relatively stable winter Aleutian low-pressure system in the Northern Hemisphere). Graham et al. (1997), however, also observed that *Macrocystis* holdfast growth decreased significantly along a gradient of increasing wave exposure, possibly due to greater disturbance to the *Macrocystis* surface canopy, which reduces translocation to haptera and thereby reduces holdfast growth (Barilotti et al. 1985, McCleneghan & Houk 1985). Thus, increased wave forces and decreased strengths of holdfast attachment can act in combination to decrease *Macrocystis* sporophyte survival; Graham et al. (1997) observed that *Macrocystis* sporophyte life-spans rarely exceeded 1 yr at their most wave-exposed sites. Although all of these described patterns may possibly exist for any *Macrocystis* life stage, the likelihood of wave-induced mortalities will be much lower for the smaller life stages due to both decreasing thallus size and decreasing water velocities within the benthic boundary layer. Additionally, other hydrographic factors can result in high sporophyte mortalities in relatively wave-protected regions (e.g., tidal surge, nutrient limitation, temperature and salinity stress; Buschmann et al. 2004a, 2006).

Biological processes also clearly play a role in mortality of *Macrocystis* sporophytes. During sea urchin population outbreaks, sea urchin grazing of *Macrocystis* holdfasts can result in (1) detachment of adult sporophytes and their removal from the population (Dayton 1985a, Tegner et al. 1995a), (2) modification of sporophyte morphology (Vásquez & Buschmann 1997) and (3) removal of entire recruits and juvenile sporophytes (Dean et al. 1984, 1988, Buschmann et al. 2004b, Vásquez et al. 2006). Unlike some locations (e.g., the Aleutian Islands; Estes & Duggins 1995), widespread destruction of Californian and Chilean *Macrocystis* populations by sea urchin grazing is rare (Castilla & Moreno 1982, Foster & Schiel 1988, Steneck et al. 2002, Graham 2004). Still, sea urchin outbreaks can result in episodic deforestation of *Macrocystis* populations up to a scale of a few kilometres (Dayton 1985a). In healthy southern California systems, sea urchins can live in *Macrocystis* holdfasts and result in holdfast cavitation and thus a decrease in sporophyte attachment strength (Tegner et al. 1995a). Although episodic and small scale, the prevalence of holdfast cavitation by sea urchins increases with increasing sporophyte age, thereby increasing the vulnerability of

large, older sporophytes to wave-induced mortality (Tegner et al. 1995a). Infestations of *Macrocystis* sporophytes by epizoites and small herbivorous crustaceans (amphipods and isopods) have also been observed worldwide (North & Schaeffer 1964, Dayton 1985b). Most outbreaks of herbivorous crustaceans simply result in sublethal biomass loss (Graham 2002), which will effectively decrease sporophyte drag and thus possibly wave-induced mortality. Crustacean infestations can also occur in the holdfasts and result in increased mortality due to decreased sporophyte attachment strength (North & Schaeffer 1964, Ojeda & Santelices 1984). When carnivorous 'picker' fishes are absent from the water column in both California and Chile, outbreaks of epiphytic sessile invertebrates (bryozoans, kelp *Pecten* spp., spirorbids) often result (Bernstein & Jung 1979, Dayton 1985b), weighing down *Macrocystis* sporophyte canopies and either (1) increasing the likelihood of detachment due to water motion or (2) bringing surface canopy biomass into contact with grazing activities of benthic herbivores (Dayton 1985b). Although seemingly important, there are very few data concerning the importance of these processes in regulating *Macrocystis* mortality worldwide. Finally, although not a natural biological disturbance, human harvesting of *Macrocystis* canopies does not appear to have significant effects on sporophyte survival (Kimura & Foster 1984, Barilotti et al. 1985, Druehl & Breen 1986).

Inter- and intraspecific competition for space and light are important in regulating the survival of *Macrocystis* microscopic stages (gametophytes and embryonic sporophytes) to macroscopic size (juveniles; less than tens of centimetres), and growth of *Macrocystis* juveniles to adult size (Schiel & Foster 2006). Smaller *Macrocystis* thalli are vulnerable to overgrowth by seaweeds and other kelps (Santelices & Ojeda 1984a, Vega et al. 2005), and even by conspecifics in monospecific stands (Schroeter et al. 1995, Graham et al. 1997). Intraspecific competition for space is likely to be most severe at the smaller size classes because critical zoospore settlement densities will result in high densities of microscopic embryonic sporophytes following fertilisation and the large size of adult *Macrocystis* holdfasts (up to 1 m diameter) necessitates that many recruits and juveniles will be smothered as nearby sporophytes grow in size. After *Macrocystis* sporophyte densities are initially thinned by competition for space, competition for light increases as sporophytes begin to grow to the water surface (Dean & Jacobsen 1984). Sporophytes that reach the surface will have enhanced photosynthetic rates and be able to translocate more photosynthates to basal meristems for new frond initiation (North 1994). As such, sporophytes that gain the competitive edge of a surface canopy may become even larger, increasing their likelihood of outcompeting neighbours. Water column nutrients further constrain the maximum amount of surface canopy biomass, apparently regulating the total number of *Macrocystis* fronds per square meter (the frond carrying capacity; North 1994, Tegner et al. 1997). The ontogenetic development of a *Macrocystis* cohort is, therefore, dominated by self-thinning (Schiel & Foster 2006), in which high densities of small individuals ultimately yield much lower densities of very large individuals (North 1994).

The applicability of this self-thinning model in *Macrocystis* populations, however, has not been tested directly. North (1994) estimated the frond carrying capacity of a typical *Macrocystis* population to be 10 fronds m<sup>-2</sup>, whereas Tegner et al. (1997) found frond carrying capacity to vary according to oceanographic climate, being higher during cooler, nutrient-rich conditions (La Niña) and lower during warmer, nutrient-poor conditions (El Niño). Schiel et al. (1995) also observed at the Chatham Islands that a site with larger *Macrocystis* sporophytes had lower population densities than a site dominated by smaller *Macrocystis* sporophytes. Many researchers have estimated that self-thinning ultimately results in adult sporophyte densities of 1 per 10 m<sup>2</sup> (Dayton et al. 1984, 1992, Graham et al. 1997), although the accuracy of this value has never been assessed experimentally. Furthermore, these studies have been restricted to *pyrifera* form populations in central, southern and Baja California. In other systems (e.g., Chile, New Zealand), *pyrifera* form individuals do not grow to large sizes or form large populations (Schiel et al. 1995) and conspicuous self-thinning of these populations has not been observed (Buschmann et al. 2004a, 2006). Similarly,

shallow-water *integrifolia*-form sporophytes exhibit vegetative propagation, resulting in coalescent holdfasts, and the concept of sporophyte self-thinning may be irrelevant to these populations (A. Vega & J.A. Vásquez, unpublished data).

As previously described, *Macrocystis* microscopic stages have high light requirements and are thus highly vulnerable to inter- and intraspecific competition for light (Schiel & Foster 2006). Due to their small size, *Macrocystis* gametophytes and embryonic sporophytes are also highly vulnerable to sand scour (Dayton et al. 1984) and smothering by sediments (Devinny & Volse 1978) and by macro- (Dean et al. 1989, Leonard 1994) and mesograzers (Sala & Graham 2002).

Finally, it should be noted that all of the above mortality agents typically result in small- to mesoscale variability in the stage and size structure of *Macrocystis* populations. During normal conditions, many factors are typically acting to regulate sporophyte survival in a probabilistic fashion, resulting in high variability in sporophyte abundance and size structure at the scale of tens to hundreds of metres (Edwards 2004). During episodic storms and ENSOs, however, multiple factors (e.g., wave intensity and nutrient limitation) may act simultaneously to produce massive stage- and size-dependent mortalities homogeneously over broad spatial scales of 10s to 100s of km (Edwards 2004).

#### *Dispersal, recruitment and population connectivity*

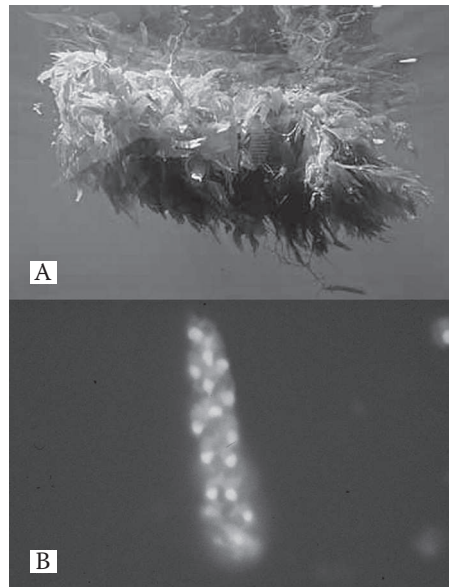
The field ecology of microscopic life-history stages is perhaps the most dynamic and least understood aspect of *Macrocystis* population biology (North 1994), and that of seaweeds in general (Santelices 1990, Amsler et al. 1992, Norton 1992). Previous life-history studies for *Macrocystis* indicate the potential for a wide variety of temporal and spatial variability in the time an individual remains within a life-history stage, or the time necessary to proceed to subsequent stages (Figure 4). This temporal flexibility in the life history begins with dispersal and ultimately results in variability in recruitment and thus demographic interactions within a population (Santelices 1990).

Adult *Macrocystis* sporophytes typically produce zoospores with limited dispersal abilities (e.g., Anderson & North 1966, Dayton et al. 1984, Gaylord et al. 2002, Raimondi et al. 2004), suggesting a tight coupling between zoospore output, dispersal and recruitment (Graham 2003). Recent studies, however, have indicated that the supply of propagules of marine organisms can be decoupled from the adult demographic and genetic patterns, as propagules are dispersed far from their natal site (e.g., Roughgarden et al. 1988, Downes & Keough 1998, Wing et al. 1998, Shanks et al. 2000). This decoupling also seems to apply to *Macrocystis* (Reed et al. 1988, 2004, 2006, Gaylord et al. 2002), especially when the populations are not large enough for modification of currents by the canopy (Jackson & Winant 1983, Jackson 1998, Graham 2003). Because of their small size, *Macrocystis* zoospores will clearly be transported as far as available currents advect them (Gaylord et al. 2002). However, if adult sporophytes modify current directions and velocities, effective zoospore dispersal can be decreased, coupling zoospore supply to relative changes in the density and size structure of the adult sporophytes (Graham 2003). Subsequently, *Macrocystis* forests can vary between ‘open’ and ‘closed’ populations, depending on their size, isolation and geographic location (Graham 2003, Reed et al. 2004, 2006). Furthermore, *Macrocystis* zoospore dispersal can be enhanced by episodic periods of high zoospore production that coincide with storms (Reed et al. 1988, 1997), large population sizes (and thus high source zoospore concentrations; Reed et al. 2004, 2006) and turbulent resuspension of zoospores within the benthic boundary layer (Gaylord et al. 2002). Together, spatial and temporal variability in water motion, zoospore output and *Macrocystis* forest size results in high variability in the effective ranges of zoospore dispersal (Reed et al. 2006).

Nevertheless, it is likely that the dispersal dynamics described for a few large *Macrocystis* forests in southern California are unique to this region (e.g., Point La Jolla and Point Loma at 1–8 km<sup>2</sup>; Dayton et al. 1984, Graham 2003, Reed et al. 2006) because most *Macrocystis* forests

worldwide are relatively small (<1 km<sup>2</sup>) and consist of narrow belts that fringe coastlines and nearshore islands. In these cases, the retention of zoospores within the small natal adult populations will be decreased, potentially reducing the probability of self-seeding of the populations and thus increasing the reliance of the population on external propagule sources (Reed et al. 2004, 2006). The potential for long-distance dispersal to effectively connect these small populations that occur over broad regions (e.g., in central California, Chile, Australia, New Zealand) has not been tested but models suggest that regional population connectivity via zoospore dispersal is likely (Reed et al. 2006). Furthermore, alternative mechanisms for colonisation and population persistence should be explored in these systems. For example, long-distance dispersal by means of drifting sporophytes or reproductive fragments has been suggested as an important mechanism for *Macrocystis* colonisation (Figure 5; Anderson & North 1966, Dayton et al. 1984, Macaya et al. 2005, Hernández-Carmona et al. 2006). Drifting reproductive sporophytes have been shown to be abundant along broad regions of the Chilean and Californian coasts (Macaya et al. 2005, Thiel & Gutow 2005a, Hernández-Carmona et al. 2006), and drifting sporophytes can remain reproductively viable in central California for over 125 days (Hernández-Carmona et al. 2006).

Clearly, dispersal distance alone cannot explain variability in local or remote recruitment, including the colonisation of new substrata (Reed et al. 1988, 2004, 2006). Critical zoospore settlement densities necessary for *Macrocystis* recruitment will inherently limit effective dispersal distance to much less than the distance travelled by individual zoospores (Gaylord et al. 2002, Reed et al. 2006). The key to long-distance colonisation, therefore, is not the arrival of a kelp propagule to new substrata, but rather the arrival of two propagules (of opposite sex) within millimetres of each other and their ultimate survival to sexual maturity. As such, new colonisations are rarely



**Figure 5** (A) Drifting *Macrocystis* sporophyte, southern California. (Published with permission of Phillip Colla/Oceanlight.com.) (B) Epi-fluorescent micrograph of drifting *Macrocystis* sporangia observed in water sample (15 m depth) from Point Loma kelp forest, southern California (note individual zoospores with plastids). (Photograph by Michael Graham.) *Macrocystis* identification based on species-specific spectrophotometric signature (Graham 1999).

observed farther than tens of metres from individual *Macrocystis* sporophytes (Anderson & North 1966, Dayton et al. 1984, Reed et al. 2004, 2006) or hundreds of metres from *Macrocystis* populations (Anderson & North 1966, Reed et al. 2004, 2006). Physical and biological processes that promote the arrival of zoospore aggregations to suitable substrata will, however, enhance the frequency of long-distance colonisation. For example, Reed et al. (1997) observed a synchronous decline in *Macrocystis* sorus area that was correlated with increased storm-induced water motion, potentially indicating a synchronous bout of reproductive output. The locally increased density of zoospores in the water column, and the high along-shore advection that occurs during such storms, may help to extend the colonisation distance (Gaylord et al. 2002). Similarly, annual *Macrocystis* populations in southern Chile exhibit increased zoospore production per soral area over short reproductive periods, potentially increasing the temporal aggregation of settled zoospores (Buschmann et al. 2006). Other kelps also synchronise reproductive output (McConnico & Foster 2005), increasing the likelihood that critical zoospore settlement densities will be exceeded, if only for a short time. Drifting *Macrocystis* sporophytes may provide an additional aggregation mechanism because reproductive sporophylls will travel together (Hernández-Carmona et al. 2006) and Dayton et al. (1984) observed a path of recruitment in the trail of a drifting reproductive *Macrocystis* sporophyte. Additionally, the detachment and dispersal of reproductive sporophylls, or even intact sporangia (Figure 5), during periods of high reproductive output may also increase colonisation distances as long as a high density of zoospores is released and they gain attachment to the substratum. Benthic invertebrates that catch and eat such drifting reproductive fragments may facilitate this process (Dayton 1985a).

In order to reach suitable settlement substratum, *Macrocystis* zoospores must enter the benthic boundary layer where they respond to a chemically, physically and biologically heterogeneous microenvironment (Amsler et al. 1992). At this microscale, zoospores can orient their movement relative to nutrient gradients (Amsler & Neushul 1989) and settle preferentially in regions of high micronutrient concentrations (Amsler & Neushul 1990); all kelp zoospores lack eyespots (Henry & Cole 1982) and therefore are not phototactic (Müller et al. 1987). Energetic resources to support zoospore swimming appear to come from a combination of zoospore photosynthesis and lipid reserves (Reed et al. 1992, 1999). These experiments suggest an adaptation that enhances the probabilities for settlement in suitable microenvironments for growth and reproduction of gametophytes (Amsler et al. 1992). Upon settlement, the survival of *Macrocystis* gametophytes is low, with <0.1% of the female gametophytes being fertilised (Deysher & Dean 1986a).

Microscopic stages, however, should not be considered simply an obstacle in the *Macrocystis* life history that must be overcome in order for populations to persist. In fact, recent studies have suggested that the microscopic stages may play a key role in population persistence by allowing *Macrocystis* to survive environmental conditions that are unfavourable to macroscopic sporophytes. Ladah et al. (1999) observed rapid and widespread *Macrocystis* recruitment following ENSO 1997–1998, which completely destroyed *Macrocystis* sporophytes over a 500-km region. The lack of nearby reproductive adults and homogeneity in recruitment over this broad region suggested that long-distance zoospore dispersal or individual drifting sporophytes were not the source of recovery (although deep-water refuges were possible; Ladah & Zertuche-Gonzalez 2004). Ladah et al. (1999) concluded that recruitment from persistent microscopic stages must have fuelled the recovery, similar to the assumption by Buschmann (1992) that over-wintering microscopic stages must link consecutive annual *Macrocystis* populations in southern Chile. Clearly, microscopic stages of many kelp taxa can persist through adverse environmental conditions, although field studies by Deysher & Dean (1986b) and Reed et al. (1997) have suggested that this is not true for *Macrocystis*. Kinlan et al. (2003) recently demonstrated that the development of *Macrocystis* embryonic sporophytes could be delayed under limited light and nutrients for at least 1 month. When resources

were restored, the surviving embryonic sporophytes grew quicker and reached larger sizes than their 'well-fed' controls. Durations of arrested development >1 month were not explored, yet the identification of *Macrocystis* embryonic sporophytes (rather than gametophytes) as a potentially persistent stage may be important because high zoospore settlement densities are no longer necessary for recruitment. In any case, the arrested development of *Macrocystis* microscopic stages probably results from negligible growth due to inadequate resources (e.g., light or nutrients) rather than a true physiological state of dormancy as in many terrestrial seed plants.

Numerous studies have identified low benthic irradiance as a key environmental factor limiting *Macrocystis* recruitment (e.g., Dean & Jacobsen 1984, Reed & Foster 1984, Santelices & Ojeda 1984a, Deysher & Dean 1986b, Schroeter et al. 1995, Kinlan et al. 2003). In the field, such light limitation along the deep limit of *Macrocystis* is typically due to poor water quality and high light extinction with depth (e.g., Spalding et al. 2003). Between the shallow and deep limits, overlying canopies of kelp, foliose and coralline algae regulate light available for *Macrocystis* recruitment (e.g., Dean & Jacobsen 1984, Reed & Foster 1984, Santelices & Ojeda 1984a). *Macrocystis* sporophytes that recruit to turf algae are typically removed by water motion before becoming firmly attached to the substratum (Leonard 1994, Graham 1997). In fact, one of the few patterns to emerge clearly for *Macrocystis* populations worldwide is that disturbances to *Macrocystis* canopies are typically followed by *Macrocystis* recruitment (Dayton & Tegner 1984, Dayton et al. 1984, 1992, 1999, Reed & Foster 1984, Santelices & Ojeda 1984a, Graham et al. 1997). However, in annual *Macrocystis* populations present in southern Chile, there is a time lag of 3–5 months between the disappearance of the canopy and subsequent recruitment (Buschmann et al. 2006). This population is also unique in that most *Macrocystis* sporophytes recruit to and grow upon the shells of large filter-feeding slipper limpets (*Crepidula*; Buschmann 1992). Finally, Raimondi et al. (2004) have recently demonstrated inbreeding depression (reduced growth) of *Macrocystis* recruits due to self-seeding in close proximity to adult sporophytes. Thus, although most zoospores may only travel short distances, inbreeding depression may select for cross-seeded recruits and enhance the effectiveness of long-distance zoospore dispersal in driving within-population recruitment. The population consequences of this intriguing result await exploration.

The vegetative propagation of *integrifolia*-form sporophytes following sporophyte recruitment may enhance the persistence of *Macrocystis* populations, especially in the absence of consistent zoospore supply. Buschmann et al. (2004a) observed low sporophyte fecundity in small and narrow northern Chilean *integrifolia*-form populations relative to the larger central Chilean and *pyrifera*-form populations, suggesting that sexual reproduction is less effective in these shallow-water populations. Therefore, the role of dispersal in *Macrocystis* population dynamics must be considered relative to the specific environmental and demographic contexts within which the populations exist, especially with regard to population size and isolation, near-shore hydrodynamics, regeneration capacity and differences in sexual and vegetative reproductive potential among *Macrocystis* forms. It is important to note that recruitment to *integrifolia*-form populations is noticeably absent in California (Setchell 1932, Graham 1996) but relatively common in British Columbia (Druehl & Wheeler 1986) and northern Chile (Vega et al. 2005).

The ultimate consequence of 20+ yr of research on *Macrocystis* sporophyte mortality, propagule dispersal and population recruitment has been the integration of available data to support the functioning of regional *Macrocystis* forests as metapopulations (Reed et al. 2006). Reed et al. (2006) estimated that the frequency of local extinctions and recolonisations for *Macrocystis* populations in southern California occurred over broad temporal scales (months to 10+ yr). Local extinction rates decreased with increasing population size and decreasing population isolation, with extinction durations rarely exceeding 2 yr. Reed et al. (2006) also identified a broad spectrum of interpopulation distances (hundreds of metres to tens of kilometres). It is suggested here that the broad array of *Macrocystis* dispersal vectors, effects of local hydrodynamics, coupling of dispersal distances

to forest size and the potential persistence of microscopic life-history stages may again be advantageous to maintaining demographic and genetic connectivity with *Macrocystis* metapopulations.

### *Demography and population cycles*

Temporal variability in *Macrocystis* sporophyte abundance ranges from highly predictable to chaotic, depending on the spatiotemporal scales of interest. In some locations, sporophyte mortality can be synchronised over broad spatial scales, typically driven by predictable seasonal mortalities, such as in the wave-exposed regions of South America (Barrales & Lobban 1975, Dayton 1985b) and California (Foster 1982, Dayton et al. 1984, Graham et al. 1997). Given the potential for continuous *Macrocystis* recruitment, recruitment suppression by surface canopies, and the potential for delayed recruitment, the response to these synchronised mortalities can be rapid and massive (Dayton & Tegner 1984, Dayton et al. 1984) or delayed (Graham et al. 1997). Graham et al. (1997) found that recruitment to adult size following winter mortalities was often delayed for many months at wave-exposed sites on the Monterey Peninsula in California, due presumably to a lack of recruits present to exploit the canopy opening. Although the cause of the recruitment delay was not identified, Graham et al. (1997) suggested that production of new adults actually occurs in two stages: first, the recruitment of macroscopic sporophytes (requiring both fertilisation and growth to macroscopic size), and second, sporophyte growth to adult size. Nevertheless, recruitment appears to drive *Macrocystis* population dynamics (Dayton et al. 1992, Graham et al. 1997, Buschmann et al. 2006).

Graham et al. (1997) further suggested that the timing and magnitude of the disturbance determined whether the recruitment stages occur in rapid succession or are separated by a delay. For example, in the Point Loma kelp forest in southern California, Dayton et al. (1984, 1992, 1999) have repeatedly observed massive recruitment to adult size following ENSOs (4- to 7-yr frequency). In this case, pre-ENSO adult populations hover around carrying capacity with ENSOs typically removing entire sporophytes from the majority of the population and allowing recruits to grow quickly to adult size. In central California, however, the primary disturbance is caused by annual storms that produce a mosaic of both lethal and sublethal mortalities (Graham et al. 1997, Edwards 2004), and the populations never truly reach carrying capacity. Individual sporophytes may be lost, but canopies often recover quickly, decreasing the likelihood that recruits can grow directly to adult size. As such, the massive synchronised recruitment that drives long-term cycles in *Macrocystis* population dynamics in southern California (Dayton et al. 1984, 1992, 1999) may be typical of regions that experience large, yet episodic disturbances (e.g., ENSO in California and Chile; Edwards 2004, Vega et al. 2005), whereas regions that experience more chronic annual disturbances may experience more unpredictable population cycling, such as in California (Graham et al. 1997) and Chile (Buschmann et al. 2004a). Such a generalisation is consistent with the population modelling studies of Nisbet & Bence (1989) and Burgman & Gerard (1990).

The effect of ENSO on *Macrocystis* population cycling also appears to vary among ENSOs. Both ENSO-induced storms and nutrient deprivation are major sources of *Macrocystis* mortality (Dayton et al. 1984, 1992, 1999, North 1994, Edwards 2004). During the 1982–1983 ENSO in California, large storms preceded the period of anomalously warm temperature and high nutrient stress (Dayton & Tegner 1984, Dayton et al. 1984), decimating *Macrocystis* populations throughout their range (Tegner & Dayton 1987). During the 1997–1998 ENSO, however, southern and Baja California kelp populations deteriorated in anomalously warm temperature prior to the massive winter storms of 1998 (Edwards 2004). As a result, some sporophytes survived in deeper water (Dayton et al. 1999, Edwards 2004, Ladah & Zertuche-Gonzalez 2004), potentially due to the decreased drag of sublethal loss of canopy biomass. Again, in both cases, the combination of open space cleared by storms, reduced canopy shading and subsequent La Niña conditions led to intense

recruitment in the spring (Dayton et al. 1984, 1992, 1999). Increased abundance of understory kelps (e.g., *Pterygophora californica*, *Laminaria farlowii* and *Eisenia arborea*), usually inferior competitors to *Macrocystis*, became well established during ENSO, persisted for many years post-ENSO (Dayton & Tegner 1984, Dayton et al. 1984, 1999) and was shown to suppress *Macrocystis* recruitment in local areas (e.g., Edwards & Hernández-Carmona 2005).

In the southeast Pacific, Soto (1985) also reported a massive mortality of *Macrocystis* from 18 to 30°S during ENSO 1982–1983, resulting in a collapse of the kelp harvest from 1983 to 1986 in northern Chile (National Fishery Service, SERNAPESCA 1980–1990). No such mortalities were witnessed, however, in northern Chile *Macrocystis* populations during ENSO 1997–1998 (Vega et al. 2005) where *Macrocystis* abundances were reduced but soon replaced by high recruitment. The absence of an ENSO-induced *Macrocystis* collapse in northern Chile suggested (1) differential effects of various ENSOs at different localities along the coastline; (2) presence of ‘source’ localities (Camus 1994), which, due to certain attributes of the habitat, were able to maintain *Macrocystis* populations that provided reproductive propagules to disturbed populations (‘sink’ localities); (3) the existence of persistent microscopic life-history stages (Santelices et al. 1995) and (4) differential effects of ENSO on intertidal versus subtidal *Macrocystis* populations. Unpredictably, *Macrocystis* populations in northern Chile began to decrease following ENSO 1997–1998, apparently as a result of La Niña 1999 (Vega et al. 2005). The direct cause remains unknown but is linked to *Macrocystis* recruitment failure.

### Ecology of *Macrocystis* communities

One of the most interesting aspects of any *Macrocystis*-dominated system is the linkage between the dynamics and productivity of *Macrocystis* populations and the diversity and structure of their associated floral and faunal communities. Indeed, the functional importance of *Macrocystis* within giant kelp communities was apparent to even the earliest kelp forest ecologists (see, e.g., Darwin 1839). Here, recent advances in *Macrocystis* community ecology are explored through a discussion of the structural role of *Macrocystis* within the system, resulting predator-prey interactions and food web dynamics, and the effects of exploitation and global climate changes on the biodiversity and stability of these coastal systems on global scales. The focus is on a mechanistic understanding of *Macrocystis* systems; a more comprehensive treatment of *Macrocystis* community ecology can be found in Foster & Schiel (1985).

#### *Macrocystis* as a foundation species

*Macrocystis* is the tallest benthic organism (Steneck et al. 2002). Due to their complex morphology, *Macrocystis* sporophytes can alter abiotic and biotic conditions by dampening water motion (Jackson & Winant 1983, Jackson 1998), altering sedimentation (North 1971), shading the sea floor (Reed & Foster 1984, Edwards 1998, Dayton et al. 1999, Clark et al. 2004), scrubbing nutrients from the water column (Jackson 1977, 1998), stabilising substrata (Neushul 1971, North 1971), providing physical habitat for organisms both above and below the benthic boundary layer (reviewed by Foster & Schiel 1985) and providing fixed carbon (from drift kelp to particulate and dissolved organic carbon) within *Macrocystis* forests (Gerard 1976) and to surrounding habitats (reviewed by Graham et al. 2003). The irony for *Macrocystis* community ecologists is that this complex role of *Macrocystis* as the foundation of its associated community is both the impetus for mechanistic community ecology studies and yet is the primary impediment to such studies.

There are three primary components to direct provision of habitat by *Macrocystis* sporophytes: the holdfast, the mid-water fronds, and the surface canopy (Foster & Schiel 1985). *Macrocystis* holdfasts are complex structures comprising numerous dichotomously branched and intertwined



haptera and are colonised by a highly diverse assemblage of algae, invertebrates and fishes (Figure 2A,B; Fosberg 1929, Andrews 1945, Cribb 1954, Ghelardi 1971, Jones 1971, Beckley & Branch 1992, Vásquez 1993, Thiel & Vásquez 2000). Haptera typically initiate from the primary stipe dichotomy, with new haptera forming above older ones. The haptera generally grow until they reach the substratum, thereby forming holdfasts that are initially 2-dimensional structures, and depending on age, may ultimately become large 3-dimensional mounds. As the holdfasts grow, new biomass accumulates along the outer surface, whereas the older biomass in the centre of the holdfast becomes necrotic and cavitates (Cribb 1954, Ghelardi 1971, Tegner et al. 1995a). As such, large holdfasts can provide different quantities and qualities of available habitat than smaller ones; large holdfasts are generally restricted to *angustifolia*-, *laevis*- and *pyrifera*-form sporophytes (Figure 2A), whereas the flat strap-like rhizomes of *integrifolia*-form sporophytes offer little habitat to kelp forest organisms (Figure 2B; Scagel 1947).

Most work on *Macrocystis* holdfast communities has focused simply on species enumeration (Ghelardi 1971, Jones 1971, Beckley & Branch 1992, Vásquez et al. 2001) and patterns of faunal abundance and diversity as a function of holdfast size (Andrews 1945, Thiel & Vásquez 2000) or time since dislodgement of holdfasts from the substratum (Vásquez 1993). Large holdfasts are often encrusted with bryozoans and sponges and serve as refuges for crustaceans (e.g., amphipods), molluscs, brittlestars and sea urchins, especially in the large cavitated centres of older holdfasts; small holdfasts typically house the more mobile invertebrates (e.g., amphipods). Occasional herbivore outbreaks within *Macrocystis* holdfasts may contribute to sporophyte mortalities, especially for large sporophytes (Jones 1971, Tegner et al. 1995a). Due to the dynamic nature of *Macrocystis* populations, high variability in sporophyte size and intersporophyte distances may be of primary importance in driving the abundance and diversity of holdfast communities within a population, as predicted by ‘island biogeography’ theory (Thiel & Vásquez 2000). Nevertheless, it has not been determined whether *Macrocystis* holdfast communities are of functional importance within the larger kelp forest system.

The mid-water fronds and surface canopies are also host to a variety of fishes, sessile and mobile invertebrates, and even birds and pinnipeds (reviewed by Graham 2004, Graham et al. 2007). Encrusting bryozoans, hydroids and occasionally bivalves (*Pecten*) may cover large portions of mid-water fronds (Scagel 1947, Wing & Clendenning 1971, Bernstein & Jung 1979, Dixon et al. 1981, Dayton 1985a,b, Hurd et al. 1994), which are inherently older than their surface-water counterparts. The bulk of the faunal biomass in the mid-water, however, is locked up in crustaceans, grazing molluscs (e.g., top and turban snails; Watanabe 1984a,b, Coyer 1985, 1987, Stebbins 1986) and juvenile and adult fishes, which use the habitat as refuge, for foraging or as a focus of aggregations (Bray & Ebeling 1975, Moreno & Jara 1984, Ebeling & Laur 1985, Hallacher & Roberts 1985, DeMartini & Roberts 1990, Holbrook et al. 1990, Stephens et al. 2006). The *Macrocystis*-fish association may be weaker, however, in areas with high relief (Stephens et al. 1984). Again, the importance of these faunal components to the system as a whole has not been addressed.

The functional importance of *Macrocystis* canopies to the dynamics of the kelp forest community, however, is well established. *Macrocystis* canopies are important recruitment sites for many species of near-shore fishes (Carr 1989, 1991, 1994, Anderson 1994, Stephens et al. 2006), and the direct link between canopy biomass, frond density or sporophyte density and fish abundance has been demonstrated (Carr 1989, 1991, 1994, DeMartini & Roberts 1990, Holbrook et al. 1990, Anderson 1994, 2001). These fish assemblages are important in controlling canopy herbivore outbreaks (Bray & Ebeling 1975, Bernstein & Jung 1979, Dayton 1985a,b, Tegner & Dayton 1987, Graham 2002), except in South America where canopy ‘picker-fish’ assemblages are apparently absent (Dayton 1985b, Vásquez et al. 2006). Nevertheless, the *Macrocystis*-fish relationship is complex. Some kelp forest fish taxa show a negative relationship with *Macrocystis* abundance

(e.g., *Embiotoca lateralis*), apparently due to the negative effect of *Macrocystis* on subsurface algal assemblages that are important fish foraging habitats (Ebeling & Laur 1985, Holbrook et al. 1990). It remains to be seen, however, whether such conspicuous habitat associations are specific to the relatively benign regions in which they have been tested (e.g., southern California) or may also be general to regions with higher spatial and temporal variability in *Macrocystis* population dynamics. Furthermore, there appear to be no studies of fish-*Macrocystis* associations that have focused on the shallow-water *angustifolia* or *integrifolia* forms.

*Macrocystis* sporophytes continue to provide habitat resources after detachment from the substratum. Holdfast, mid-water fronds and canopies can retain epifaunal fishes and mobile and sessile invertebrates even when drifting sporophytes travel long distances (Edgar 1987, Vásquez 1993, Helmuth et al. 1994, Hobday 2000a,b,c, Smith 2002, Macaya et al. 2005, Thiel & Gutow 2005a,b). In some cases, new species are added from the plankton to the communities on the *Macrocystis* drifters (Hobday 2000c, Thiel & Gutow 2005b). Eventually the drifters (1) are deposited onto coastal beaches where they can be buried or the pneumatocysts may break causing sporophytes that are resuspended by high tides to be transported to deep water habitats (Zobell 1971), (2) lose their buoyancy at sea and sink directly to deep-water habitats (Harrold & Lisin 1989), (3) aggregate at convergence zones where they may grow vegetatively for undetermined durations (North 1971, van Tüssenbroek 1989b, Thiel & Gutow 2005a) or (4) reconnect with coastal *Macrocystis* populations (Hobday 2000a, Thiel & Gutow 2005b).

Additional habitat and trophic associations become apparent at the scale of *Macrocystis* populations rather than individuals, probably due to the variety of ways that kelp forests affect the near-shore environment. Kelp forests tend to be darker, less hydrodynamic habitats than adjacent rocky reefs (Dayton 1985a, Foster & Schiel 1985) and it has been hypothesised that large kelp forests may be sites where fixed carbon accumulates in the form of detritus (from drift kelp to small particulates) (Gerard 1976, Harrold & Reed 1985, Graham et al. 2007). It is therefore not surprising that up to 35% of 275 common kelp forest taxa (flora and fauna) in the southern California Channel Islands were found to be associated with the presence of *Macrocystis* (Graham 2004), 25% of which were obligate associates; >90% of the taxa were more common in forested areas than deforested areas. Many of these associates had either clear trophic linkages with *Macrocystis* (e.g., abalones) or the associations were driven by habitat provision (e.g., kelp surfperch *Brachyistius frenatus*).

Similar forestwide associations are found for *Macrocystis* populations in northern Chile, although species richness is much less than in California (Figure 6). Interestingly, the Chilean data show first that the presence of other kelp taxa (e.g., *Lessonia*) can also drive changes in kelp forest assemblage structure, and second that different species of kelp (e.g., *Macrocystis* vs. *Lessonia*) may differ in the quality and quantity of habitat that they provision. Furthermore, Vega et al. (2005) recently demonstrated that the morphology of the understory subtidal kelp *Lessonia trabeculata* varies in the presence/absence of *Macrocystis*, potentially resulting in additional effects of *Macrocystis* distribution on community structure. Still, these studies have relied on natural kelp deforestations, for example due to sea urchin overgrazing, which can produce various factors that confound variability in kelp presence. As such, the direct isolation of the importance of *Macrocystis* energy and habitat provision relative to that of other kelps or non-kelp macroalgae species remains elusive (Graham et al. 2007). Finally, due to the different growth rates and distribution of canopy biomass among the different forms of *Macrocystis* (e.g., *pyrifera* vs. *integrifolia* forms), shallow- and deep-water *Macrocystis* populations may also provide trophic and habitat resources in different ways. For example, interfrond distances among shallow *integrifolia*- and *angustifolia*-form sporophytes (Figure 2D) are much more homogeneous than their deeper *pyrifera*-form counterparts (Figure 2C), where high stipe densities are aggregated around individual sporophytes that are widely spaced. Such ecotypic variability in the spatial distribution of suitable habitat (i.e., canopy fronds) may

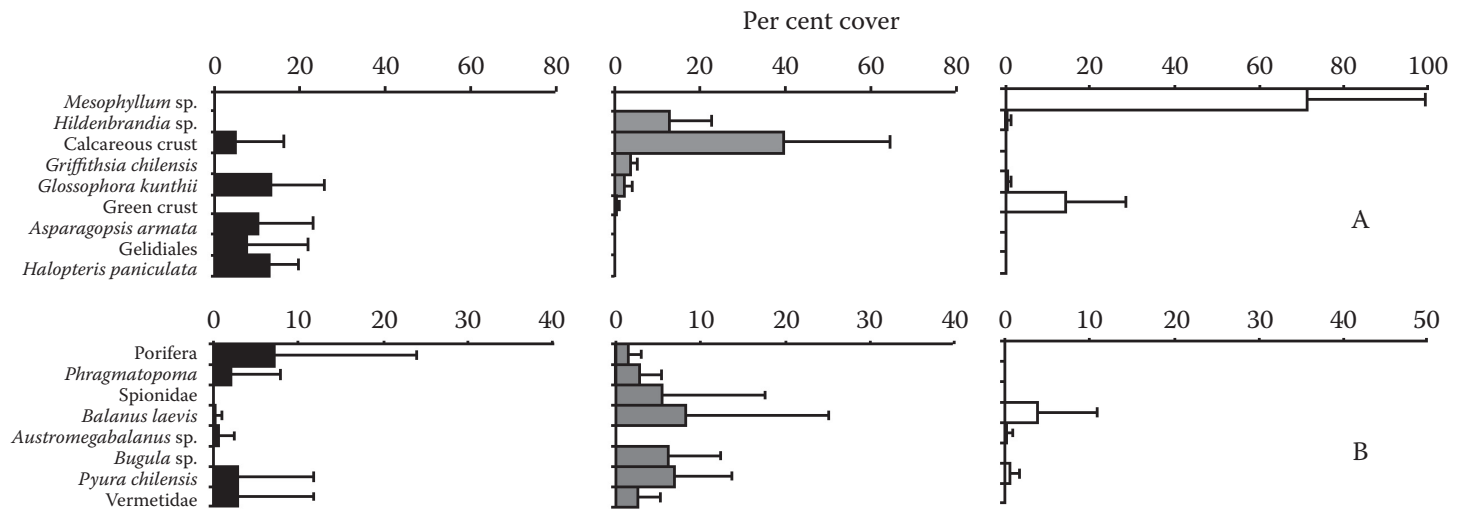
affect the nature and strength of species associations in shallow versus deep water, especially among fish taxa that preferentially use the canopy, mid-water fronds or water column spaces.

### *Trophic interactions and food webs*

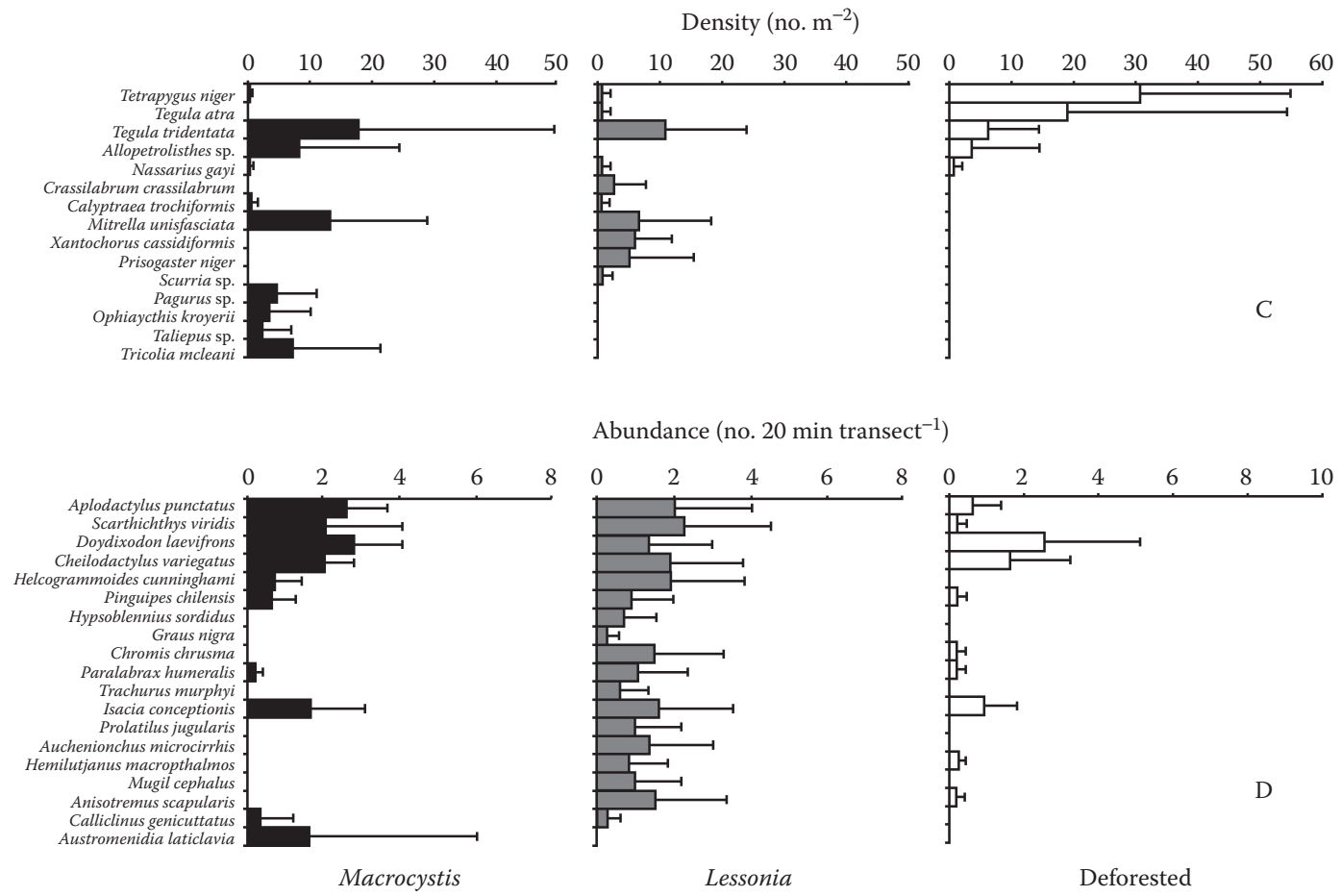
During his initial observations of *Macrocystis* forests in southern Chile, Darwin (1839) was struck by the high diversity of species that appeared to be trophically linked to energy provision by *Macrocystis*. He professed “The number of living creatures of all orders, whose existence intimately depends on the kelp, is wonderful”. Indeed, all described *Macrocystis* forests harbour tens to hundreds of species, most of which feed either on *Macrocystis*-derived fixed carbon (from direct grazing to filter-feeding on *Macrocystis* detritus) or within some predatory trophic subweb founded upon *Macrocystis*-based herbivores (Graham et al. 2007). Although food web studies are rare (reviewed by Graham et al. in press), most species lists from within *Macrocystis* forests contain taxa from multiple trophic levels, often with numerous taxa within each level, and typically a wide variety of generalist and specialist species. It therefore seems unnecessary to review here the nature of trophic interactions within *Macrocystis* forests. Instead, the focus is specifically on recent studies of the fate of *Macrocystis*-based primary productivity and the importance of trophic interactions in the dynamics and stability of *Macrocystis* forests because these are topics of global interest.

Gerard (1976) and Pearse & Hines (1976) estimated that although central Californian *Macrocystis* sporophytes had very high standing stock, most *Macrocystis*-based productivity entered the food web through detrital pathways. Storm waves rip entire sporophytes from the substratum, break fronds and erode senescent blades, sending detrital material of a wide size range to either the kelp forest floor or out of the forest to other systems. Large detrital pieces (i.e., drift) collect near the bottom where they are heavily grazed by asteroids, crustaceans (crabs, amphipods, isopods), snails and fishes (Leighton 1966, Feder et al. 1974, Gerard 1976, Pearse & Hines 1976, Beckley & Branch 1992, Kenner 1992, Hobson & Chess 2001; see also reviews by Castilla 1985, Foster & Schiel 1985, Graham et al. 2007). When present, large pieces of *Macrocystis* drift make up the primary diet of sea urchins (Leighton 1966, Castilla & Moreno 1982, Dayton et al. 1984, Vásquez et al. 1984, Castilla 1985, Ebeling et al. 1985, Harrold & Reed 1985). In Chile, *Tetrapygyus niger* and *Loxechinus albus* can catch drift in *Macrocystis* forests (Castilla 1985, Rodriguez 2003) but to a lesser extent than *Strongylocentrotus franciscanus* or *S. purpuratus* in the northeast Pacific (Harrold & Reed 1985, Harrold & Pearse 1987). When deprived of drift, *S. franciscanus* or *S. purpuratus* abandon their normal ‘sit and catch drift’ strategy in search of attached algae (Mattison et al. 1977, Ebeling et al. 1985, Harrold & Reed 1985, Harrold & Pearse 1987), a behavioural switch not observed for other sea urchin taxa (Vásquez & Buschmann 1997, Steneck et al. 2002). *Macrocystis* drift is also the main component of the diet of abalone in California (Leighton 1966, Tutschulte & Connell 1988) and sea urchins and abalone are thought to compete strongly when *Macrocystis* drift is in short supply (Tegner & Levin 1982). In the absence of drift, abalones often decrease in abundance or disappear from the local system entirely (e.g., Graham 2004). Smaller detrital pieces (i.e., particulate organ carbon, POC) make *Macrocystis*-based productivity accessible to many more taxa (e.g., polychaetes, bivalves, sponges, crustaceans, ophiuroids, mysids or basically any kelp forest detrital or filter feeder; Clarke 1971, Foster & Schiel 1985, Beckley & Branch 1992, Kim 1992, Graham 2004, Graham et al. 2007). Therefore, it is not surprising that sessile filter feeders and mobile herbivores can be extremely diverse in *Macrocystis* forests (100+ taxa), with many taxa disappearing during local *Macrocystis* deforestation (Graham 2004).

The direct grazing pathway is also utilised by a high diversity of kelp forest herbivores (Rosenthal et al. 1974, Gerard 1976, Pearse & Hines 1976, Moreno & Sutherland 1982, Castilla 1985, Foster & Schiel 1985, Graham 2004, Graham et al. 2007). Snails, crustaceans, asteroids and fishes can graze the benthic and water column biomass of *Macrocystis* sporophytes. These herbivores



**Figure 6** Macroscopic species abundances in areas of sea urchin overgrazing (deforested), *Lessonia trabeculata* forests and *Macrocystis (integrifolia-form)* forests for northern Chile (3–15 m depth). (A) Per cent cover of macroalgae; (B) per cent cover of sessile invertebrates.



**Figure 6** (continued) (C) density of mobile invertebrates (no. m<sup>-2</sup>); (D) abundance (no. 20 min<sup>-1</sup> of visual survey) of fishes. Data are means ± SD; sample sizes range from 34 to 136. Data are from Nuñez & Vásquez (1987), Vásquez et al. (1998), Salinas (2000) and W. Stotz, J. Aburto & L. Cailleaux, unpublished data.

generally have low per capita consumption rates (e.g., Jones 1971, Sala & Graham 2002) and probably have little impact on *Macrocystis* standing stock, except during population explosions (Jones 1971, Tegner & Dayton 1987, Graham 2002) or when *Macrocystis* sporophytes are small in size (e.g., during recruitment or recovery following disturbance; Moreno & Sutherland 1982, Harris et al. 1984, Castilla 1985, Sala & Graham 2002, Buschmann et al. 2004b). It is unknown whether the diversity of these herbivores within *Macrocystis* forests may enhance or lessen the effects of herbivory on *Macrocystis* survival and population dynamics, through complementarity or competition, respectively.

It is well known, however, that sea urchins can have a great impact on *Macrocystis* standing stock through direct grazing (Lawrence 1975, Pearse & Hines 1979, Schiel & Foster 1986, Harrold & Pearse 1987, Vásquez & Buschmann 1997, Steneck et al. 2002, Vásquez et al. 2006). In some systems (e.g., southern Chile), *Macrocystis* fronds can be weighted down by epizoites and sea urchins can heavily graze water column biomass directly (Dayton 1985b). In most cases, however, the greatest impact of sea urchin grazing on *Macrocystis* biomass is when sea urchins aggregate on holdfasts and detach entire sporophytes, which then drift out of the system (North 1971, Foster & Schiel 1985); sea urchins (and potentially other herbivores) may then keep the system in a deforested state by grazing directly on *Macrocystis* recruits. Again, such overgrazing by *Strongylocentrotus* is apparently limited to periods of low drift availability (Ebeling et al. 1985, Harrold & Reed 1985), which occur episodically at local scales within southern California (Foster & Schiel 1988, Steneck et al. 2002, Graham 2004). Sea otters (*Enhydra lutris*) inhibit sea urchin overgrazing throughout the otter's range (McLean 1962, Harrold & Pearse 1987, Foster & Schiel 1988, Watanabe & Harrold 1991), which at present is limited mostly to the Northern Hemisphere north of Point Conception (Laidre et al. 2001). Cowen et al. (1982) also observed that high wave action in central California curtailed sea urchin foraging and allowed algal recovery. In this region, seasonal variability in wave intensity was suggested as the most important factor regulating the abundance and structure of macroalgal assemblages (Cowen et al. 1982, Foster 1982).

The mechanisms controlling sea urchin overgrazing in southern California (south of Point Conception), however, are controversial. In the absence of sea otters, various forms of abiotic and biotic regulation of sea urchin populations have been proposed (see Foster & Schiel 1988, Steneck et al. 2002). For example, storms and/or disease can wipe out large sea urchin aggregations over relatively broad spatial scales (Ebeling et al. 1985, Tegner & Dayton 1991, Lafferty 2004), whereas recruitment failure can limit replenishment of local sea urchin populations (Pearse & Hines 1987). Nevertheless, the most popular explanation for the lack of large-scale sea urchin barrens in the absence of sea otters in southern California is that other predators are controlling sea urchin abundance. Various kelp forest predators eat sea urchins (see review by Graham et al. 2007), although most only eat small sea urchins that are incapable of inflicting significant damage to *Macrocystis* holdfasts. Sheephead (*Semicossyphus*), lobsters (*Panulirus*) and the sunflower stars (*Pycnopodia*) appear to be the only Californian kelp forest predators other than sea otters that can feed on adult sea urchins. In some southern California kelp forests, data suggest that sheephead and lobster predation are important in controlling urchin abundance (e.g., Cowen 1983, Lafferty 2004) although the diets of these species are highly variable in space and may not include sea urchins even when sea urchins are present (e.g., Cowen 1986). Furthermore, in most cases the predation hypothesis is invoked in the absence of field experimentation (but see Cowen 1983), which is problematic since sheephead and lobsters have become relatively rare in southern California kelp forests (Dayton et al. 1998), yet deforested areas are also relatively rare (Foster & Schiel 1988). Sea urchin populations in southern California, therefore, are clearly regulated by multiple abiotic and biotic processes, probably resulting in the low frequency of sea urchin barrens in the Southern California Bight.

The only other *Macrocystis* systems for which sea urchin overgrazing has been observed are in South America, although like California, large-scale overgrazing is rare (Vásquez & Buschmann 1997, Steneck et al. 2002). In northern Chile, large-scale overgrazing of *Macrocystis* by *Tetrapygyus niger* appears to be limited by high water motion in the region where *Tetrapygyus* and *Macrocystis* distributions overlap (Vásquez & Buschmann 1997). Sea urchin overgrazing in northern Chile is subsequently restricted to particular depth zones. Also, the asteroids *Luidia* and *Meyenaster* are solitary hunters within subtidal habitats and are important predators on *Tetrapygyus niger* and other echinoids and asteroids (Viviani 1979, Vásquez & Buschmann 1997, Vásquez et al. 2006). Again, as in California, the role of sea urchin grazing in regulating *Macrocystis* populations in southern Chile is more controversial. Initial experimental results detected no effect of *Loxechinus albus* grazing on *Macrocystis* populations in the Beagle Channel (Castilla & Moreno 1982). On the other hand, Dayton (1985b) argued that *Loxechinus albus* grazing should significantly affect *Macrocystis* abundance along the protected coast of southern Chile where large asteroid predators could serve as a controlling factor and further suggested that the results of Castilla & Moreno (1982) were only relevant to the southernmost subpolar area (Beagle Channel). Additionally, density of an annual *Macrocystis* population in the archipelago region of southern Chile was significantly reduced from 24 to 2 sporophytes m<sup>-2</sup> when *Loxechinus albus* densities exceeded 20 m<sup>-2</sup> (Buschmann et al. 2004b). These contradictions have developed into an unresolved controversy about the ecological role of sea urchins in structuring Chilean *Macrocystis* populations (Vásquez & Buschmann 1997).

Based on these numerous field studies spanning the global range of *Macrocystis*, simple trophic cascades do not seem to exist in *Macrocystis*-based systems. Various instances of overgrazing have been described (Steneck et al. 2002) but they are generally short-lived, observed at local scales and are often the result of overgrazing by particular trophic groups (e.g., sea urchins and amphipods). Nevertheless, due to the high diversity and productivity of *Macrocystis*-based food webs (Rosenthal et al. 1974, Pearse & Hines 1976, Castilla 1985, Foster & Schiel 1985, Graham 2004, Graham et al. 2007), these rare overgrazing events can have conspicuous ecological consequences (e.g., Graham 2004). The question still remains, however, as to why overgrazing is less frequent in *Macrocystis*-based systems than in other kelp-based systems (e.g., Aleutians, North Atlantic, Japan; Steneck et al. 2002).

Three striking features are common to *Macrocystis* systems worldwide and may be important in buffering *Macrocystis* communities from overexploitation. The first is that all *Macrocystis*-based food webs are relatively diverse. Such high diversity, especially when it occurs at higher-order trophic levels, may provide a wider range of trophic interactions than less-diverse systems, minimizing the impact of grazing by any given herbivore species. Such ecological effects of high diversity are supported by the field and experimental mesocosm studies of Byrnes et al. (2006), who found that increased predator diversity decreased the impact of an assemblage of grazers on *Macrocystis* biomass. In addition to the highly diverse systems of California, Beckley & Branch (1992) enumerated 200+ taxa in a *Macrocystis* system at the Prince Edwards Islands. Castilla (1985) identified 30+ herbivores and primary predators for the *Macrocystis*-based food web in the Beagle Channel, culminating with the generalist asteroid *Cosmarestias lurida*; Adami & Gordillo (1999) observed a similar system on the other side of the channel, although *Loxechinus albus* was conspicuously absent. Vásquez et al. (1998) observed similar trophic diversity in the *Macrocystis* system of northern Chile, which can include the Southern Hemisphere sea otter *Lontra felina*. Although *L. felina* does not feed on sea urchins (Ebensperger & Botto-Mahan 1997, Villegas 2002), these sea otters do forage on fishes, crustaceans and molluscs and may represent a diversifying component in these systems (Castilla & Bahamondes 1979). A poleward decrease in the diversity of *Macrocystis* systems appears to be present in both the Northern (Graham 2004, Graham et al. 2007) and Southern Hemispheres (Castilla 1985, Vásquez et al. 1998). The second commonality

among *Macrocystis* systems is that they are all imbedded within high-productivity systems necessary to support *Macrocystis* survival, growth and reproduction. Therefore, the inherently high delivery of nutrients to global *Macrocystis* populations may simply override consumptive processes in regulating community structure and ecosystem processes over broad temporal and spatial scales. Finally, sea urchin recruitment appears to be more variable in space and time at low latitudes compared with high latitudes (Castilla & Moreno 1982, Foster & Schiel 1988, Buschmann et al. 2004b, Vega et al. 2005), potentially destabilising sea urchin population dynamics and decreasing the likelihood of large-scale sea urchin population explosions (Foster & Schiel 1988).

Despite the numerous trophic studies of kelp forest organisms, however, there is a dearth of research on communitywide patterns of energy flow. Stable isotope methods have demonstrated the important role of detrital pathways in *Macrocystis* forests (e.g., Kaehler et al. 2000) and other systems (Duggins et al. 1989, Bustamante & Branch 1996, Fredriksen 2003). *Macrocystis* productivity is also exported to other systems (e.g., sandy beaches, deep-sea basins, coastal islands) where it may contribute greatly as an allochthonous energy source (Lavoie 1985, Inglis 1989, Vetter 1994, Harrold et al. 1998, Orr et al. 2005). The trophic consequences of *Macrocystis* production, however, have rarely been considered beyond the finite boundaries of the kelp forest.

Clearly, *Macrocystis* systems are energy rich. Trophic interactions among kelp forest organisms can be conspicuous and are interesting avenues for ecological research. Yet, the emerging pattern over the last 150 yr of research is that at the community or ecosystem level, the diversity and productivity of *Macrocystis* systems are driven primarily by oceanographic processes that regulate the distribution, abundance and standing stock of the main foundation species, *Macrocystis*. It has recently been proposed, however, that the primary structural force for *Macrocystis*-based systems in southern California (Channel Islands National Park) is 'top-down' consumption (Halpern et al. 2006). Halpern et al. (2006) used satellite-derived chlorophyll-*a* data to estimate nutrient delivery to kelp beds as a proxy for 'bottom-up' processes. The effect of nutrients on algal abundance (primarily that of *Macrocystis*) was then determined to be significantly lower than consumptive effects. Off-shore chlorophyll-*a* concentrations, however, are not indicative of processes acting in the near shore (Blanchette et al. 2006) and nutrient delivery to off-shore plankton assemblages and near-shore kelp beds are two fundamentally different and negatively correlated processes (Broitman & Kinlan 2006). Additionally, it is well established that variability in *Macrocystis* sporophyte density (the abundance variable used by Halpern et al. 2006) is driven primarily by self-thinning and is unrelated to nutrient supply (North 1994), whereas nutrient supply and *Macrocystis* biomass are tightly coupled (North 1994, Tegner et al. 1996, 1997, Dayton et al. 1999). It would be interesting to know whether Halpern et al. (2006) would have obtained different results if they had used *Macrocystis* canopy biomass data available for the same region (Reed et al. 2006) and conducted their study beyond 1999–2002, which was the most 'nutrient benign' period of the last 50 yr. In fact, their study period did not include any of the conspicuous El Niño or La Niña events known to drive maxima and minima in community structure and energy flow within these systems (Dayton et al. 1999, Edwards 2004).

A final concern with the approach of Halpern et al. (2006) is the inability of their correlative analyses to disentangle the confounding effects of habitat versus trophic associations. For example, one of their four conspicuous species that was correlated with *Macrocystis* abundance, and thus identified as a key consumer, was the striped surfperch (*Embiotoca lateralis*). Previous studies have repeatedly observed a negative association between *E. lateralis* and *Macrocystis* (Ebeling & Laur 1985, Holbrook et al. 1990). The mechanism underlying the association, however, is not a top-down trophic interaction but rather the negative effect of *Macrocystis* surface canopies on preferred foraging habitat (foliose algae) of *Embiotoca lateralis*. Another of the conspicuous species, the scavenger *Kelletia kellestii*, was found previously to be associated with sea urchin barrens rather than kelp forests (Behrens & Lafferty 2004), the exact opposite pattern from that predicted by the



top-down hypothesis. The confounding nature of habitat versus trophic interactions in driving kelp forest associations is probably ubiquitous among *Macrocystis* systems due to this species simultaneous provision of primary habitat and energy throughout much of its range (see ‘*Macrocystis* as a foundation species,’ p. 62). This criticism of the results of Halpern et al. (2006) does not mean that predation is unimportant in regulating the structure and dynamics of *Macrocystis* systems, but simply argues for greater caution when using correlative data to understand regulatory processes in this complex system.

#### *Community consequences of climate change and kelp forest exploitation*

Climate change and human exploitation can affect the diversity and productivity of *Macrocystis* systems either by indirect modification of *Macrocystis* distribution, abundance and productivity or by directly modifying distribution, abundance and productivity of the flora and fauna that inhabit *Macrocystis* forests. *Macrocystis* productivity and distributional limits are largely constrained by environmental processes (see ‘Organismal biology’ section, p. 42). Studies of environmental control on *Macrocystis* systems, however, have been limited entirely to ecological timescales (e.g., Dayton et al. 1999). Over periods of years to decades, temporal changes in nutrient availability (as measured through sea-surface temperature proxies), sedimentation and substratum composition, storms and light have all been shown to modify the living space and carrying capacity of *Macrocystis* (e.g., North & Schaeffer 1964, Zimmerman & Robertson 1985, Seymour et al. 1989, North 1994, Tegner et al. 1996, 1997, Dayton et al. 1999, Edwards 2004). Such responses to short-term climate change have typically been associated with ENSOs (4- to 7-yr frequency; Dayton et al. 1999, Edwards 2004) and cycles in the Pacific Decadal Oscillation (PDO, 10- to 20-yr frequency; Dayton et al. 1999). In California, strong ENSOs affect *Macrocystis* populations in two primary ways: nutrient stress associated with deepening of the thermocline and destructive storm waves. The relative impacts of each of these processes, however, vary latitudinally (Edwards 2004). Conspicuous second-order community responses often result, for example, from reduction in the availability of *Macrocystis* standing stock and drift and subsequent overgrazing by sea urchins or crustaceans (Ebeling et al. 1985, Harrold & Reed 1985, Tegner & Dayton 1987, Graham 2002, Behrens & Lafferty 2004). Ecologically important echinoderms (e.g., sea urchins and seastars) often suffer mass mortalities that may also be associated with ENSOs (Tegner & Dayton 1987, Dayton & Tegner 1989, Dayton et al. 1992, Behrens & Lafferty 2004, Lafferty 2004). These high-frequency ENSO cycles are overlaid on longer-frequency PDO cycles, with warm PDO periods exacerbating ENSO cycles (Dayton et al. 1999); the two most destructive ENSOs on record (1982–1983 and 1997–1998) occurred during the most recent warm PDO period. Nevertheless, the most well-established effect of PDO cycling on *Macrocystis* systems is the correlation between larger *Macrocystis* sporophyte sizes during PDO cold periods relative to warm periods (Tegner et al. 1996, 1997).

The importance of short-term oceanographic phenomena (e.g., ENSO) in regulating other *Macrocystis* systems is essentially unknown. During the 1997–1998 El Niño, northern Chilean *Macrocystis* populations increased, while black sea urchins (*Tetrapygus niger*) decreased (Vega et al. 2005), a pattern opposite to that observed in southern California. The 1997–1998 El Niño devastated *Macrocystis* populations in central Perú, decreasing sporophyte density and the diversity of associated species (Llellish et al. 2001). The subsequent 1998–1999 La Niña, however, triggered high *Tetrapygus niger* recruitment and a significant increase in *T. niger* adult populations (Vásquez et al. 2006), which corresponded with a crash in *Macrocystis* populations (Vega et al. 2005). The 1997–1998 El Niño also affected northern Chilean asteroid populations. *Luidia* and *Meyenaster* are considered to be top predators in littoral benthic food chains of northern Chile, and both species prey upon *Heliaster* and *Stichaster* (Viviani 1979). *Luidia* and *Meyenaster* coexist and restrict the

bathymetric distribution of *Stichaster* and *Heliaster* in the intertidal and subtidal zones (Viviani 1979). *Meyenaster* and *Luidia* decreased significantly within *Macrocystis* populations during the 1997–1998 El Niño, potentially migrating to deeper water, whereas *Heliaster* and *Stichaster* increased in abundance during the same period (Vásquez et al. 2006). It remains to be determined whether the ENSO-driven decreases in *Luidia* and *Meyenaster* abundances, both important predators on *Tetrapygyus* (Viviani 1979, Vásquez 1993, Vásquez & Buschmann 1997), were the ultimate causes of the 1998–1999 *T. niger* population explosion (Vega et al. 2005, Vásquez et al. 2006).

Although nutrient deprivation is the most conspicuous intra- and interdecadal oceanographic stressor on *Macrocystis* physiology and survival, it has recently been shown that temperature shifts alone can have rapid impacts on *Macrocystis* systems from the organismal to community levels. Schiel et al. (2004) used an 18-yr dataset to study changes in the structure of a local *Nereocystis* kelp bed after 10 yr of increased ocean temperature (+3.5°C) due to the thermal outfall of a power-generating station. Similar to the changes observed following deforestation in southern California (Graham 2004), Schiel et al. (2004) detected significant communitywide changes in 150 species of algae and invertebrates since the initiation of the thermal outfall. These community changes, however, were not consistent with a northern shift in the distribution of southern species, but rather a shift in the dominant canopy-forming kelp from *Nereocystis* to *Macrocystis*, and the potential shading effect of the *Macrocystis* surface canopy. These data demonstrate the difficulty in disentangling the direct effect of climate change on giant kelp communities from the indirect effect of climate change on the distribution, abundance and productivity of key habitat-forming and energy-producing species, like *Macrocystis*.

Studies of the effects of natural and anthropogenic climate change on *Macrocystis* systems have been limited to the last few decades. The frequency and severity of ENSOs have been highly variable over geological timescales (Rosenthal & Broccoli 2004) and it has been suggested that their frequency is increasing (Diaz et al. 2001). Still, the ecological consequences of such long-term climate change to *Macrocystis* systems seem obvious; Schimmelmann & Tegner (1991) detected an ENSO signal in the flux of *Macrocystis*-derived organic carbon to the floor of the Santa Barbara Basin over 1500 yr. Less obvious, however, are interactions between long-term changes in ocean temperature, near-shore sedimentation, light and sea level that are driven by glacial-interglacial cycling (Graham et al. 2003). *Macrocystis* has limited depth, substratum composition and nutrient ranges, and ice age redistribution and modification of environmental conditions may have had massive impacts on *Macrocystis* distribution, abundance and productivity. For example, late-Quaternary sea-level rise probably led to large changes in inhabitable *Macrocystis* reef area around the Californian Channel Islands and mainland as broad near-shore rocky platforms became exposed, shrank and even fragmented (Graham et al. 2003, Kinlan et al. 2005). A recent study predicted that southern Californian *Macrocystis* kelp forest area and biomass increased up to 3-fold from the last glacial maximum to the mid-Holocene, but then rapidly declined by 40–70% during the late Holocene to current area and biomass levels (M.H. Graham, B.P. Kinlan, R.K. Grossberg, unpublished data). Furthermore, the early Holocene peak in *Macrocystis* distribution and abundance coincided with highly productive palaeo-oceanographic conditions, probably yielding a subsequent peak in *Macrocystis* productivity during that period. This shift overlapped with conspicuous changes in total biomass of kelp-associated species, such as abalone, sea urchins and turban snails in native American shell middens on the Channel Islands (Erlandson et al. 2005). The community and ecosystem consequences of such long-term climate change on *Macrocystis* systems can be predicted but critical tests of such predictions will require application of contemporary palaeo-ecological tools (e.g., stable isotopes) because *Macrocystis* sporophytes do not fossilise (Graham et al. 2003).

Poor strategies of sewage discharge in the 1950s and 1960s were associated with the decimation of a few very large *Macrocystis* forests in southern California (North & Schaeffer 1964, North & Hubbs 1968, North 1971, Tegner & Dayton 1991). Stringent regulations, however, quickly remedied

the impacts. Tegner et al. (1995b) later found that nitrogenous wastes originating from breakage in sewage outfalls can actually have positive effects on *Macrocystis* recruitment, especially during periods of nutrient deprivation. It was also noted by Dawson et al. (1960) that an oil spill in Baja California, Mexico, had no direct impacts on *Macrocystis* physiology, yet positively affected *Macrocystis* survival by causing high local mortality of sea urchins. Effects of other pollutants, such as some metals and aqueous petroleum waste, on *Macrocystis* microscopic stages can inhibit microtubule dynamics, DNA replication, photosynthetic processes and overall physiology (Anderson et al. 1990, Garman et al. 1994, 1995, Reed & Lewis 1994). Despite these localised impacts, there is little evidence that chemical pollution currently restricts *Macrocystis* distribution, abundance and productivity over broad spatial and temporal scales.

Finally, *Macrocystis* systems have been subjected to long-term anthropogenic exploitation, spanning a period of at least 11,000 yr (Erlandson et al. 2005). Recent attention has focused on direct exploitation of *Macrocystis* populations and *Macrocystis*-associated organisms, especially in southern California where *Macrocystis* has been harvested for algin extraction since the 1920s (North 1994). Californian harvests are limited to the upper 1–2 m of the water column and have been shown to have minimal impacts on sporophyte survival (see p. 56). Indeed, while there is considerable temporal variability in *Macrocystis* populations due to physical and biological factors, the long-term stability of the *Macrocystis* harvest suggests that it is one of the best-managed marine harvests of wild populations worldwide (Dayton et al. 1998). Nevertheless, in southern Chile, *Macrocystis* is harvested by abalone farmers who require biomass all year round and *Macrocystis* cultivation is now required to offset heavy exploitation of natural *Macrocystis* populations (Gutierrez et al. 2006). Due to the patchy distribution of *integrifolia*-form populations in northern Chile, *Macrocystis* harvesting near abalone farms has had a great impact on the dynamics of local *Macrocystis* populations, with subsequent effects on *Macrocystis*-associated communities (J.A. Vásquez, unpublished data).

Although *Macrocystis* populations themselves appear to be relatively immune to episodic harvesting of the surface canopy, *Macrocystis*-associated organisms are not. Overfishing has resulted in virtual elimination of large predators in southern California *Macrocystis* forests (Dayton et al. 1998). The ecological impacts of overfishing on *Macrocystis* populations are unclear because some correlative studies suggest cascading impacts whereas others do not (Foster & Schiel 1988, Dayton et al. 1998, Steneck et al. 2002, Behrens & Lafferty 2004, Lafferty 2004, Graham et al. 2007). Although predators may or may not be more common within marine reserves (Paddack & Estes 2000, Behrens & Lafferty 2004, Lafferty 2004), predators within reserves are typically larger in size (Paddack & Estes 2000). Again, the problem lies in deciphering the various types and strengths of species interactions operating in *Macrocystis* forests (e.g., *Macrocystis*-derived habitat and energy provision compared with predation). One thing is clear, however, despite the ubiquitous role of *Macrocystis*-derived habitat and energy provision in enhancing kelp forest diversity and productivity worldwide, kelp forest organisms cannot survive targeted exploitation over large temporal and spatial scales (Dayton et al. 1998).

## Conclusion

The global scientific literature indicates that *Macrocystis* is an important provider of habitat and energy to its associated communities wherever it is present. It is also clear that, despite non-trivial gene flow among global *Macrocystis* populations, *Macrocystis* morphology and physiology are highly variable in response to the environmental conditions within which sporophytes recruit, grow and reproduce. These conspicuous ecotypic differences have generally led researchers to study *Macrocystis* population dynamics and community interactions from a regional perspective. Patterns observed for some large conspicuous giant kelp forests in southern California have subsequently

dominated the literature and become the paradigms against which the ecologies of other *Macrocystis* systems are compared. When viewed from a global perspective, however, regional differences in the results of prior descriptive and experimental studies can be reconciled by an appreciation of great plasticity in *Macrocystis* form and function. The origin, nature and potential restriction of such plasticity to *Macrocystis* are appealing paths for future research.

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