

## NOTE

## Deep occurrence of the giant kelp *Macrocystis laevis* in the Southern Ocean

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**ABSTRACT:** During a combined hydroacoustic-trawling survey at the Prince Edward Archipelago, a kelp bed of *Macrocystis laevis* growing at a maximum depth of 68 m was repeatedly observed in the open shelf area. This is the deepest population ever described for any species of giant kelp. Nutrient availability and temperature in the area were found to have no significant impact on kelp production and distribution. Likewise, measurements of photon flux density showed that neither plant growth nor sporophyte formation was likely to have been light-inhibited during the period of the observations. However, since irradiance levels in the deep kelp bed were close to the lower threshold for growth, the absence of plants below 68 m depth was probably determined by light availability. Around Marion Island, where *M. laevis* is found only within the 20 m isobath, the offshore limit of the kelp beds is controlled by availability of suitable rock substrata. The inshore limit appears to be set by the maximum height of storm-induced waves.

Four species of *Macrocystis* are generally recognized: *M. integrifolia*, *M. angustifolia*, *M. pyrifera* and the recently described *M. laevis* (Womersley 1954, Neushul 1971, Hay 1986, Brostoff 1988). *Macrocystis* kelps are found in cold temperate oceans with surface temperatures varying from 0 to 20 °C, and their main distribution is circumpolar in the Southern Hemisphere, between 40 and 60° S (Table 1; Cribb 1954, Michanek 1983). They are also present in the major coastal upwelling areas. On the west coast of South Africa they occur between 33°24' and 34°8' S and on the Pacific coast of South America extend almost to the equator, reappearing in North America along Baja California and reaching southern Alaska to the north (Table 1).

Only 2 species of *Macrocystis* are represented in the Southern Ocean: *M. pyrifera* and *M. laevis*. While *M. pyrifera* is widely distributed from subantarctic South America to New Zealand, and occurs at most islands in the Atlantic and Indian sectors of the Southern Ocean, *M. laevis* is endemic to the Prince Edward Archipelago (Hay 1986).

Along rocky coasts, the inshore limit of *Macrocystis*

forests is usually controlled by wave action and tidal ranges (North 1971, Seymour et al. 1989). The offshore limit appears to be determined by different factors for the various species. *M. integrifolia* and *M. angustifolia* are restricted to shallow intertidal and subtidal areas (Table 1) and their lower depth limits are set by sea urchin grazing and wave action, respectively (Papenfuss 1942, Druehl 1978). *M. pyrifera* and *M. laevis* extend to deeper subtidal depths and further offshore (Table 1). Their lower limits seem to be primarily controlled by light intensity at the bottom (Neushul & Haxo 1963, Peres 1982, Dean & Jacobsen 1984). *M. pyrifera* beds in turbid waters usually do not extend below 10 to 20 m, but in clearer offshore waters they may reach 30 to 40 m (Grua 1964, North 1971).

The deepest occurrence of *Macrocystis pyrifera* was recorded at 54.9 m in southern Argentina by Neushul (1971), who described this finding as 'enigmatic'. Similarly, Hay (1986) expressed scepticism about the earliest record of *M. laevis* at Marion Island, supposedly collected from a depth of 40 fathoms, ca 73 m (Dickie 1877). Here, we provide evidence that *M. laevis* in the Prince Edward Archipelago can occur down to a depth of at least 60 to 65 m.

Observations on the depth distribution of *Macrocystis laevis* were made from the SA 'Agulhas' in April/May and August 1989. On both occasions, acoustic records were taken along 2 transects crossing the islands' shelf with 12 kHz NEC NS-74 and 120 kHz SIMRAD EKS echo-sounders. Samples of kelp were collected in April 1989 using an opening-closing RMT-2 net towed at 2.5 to 3.0 knots. Haul depth was controlled by a Universal Underwater Unit (Robertson et al. 1981).

Conductivity, temperature and depth (CTD) casts in the area were made using a Neil Brown MK III probe. At selected depths (0, 10, 20, 50 and 100 m), the concentrations of nitrogenous nutrients (nitrate, nitrite, ammonia and urea) were measured with a Technicon

*Macrocystis* spp. Geographic distribution and maximum depth of occurrence

Species	Distribution	Depth (m)	Source
<i>M. angustifolia</i>	South Africa	8	Isaac (1937)
	South Australia	6	Womersley (1954)
<i>M. integrifolia</i>	British Columbia	10	Druehl (1978)
	US Pacific coast	9	Michanek (1983)
	Chile	8	Neushul (1971)
	Peru	20	Juhl-Noodt (1958)
<i>M. pyrifera</i>	Southern California	30	Neushul & Haxo (1963)
	Baja California	40	North (1971)
	Southern Chile	10	Dayton et al. (1973)
	Peru	40	Juhl-Noodt (1958)
	Southern Argentina	55	Neushul (1971)
	Tasmania	30	Michanek (1983)
	New Zealand	16	Hay (1990)
	Kerguelen Is.	40	Grua (1964)
	Crozet Is.	25	Delépine (1966)
	St. Paul–Amsterdam Is.	20	Delépine (1966)
	Falkland Is.	25	Powell (1981)
	South Georgia Is.	25	Skottsberg (1941)
	Gough-Tristan Is.	30	Baardseth (1941)
<i>M. laevis</i>	Prince Edward Is.	73	Dickie (1877)

Autoanalyzer II system (Strickland & Parsons 1968, Mostert 1983). In April/May 1989, 16 depth profiles of photosynthetically available radiation (PAR) were obtained in the shelf and circumsular waters of the archipelago using a Biospherical Instruments irradiance meter (model QSP 170B). Surface irradiance levels were measured at regular intervals of 2 to 4 h throughout the survey.

*Macrocystis laevis* in the Prince Edward Archipelago is abundant along the east coast of Marion Island, with a few isolated patches on the exposed west and southern shores (Fig. 1; Attwood et al. 1991). These kelp beds cover a total area of ca 5.5 km<sup>2</sup> and extend more than 100 m offshore, at depths between 5–10 and 20 m (De Villiers 1976, Attwood et al. 1991, Beckley & Branch in press). They all form dense canopies at the surface.

Well-developed beds of *Macrocystis laevis* were observed during both autumn and winter surveys (April/May and August 1989) on Natal Bank, an isolated prominence shoaling to 45 m below sea level and located on the shelf between Marion and Prince Edward Islands (Fig. 1). Kelp was recorded on both the 12 and 120 kHz echograms and extended upward towards the surface from a maximum bottom depth of ca 68 m (Figs. 2 & 3). They were never observed to form canopies at the surface and, according to the echograms, the longest stipes reached a length of 20 to 25 m. This indicates that the apical portions of the plants were > 30 m below the sea surface. On 26 April fronds were collected while towing the RMT-2 net at between 52 and 67 m.

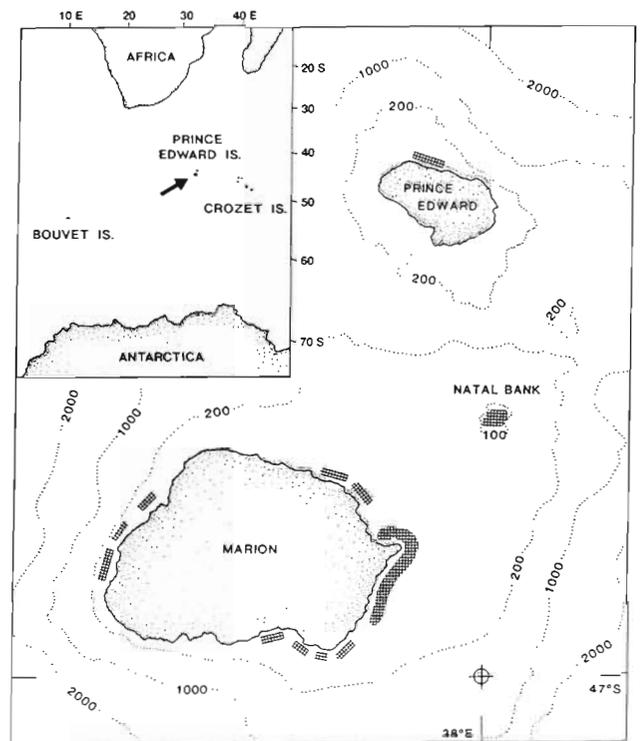


Fig. 1. Bottom topography (depth contours in metres) and distribution (shaded areas) of *Macrocystis laevis* around the Prince Edward Islands

An estimation, based on echograms, of kelp cover within the 60 m isobath on Natal Bank gives values of about 53 and 46% of the total area in April and August, respectively (Fig. 3). An area of about 2.5 km<sup>2</sup> lies

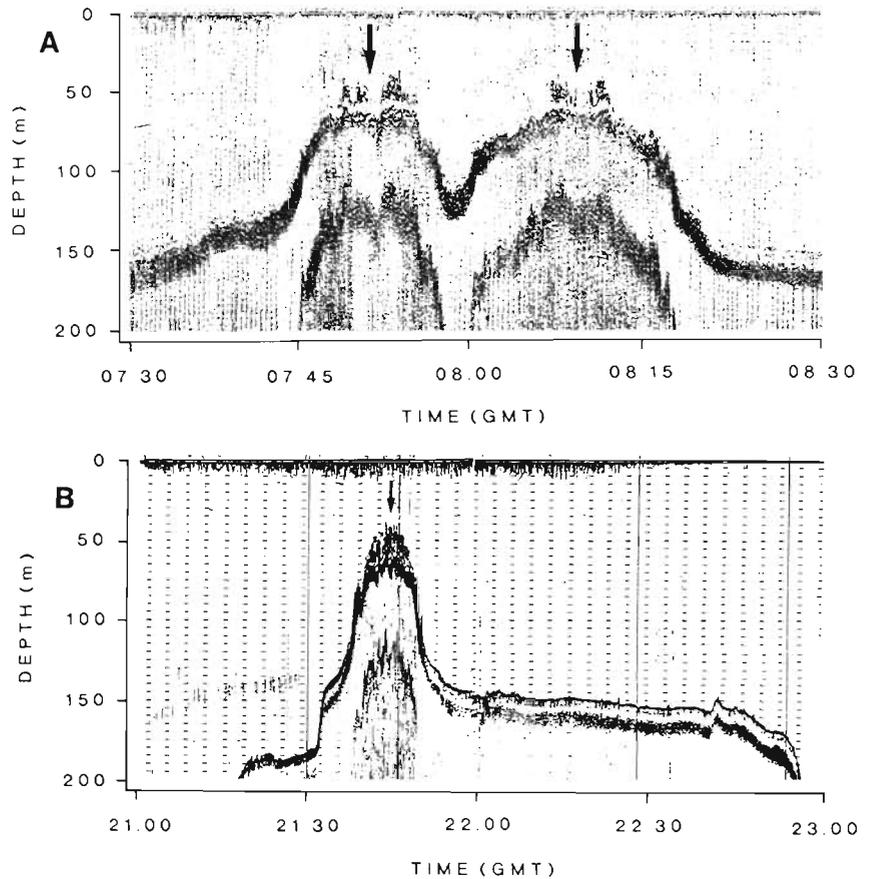


Fig. 2. 120 kHz acoustic records along a transect crossing the Natal Bank. (A) 26 April 1989; (B) 23 August 1989. Arrows indicate deep kelp beds of *Macrocystis laevis*

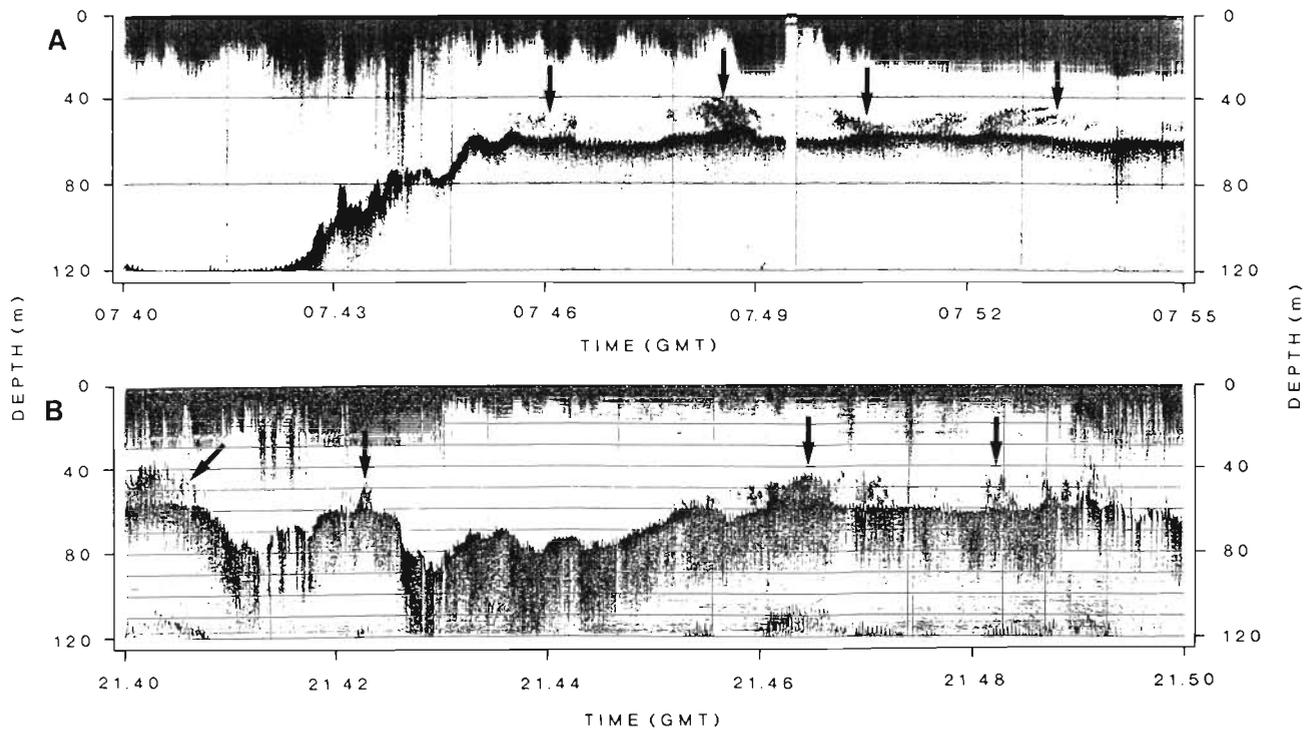


Fig. 3. 12 kHz acoustic records along a transect crossing the Natal Bank. (A) 26 April 1989; (B) 23 August 1989. Arrows indicate deep kelp beds of *Macrocystis laevis*

within the 60 m isobath, indicating a kelp forest of 1.0 to 1.3 km<sup>2</sup>, i.e. about one-fifth of the population found around Marion Island. Assuming plant weights and densities similar to those of the coastal population (i.e. 0.875 holdfasts m<sup>-2</sup> and 13.21 kg plant<sup>-1</sup>; Attwood et al. 1991), the total biomass of *Macrocystis laevis* on Natal Bank could amount to ca 1.1 to 1.5 × 10<sup>4</sup> t (wet wt), or ca 700 to 900 t (carbon).

To our knowledge, the population of *Macrocystis laevis* in the Prince Edward Archipelago is the deepest ever described for any species of giant kelp. There are 2 previous records of *M. laevis* at great depths. During the 'Challenger' expedition the kelp was hauled from 40 fathoms (1 fathom = 1.83 m; Dickie 1877), and in March 1976 it was dredged at 58 m on Natal Bank by the 'Marion-Dufresne' (Arnaud & Hureau 1979).

The most important factors controlling *Macrocystis* production and distribution are nitrogen availability (Jackson 1977, Wheeler & North 1981, Gerard 1982), temperature (North 1971, Dean & Jacobsen 1984, Hay 1990), nature of the substratum (Cribb 1954, North 1971, Druehl 1978, Peres 1982), herbivore grazing (Leighton 1971, Druehl 1978, Dean et al. 1984), irradiance (Neushul & Haxo 1963, Neushul 1971, Dean & Jacobsen 1984, Reed & Foster 1984, Deysher & Dean 1986) and wave action (ZoBell 1971, Dayton et al. 1984, Seymour et al. 1989). Most of these act synergistically and their relative importance is often variable, depending on season and location (North 1971, Druehl 1978, Dean & Jacobsen 1984, Hay 1990).

Most studies on the physiological and ecological requirements of *Macrocystis* have been carried out on the widely distributed *M. pyrifera*. Until its recent description as a separate species, *M. laevis* has been confused with this congeneric kelp (De Villiers 1976, Hay 1986, Attwood et al. 1991). Both species (mutually exclusive) occur in the subantarctic zone of the Southern Ocean, and are biogeographically linked by the Antarctic Circumpolar Current. It seems reasonable, therefore, to assume that their physiology and ecology are very similar (Attwood et al. 1991).

Analysis of environmental control of seaweed growth and distribution requires a combination of in situ and laboratory measurements of all the parameters involved, taking into account daily, monthly and seasonal variations. Admittedly, the data set available for the Prince Edward Island seas still lacks this comprehensiveness. Nevertheless, data on many environmental variables have been collected over the past decade with sufficient regularity to allow the elaboration of some preliminary results and hypotheses.

Ambient nitrate (NO<sub>3</sub>) concentrations in the area (13 to 26 μmol N l<sup>-1</sup>, Fig. 4; Duncombe Rae 1989, Van Ballegooyen et al. 1989, Perissinotto et al. 1990) are well above growth-limiting levels for *Macrocystis* of

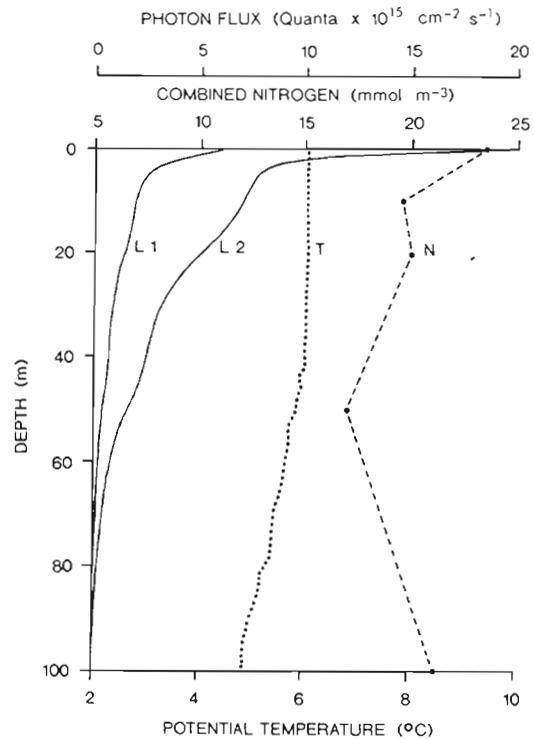


Fig. 4. Selected vertical profiles of temperature (T, dotted line), combined nitrogenous nutrients (N, dashed line) and light intensity (continuous lines) representative of the physico-chemical environment on Natal Bank during April 1989. L1 and L2 represent light profiles under the heaviest and lightest overcast conditions, respectively

< 1 μmol N l<sup>-1</sup> (Jackson 1977, Gerard 1982, Dean & Jacobsen 1984), and tissue nitrogen content (2.1 to 2.9% of dry weight; Attwood et al. 1991) far exceeds levels for nitrogen-deficient *Macrocystis* (0.7 to 1.1%; Gerard 1982). Maximum and minimum temperatures (8.0 and 2.1 °C, respectively; Schulze 1971) also lie within the optimal range of 0 to 18 °C for *Macrocystis* growth (Cribb 1954, Womersley 1954, Michanek 1983).

Data on the diet of the local herbivore community are still too limited to permit conclusions on grazing effects on *Macrocystis laevis*. However, the 2 most abundant grazers (the sea urchin *Pseudochinus marionus* and the isopod *Dynamenella huttoni*) appear to feed primarily on kelp detritus rather than living plants (Attwood et al. 1991).

The effect of underwater irradiance on depth limitation deserves particular attention. Light availability may be limiting, as predominantly overcast conditions at the archipelago reduce the annual sunshine duration to < 30% of the maximum possible, and yearly average photon flux density (ca 40 mol m<sup>-2</sup> d<sup>-1</sup>) is less than 30% of the estimated world average (Schulze 1971, Smith 1987). In the absence of nutrient and temperature limitations, *Macrocystis* requires a minimum

photon flux of ca 0.24 to 0.42 mol m<sup>-2</sup> d<sup>-1</sup> for growth (Neushul & Haxo 1963, Clendenning 1971, Dean & Jacobsen 1984) and ca 0.20 to 0.25 mol m<sup>-2</sup> d<sup>-1</sup> for sporophyte production by gametophytes (Deysher & Dean 1984, 1986).

In April/May 1989, surface irradiation around the Prince Edward Archipelago ranged from 5.8 to 115 mol m<sup>-2</sup> d<sup>-1</sup>, depending on cloud cover, and averaged 39.8 mol m<sup>-2</sup> d<sup>-1</sup>. The water column in the immediate vicinity of the deep kelp bed at Natal Bank was very clear at the time of the survey (Fig. 4). The extinction coefficient was remarkably low (0.059 to 0.054 m<sup>-1</sup>), while the euphotic zone reached 78 to 85 m. In the absence of canopy shading, the deepest depths at which *Macrocystis laevis* was attached (ca 68 m) received a photon flux of ca 0.29 to 0.43 mol m<sup>-2</sup> d<sup>-1</sup>, i.e. just above the thresholds for both growth and sporophyte formation. Recruitment of young plants on the bank is possible under these conditions, but below 68 m depth their growth is probably inhibited by insufficient light.

Irradiance levels at the depth of the upper extent of their stipes in the water column (ca 35 to 40 m) ranged between 1.2 and 2.0 mol m<sup>-2</sup> d<sup>-1</sup>. These values fall within, or close to, the light saturation range for *Macrocystis* growth of 1.8 to 3.0 mol m<sup>-2</sup> d<sup>-1</sup> (Neushul & Haxo 1963, Dean & Jacobsen 1984). Although shortening of the photoperiod during winter must affect growth rates, acoustic records taken over the Natal Bank (Figs. 2 & 3) show no obvious difference in kelp bed cover between autumn (April/May) and winter (August).

The shelf area of the archipelago exhibits an island mass effect which results in the periodic formation of dense phytoplankton blooms (Allanson et al. 1985, Boden 1988, Perissinotto & Duncombe Rae 1990, Perissinotto et al. 1990). Phytoplankton cells can dramatically reduce the light penetration by absorption and scattering and may cause periodical inhibition in the growth of the deepest kelp beds (Clendenning 1971).

In contrast to its deep occurrence on Natal Bank, around Marion Island *Macrocystis laevis* is usually restricted to a depth of ca 20 m. This limit probably reflects the availability of suitable substrata. *Macrocystis* requires a hard substratum for attachment and even when solidly anchored, burial of the holdfast by sand or mud may cause the removal of entire kelp beds (Cribb 1954, North 1971, Reed & Foster 1984, Schiel & Foster 1986). Turbulence near the bottom may also resuspend fine sediment in the water column, reducing the photon flux below the sea surface (Foster 1975, Schiel & Foster 1986).

The shelf area is extensively covered with sediments, from fine mud to small cobbles, which extend inshore to at least the 25 m isobath (Arnaud & Hureau 1979). *Macrocystis laevis* is densest in shallower waters where

lava platforms and boulders (1 to 3 m diameter; De Villiers 1976) form the substratum, but extends much deeper where rock surfaces emerge from the sediments, for example Natal Bank and on the east coast of Marion Island, where kelp has been collected at 50 m (Arnaud & Hureau 1979).

Finally, differences in distribution and abundance between the eastern and the other shores of Marion Island can be explained by wave exposure. The climate of the archipelago is dominated by northwesterly winds which reach gale force (> 55 km h<sup>-1</sup>) on average on 107 days per year (Schulze 1971, Smith 1987). This generates swells up to 20 m high on the west shore, while the eastern or lee shore has a maximum wave height of only ca 4 m (De Villiers 1976, Lutjeharms 1990). Waves break when the ratio of wave height to water depth is about 0.8 (Knauss 1978) and can cause severe damage to *Macrocystis* (Seymour et al. 1989). This may explain why *M. laevis* beds can extend inshore to the 5 m isobath on the eastern shore (Attwood et al. 1991), but occur only further offshore on the south and northwest coasts (De Villiers 1976).

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