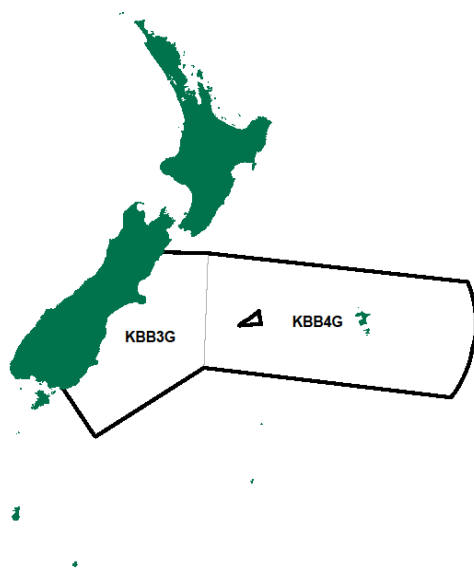


BLADDER KELP ATTACHED (KBB G)*(Macrocystis pyrifera)***1. FISHERY SUMMARY**

Attached bladder kelp (KBB G) was introduced into the Quota Management System (QMS) on 1 October 2010, only within FMA 3 and FMA 4, which have the reporting codes KBB 3G and KBB 4G, respectively. The Total Allowable Catch (TAC), Total Allowable Commercial Catch (TACC), recreational, customary, and other mortality allowances issued to KBB G on entering the QMS remain unchanged and are presented in Table 1.

Bladder kelp, like all other large seaweeds, occurs in one of three states: attached (growing on the substrate), free-floating, and beach-cast. The attached growing state of bladder kelp is the only state managed under the QMS. Fisheries New Zealand will continue to monitor the use of beach-cast and free-floating seaweeds in FMAs 3 and 4 and will reconsider introducing these states into the QMS if sustainability and utilisation risks are identified in the future. Separate codes refer to beach-cast bladder kelp in FMA 3 (KBB 3B) and free-floating bladder kelp in FMA 3 and 4 (KBB 3F and KBB 4F). Unless explicitly stated, this section refers to only attached bladder kelp.

Table 1: Total Allowable Catch (TAC, t), Total Allowable Commercial Catches (TACC, t), customary non-commercial (t), recreational (t), and other mortality allowances (t) for attached bladder kelp on entering the QMS on 1 October 2010.

| Fishstock | Description | TAC (t) | Customary Allowance (t) | Recreational Allowance (t) | Other sources of mortality (t) | TACC (t) |
|-----------|---------------------------|---------|-------------------------|----------------------------|--------------------------------|----------|
| KBB 3G | South-East (coast) | 1 238 | 0.1 | 0.1 | 1.0 | 1 237 |
| KBB 4G | South-East (Chatham Rise) | 274 | 0.1 | 0.1 | | 273 |

1.1 Commercial fisheries

Bladder kelp has been used for the production of potash, alginates, dietary supplements, and fertiliser, as well as for abalone and sea urchin feed, and it is also cultivated for bio-remediation purposes (Buschmann et al 2006, Gutierrez et al 2006, Barrento et al 2016, Correa et al 2016). There is current research evaluating the utilisation of bladder kelp as feed for other aquaculture species such as shrimps (Buschmann et al 2006, Cruz-Suárez et al 2009), as well as an evaluation as a possible feedstock for conversion into ethanol for biofuel use (Wargacki et al 2012, Camus et al 2016). Because of the growing demand for bladder kelp, Fisheries New Zealand considered that the bladder kelp resource requires active management to ensure its sustainable use, and that management under the QMS was the most appropriate mechanism. The fishing year for commercial harvest of KBB G is 1 October to 30 September, and catch is measured in greenweight (tonnes).

BLADDER KELP ATTACHED (KBB G)

Restrictions on New Zealand harvests of KBB G have been based on the Californian fishery (where the majority of research into harvesting effects has been conducted) and modified to take into account differences between California and New Zealand. These differences include reduced nutrients in New Zealand waters, the shallower depth at which KBB G is harvested in New Zealand, and the lack of information on New Zealand stocks. Harvesting strategies for wild harvest of *Macrocystis* have also been developed in Chile where *Macrocystis* has a wide geographic range (e.g., Borrás-Chavez et al 2012, Almanza & Buschmann 2013, Buschmann et al 2014b).

KBB G harvest is restricted to a maximum cutting depth of 1.2 m, implemented on introduction to the QMS on 1 October 2010. Also, harvest of attached kelp is prohibited within the East Otago Taiāpure.

Harvest of KBB G mainly occurs in QMA 3 and has varied since 2001–02 from 3 t to 105 t (Table 2 and Figure 1). Landings of KBB G in QMA 4 are minimal, with a total of only 2.49 t reported (Table 2).

Table 2: Reported landings for KBB G in greenweight (t) by fishing year. Blank cells indicate nil catches. Values above and below the horizontal line represent historical landings prior to QMS introduction and landings post QMS introduction, respectively. * Pre 2010 landings in KBB 3G include a combination of beach-cast, free-floating, and attached bladder kelp. Pre 2010 landings in KBB 4G may include a combination of free-floating and attached bladder kelp. Post 2010, the reported landings are for attached bladder kelp only.

| Fishing Year | KBB 3G | KBB 4G |
|--------------|---------|--------|
| 2001–02 | 104.50* | 0.37* |
| 2002–03 | 37.00* | |
| 2003–04 | 7.53* | |
| 2004–05 | 17.90* | |
| 2005–06 | 2.82* | |
| 2006–07 | 8.35* | |
| 2007–08 | 6.43* | 2.10* |
| 2008–09 | 63.50* | |
| 2009–10 | 28.37* | |
| 2010–11 | 53.34 | |
| 2011–12 | 34.25 | |
| 2012–13 | 5.00 | |
| 2013–14 | 94.00 | 0.00 |
| 2014–15 | 62.00 | 0.02 |
| 2015–16 | 30.54 | 0.00 |
| 2016–17 | 41.77 | 0.00 |
| 2017–18 | 40.81 | 0.00 |
| 2018–19 | 67.24 | 0.00 |
| 2019–20 | 72.83 | 0.00 |
| 2020–21 | 94.03 | 0.00 |
| 2021–22 | 77.33 | 0.00 |

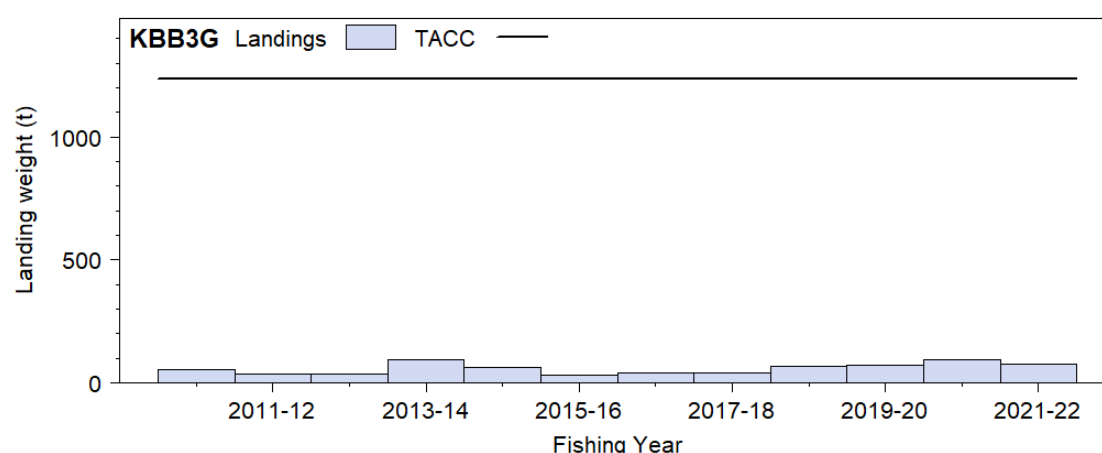


Figure 1: Reported commercial landings and TACC for KBB 3G (east coast, South Island). Note that this figure does not show data prior to entry into the QMS.

1.2 Recreational fisheries

There is no quantitative estimate of recreational harvest of bladder kelp at this time, although it is assumed to be restricted to the collection of beach-cast seaweed for composting. Consequently, recreational harvest of attached bladder kelp is assumed to be negligible.

1.3 Customary non-commercial fisheries

The customary harvest of bladder kelp is currently unrestricted. There is no quantitative information on the extent of customary harvest of attached bladder kelp (or any other state) in FMAs 3 and 4; however, the customary harvest of attached bladder kelp is likely to be negligible.

1.4 Illegal catch

There is some qualitative data to suggest illegal, unreported, unregulated activity in this Fishery.

1.5 Other sources of mortality

Hydrographic factors (e.g., tidal surge, nutrient limitation, temperature, and salinity stress) have been demonstrated to result in significant mortality of bladder kelp (Buschmann et al 2004, 2006, Schiel & Foster 2015). Wave action, both orbital size and velocity, has been shown to be a significant predictor variable for the distribution of kelp beds (Young et al 2015). Reductions in population densities of existing *M. pyrifera* populations have been linked to El Niño cycling and winter storm activity (Zimmerman & Robertson 1985, Seymour et al 1989).

Due to their large size and high drag, adult bladder kelp are vulnerable to removal by high water motion (Dayton et al 1984, Seymour et al 1989, Schiel et al 1995, Fyfe & Israel 1996, Graham et al 1997, Fyfe et al 1999), which is considered the primary agent of mortality. In 1994, Fyfe et al (1999) found that winter storms extensively removed floating surface canopies at Pleasant River (north of Dunedin), and, that by February 1995, 50% of surface canopies had reformed. High seasonal and year-to-year variability in wave intensity and plant biomass results in high intra- and inter-annual variability in mortality. In California, uprooted plants may become entangled with attached plants, increasing drag and the likelihood of detachment, which may result in a ‘snowball effect’ capable of clearing large swaths in the local population (Dayton et al 1984). For example, Seymour et al (1989) observed that mortality of bladder kelp in California due to storm-induced plant detachment and entangled was as great as 94%. Graham et al (1997) observed that bladder kelp holdfast growth in California decreased significantly along a gradient of increasing wave exposure, possibly due to greater disturbance to the bladder kelp surface canopy, which reduces holdfast growth (Barilotti et al 1985, McCleneghan & Houk 1985). Thus, increased water motion and decreased holdfast strength can act in combination to decrease plant survival.

Light is a key indicator for the distribution of *M. pyrifera* (e.g., Desmond et al 2015, Tait 2019, Tait et al 2021). Sedimentation (coastal erosion, land use changes) negatively affects both the settlement and survival of spores and early growth stages of *M. pyrifera* (e.g., Geange et al 2014, Glover 2020), but also influences the light environment, reducing productivity (e.g., Desmond et al 2015). Movement of bottom sediments can scour or bury bladder kelp spores and recruits, and the resuspension of sediments can reduce the amount of light reaching sub-canopy algae, preventing the attachment and development of spores, and inhibiting the growth of bladder kelp recruits (Dean & Jacobson 1984, Pirker 2002, Tait 2019). Research within the East Otago Taiāpure has demonstrated that kelp forests in the taiāpure are light limited for much of the year and that sediment run-off from the land can reduce their productivity and the extent of the kelp beds (Hepburn et al 2011, Pritchard et al 2013, Desmond et al 2015).

Temperature can influence the timing of the reproductive cycle in *M. pyrifera* (Kain 1982), as well as affecting the viability of different life stages (Kain 1982, Hay 1990, Ladah et al 1999). For example, Le et al. (2022) found that spore settlement for *M. pyrifera* suffered significant declines when temperatures increased above 23.8°C. Over large spatial scales, elevated temperature also appears to be a major influence on bladder kelp mortality and is likely to limit the northern distribution of bladder kelp within New Zealand (Hay 1990). For example, Hay (1990) described an apparent retraction of the distribution of bladder kelp within Cook Strait since 1942, presumably due to increasing surface water temperatures. Cavanaugh et al (2011) compared changes in canopy biomass with oceanographic and climatic data in California. They revealed that winter losses of regional kelp canopy biomass were positively correlated

with significant wave height, whereas spring recoveries were negatively correlated with sea surface temperature. On inter-annual timescales, regional kelp-canopy biomass lagged the variations in wave height and sea surface temperatures by 3 years, indicating that these factors affect cycles of kelp recruitment and mortality. The dynamics of kelp biomass in exposed regions were related to wave disturbance, whereas kelp dynamics in sheltered regions tracked sea surface temperatures more closely. In different parts of its geographic and ecological distribution, *M. pyrifera* shows morphological plasticity to different temperature ranges (e.g., Rothäusler et al 2011, Buschmann et al 2014a).

As well as warming oceans, marine heatwaves are being reported throughout the globe, becoming stronger and more frequent. The duration and intensity of these events influences their impacts, and there is strong evidence that these impacts are exacerbated by other stressors. Tait et al (2021) tested the association of surface canopy cover of *M. pyrifera* with sea surface temperature, temperature anomalies, chlorophyll a (a proxy for nutrient availability), and water clarity, using satellite imagery of surface canopies in 4 regions along the east and south coasts of New Zealand. They found a reduced cover of kelp across all regions during and after the marine heat wave of 2017/2018. The least impact was found in the southern region where water temperatures did not exceed 18°C. A very important observation was the significant interaction with water clarity: temperature-induced kelp loss was greater when water clarity was poor.

In Tasmania *Macrocystis* kelp beds were once sufficiently large to be commercially harvested but have declined by approximately half along the east coast since 1944 (Edyvane 2003) effectively being functionally extinct (Butler et al 2020). A further study of the extent of these *Macrocystis* beds, based on a time series of aerial photographs (1946–2007), showed an average canopy extent in the last decade of about 9% of the average canopy extent in the 1940s. The declines were estimated to be up to 95–98% in some locations. In general, declines were less pronounced in southern regions of Tasmania than in northern and eastern regions. The decline in *Macrocystis* has been linked with the progressive southward penetration of warm, salty, nutrient-poor EAC water, which has extended about 350 km further south than 60 years ago (Johnson et al 2011). Because of this decline and the ecosystem functions that this species provides, *Macrocystis* forests were declared an endangered ecological community under the federal Environmental Protection and Biodiversity Conservation Act 1999 in 2012. This dramatic loss of kelp forests is considered to have been driven by a combination of increasing temperature, decreasing nutrients, increased fishing, and increased herbivory by the expanding range of herbivores (Johnson et al 2011, Wernberg et al 2011, Butler et al 2020).

In New Zealand, with current seawater warming trends, including strong evidence of relatively rapid warming within southern waters (Shears & Bowen 2017), the cover of *Macrocystis* across much of its current range in southern New Zealand will be negatively affected. Although temperature was the major driver identified in *Macrocystis* canopy cover decline by Tait et al (2021), it is also evident that declining water clarity (high turbidity and low-light penetration) has negative effects on giant kelp (Desmond et al. 2015, Tait 2019, Tait et al. 2021).

Other human-induced threats include various pollutants that negatively affect bladder kelp. Leal et al (2016) examined the impact of exposure to chronic and high concentrations of copper in both *Macrocystis* and *Undaria* in New Zealand and found that there were differential impacts on meiospore germination, and arrested development of gametogenesis occurred in both species.

Coastal eutrophication has been shown globally to be a key stressor driving losses of major kelp forests (Wernberg et al 2011, Filbee-Dexter & Wernberg 2018). Glover (2020) discusses the impact of land conversion to pasture in New Zealand and the particular implications for increased phosphorous, nitrogen, and *Escherichia coli* (*E. coli*) in local bodies of water, with particular reference to East Otago. While seasonally nutrient concentrations can be limiting for *M. pyrifera* in New Zealand (e.g., Stephens & Hepburn 2016), the nutrients associated with land-use intensification can result in a system shift to turf-dominated ecosystems.

Although wave disturbance and sea surface temperature appear to be the predominant abiotic sources of bladder kelp mortality, there are no quantitative estimates for these sources of mortality available for New Zealand. Further, the relevance of results from studies conducted outside New Zealand may be

limited due to differences in hydrographic environment between New Zealand and other locations.

In terms of biological processes, Californian and Chilean studies have shown that grazing by sea urchins can result in the detachment of adult plants and their removal from the population (Dayton 1985a, Tegner et al 1995), and/or the removal of recruits and juvenile plants (Dean & Jacobsen 1984, Dean et al 1988, Vásquez et al 2006). Wernberg et al (2011) discuss the interactions and roles of range extensions of herbivores, over harvest of predators, and introduction of non-indigenous species in conjunction with climate change stressors and the consequent negative impacts on ecological functioning and resilience of kelp forests. The invasive kelp *Undaria pinnatifida*, an opportunistic species that competes with *M. pyrifera* for space (Desmond et al 2019) but offers dramatically reduced ecosystem benefits (Suárez-Jiménez et al 2017, Desmond et al 2018), is also a significant stressor in parts of the kelp's range.

In Chile, infestations of bladder kelp holdfasts by crustaceans (e.g., amphipods and isopods) may increase mortality by decreasing attachment strength (Ojeda & Santelices 1984). Buschmann et al (2014b) summarise information about diseases, covering a range of pathogens and diseases known to occur in kelps, including prokaryotes, viruses, oomycetes, and fungi. Epiphytic and endophytic microscopic algae can also negatively affect kelp. Endophytic diseases can result in tumour-like growths, loss of photosynthetic tissue, and deformation of thalli.

2. BIOLOGY

Historically, two species of bladder kelp, *Macrocystis pyrifera* (Linnaeus) C. Agardh and *M. integrifolia* Bory, were reported from both Northern and Southern hemispheres, and *M. angustifolia* Bory and *M. laevis* Hay were reported from the Southern Hemisphere. However, *M. angustifolia*, *M. integrifolia*, and *M. laevis* are currently regarded as taxonomic synonyms of *M. pyrifera* (Graham et al 2007, Demes et al 2009). The four previously recognised species are referred to as bladder kelp, *Macrocystis pyrifera*. Macaya & Zuccarello (2010a, b) assessed the genetic structure of *M. pyrifera* across a broad latitudinal range in the southern hemisphere, finding low levels of genetic diversity.

In the 2019 evaluation of the threat status of New Zealand marine macroalgae, *Macrocystis pyrifera* was recorded as “At Risk, Declining”, based on the information available at that time (Nelson et al 2019).

Bladder kelp is globally widespread. It is found in the Atlantic Islands (Baardseth 1941, Chamberlain 1965); North America from Alaska to California, Baja, and Mexico (e.g., Carr 1994, Graham et al 2007, Cavanaugh et al 2011); Central America (Taylor 1945); South America from Peru to Chile, Argentina, and Uruguay (e.g., Vásquez et al 2006, Thiel et al 2007, Macaya & Zuccarello 2010b); the Indian Ocean (Silva et al 1996); Tasmania (Cribb 1954, Womersley 1987); sub-Antarctic islands (Ricker 1987, John et al 1994); and New Zealand (Hay 1990, Fyfe & Israel 1996, Brown et al 1997, Hepburn et al 2007).

In New Zealand, bladder kelp has a broad latitudinal distribution (Figure 2), occurring around the southern North Island, the South Island, as well as Stewart, Chatham, Bounty, Antipodes, Auckland, and Campbell islands (Adams 1994, Harper et al 2012). According to Hay (1990) bladder kelp does not persist in New Zealand waters where maximum temperatures exceed 18–19 °C for several days. The northern limit of bladder kelp in the North Island has been reported to be between Castlepoint and Cape Turnagain on the east coast of the North Island, and Kapiti Island on the west coast. No *Macrocystis* has been seen at Castlepoint for at least 40 years, and there are no recent sightings of it at Kapiti Island. The current northern limit of the species appears to be on D’Urville Island in the western Marlborough Sounds (Desmond, pers. comm.), on the west coast of the North Island near Mana Island, and on the east coast of the North Island in Palliser Bay. Hay (1990) considered the distribution of bladder kelp corresponds to the Southland current, which brings cool nutrient-rich water north from the south. The distribution of bladder kelp is generally patchy, and there is both seasonal and inter-annual variation in abundance (Hay 1990, Pirker et al 2000). D’Archino et al (2019) evaluated the known distribution of *M. pyrifera* in the Wellington region, reports of declining populations over time, and methods to monitor populations of *Macrocystis*. The main drivers of retraction in range and declining populations are

BLADDER KELP ATTACHED (KBB G)

considered to be a combination of increased sea surface temperature, a combination of reduced light availability and increased sedimentation from terrestrial runoff, and, in some parts of its range, invasion by *Undaria pinnatifida* (Desmond et al 2015, 2018, 2019, Tait et al 2021).

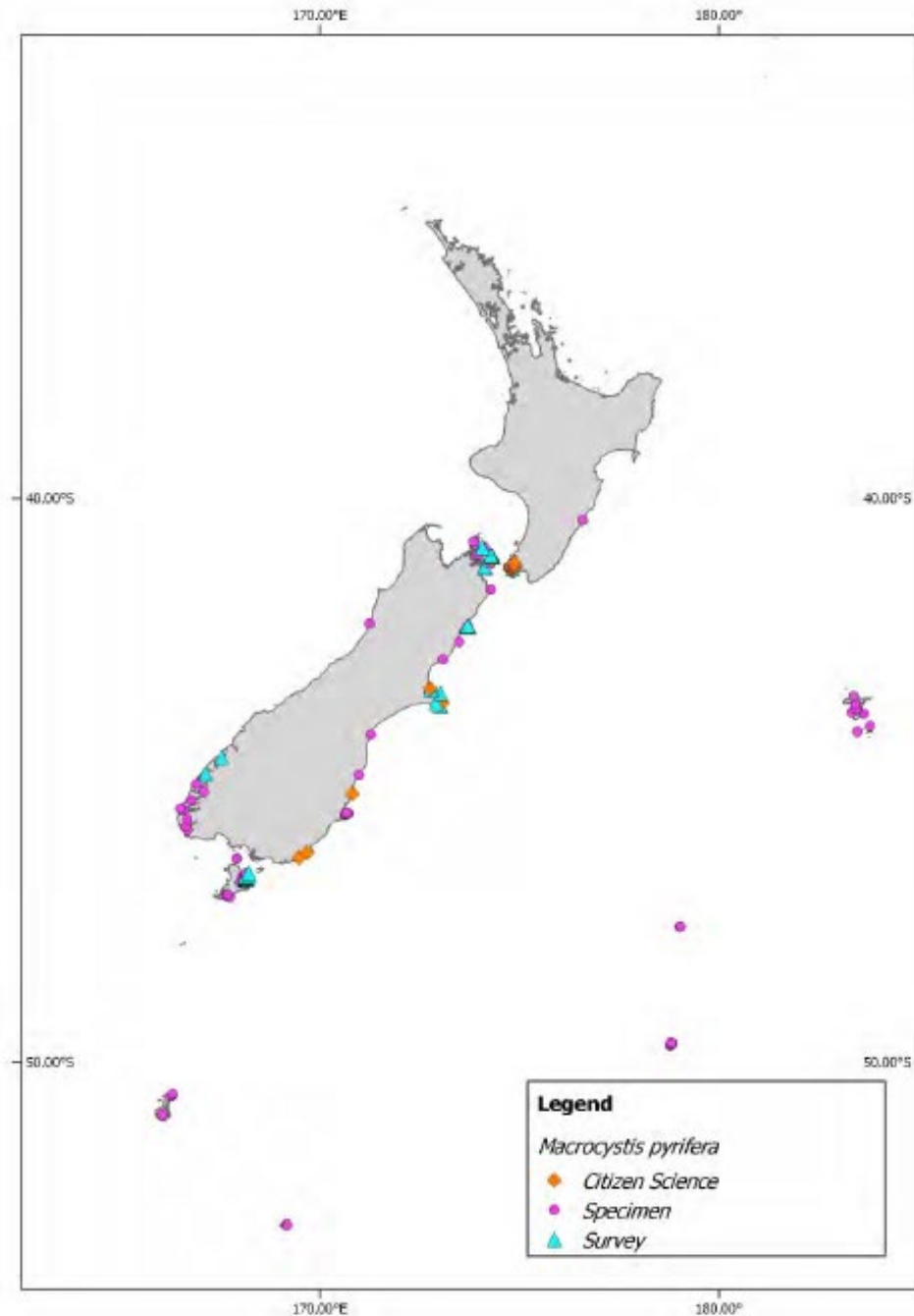


Figure 2: The New Zealand distribution of *Macrocyctis pyrifera* (Laminariales) as recorded by citizen science, specimen, and survey records (D’Archino et al 2019).

Schiel & Foster (2015) published a detailed treatment of all aspects of the biology and ecology of *Macrocyctis*. Bladder kelp is a large perennial kelp and can grow up to 45 m long in New Zealand, occurring in water 3–20 m deep. Where the bottom is rocky and affords places for it to anchor, bladder kelp grows in extensive beds with large floating canopies and frequently forms colonies or large populations in calm bays, harbours, or in sheltered offshore waters. It can tolerate a wide range of water motion in New Zealand, including areas where tidal currents reach 5–7 knots (Hay 1990). Smaller plants can be found in shallow pools and channels.

Macrocyctis has a heteromorphic life history with a conspicuous kelp phase, the sporophyte, and

microscopic gametophytes. Individuals of the kelp phase persist for up to five years in California (North 1994). The life history progresses from planktonic zoospores (less than three days longevity) to microscopic benthic gametophytes (7–30 days longevity) and finally macroscopic benthic sporophytes (the large plants visible along the coast) (Figure 3). Adult sporophytes typically consist of numerous vegetative fronds that arise from longitudinal splits in meristem tissue (undifferentiated plant tissue which gives rise to new cells) located just above the holdfast. Vegetative fronds consist of a stipe (stem) terminating in an apical meristem (the primary point of growth at the tip of a frond) which gives rise to new vegetative blades as the frond develops (Figure 3). Blades are attached to the stipe by a single pneumatocyst (gas bladder), which provides buoyancy to the frond. Continued elongation of the stipe, combined with the production of new blades by the apical meristem, results in elongation of the frond and increases in the number of blades. Fronds continue to grow after reaching the surface, forming canopies (Figure 3). Finally, meristem activity ceases in the apical blade and a terminal blade is formed. In California, frond elongation has been observed occurring at a rate of up to 30 cm per day, making bladder kelp one of the fastest growing organisms on earth. Reproductive blades (called sporophylls) are clustered above the holdfast, forming from the lowermost two to six blades on each frond (Figure 3). Sporophylls develop reproductive sporangia (spores) that are densely packed in sori (a cluster of sporangia) on the surface of the sporophylls. Californian studies have shown spores within sporangia take about 14 days to mature, with a mean residence time of about 30 days (Tugwell & Branch 1989). Each sporangium releases numerous mature zoospores that develop into gametophytes (North 1986).

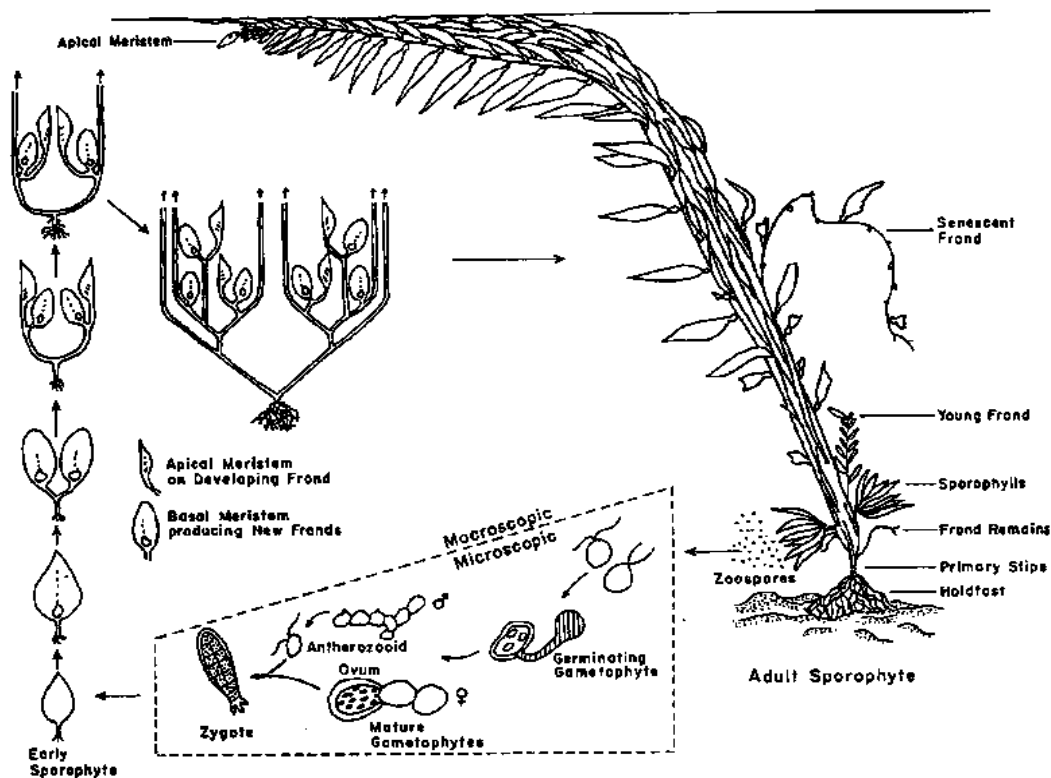


Figure 3: Diagram of the bladder kelp life cycle showing (left side) development of the young diploid sporophyte, increasing frond numbers through production of basal and apical meristematic blades; (right side) growth habit of an adult diploid sporophyte about two years old, standing in 10 m of water depth, and liberating haploid zoospores; (below centre) development of haploid gametophytes from settled zoospores, proceeding to gametogenesis, and fertilisation yielding the zygote and, thence, a diploid embryonic sporophyte. From North (1986).

A floating surface canopy consisting of numerous vegetative fronds characterises adult plants. In California, the floating surface canopy comprises 33–50% of total plant biomass and produces approximately 95% of organic production (Towle & Pearse 1973).

Unlike other perennial kelp genera, bladder kelp has limited nutrient and photosynthate storage capabilities, which in New Zealand is about 2 weeks (Brown et al. 1997); consequently, growth by young fronds, reproductive material, holdfasts, and other tissues near the base of the plant is supported

by translocation of photosynthates from the canopy, which follows a source-sink relationship (North 1986). Mature canopy tissue exports both upward to the apical meristem at the frond apex, and downward to sporophylls, meristem tissue, holdfasts, and into apical regions of juvenile fronds (Schmitz & Lobban 1976, Lobban 1978, Manley 1984). The ability of bladder kelp to translocate photosynthates allows it to grow in dense aggregations with overlapping canopies that effectively shade out competitors on the bottom, yet support rapid growth by young fronds, sporophylls, holdfasts, and other tissues near the base of the plant. In a bed of *M. pyrifera* in Stewart Island, Stephens & Hepburn (2016) investigated how *in situ* pulses of nitrate (NO_3^-) affected the growth and nitrogen physiology of *M. pyrifera*, measuring multiple parameters (e.g., growth, pigments, soluble NO_3^-) in distinct tissues throughout entire fronds (apical meristem, stipe, adult blade, mature blade, sporophyll, and holdfast). Labelled ^{15}N was used to trace nitrogen uptake and translocation from nitrogen sources in the kelp canopy to sinks in the holdfast, 10 m below. Their research provided the first evidence of long-distance (> 1 m) transport of N in macroalgae.

Macrocystis pyrifera is a species that demonstrates high morphological, physiological, and life-history plasticity, allowing it to adapt to different nitrogen environments around the globe (refer Graham et al 2008, Buschmann et al 2014a, Schiel & Foster 2015). Patterns in physiological parameters suggest that *M. pyrifera* displays functional differentiation between canopy and basal tissues that may aid in nutrient-tolerance strategies, similar to those seen in higher plants and unlike those seen in more simple algae (i.e., non-kelps). In a study conducted at Stewart Island, Stewart (2015) showed that *M. pyrifera* growing on the edge of a kelp bed displayed higher growth rates and higher tissue carbon and nitrogen concentrations than kelp found in the interior of the same bed. He attributed these differences primarily to edge individuals receiving more light than interior individuals. Stephens & Hepburn (2014) examined intra-specific differences in kelp growth, physiology, and tissue chemistry and whether these can be attributed to differences in mass-transfer within the same bed. They investigated whether a mass transfer gradient across *M. pyrifera* kelp beds exists, and then whether this exposure gradient influences growth, erosion, pigment concentrations, tissue nitrogen, and C:N ratios. While variation in kelp growth has been previously demonstrated to occur between beds (Gerard & Mann 1979, Hepburn et al 2007), Stephens & Hepburn (2014) provided the first evidence that *M. pyrifera* growth within a singular site is not uniform and that the differences in growth rates presented here can be attributed to hydrodynamic gradients over relatively small spatial scales (tens of metres).

Macrocystis blades from wave-exposed locations have been found to have thicker tissue and are narrower than blades collected from wave sheltered locations (Hurd & Pilditch 2011). The blades from exposed sites exhibited surface corrugations, while those from sheltered sites were smooth, altering the diffusion boundary layer and modifying uptake of nutrients. Stephens & Hepburn (2016) found that nitrogen fertilisation did not enhance elongation rates within the frond, but instead thickness (biomass per unit area) increased in adult blades. They considered that increased blade thickness may enhance tissue integrity because fertilised kelp had lower rates of blade erosion.

The reliance on surface fronds for translocated photosynthate, combined with their vulnerability to disturbance, results in considerable spatial and temporal variability in bladder kelp productivity and size. For example, Graham et al (1997) observed that bladder kelp holdfast growth in California decreased significantly along a gradient of increasing wave exposure, possibly due to greater disturbance to the bladder kelp surface canopy. Similarly, Miller & Geibel (1973) and McCleneghan & Houk (1985) observed reduced holdfast growth in bladder kelp following the experimental removal of surface canopies in California. Reed (1987) demonstrated that a 75% thinning of vegetative fronds in California led to an approximate 75% decrease in the generation of reproductive blades.

Understanding the morphological variation and adaptation in *M. pyrifera* has important implications for understanding intra-site nutrient acquisition, the excretion of wastes, and, therefore, for primary productivity. Stephens & Hepburn (2014) showed that there is greater hydrodynamic variability within and across relatively small macroalgal beds than previously understood and this fine-scale variability also has important implications for key processes surrounding nutrient uptake and for photosynthesis and primary productivity.

Graham (2002) identified shifts in the reproductive condition of Californian bladder kelp from fertile to completely sterile in response to episodic, sub-lethal frond grazing by amphipods. This change in reproductive condition occurred despite relatively constant sporophyll biomass. Finally, in a New Zealand study, Geange (2014) identified an apparent trade-off between vegetative growth and the generation of reproductive sporophylls. Relative to controls, the removal of surface canopies did not result in decreased frond generation, despite an 86% reduction in the generation of reproductive blades. Geange (2014) also found that 89% of plants became completely sterile 50 days after canopy removal, with effects persisting for up to 83 days.

Growth of bladder kelp in New Zealand appears to be seasonal. Autumn and winter growth rates in 1988 in Otago Harbour were estimated at approximately 1–20 mm per day (Table 3, Brown et al 1997). Brown et al (1997) identified a seasonal pattern of blade relative growth rate (RGR) in Otago Harbour, where blade RGRs during 1986–87 were similar year-round, except for summer when lower rates were recorded. Brown et al (1997) concluded that sufficiently high irradiance levels and seawater nutrient concentrations support relatively constant growth throughout most of the year, but that growth was nutrient-limited during summer months when seawater nitrate levels decline. However, the research of Hepburn et al (2007) and Hurd (2017) showed growth rates to be enhanced by water velocity in modifying the seasonal pattern of *M. pyrifera* growth by ameliorating the negative effect of low seawater nitrogen concentrations during summer and autumn.

Table 3: Growth parameters for KKB G canopy (> 2.25 m) and submerged fronds at Aquarium Point, Otago Harbour during autumn (March/April/May) and winter (June/July/August) 1988. Adapted from Brown et al (1997).

| Growth parameter | Canopy | Frond type Submerged |
|--|----------------------------|----------------------------|
| <i>Frond-elongation rate</i> | | |
| autumn | 1.90 cm d ⁻¹ | 1.20 cm d ⁻¹ |
| winter | 2.00 cm d ⁻¹ | 1.30 cm d ⁻¹ |
| <i>Relative frond-elongation rate</i> | | |
| autumn | 0.0065 d ⁻¹ | 0.0080 d ⁻¹ |
| winter | 0.0066 d ⁻¹ | 0.0130 d ⁻¹ |
| <i>Node-initiation rate</i> | | |
| autumn | 0.33 nodes d ⁻¹ | 0.28 nodes d ⁻¹ |
| winter | 0.30 nodes d ⁻¹ | 0.30 nodes d ⁻¹ |
| <i>Relative node-initiation rate</i> | | |
| autumn | 0.0047 d ⁻¹ | 0.0064 d ⁻¹ |
| winter | 0.0044 d ⁻¹ | 0.0089 d ⁻¹ |
| <i>Net blade-elongation rate</i> | | |
| autumn | 9.40 cm d ⁻¹ | 5.40 cm d ⁻¹ |
| winter | 12.80 cm d ⁻¹ | 12.10 cm d ⁻¹ |
| <i>Elongation rate of immature blades</i> | | |
| autumn | 0.22 cm d ⁻¹ | 0.08 cm d ⁻¹ |
| winter | 0.21 cm d ⁻¹ | 0.10 cm d ⁻¹ |
| <i>Relative elongation rate of immature blades</i> | | |
| autumn | 0.0380 d ⁻¹ | 0.0010 d ⁻¹ |
| winter | 0.0360 d ⁻¹ | 0.0010 d ⁻¹ |

3. STOCKS AND AREAS

In New Zealand, patches of bladder kelp are typically small and discrete, usually less than 100 m², although large beds (less than 1 km²) are found along the North Otago coast (Fyfe et al 1999). Although there are anecdotal accounts of changes in the distribution of *Macrocystis* in New Zealand, particularly in the northern portion of its range near Cape Campbell and in the Marlborough Sounds, and also in offshore Otago sites, baseline data are very limited, and the extent of population and distributional declines remain unclear (D'Archino et al 2019). Although there are currently no data evaluating stock structure for bladder kelp in New Zealand, Alberto et al (2010, 2011) found low, but significant, genetic differentiation over a 70 km stretch of coast in the Santa Barbara Channel in southern California. In a New Zealand context, where stands of bladder kelp are small and discrete, these results suggest that stocks may display strong spatial structuring; however, these results should be viewed with caution because current regimes in the Santa Barbara Channel are strongly unidirectional. Research conducted

at University of Otago is currently investigating genetic structure of *M. pyrifera* around New Zealand (Desmond & Le pers. comm.).

4. ENVIRONMENTAL AND ECOSYSTEM CONSIDERATIONS

This section was first introduced to the May 2013 Plenary after review by the Aquatic Environment Working Group and has been updated subsequently as relevant research has been undertaken and published.

4.1 Role in the ecosystem

Macrocystis pyrifera is a large and complex organism that can alter the surrounding physical environment and buffer interior kelp individuals from wave and current movement. Forests of bladder kelp are amongst the most productive marine communities in temperate waters. They act as keystone species, altering the abiotic environment and providing vast amounts of energy and highly structured three-dimensional habitat (Foster & Schiel 1985, Graham 2004, Graham et al 2008, Schiel & Foster 2015, Hepburn 2019). Kelp forests provide a key habitat for reef fishes (Win 2011) and their canopy provides a surface for attachment for many organisms (Hepburn & Hurd 2005), providing physical habitat for organisms both above and below the benthic boundary layer (Foster & Schiel 1985). Kelp forests are key kōhanga (nursery) areas for fish (Win 2011) and are thought to allow for the settlement of larvae of kōura (crayfish, *Jasus edwardsii*) and perhaps pāua by slowing water flow, allowing passing larvae to reach the seabed and providing a refuge for newly settled recruits (Hinojosa et al 2015, Hesse et al 2016, Hepburn 2019).

In California, bladder kelp has been identified as altering abiotic and biotic conditions by dampening water motion and as a result may help prevent coastal erosion (Jackson & Winant 1983, Jackson 1998, Gaylord et al 2012), 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), and stabilising substrata (North 1971).

There are three primary components to the provisioning of habitat by attached bladder kelp: the holdfast, the midwater fronds, and the surface canopy (Foster & Schiel 1985). Studies from California, Canada, Chile, the Sub-Antarctic, Tasmania, and New Zealand have shown that a highly diverse assemblage of organisms colonises each of these three components. Holdfasts are primarily colonised by algae and invertebrates and encrusted with bryozoans and sponges. The midwater fronds and surface canopies are host to a variety of sessile and mobile invertebrates (e.g., amphipods, top snails, and turban snails), encrusting bryozoans, and hydroids. Juvenile and adult fishes may also associate with midwater and canopy fronds, although kelp-fish associations in New Zealand appear to be weaker than those reported in California.

Although the following associations are not exclusive, the major species associated with bladder kelp forests in New Zealand include: (i) understory brown algae, *Ecklonia radiata*, *Carpophyllum flexuosum*, *Marginariella boryana*, and *Cystophora platylobium*; (ii) a rich fauna of sessile invertebrates, including *Callana* spp., *Calliostoma granti*, *Cookia sulcata*, *Evechinus chloroticus*, *Haliotis iris*, *Trochus* spp.; and (iii) fishes, including *Notolabrus celidotus*, *N. cinctus*, *Odax pullus*, and *Parika scaber* (Pirker et al 2000, Shears & Babcock 2007). Large stands of *Macrocystis pyrifera* play a particularly important role in supporting culturally and commercially important local fisheries species such as *Haliotis iris* (pāua), *Jasus edwardsii* (southern rock lobster), *Parapercis colias* (blue cod), *Evechinus chloroticus* (kina), and *Odax pullus* (greenbone) (Fyfe et al 1999, Hinojosa et al 2015). D'Archino et al (2019) present an example of a community food web based on survey data from the East Otago Taiāpure community, showing the relationships and patterns of association between species or among groups. The *Macrocystis* node was found to be strongly linked to other species, emphasising its role as a foundational member of the community.

A significant proportion of annual kelp production becomes free-floating and beach-cast in response to storm events, seasonal mortality, or ageing. Bladder kelp continues to provide habitat resources after

detachment from the substratum. Studies from California, Chile, Macquarie Island, South Georgia, and Tasmania have shown that holdfasts, midwater fronds, and canopies can retain epifaunal fishes and mobile and sessile invertebrates when drifting long distances and play an important role in the dispersal of invertebrates and fishes (Edgar 1987, Vásquez 1993, Helmuth et al 1994, Hobday 2000a, b, c, Smith 2002, Macaya et al 2005, Thiel & Gutow 2005a, b). Mature free-floating individuals may also be important in the connectivity of bladder kelp populations and may explain low genetic diversity of bladder kelp over large geographic extents in the south-eastern Pacific (Thiel et al 2007, Macaya & Zuccarello 2010b).

The beach-cast state is either washed back into the sea over subsequent tidal cycles or remains in the beach environment. New Zealand and Californian studies demonstrate that it is incorporated into physical beach processes, or into the terrestrial or marine food webs through consumption and decomposition (Inglis 1989, Lastra et al 2008). In New Zealand, beach-cast material supports a diverse ecology of organisms through nutrient cycling and decomposition, including various micro- and macro-fauna (Inglis 1989, Marsden 1991) and, if washed up high enough on the beach, can aid sand dune formation.

4.2 Incidental catch (fish and invertebrates)

Small scale harvesting experiments carried out in Akaroa Harbour showed that harvesting canopy biomass had no measurable effect on bladder kelp and the dominant understory species (Pirker et al 2000).

4.3 Incidental catch (marine mammals, seabirds, and protected fish)

None known.

4.4 Benthic interactions

None known.

4.5 Other considerations

None known.

5. STOCK ASSESSMENT

Currently there is insufficient information on canopy area and density to allow for a stock assessment for KBB G. Furthermore, due to large temporal and spatial variation in bladder kelp growth, estimates of biomass should be looked at conservatively when applying regional scale management.

Large spatial and temporal fluctuations in biomass within and between individual kelp forests necessitates the need for initial annual stock assessments of targeted beds to determine credible biomass and sustainable yield information to ensure long-term sustainability (Pirker et al 2000). A combination of aerial photography and *in situ* measurements provide a useful approach for assessing canopy biomass (Fyfe & Israel 1996, Fyfe et al 1999, Pirker et al 2000), although in some populations canopies are not present at the water surface and may remain undetected. Additional approaches to monitoring kelp beds are discussed by D'Archino et al (2019) and D'Archino & Piazzini (2021).

5.1 Estimates of fishery parameters and abundance

No estimates of fishery parameters or abundance are available at present.

5.2 Biomass Estimates

Maximum biomass occurs in winter (Cummack 1981, Pirker et al 2000). Growth rates and peaks in biomass can vary significantly over very short distances (i.e., kilometres) and temporal scales (i.e., seasonally) in response to changes in currents, light, nutrient levels, and other environmental factors. Fyfe et al (1999) found that the wet biomass of closed canopy at Pleasant River in KBB 3 fluctuated from an estimated 10 639 g m⁻² (SE = 1566) in November 1995 to 3761 g m⁻² (SE = 1237) in November 1996. Pirker et al (2000) noted that marked differences exist in the demography of bladder kelp at a spatial scale of only a few kilometres—and that beds decline and regenerate at different times. Because

BLADDER KELP ATTACHED (KBB G)

of the apparent rapid spatio-temporal fluctuations in biomass, the status of KBB 3G and KBB 4G biomass is unknown and unable to be reliably estimated using currently available information. Therefore, Fisheries New Zealand was unable to ascertain whether the current biomass of both attached bladder kelp stocks is stable, increasing, or decreasing.

There is some limited information on past harvestable bladder kelp biomass and potential yield at three sites in Akaroa Harbour (Wainui, Ohinepaka, and Mat White bays, located in KBB 3G) where Pirker et al (2000) estimated a combined annual harvestable canopy biomass of 377 tonnes for 1999. Further, Pirker et al (2000) concluded that at Akaroa Harbour sites no one forest was capable of supporting the removal of consistent amounts of canopy, although two harvests could be sustained per year—one in late spring/early summer just prior to frond senescence, and then another cut in late autumn/early winter. However, this estimate should be treated with caution; the survey provides only seasonal point estimates of harvestable biomass during the time the survey was conducted, with the 1999 estimate being the highest. Further, the 1999 estimate does not provide an indication of biomass at a QMA level.

There is also some limited information on the location of bladder kelp beds throughout KBB 3, although the biomass of floating surface canopies is unknown. In November 1995, Fyfe et al (1999) used aerial photography to quantify whole plant biomass (surface canopies and subsurface fronds) of bladder kelp forests at Pleasant River. They estimated 42 ha of closed bladder kelp canopy and 43 ha of broken canopy, with a combined biomass of 7900 tonnes (± 1300).

5.3 Yield estimates and projections

MCY cannot be estimated because absolute biomass has not been estimated.

CAY cannot be estimated.

5.4 Other yield estimates and stock assessment results

No information is available.

5.5 Other factors

It is not known whether the biomass of bladder kelp is stable or variable, but the latter is considered more likely.

6. STATUS OF THE STOCKS

KBB 3G - South-East (coast)

Stock Structure Assumptions

No information is currently available to determine biological stocks for bladder kelp. Therefore, where quota has been allocated this has been to existing fishery management areas (3 and 4).

| Stock Status | |
|-----------------------------------|--|
| Year of Most Recent Assessment | 1995 and 1999 |
| Assessment Runs Presented | Survey biomass from different parts of KBB 3 |
| Reference Points | Interim Target: 40% B_0 Interim Soft Limit: 20% B_0 Interim Hard Limit: 10% B_0 Interim Overfishing threshold: F_{MSY} |
| Status in relation to Target | Due to the relatively low levels of exploitation it is likely that all stocks are still effectively in a virgin state, therefore they are Very Likely (> 90%) to be at or above the target |
| Status in relation to Limits | Very Unlikely (< 10%) to be below the soft and hard limits |
| Status in relation to Overfishing | Overfishing is Very Unlikely (< 10%) to be occurring |

| Historical Stock Status Trajectory and Current Status | |
|---|--|
| - | |

| Fishery and Stock Trends | |
|--|--|
| Recent Trend in Biomass or Proxy | Unknown |
| Recent Trend in Fishing Intensity or Proxy | Fishing is light in KBB 3G averaging 41 t since 2001–02, with a maximum of 104.5 t in 2001–02. |
| Other Abundance Indices | - |
| Trends in Other Relevant Indicators or Variables | - |

| Projections and Prognosis | |
|---|--|
| Stock Projections or Prognosis | Unknown |
| Probability of Current Catch or TACC causing Biomass to remain below, or to decline below, Limits | Current catches are Very Unlikely (< 10%) to cause declines below soft or hard limits |
| Probability of Current Catch or TACC causing Overfishing to continue or to commence | Current catches are Very Unlikely (< 10%) to cause overfishing to continue or commence |

| Assessment Methodology and Evaluation | | |
|--|--|--|
| Assessment Type | Level 2 Partial quantitative stock assessment | |
| Assessment Method | Ground-truthed remote sensing biomass surveys | |
| Assessment Dates | Latest assessment: 1995 and 1999 (in different areas of KBB 3) | Next assessment: Unknown |
| Overall assessment quality rank | 1-High quality: it is very likely that fishing is light and having little impact | |
| Main data inputs (rank) | Biomass surveys | 2 - Medium or mixed quality because surveys only cover part of the range and are dated |
| Data not used (rank) | - | - |
| Changes to Model Structure and Assumptions | - | - |
| Major Sources of Uncertainty | - | - |

| Qualifying Comments |
|---|
| There are large temporal and spatial fluctuations in biomass within and between beds; therefore, biomass estimates should be utilised conservatively. |

| Fishery Interactions |
|---|
| Bladder kelp plays an important role in structuring habitats and provides both dissolved and particulate carbon to nearshore food chains, and also contributes drift material that ends up in the deep ocean as well as being beach-cast (and potentially resuspended) with breakdown products contributing to both terrestrial and marine food webs. Effects of harvesting canopy biomass on associated or dependent species has not been measured in New Zealand and would be dependent upon the methods used and the quantities taken relative to the population size and standing crop. |

KBB 4G - South-East (Chatham Rise)

Stock Structure Assumptions

No information is currently available to determine biological stocks for bladder kelp. Therefore, where quota has been allocated this has been to existing fishery management areas (3 and 4).

BLADDER KELP ATTACHED (KBB G)

| Stock Status | |
|--------------------------------|------|
| Year of Most Recent Assessment | None |
| Assessment Runs Presented | None |

| | |
|-----------------------------------|--|
| Reference Points | Interim Target: 40% B_0 Interim Soft Limit: 20% B_0 Interim Hard Limit: 10% B_0 Interim Overfishing threshold: F_{MSY} |
| Status in relation to Target | Due to the relatively low levels of exploitation it is likely that all stocks are still effectively in a virgin state, therefore they are Very Likely (> 90%) to be at or above the target |
| Status in relation to Limits | Very Unlikely (< 10%) to be below the soft and hard limits |
| Status in relation to Overfishing | Overfishing is Very Unlikely (< 10%) to be occurring |

| Historical Stock Status Trajectory and Current Status |
|---|
| - |

| Fishery and Stock Trends | |
|--|--|
| Recent Trend in Biomass or Proxy | Unknown |
| Recent Trend in Fishing Intensity or Proxy | Fishing is very light in KBB 4G with less than 3 t reported since 2001–02. |
| Other Abundance Indices | - |
| Trends in Other Relevant Indicators or Variables | - |

| Projections and Prognosis | |
|---|--|
| Stock Projections or Prognosis | Unknown |
| Probability of Current Catch or TACC causing Biomass to remain below, or to decline below, Limits | Current catches are Very Unlikely (< 10%) to cause declines below soft or hard limits |
| Probability of Current Catch or TACC causing Overfishing to continue or to commence | Current catches are Very Unlikely (< 10%) to cause overfishing to continue or commence |

| Assessment Methodology and Evaluation | | |
|--|---|--------------------------|
| Assessment Type | - | |
| Assessment Method | - | |
| Assessment Dates | - | Next assessment: Unknown |
| Overall assessment quality rank | - | |
| Main data inputs (rank) | - | - |
| Data not used (rank) | - | - |
| Changes to Model Structure and Assumptions | - | |
| Major Sources of Uncertainty | - | |

| Qualifying Comments |
|---|
| There are large temporal and spatial fluctuations in biomass within and between beds; therefore, any biomass estimates in the future should be utilised conservatively. |

| Fishery Interactions |
|--|
| Bladder kelp plays an important role in structuring habitats and provides both dissolved and particulate carbon to nearshore food chains, and also contributes drift material that ends up in the deep ocean as well as being beach-cast (and potentially resuspended) with breakdown products |

contributing to both terrestrial and marine food webs. Effects of harvesting canopy biomass on associated or dependent species has not been measured in New Zealand and would be dependent upon the methods used and the quantities taken relative to the population size and standing crop.

7. FUTURE RESEARCH CONSIDERATIONS

Future high priority research areas include: (i) updated (or new in the case of KBB 4G) biomass surveys; (ii) an evaluation of stock structure and inter-stock genetic differentiation; and (iii) quantitative estimates for different sources of mortality.

8. FOR FURTHER INFORMATION

- Adams, N M (1994) *Seaweeds of New Zealand*. Canterbury University Press, 360 p.
- Alberto, F; Raimondi, P; Reed, D C; Coelho, N C; Leblois, R; Whitmer, A; Serrão, E A (2010) Habitat continuity and geographic distance predict population genetic differentiation in giant kelp. *Ecology* 91: 49–56.
- Alberto, F; Raimondi, P T; Reed, D C; Watson, J R; Siegel, D A; Mitari, S; Coelho, N; Serrão, E A (2011) Isolation by oceanographic distance explains genetic structure for *Macrocystis pyrifera* in the Santa Barbara Channel. *Molecular Ecology* 20: 2543–2554.
- Almanza, V; Buschmann, A H (2013) The ecological importance of *Macrocystis pyrifera* (Phaeophyta) forests towards a sustainable management and exploitation of Chilean coastal benthic co-management areas. *International Journal of Environment and Sustainable Development* 12(4): 341360. <http://dx.doi.org/10.1504/IJESD.2013.056331>
- Anderson, T W (1994) Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Marine Ecology Progress Series* 113: 279–290.
- Andrews, N L (1945) The kelp beds of the Monterey region. *Ecology* 26: 24–37.
- Baardseth, E (1941) The marine algae of Tristan da Cunha. Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937–1938 No. 9: 1–173.
- Barilotti, D C; McPeak, R H; Dayton, P K (1985) Experimental studies on the effects of commercial kelp harvesting in central and southern California *Macrocystis pyrifera* kelp beds. *California Fish and Game* 71: 4–20.
- Barrento, S; Camus, C; Sousa-Pinto, I; Buschmann, A H (2016) Germplasm banking of the giant kelp: Our biological insurance in a changing environment. *Algal Research* 13: 134–140.
- Beckley, L E; Branch, G M (1992) A quantitative scuba-diving survey of the sublittoral macrobenthos at subantarctic Marion Island. *Polar Biology* 11: 553–563.
- Bernstein, B L; Jung, N (1979) Selective pressures and coevolution in a kelp canopy community in southern California. *Ecological Monographs* 49: 335–355.
- Borras-Chavez, R; Edwards, M; Vásquez, J A (2012) Testing sustainable management in Northern Chile: harvesting *Macrocystis pyrifera* (Phaeophyceae, Laminariales). A case study. *Journal of Applied Phycology* 24: 1655–1665.
- Bray, R N; Ebeling, A W (1975) Food, activity, and habitat of three ‘picker-type’ microcarnivorous fishes in the kelp forests off Santa Barbara, California. *Fishery Bulletin* 73: 815–829.
- Brown, M T; Nyman, M A; Keogh, J A; Chin, N K M (1997) Seasonal growth of the giant kelp *Macrocystis pyrifera* in New Zealand. *Marine Biology* 129: 417–424.
- Buschmann, A H; Moreno, C A; Vásquez, J A; Hernández-González, M C (2006) Population and reproduction strategies of *Macrocystis pyrifera* (Phaeophyta) in southern Chile. *Journal of Applied Phycology* 18: 575–582.
- Buschmann, A H; Pereda, S V; Varela, D A; Rodríguez-Maulen, J; Lopez, A; Gonzalez-Carvajal, L; Schilling, M; Henriquez-Tejo, E A; Hernandez-Gonzalez, M C (2014a) Ecophysiological plasticity of annual populations of giant kelp (*Macrocystis pyrifera*) in a seasonally variable coastal environment in the Northern Patagonian Inner Seas of Southern Chile. *Journal of Applied Phycology* 26(2): 837–847. <http://dx.doi.org/10.1007/s10811-013-0070-z>
- Buschmann, A H; Prescott, S; Potin, P; Faugeron, S; Vásquez, J A; Camus, C; Infante, J; Hernández-González, M C; Gutiérrez, A; Varela, D A (2014b) The Status of Kelp Exploitation and Marine Agronomy, with Emphasis on *Macrocystis pyrifera*, in Chile. In: Nathalie, B. (ed.), pp. 161–188. *Advances in Botanical Research*. Academic Press.
- Buschmann, A H; Vásquez, J A; Osorio, P; Reyes, E; Filún, L; Hernández-González, M C; Vega, A (2004) The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. *Marine Biology* 145: 849–862.
- Butler, C L; Lucieer, V L; Wotherspoon, S J; Johnson, C R (2020) Multidecadal decline in cover of giant kelp *Macrocystis pyrifera* at the southern limit of its Australian range. *Marine Ecology Progress Series* 653: 1–18. doi: 10.3354/meps.
- Camus, C; Ballerino, P; Delgado, R; Olivera-Nappa, Á; Leyton, C; Buschmann, A H (2016) Scaling up bioethanol production from G. Gao et al.: Macroalgae for biofuel the farmed brown macroalga *Macrocystis pyrifera* in Chile. *Biofuels Bioproducts and Biorefining* 10: 673–685
- Carr, M H (1989) Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* 126: 59–76.
- Carr, M H (1991) Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* 146: 113–137.
- Carr, M H (1994) Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75: 1320–1333.
- Cavanaugh, K C; Siegel, D A; Reed, D C; Dennison, P E (2011) Environmental controls of giant kelp biomass in the Santa Barbara Channel. *Marine Ecology Progress Series* 429: 1–17.
- Chamberlain, Y M (1965) Marine algae of Gough Island. *Bulletin of the British Museum (Natural History) Botany* 3: 176–232.
- Clark, R P; Edwards, M S; Foster, M S (2004) Effects of shade from multiple kelp canopies on an understory algal assemblage. *Marine Ecology Progress Series* 267: 107–119.
- Correa, T; Gutiérrez, A; Flores, R; Buschmann, A H; Cornejo, P; Bucarey, C (2016) Production and economic assessment of giant kelp *Macrocystis pyrifera* cultivation for abalone feed in the south of Chile. *Aquaculture Research* 47: 698–707.
- Coyer, J A (1987) The mollusk assemblage associated with fronds of giant kelp (*Macrocystis pyrifera*) off Santa Catalina Island, California. *Bulletin of the Southern California Academy of Sciences* 85: 129–138.
- Cribb, A B (1954) *Macrocystis pyrifera* (L.) Ag. in Tasmanian waters. *Australian Journal of Marine and Freshwater Research* 5: 1–34.

- Cruz-Suárez, L; Tapia-Salazar, M; Nieto-López, M; Guajardo-Barbosa, C; Ricque-Marie, D (2009) Comparison of *Ulva clathrata* and the kelps *Macrocystis pyrifera* and *Ascophyllum nodosum* as ingredients in shrimp feeds. *Aquaculture Nutrition* 15: 421–430.
- Cummack, B T (1981) Ecology of *Macrocystis pyrifera* with special reference to growth and development of the sporophyte. MSc Thesis, University of Canterbury. 145 p.
- D'Archino, R; Neill, K F; Nelson, W A; Fachon, E; Peat, C (2019) New Zealand Macroalgae: Distribution and Potential as National Scale Ecological Indicators. *New Zealand Aquatic Environment and Biodiversity Report No. 207*. 217 p.
- D'Archino, R; Piazzini, L (2021) Macroalgal assemblages as indicators of the ecological status of marine coastal systems: A review. *Ecological Indicators* 129: 107835.
- Dayton, P K (1985a) Ecology of kelp communities. *Annual Review of Ecology and Systematics* 16: 215–245.
- Dayton, P K (1985b) The structure and regulation of some South American kelp communities. *Ecological Monographs* 55: 447–468.
- Dayton, P K; Currie, V; Gerrodette, T; Keller, B D; Rosenthal, R J; Van Tresca, D (1984) Patch dynamics and stability of some California kelp communities. *Ecological Monographs* 54: 253–289.
- Dayton, P K; Tegner, M J; Edwards, P B; Riser, K L (1999) Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecological Monographs* 69: 219–250.
- Dean, T A; Jacobsen, F R (1984) Growth of juvenile *Macrocystis pyrifera* (Laminariales) in relation to environmental factors. *Marine Biology* 83: 301–311.
- Dean, T A; Jacobsen, F R; Thies, K; Lagos, S L (1988) Differential effects of grazing by white sea urchins on recruitment of brown algae. *Marine Ecology Progress Series* 48: 99–102.
- DeMartini, E E; Roberts, D A (1990) Effects of giant kelp *Macrocystis* on the density and abundance of fishes in a cobble-bottom kelp forest. *Bulletin of Marine Science* 46: 287–300.
- Demes, K W; Graham, M H; Suskiewicz, T S (2009) Phenotypic plasticity reconciles incongruous molecular and morphological taxonomies: the giant kelp, *Macrocystis* (Laminariales, Phaeophyceae), is a monospecific genus (note). *Journal of Phycology* 45: 1266–1269.
- Desmond, M J; Pritchard, D W; Hepburn, C D (2015) Light limitation within southern New Zealand kelp forest communities. *PLoS ONE* 10(4): 1–18. doi: 10.1371/journal.pone.0123676.
- Desmond, M J; Pritchard, D W; Hurd C L; Richards, D K; Schweikert, K; Wing S; Hepburn C D (2019) Superior photosynthetic performance of the invasive kelp *Undaria pinnatifida* may contribute to continued range expansion in a wave-exposed kelp forest community. *Marine Biology* 166: 139. doi: 10.1007/s00227-019-3593-2
- Desmond, M J; Suárez-Jiménez, R; Nelson, W; Hepburn C (2018) Epifaunal community structure within southern New Zealand kelp forests. *Marine Ecology Progress Series* 596: 71–81. doi: 10.3354/meps12587
- Dixon, J; Schroeter, S C; Kastendiek, J (1981) Effects of the encrusting bryozoan, *Membranipora membranacea*, on the loss of blades and fronds by the giant kelp, *Macrocystis pyrifera* (Laminariales). *Journal of Phycology* 17: 341–345.
- Ebeling, A W; Laur, D R (1985) The influence of plant cover on surfperch abundance at an offshore temperate reef. *Environmental Biology of Fishes* 12: 169–180.
- Edgar, G J (1987) Dispersal of faunal and floral propagules associated with drifting *Macrocystis pyrifera* plants. *Marine Biology* 95: 599–610.
- Edwards, M S (1998) Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F). *Journal of Experimental Marine Biology and Ecology* 228: 309–326.
- Edyvane, K S (2003) Conservation, Monitoring & Recovery of Threatened Giant Kelp (*Macrocystis pyrifera*) Beds in Tasmania –Final Report. Report to Environment Australia (Marine Species Protection Program). 39 p.
- Filbee-Dexter, K; Wernberg, T (2018) Rise of turfs: A new battleground for globally declining kelp forests. *Biological Oceanography* 68(2): 64–76. doi: 10.1093/biosci/bix147.
- Foster, M S; Schiel, D (1985) The ecology of giant kelp forests in California: A community profile. *U.S. Fish and Wildlife Service Biological Report* 85(7).
- Fyfe, J E; Israel, S A (1996) A window on an underwater habitat: Quantifying differences in giant kelp beds using colour aerial photographs and image processing software. 8th International Colloquium of the Spatial Information Research Centre, University of Otago, New Zealand, pp 95–102.
- Fyfe, J; Israel, S A; Chong, A; Ishmail, N; Hurd, C L; Probert, K (1999) Mapping marine habitats in Otago, Southern New Zealand. *Geocarto International* 14: 17–26.
- Gaylord, B; Nickols, K J; Jurgens, L (2012) Roles of transport and mixing processes in kelp forest ecology. *Journal of Experimental Biology* 215(6): 997–1007.
- Geange, S (2014) Growth and reproductive consequences of photosynthetic tissue loss in the surface canopies of *Macrocystis pyrifera* (L.) C. Agardh. *Journal of Experimental Marine Biology and Ecology* 453: 70–75.
- Geange, S W; Powell, A; Clemens-Seely, K; Cárdenas, C A (2014) Sediment load and timing of sedimentation affect spore establishment in *Macrocystis pyrifera* and *Undaria pinnatifida*. *Marine Biology* 161(7): 1583–1592. doi: 10.1007/s00227-014-2442-6
- Gerard, V A; Mann, K H (1979) Growth and production of *Laminaria longicruris* (Phaeophyta) populations exposed to different intensities of water movement. *J. Phycol.* 15: 33–41
- Ghelardi, R J (1971) The biology of giant kelp beds (*Macrocystis*) in California: species structure of the holdfast community. *Nova Hedwigia* 32: 381–420.
- Glover, M (2020) The lost kelp forest: a multi-disciplinary approach to understand change of *Macrocystis pyrifera* habitat in Otago, New Zealand. MSc Thesis, University of Otago, Dunedin. 133 p.
- Graham, M H (1997) Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, U.S.A. *Journal of Experimental Marine Biology and Ecology* 218: 127–149.
- Graham, M H (2002) Prolonged reproductive consequences of short-term biomass loss in seaweeds. *Marine Biology* 140:901–911.
- Graham, M H (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7: 341–357.
- Graham, M; Halpern, B; Carr, M (2008) Diversity and dynamics of California subtidal kelp forests. In: McClanahan, T; Branch, G (editors), pp. 103–134. *Food webs and the dynamics of marine benthic ecosystems*. Oxford, UK: Oxford University Press.
- Graham, M H; Harrold, C; Lisin, S; Light, K; Watanabe, J M; Foster, M S (1997) Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. *Marine Ecology Progress Series* 148: 269–279.
- Graham, M H; Vásquez, J A; Buschmann, A H (2007) Global ecology of the giant kelp *Macrocystis*: from ecotypes to ecosystems. *Oceanography and Marine Biology: An Annual Review* 45: 39–88.
- Gutierrez, A; Correa, T; Muñoz, V; Santibañez, A; Marcos, R; Cáceres, C; Buschmann, A H (2006) Farming of the Giant Kelp *Macrocystis Pyrifera* in Southern Chile for Development of Novel Food Products. *Journal of Applied Phycology* 18: 259–267.
- Hallacher, L E; Roberts, D A (1985) Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California [U.S.A.]. *Environmental Biology of Fishes* 12: 91–110.
- Harper, M A; Cassie Cooper, V; Chang, F H; Nelson, W A; Broady, P A (2012) Phylum Ochrophyta: brown and golden-brown algae, diatoms, silicoflagellates, and kin. In: Gordon, D P (Ed), pp. 114–163. *New Zealand inventory of biodiversity. Volume Three. Kingdoms Bacteria, Protozoa, Chromista, Plantae, Fungi*. Canterbury University Press, Christchurch.

- Hay, C H (1990) The distribution of *Macrocystis* (Phaeophyta: Laminariales) as a biological indicator of cool sea surface temperature, with special reference to New Zealand. *Journal of the Royal Society of New Zealand* 20: 313–336.
- Helmuth, B S; Veit, R R; Holberton, R (1994) Long-distance dispersal of subantarctic brooding bivalve (*Gaimardia trapesina*) by kelp rafting. *Marine Biology* 120: 421–426.
- Hepburn, C D (2019) Local, community-led interventions to address global-scale problems and environmental extremes in coastal ecosystems. In: Techera, E J; Winter, G (Eds), pp. 141–158. *Marine extremes: Ocean safety, marine health and the blue economy*. Abingdon, UK: Routledge.
- Hepburn, C D; Holborow, J D; Wing, S R; Frew, R D; Hurd, C L (2007) Exposure to waves enhances the growth rate and nitrogen status of the giant kelp *Macrocystis pyrifera*. *Marine Ecology Progress Series* 339: 99–108.
- Hepburn, C D; Hurd, C L (2005) Conditional mutualism between the giant kelp *Macrocystis pyrifera* and colonial epifauna. *Marine Ecology Progress Series* 302: 37–48. <http://dx.doi.org/10.3354/meps302037>
- Hepburn, C D; Pritchard, D W; Cornwall, C E; McLeod, R J; Beardall, J; Raven, J A; Hurd, C L (2011) Diversity of carbon use strategies in a kelp forest community: implications for a high CO₂ ocean. *Global Change Biology* 17(7): 2488–2497. <http://dx.doi.org/10.1111/j.1365-2486.2011.02411.x>
- Hesse, J; Stanley, J A; Jeffs, A G (2016) Relative predation risk in two types of habitat for juvenile Australasian spiny lobsters, *Jasus edwardsii*. *Marine Biology Research* 12(9): 895–906.
- Hinojosa, I A; Green, B S; Gardner, C; Jeffs, A (2015) Settlement and early survival of southern rock lobster, *Jasus edwardsii*, under climate-driven decline of kelp habitats. *ICES Journal of Marine Science* 72: 59–68. doi: 10.1093/icesjms/fsu199
- Hobday, A J (2000a) Abundance and dispersal of drifting kelp *Macrocystis pyrifera* rafts in the Southern California Bight. *Marine Ecology Progress Series* 195: 101–116.
- Hobday, A J (2000b) Age of drifting *Macrocystis pyrifera* (L.) C. Agardh rafts in the Southern California Bight. *Journal of Experimental Marine Biology and Ecology* 253: 97–114.
- Hobday, A J (2000c) Persistence and transport of fauna on drifting kelp (*Macrocystis pyrifera* (L.) C. Agardh) rafts in the Southern California Bight. *Journal of Experimental Marine Biology and Ecology* 253: 75–96.
- Holbrook, S J; Carr, M H; Schmitt, R J; Coyer, J A (1990) Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bulletin of Marine Science* 47: 104–114.
- Hurd, C L (2017) Shaken and stirred: the fundamental role of water motion in resource acquisition and seaweed productivity. *Perspectives in Phycology* 4: 73–81.
- Hurd, C L; Durante, K M; Chia, F S; Harrison, P J (1994) Effect of bryozoan colonization on inorganic nitrogen acquisition by the kelps *Agarum fimbriatum* and *Macrocystis integrifolia*. *Marine Biology* 121: 167–173.
- Hurd, C L; Pilditch, C A (2011) Flow-induced morphological variations affect diffusion boundary-layer thickness of *Macrocystis pyrifera* (Heterokontophyta, Laminariales). *Journal of Phycology* 47: 341–351.
- Inglis, G (1989) The colonisation and degradation of stranded *Macrocystis pyrifera* (L.) C. Ag. by the macrofauna of a New Zealand sandy beach. *Journal of Experimental Marine Biology and Ecology* 125: 203–217.
- Jackson, G A (1977) Nutrients and production of giant kelp, *Macrocystis pyrifera*, southern California. *Limnology and Oceanography* 22: 979–995.
- Jackson, G A (1998) Currents in the high drag environment of a coastal kelp stand off California. *Continental Shelf Research* 17: 1913–1928.
- Jackson, G A; Winant, C D (1983) Effect of a kelp forest on coastal currents. *Continental Shelf Research* 2: 75–80.
- John, D M; Pugh, P J A; Tittley, I (1994) Observations on the benthic marine algal flora of South Georgia: a floristic and ecological analysis. *Bulletin of the Natural History Museum, London, Botany* 24(2): 101–114.
- Johnson, C R; Banks, S C; Barrett, N S; Cazassus, F; Dunstan, P K; Edgar, G J; Frusher, S D; Gardner, C; Haddon, M; Helidoniotis, F; Hill, K L; Holbrook, N J; Hosie, G W; Last, P R; Ling, S D; Melbourne-Thomas, J; Miller, K; Peel, G T; Richardson, A J; Ridgway, K R; Rintoul, S; Ritz, D; Ross, D; Sanderson, J; Shepherd, S; Slotwinski, A; Swadling, K M; Taw, N (2011) Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology* 400(1–2): 17–32. <http://dx.doi.org/10.1016/j.jembe.2011.02.032>
- Jones, L G (1971) The biology of giant kelp beds (*Macrocystis*) in California: Studies on selected small herbivorous invertebrates inhabiting *Macrocystis* canopies and holdfasts in southern Californian kelp beds. *Nova Hedwigia* 32: 343–367.
- Kain, J M (1982) Morphology and growth of the giant kelp in New Zealand and California. *Marine Biology* 67: 143–157.
- Ladah, L; Zertuche-Gonzalez, J; Hernandez-Carmona, G (1999) Giant kelp (*Macrocystis pyrifera*, Phaeophyceae) recruitment near its southern limit in Baja California after mass disappearance during ENSO 1997–1998. *Journal of Phycology* 35: 1106–1112.
- Lastra, M; Page, H M; Dugan, J E; Hubbard, D M; Rodil, I F (2008) Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. *Marine Biology* 154: 163–174.
- Le, D M; Desmond, M; Pritchard, D W; Hepburn, D (2022) Effect of temperature on sporulation and spore development of giant kelp (*Macrocystis pyrifera*). *PLoS ONE* 17(12): e0278268.
- Leal, P P; Hurd, C L; Sander, S G; Kortner, B; Roleda, M Y (2016) Exposure to chronic and high dissolved copper concentrations impedes meiospore development of the kelps *Macrocystis pyrifera* and *Undaria pinnatifida* (Ochrophyta). *Phycologia* 55(1): 12–20. <http://dx.doi.org/10.2216/15-87.1>
- Lobban, C S (1978) Translocation of ¹⁴C in *Macrocystis pyrifera* (Giant Kelp). *Plant Physiology* 61: 585–589.
- Macaya, E C; Boltaña, S; Hinojosa, I A; Macchiavello, J E; Valdivia, N A; Vásquez, N R; Buschmann, A H; Vásquez, J A; Vega, J M A; Thiel, M (2005) Presence of sporophylls in floating kelp rafts of *Macrocystis* spp. (Phaeophyceae) along the Chilean Pacific coast. *Journal of Phycology* 41: 913–922.
- Macaya, E C; Zuccarello, G C (2010a) DNA Barcoding and Genetic Divergence in the Giant Kelp *Macrocystis* (Laminariales)1. *Journal of Phycology* 46(4): 736–742. <http://dx.doi.org/10.1111/j.1529-8817.2010.00845.x>
- Macaya, E C; Zuccarello, G C (2010b) Genetic structure of the giant kelp *Macrocystis pyrifera* along the southeastern Pacific. *Marine Ecology Progress Series* 420: 103–112.
- Manley, S L (1984) Micronutrient uptake and translocation by *Macrocystis pyrifera* (Phaeophyta). *Journal of Phycology* 20: 192–201.
- Marsden, I D (1991) Kelp-sandhopper interactions on a sand beach in New Zealand. I. Drift composition and distribution. *Journal of Experimental Marine Biology and Ecology* 152: 61–74.
- McCleneghan, K; Houk, J L (1985) The effects of canopy removal on holdfast growth in *Macrocystis pyrifera* (Phaeophyta; Laminariales). *California Fish and Game* 71: 21–27.
- Miller, D J; Geibel, J J (1973) Summary of blue rockfish and lingcod life histories, a reef ecology study, and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. State of California, Department of Fish and Game. *Fish Bulletin* 158. 135 p.
- Moreno, C A; Jara, H F (1984) Ecological studies of fish fauna associated with *Macrocystis pyrifera* belts in the south of Feuguian Islands, Chile. *Marine Ecology Progress Series* 15: 99–107.
- Nelson, W A; Neill, K; D'Archino, R; Rolfe, J R (2019) Conservation status of New Zealand macroalgae, 2019. *New Zealand Threat Classification Series* 30. Department of Conservation, Wellington. 33 p.
- North, W J (1971) The biology of giant kelp beds (*Macrocystis*) in California: introduction and background. *Nova Hedwigia* 32: 1–68.

- North, W J (1986) Biology of the *Macrocystis* resource in North America. *Fisheries Technology Papers, Food and Agriculture Organization (FAO), United Nations* 281: 265–312.
- North, W J (1994) Review of *Macrocystis* biology. In: Akatsuka, I (Ed) *Biology of Economic Algae*. Academic Publishing, The Hague, The Netherlands.
- Ojeda, F P; Santelices, B (1984) Ecological dominance of *Lessonia nigrescens* (Phaeophyta) in central Chile. *Marine Ecology Progress Series* 19: 83–91.
- Pirker, J J (2002) Demography, biomass production and effects of harvesting giant kelp *Macrocystis pyrifera* (Linnaeus) in southern New Zealand. PhD Thesis. University of Canterbury.
- Pirker, J J; Schiel, D R; Lees, H (2000) Seaweed Products for Barrel Culture Paua Farming. Unpublished Report for Foundation for Research Science and Technology's Technology for Business Growth Development project. 88 p.
- Pritchard, D W; Hurd, C L; Beardall, J; Hepburn, C D (2013) Survival in low light: photosynthesis and growth of a red alga in relation to measured in situ irradiance. *Journal of Phycology* 49: 867–879. doi: 10.1111/jpy.12093
- Reed, D C (1987) Factors affecting the production of sporophylls in the giant kelp *Macrocystis pyrifera* (L.) C.Ag. *Journal of Experimental Marine Biology and Ecology* 113: 61–69.
- Reed, D C; Foster, M S (1984) The effects of canopy shading on algal recruitment and growth of a giant kelp (*Macrocystis pyrifera*) forest. *Ecology* 65: 937–948.
- Ricker, R W (1987) *Taxonomy and biogeography of Macquarie Island seaweeds*. pp. i–vi, [2], 1–344. London: British Museum (Natural History).
- Rothäusler, E; Gómez, I; Karsten, U; Tala, F; Thiel, M (2011) Physiological acclimation of floating *Macrocystis pyrifera* to temperature and irradiance ensures long-term persistence at the sea surface at mid-latitudes. *Journal of Experimental Marine Biology and Ecology* 405: 33–41. doi: 10.1016/j.jembe.2011.05.018
- Schiel, D R; Andrew, N J; Foster, M S (1995) The structure of subtidal algal and invertebrate assemblages at the Chatham Islands, New Zealand. *Marine Biology* 123: 355–367.
- Schiel, D R; Foster, M S (2015) *The Biology and Ecology of Giant Kelp Forests*. University of California Press Nature. 395 p.
- Schmitz, K; Lobban, C.S. (1976) A survey of translocation in Laminariales (Phaeophyta). *Marine Biology* 36: 207–216.
- Seymour, R J; Tegner, M J; Dayton, P K; Parnell, P E (1989) Storm wave induced mortality of giant kelp *Macrocystis pyrifera* in southern California. *Estuarine Coastal and Shelf Science* 28: 277–292.
- Shears, N T; Babcock, R C (2007) Quantitative description of mainland New Zealand's shallow subtidal reef communities. *Science for Conservation* 280. Department of Conservation, Wellington.
- Shears N T; Bowen M M (2017) Half a century of coastal temperature records reveal complex warming trends in western boundary currents. *Scientific Reports* 7: 14527. doi: 10.1038/s41598-017-14944-2
- Silva, P C; Basson, P W; Moe, R L (1996) Catalogue of the benthic marine algae of the Indian Ocean. *University of California Publications in Botany* 79: 1–1259.
- Smith, S D A (2002) Kelp rafts in the Southern Ocean. *Global Ecology and Biogeography* 11: 67–69.
- Stebbins, T D (1986) Density, distribution, and feeding of the marine snail *Norrisia norrisi* (Mollusca: Gastropoda) on the kelp *Macrocystis pyrifera* (Phaeophyta: Laminariales). *Bulletin of the Southern California Academy of Sciences* 85: 69–73.
- Stephens, J S; Morris, P M; Zerba, K; Love, M (1984) Factors affecting fish diversity on a temperature reef: the fish assemblage of Palos Verdes Point [California, U.S.A.], 1974–1981. *Environmental Biology of Fishes* 11: 259–275.
- Stephens, T A; Hepburn, C D (2014) Mass-transfer gradients across kelp beds influence *Macrocystis pyrifera* growth over small spatial scales. *Marine Ecology Progress Series* 515: 97–109. <http://dx.doi.org/10.3354/meps10974>
- Stephens, T A; Hepburn, C D (2016). A kelp with integrity: *Macrocystis pyrifera* prioritises tissue maintenance in response to nitrogen fertilisation. *Oecologia* 182(1): 71–84. <http://dx.doi.org/10.1007/s00442-016-3641-2>
- Stewart, C J (2015) The in situ nitrogen (ammonium and nitrate) uptake kinetics of *Macrocystis pyrifera* (L.) C. Agardh: applications for integrated multi-trophic aquaculture (IMTA) in Big Glory Bay, Stewart Island, New Zealand. MSc thesis. University of Otago. 126 p.
- Suárez-Jiménez, R; Hepburn, C; Hyndes, G; McLeod, R; Taylor, R; Hurd, C (2017) The invasive kelp *Undaria pinnatifida* hosts an epifaunal assemblage similar to native seaweeds with comparable morphologies. *Marine Ecology Progress Series* 582: 45–55. doi: 10.3354/meps12321
- Tait L (2019) Giant kelp forests at critical light thresholds show compromised ecological resilience to environmental and biological drivers. *Estuarine, Coastal and Shelf Science* 219: 231–241.
- Tait, L W; Thorall, F; Pinkerton, M H; Thomsen, M S; Schiel, D R (2021) Loss of Giant Kelp, *Macrocystis pyrifera*, Driven by Marine Heatwaves and Exacerbated by Poor Water Clarity in New Zealand. *Frontiers in Marine Science* 8: 721087. doi: 10.3389/fmars.2021.721087
- Taylor, W R (1945) Pacific marine algae of the Allan Hancock Expeditions to the Galapagos Islands. *Allan Hancock Pacific Expeditions* 12: i–iv, 1–528.
- Tegner, M J; Dayton, P K; Edwards, P B; Riser, K L (1995) Sea urchin cavitation of giant kelp (*Macrocystis pyrifera*) holdfasts and its effects on kelp mortality. *Journal of Experimental Marine Biology and Ecology* 191: 82–99.
- Thiel, M; Gutow, L (2005a) The ecology of rafting in the marine environment. I: The floating substrata. *Oceanography and Marine Biology: An Annual Review* 42: 181–264.
- Thiel, M; Gutow, L (2005b) The ecology of rafting in the marine environment. II: The rafting organisms and community. *Oceanography and Marine Biology: An Annual Review* 43: 279–418.
- Thiel, M; Macaya, E C; Acuña, E; Arntz, W E; Bastias, H; Brokordt, K; Camus, P A; Castilla, J C; Castro, L R; Cortés, M; Dumont, C P; Escribano, R; Fernandez, M; Gajardo, J A; Gaymer, C F; Gomez, I; González, A E; González, H E; Haye, P A; Illanes, J E; Iriarte, J L; Lancellotti, D A; Luna-Jorquera, G; Luxoro, C; Manriquez, P H; Marín, V; Muñoz, P; Navarrete, S A; Perez, E; Poulin, E; Sellanes, J; Sepúlveda, H H; Stotz, W; Tala, F; Thomas, A; Vargas, C A; Vasquez, J A; Vega, J M (2007) The Humboldt current system of northern-central Chile: oceanographic processes, ecological interactions and socioeconomic feedback. *Oceanography and Marine Biology: An Annual Review* 45: 195–344.
- Thiel, M; Vásquez, J A (2000) Are kelp holdfasts islands on the ocean floor? Indication for temporarily closed aggregations of peracarid crustaceans. *Hydrobiologia* 440: 45–54.
- Towle, D W; Pearse, J S (1973) Production of giant kelp, *Macrocystis*, estimated by in situ incorporation of C-14 in polyethylene bags. *Limnology and Oceanography* 18: 155–158.
- Tugwell, S; Branch, G M (1989) Differential polyphenolic distribution among tissues in the kelps *Eklonia maxima*, *Laminaria pallida* and *Macrocystis angustifolia* in relation to plant-defence theory. *Journal of Experimental Marine Biology and Ecology* 129:219–230.
- Vásquez, J A (1993) Effects on the animal community of dislodgement of holdfasts of *Macrocystis pyrifera*. *Pacific Science* 47:180–184.
- Vásquez, J A; Vega, J M A; Buschmann, A H (2006) Long term studies on El Niño-La Niña in northern Chile: effects on the structure and organization of subtidal kelp assemblages. *Journal of Applied Phycology* 18: 505–519.

- Wargacki, A J; Leonard, E; Win, M N; Regitsky, D D; Santos, C N S; Kim, P B; Cooper, S R; Raisner, R M; Herman, A; Sivitz, A B; Lakshmanaswamy, A; Kashiya, Y; Baker, D; Yoshikuni, Y (2012). An engineered microbial platform for direct biofuel production from brown macroalgae. *Science* 335: 308–313.
- Watanabe, J M (1984a) Food preference, food quality and diets of three herbivorous gastropods (Trochidae: *Tegula*) in a temperate kelp forest habitat. *Oecologia* 62: 47–52.
- Watanabe, J M (1984b) The influence of recruitment, competition, and benthic predation on spatial distributions of three species of kelp forest gastropods (Trochidae: *Tegula*). *Ecology* 65: 920–936.
- Wernberg, T; Russell, B D; Moore, P J; Ling, S D; Smale, DA; Campbell, A; Coleman, M A; Steinberg, P D; Kendrick, G A; Connell, S D (2011) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *Journal of Experimental Marine Biology and Ecology* 400: 7–16.
- Win, R (2011) The Importance of Macroalgae on Rocky Reefs: A Critical Aspect for Fish and Epifauna of the East Otago Coastline. MSc Thesis. University of Otago, New Zealand.
- Womersley, H B S (1987) *The marine benthic flora of southern Australia*. Part II. South Australian Government Printing Division, Adelaide. 481 p.
- Young, M; Ierodiaconou, D; Womersley, T (2015) Remote sensing of environment forests of the sea: predictive habitat modelling to assess the abundance of canopy forming kelp forests on temperate reefs. *Remote Sensing of Environment* 170: 178–187. doi: 10.1016/j.rse.2015.09.020
- Zimmerman, R C; Robertson, D L (1985) Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. *Limnology and Oceanography* 30(6): 1298–1302. doi: 10.4319/lo.1985.30.6.1298

