

The influence of stranded kelp (*Durvillaea antarctica*) on the macrofaunal assemblages of a southern New Zealand exposed sandy beach

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Stranded *Durvillaea antarctica*

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Abstract

Sandy beaches are dynamic ecosystems occurring between temperate to tropical latitudes. In-situ primary productivity of wave-exposed sandy beaches is often low, but the food web of such shores may be supported by marine subsidies in the form of stranded macrophyte material. The input of washed-up seaweed, also termed wrack, varies seasonally and between zones. *Durvillaea antarctica* and *D. willana* are two species of kelp that dominate the exposed shores of New Zealand. Research on the relationship between stranded seaweed and macrofaunal assemblages on New Zealand sandy shores is limited, hence this study aimed to produce a quantitative list of the macrofaunal species associated with stranded *D. antarctica* on an Otago exposed sandy beach, and to investigate its decomposition rate over a 30-day period in autumn and winter.

In autumn and winter 2008, six mesh bags containing 1 kg samples of *D. antarctica* were placed at four sites along Victory Beach. On days 1, 3, 6, 10, 20 and 30, kelp samples were randomly selected from each site and a 10 x 10 cm core for macrofauna was taken directly under the kelp (0 m), at 0.5 and 1 m distance away. Core and kelp samples were sieved on a 1 mm mesh to extract macrofauna, which were identified and counted. Amphipods were separated into adult and juvenile stages. Macrofaunal biomass was also determined. The water, carbon and nitrogen content of the kelp samples were measured.

Twenty macroinvertebrate taxa were found to be associated with the samples of *D. antarctica* during both seasons. Amphipoda, Staphylinidae, other Coleoptera and Diptera made up 99.9% of total macrofauna abundance and biomass. All four taxa were present on day 1 of sampling. Amphipoda was the dominant coloniser in terms of abundance and biomass for both seasons. On average, it comprised 74-96% of total abundance and 53-98% of total biomass. Amphipoda and Staphylinidae differed significantly in abundance between days of exposure, where amphipods were most abundant during early stages of colonisation and staphylinids were most abundant on day 20 of exposure. All main taxonomic groups, except other Coleoptera, differed in biomass between days of exposure and between seasons, with autumn having the highest biomass. The presence of *D. antarctica* significantly impacted the abundance of macroinvertebrate species, where abundance was highest directly under the kelp. The abundance and biomass of adult and juvenile amphipods in kelp and sediment

samples were influenced by different factors. Core abundance indicated that adults are more dependent on the presence of stranded *D. antarctica*.

Decomposition rate and moisture content of *D. antarctica* differed significantly between days of exposure and between seasons. *D. antarctica* dried and decomposed at a faster rate in autumn than in winter. Carbon content ranged between 22-35% and differed significantly over time. The nitrogen content ranged between 0.78-1.26%. Correlations between macrofaunal abundance and the decomposition rate, and total macrofaunal abundance and the C:N ratio, suggest that the macrofaunal community on Victory Beach prefers old wrack over fresh wrack and a carbon-rich food source.

Beach grooming and/or seaweed harvesting has been implicated as one of the main management concerns for the future of the ecology of sandy shores. To determine the effects of removing beach-cast seaweed on associated fauna it is essential to investigate its ecological significance in sandy beach food webs. The present study contributes to our understanding of the significant role of stranded seaweed in sandy shore foodwebs.

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Chapter 1: General Introduction



Uses of sandy shores by wildlife (sealion (C), yellow-eyed penguin (D)) and humans (walking/tourism (A), surfing (B)) on the Otago Peninsula, New Zealand (author's photos).

1.1 Sandy Beaches

Sandy beaches are dynamic ecosystems occurring from temperate to tropical latitudes (Rodil *et al.*, 2007; Gonçalves *et al.*, 2009). Pinnipeds and birds use these shores as breeding and nesting grounds (Dugan *et al.*, 2000) while humans use them for recreational (e.g. 4WD, swimming, surfing) and commercial (e.g. seaweed harvesting, mining) purposes (McLachlan, 1996; Stephenson, 1999; Priskin, 2001). Sandy beach ecosystems can be divided into three tidal levels: upper, middle and lower (McLachlan & Brown, 1990). The upper shore is the zone that extends from MHWS (Mean High Water Spring) to EHWS (Extreme High Water Spring). Driftwood and detritus that accumulates and forms a line at the recent high tide mark is known as the 'strand line' and lies within the upper shore (Svarney & Barnes-Svarney, 2003). For this study, the upper shore was identified as the area 3 metres from above the strand line to the start of dune vegetation (after Olabarria *et al.*, 2007). The upper shore is inhabited by semi-terrestrial species that are capable of surviving in a dry environment, while marine species occupy the middle and lower shore level of the intertidal zone as they require moisture for their excretion (Colombini *et al.*, 2002; De La Huz & Lastra, 2008). For instance, crustaceans dominate the upper shores, while polychaetes and molluscs inhabit the middle and lower shore level as they are more prone to desiccation (Colombini *et al.*, 2002; Rodil *et al.*, 2007).

The marine/terrestrial interface lies within the upper shore and undergoes a continuous exchange of material between the two habitats (Fig. 1.1). For instance, wind causes insects and litter from the dunes to be dispersed onto the beach, and marine invertebrates and detritus from the strand line to be scattered into the terrestrial habitat (Fig 1.1) (Stephenson, 1999). The input of marine subsidies, which in turn is influenced by the level of exposure, is therefore, important for sustaining marine and terrestrial food webs in these dynamic ecosystems.

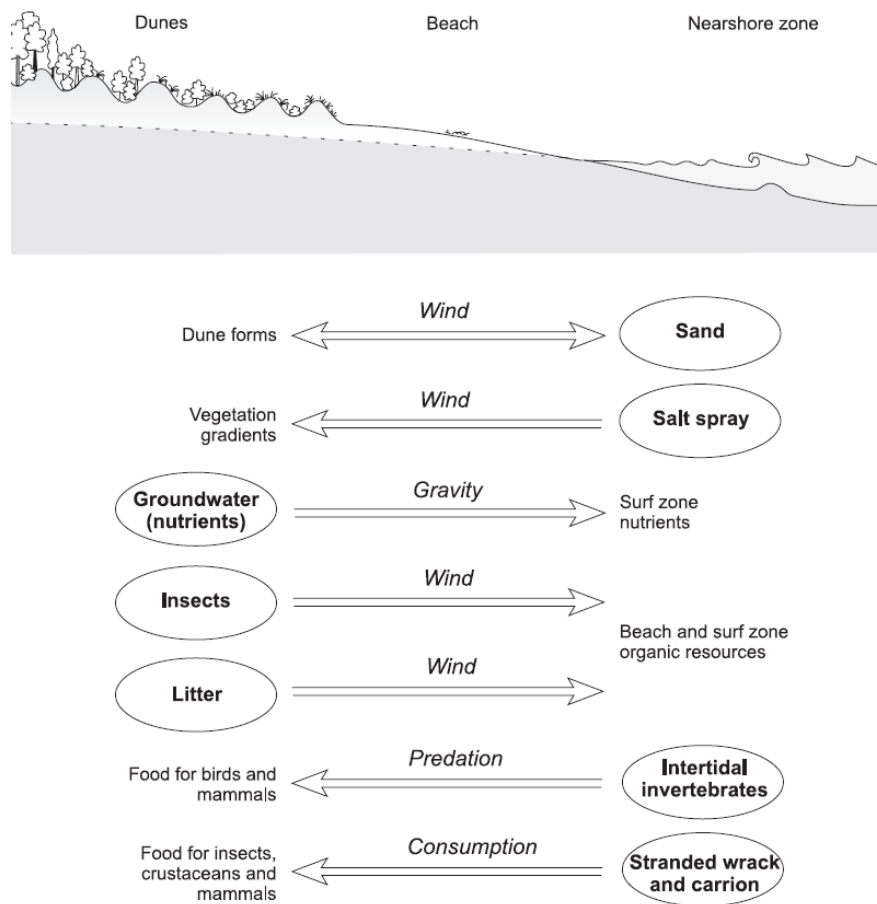


Figure 1.1 Exchange of materials at the marine-terrestrial interface (Stephenson 1999: adapted from McLachlan, 1988).

1.2 Impact of exposure

Sandy beaches can be categorised by their level of exposure. McLachlan (1980) suggested a simple rating system for assessing the degree of exposure of sandy beaches by using the following parameters of the intertidal zone: wave energy, beach slope, sediment particle size, macrofauna burrows and sediment oxidation. A very exposed beach is usually characterised by heavy wave action, deep reduced layers if present, coarse sediments, steep slope and no macrofaunal burrows (Table 1.1). On the other hand, a very sheltered beach is characterised by no wave action, shallow reduced layers, fine sediments, a flat beach slope and the presence of macrofaunal burrows (Table 1.1). The macrofaunal community structure and sediment organic matter vary between levels of exposure, where highest values are found with decreasing exposure (Defeo *et al.*, 1997; Veloso & Cardoso, 2001; Orr *et al.*, 2005; Rodil *et al.*, 2007; De La Huz & Lastra, 2008). For instance, Rodil *et al.* (2007), who sampled three

exposed and three sheltered beaches on the coast of Spain, found a macrofaunal abundance of 1535 ± 358 to 15062 ± 5771 individuals m^{-2} on sheltered beaches and 150 ± 41 to 5518 ± 1986 individuals m^{-2} on exposed beaches. De la Huz & Lastra (2008) have shown that, while the intertidal fauna is controlled by the physical factors mentioned above, the upper shore macrofaunal community is better explained by biological factors such as food availability and human impact.

Table 1.1 Categories suggested by McLachlan (1980) for classifying sandy beaches by level of exposure.

Score	Beach type	Description
1-5	Very sheltered	Virtually no wave action, shallow reduced layers, abundant macrofaunal burrows.
6-10	Sheltered	Little wave action, reduced layers present, usually no macrofaunal burrows.
11-15	Exposed	Moderate to heavy wave action, reduced layers deep if present, usually no macrofaunal burrows.
16-20	Very Exposed	Heavy wave action, no reduced layers, macrofauna only of robust motile forms.

1.3 Food web

In temperate regions, food webs of exposed sandy beaches are supported by marine subsidies (such as washed up macroalgae and seagrasses) as little primary productivity occurs within the beach itself (Figure 1.2) (Brown & McLachlan, 1990; Dugan *et al.*, 2003; Colombini & Chelazzi, 2003; Lastra *et al.*, 2008). The input of washed-up macrophytes, also termed wrack, varies seasonally and between zones (Marsden, 1991a; Ochieng & Erftmeijer, 1999; Dugan *et al.*, 2003; Orr *et al.*, 2005). Variable deposition rates are due to the buoyancy characteristics of the species that is stranded onto the beach, the level of exposure and the nearshore hydrodynamics (Orr *et al.*, 2005). Examples of wrack biomass estimates on sandy shores are as follows: a monthly input of 11.23 kg wet wt 5 m^{-1} on a sandy beach in New Zealand (Marsden, 1991a); Dugan *et al.* (2003), who sampled 15 beaches in Southern California, calculated an average cover of $0.03\text{-}5.03 \text{ m}^2 \text{ m}^{-1}$; around 0.2 kg m^{-1} of shoreline for two sandy beaches sampled in British Columbia (Orr *et al.*, 2005); mean volume of $0.00\text{-}0.09 \text{ m}^3$ wrack m^{-2} and $0.27\text{-}1.07 \text{ m}^3$ wrack m^{-2} on low-wrack and high-wrack beaches, respectively, on the west coast of Australia (Ince *et al.*, 2007); $0.61 \text{ kg wet wt m}^{-1}$ on a sandy beach in Spain and $21.4 \text{ Kg wet wt m}^{-1}$ on a southern Californian Beach (Lastra *et al.*, 2008). Figure 1.2 shows the energy cycling of stranded macrophytes as it is processed by bacteria and macrofauna at different trophic levels on a sandy shore (Robertson, 1994; Griffiths & Stenton-Dozey, 1981;

Inglis 1989). Of the total biomass, 30% of the beach-cast seaweed is returned to the sea and the remainder is consumed by primary consumers (Robertson, 1994).

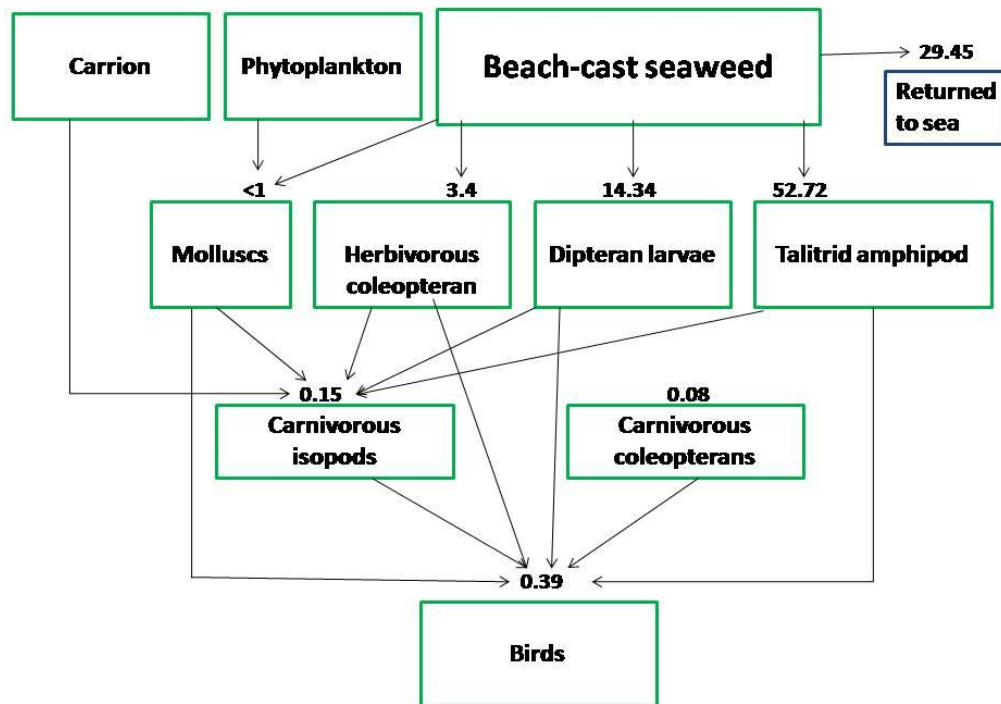


Figure 1.2 Energy cycling of beach-cast seaweeds. Numbers represent percentage of stranded seaweed transferred to the next level (Zemke-White *et al.*, 2005; adapted from Griffiths *et al.*, 1983).

Stable isotope analysis has allowed scientists to quantify whether wrack is directly consumed by primary consumers (Adin & Riera, 2003; Ince *et al.*, 2007; Olabarria *et al.*, 2009). Wrack is the main food source for a range of invertebrates throughout their life cycle (Ince *et al.*, 2007; Olabarria *et al.*, 2009). For instance, on a south-western Australian sandy beach, amphipods, dipteran flies and coleopteran beetles were found to feed on red and brown seaweeds, seagrasses and dune vegetation (Ince *et al.*, 2007). Of the total stranded seaweed, 53% was transferred to talitrid amphipods, 14% to dipteran larvae and 3% to herbivorous coleoptera in a beach food web off the Western Cape Coast of South Africa (Fig. 1.2) (Zemke-White *et al.*, 2005). Wrack also provides shelter for consumer species against predators (Inglis 1989; Colombini & Chelazzi, 2003). Invertebrate predators include shorebirds, seabirds, lizards, rodents and marine mammals (Polis *et al.*, 1997; Hubbard & Dugan, 2003). Shorebird populations have been found to be positively correlated with macrophyte biomass and the abundance of wrack-associated invertebrates (Dugan *et al.*, 2003). Wrack, therefore, supports both marine and terrestrial food webs.

Kelp sample species

Four species of brown seaweeds belonging to the genus *Durvillaea* occur in New Zealand. *Durvillaea antarctica* and *D. willana* are two of the species found throughout the exposed shores of New Zealand, including the South Island, whereas *D. chathamensis* and *Durvillaea* sp. ‘Antipodes Is’ are confined to Chatham Island and Antipodes Islands respectively (Adams, 1997). *Durvillaea antarctica* has been found to make up more than 80% of the total macrophyte biomass stranded on five beaches on the Otago peninsula, while *D. willana* made up 14% of total wrack. The holdfasts (organ of attachment) are sometimes still attached to the plants when deposited on the beach, bringing in rocks, carbonate material and associated macrofaunal species (Garden, 2005) (Fig. 1.3). *Durvillaea antarctica* was chosen for this study due to its wide distribution and abundance on the exposed shores of Otago and its easy access for collection (Hay, 1994; Stevens *et al.*, 2002). It is usually 3-5 m long, but can grow up to 10 m in length, and attaches itself to rocky surfaces (via its holdfast) in the lower intertidal zone where it is exposed at low tide (Batham, 1958; Hay, 1994; Adams, 1997). It is a popular food source for grazers, such as abalone (*Haliotis australis*) (Moss, 1998), and the holdfast offers a sheltered habitat for a range of species occupying the intertidal zone (Smith & Simpson, 1995; Smith & Simpson, 2002). For instance, Smith & Simpson (2002) recorded a total of 94 taxa associated with the holdfast of *D. antarctica*. Little focus has been given to the role of stranded macrophyte material on sandy shores of New Zealand; thus, this study was undertaken to analyse the role of *D. antarctica* as a marine subsidy on exposed sandy shores.



Figure 1.3 Photo of stranded *Durvillaea antarctica* with attached holdfast, on Allans Beach. (author's photo).

1.4 New Zealand research

A few studies have outlined the macrofaunal species of exposed beaches of New Zealand (Table 1.2). The upper beach is dominated by isopod, amphipod, coleopteran and dipteran species, while bivalves, gastropod and annelid species dominate the middle and lower beach (MacIntyre, 1963; Morton & Miller, 1968; Inglis, 1989; Stephenson, 1998; Dufour unpublished data, 2007). Fincham (1977) studied macrofaunal abundance across tidal heights on 14 North Island beaches of New Zealand. The macrofaunal community was dominated by amphipods, with an average abundance of 31-208 individuals/m², constituting 54% of the total abundance. Sandy beaches of Otago (Allans Beach, Warrington Beach), on the other hand, have been found to be dominated by the opheliid polychaete *Euzonus otagoensis* (46% of total abundance on Allans Beach) and amphipods (44% of total abundance on Warrington Beach) (Dufour unpublished data, 2007). The macrofaunal density found on these shores ranged between 76 - 304.8 individuals/m² for Allans Beach and 355.6 - 685.8 individuals/m² on Warrington Beach. Species occupying the middle and low beach level filter feed on plankton or predate on other species. Upper shore species rely on wrack or feed on other invertebrates (Morton & Miller, 1968). Macrofauna associated with seaweed are then consumed by seabirds such as the pied oystercatcher and the banded dotterel (Morton & Miller, 1968).

There is a lack of research focusing on the relationship between stranded seaweed and macrofaunal assemblages, as previous research has focused mainly on the vertical distribution of species on sandy shores. Inglis (1989) and Marsden (1991a) investigated the relationship between kelp and macrofauna on sandy shores. Both studies were carried out on Pegasus Bay (Canterbury, New Zealand) and are the only New Zealand studies published to date. Inglis (1989) looked at the colonisation and the decomposition of stranded bladder kelp *Macrocystis pyrifera* on the upper shore over a period of 18 days. Marsden (1991a), on the other hand, studied the composition and distribution of wrack up the shore, and the distribution of the common talitrid sandhopper *Bellorchestia quoyana* as a response to substrate type (sand and macrophyte). A total of nine species of macrophyte were identified in the composition of the detritus on Pegasus Bay. *Macrocystis pyrifera* and *D. antarctica* were the two dominant species, whereas the remaining seven species of macrophyte identified constituted less than 16% of the total biomass. The amount of material stranded varied between seasons, and different species had variable distribution rates along the shore, with *D. antarctica* more

abundant on the upper shore (Marsden, 1991a). Further research on the ecological role of stranded macrophytes within sandy shores is required, as there are implications resulting from the removal of stranded macrophytes on associated fauna (Kirkman & Kendrick, 1997).

Table 1.2 Summary of taxonomic groups and their corresponding number of species identified within NZ shores (McIntyre, 1963; Morton & Miller, 1968; Inglis 1989; Stephenson, 1998). Dash symbolises lower taxonomic level not mentioned.

Taxonomic groups		Species mentioned
Crustacea	Amphipoda	6
	Isopoda	9
	Decapoda	2
	Stomatopoda	1
Insecta	Coleoptera	17
	Diptera	5
	Hemiptera	1
	Hymenoptera	1
	Juliformia	1
Myriapoda	Chilopoda	3
	Geophilomorpha	1
Mollusca	Bivalvia	6
	Mactridae	5
	Tellinacea	2
	Sanguinolariidae	2
	Gastropoda	6
Polychaeta	Nephtyidae	1
	Glyceridae	3
	Orbiniidae	2
	Opheliidae	3
Nemertea	-	1

Aims

The aims of this study were to produce a quantitative list of the macrofaunal species associated with stranded *D. antarctica* on an Otago exposed sandy beach, and to investigate its decomposition rate over a period of 30 days.

Within these overall aims, this study seeks:

- (1) To quantify the number of macrofaunal species present on stranded *D. antarctica*.

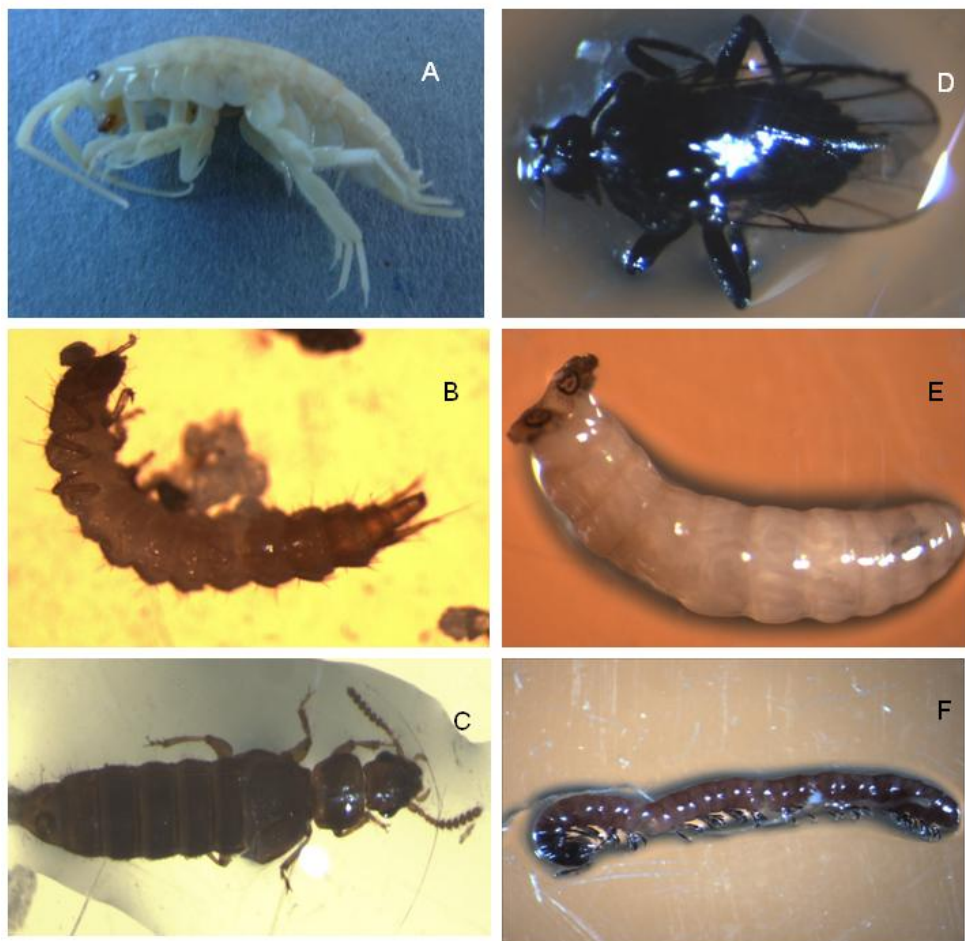
(2) To analyse the pattern of colonisation within a 30-day sampling period during autumn and winter (Chapter 2).

(3) To determine if macrofaunal abundance within the sediment is affected directly beneath *D. antarctica* samples, and at distances of 0.5 m and 1 m away (Chapter 3).

(4) To assess carbon and nitrogen content, C:N ratio, weight loss and water content of stranded *D. antarctica* over a 30-day period in both autumn and winter (Chapter 4).

Finally, implication of this research for sandy beach food webs will be discussed (Chapter 5).

Chapter 2 Seasonal and spatial variability of macrofauna assemblages on washed-up *Durvillaea antarctica*, on an Otago exposed sandy beach.



Macrofaunal species (Talitrid amphipod, *Bellorchestia quoyana* (A), Tenebrionid larvae, *Chaerodes trachyscelides* (B), Staphylinid beetle (C), Mycetophilid adult (D) and pupa (E), Diplopod (F)) found on the upper shore of Victory Beach, Otago Peninsula (author's photos).

2.1. Introduction

2.1.1 Importance of kelp

Macroalgal material often accumulates in the strand zone of open ocean sandy beaches, particularly following storm events, which can uproot kelp from neighbouring kelp beds (MacIntyre, 1963; Griffiths & Stenton-Dozey 1981; Behbehani & Croker, 1982). In New Zealand, kelp beds are dominated by *Macrocystis pyrifera*, *Ecklonia radiata*, *Lessonia variegata* and *Durvillaea spp* (Morton & Miller 1968; Adams, 1997; Steneck *et al.* 2002). These kelp species act as a source of nutrients and shelter for interstitial and supralittoral fauna of sandy shores (MacIntyre 1963; Inglis 1989; Jedrzejczak, 2002b).

Exposed rocky shores of Otago are dominated by the bull kelp *D. antarctica*, which has an air-filled honeycomb blade structure that allows it to be flexible and buoyant in a harsh environment (Batham, 1958; Morton & Miller 1968; Stevens *et al.* 2002). *Durvillaea antarctica* as washed-up detritus can be highly abundant on the upper shore of sandy beaches, but varies seasonally (Marsden 1991a). In New Zealand, Marsden (1991a) obtained a monthly average of algal input of 11.25 kg 5 m⁻¹ (on Pegasus Bay, Canterbury), which is a low input compared to that found on South African beaches where the organic input has been found to be over 2000 kg m⁻¹ yr⁻¹ (Colombini & Chelazzi, 2003).

2.1.2 Macrofauna and washed up kelp

The fauna commonly found on the upper shore of sandy beaches includes talitrid amphipods, oniscoidean isopods, coelopid and sphaerocerid flies, and tenebrionid and staphylinid beetles (Inglis, 1989; Brown & McLachlan, 1990; Harris, 1991; Jedrzejczak, 2002b; Colombini and Chelazzi, 2003; Dugan *et al.* 2003). Seaweed and detritus that washes up ashore is used as a source of food and shelter by the adult and larval stages of these primary consumers, scavengers and carnivores (MacIntyre, 1963; Inglis, 1989; Jedrzejczak, 2002b). For instance, talitrid amphipods have been shown to feed on the brown alga *M. pyrifera* (Inglis, 1989), seagrass *Posidonia sp.*, red algae and the dune grass *Spinifex longifolia* (Ince *et al.* 2007). In turn, carnivorous taxa, such as the muscid fly belonging to the genus *Paralimnophora*, rove beetles (Staphylinidae), hister beetles (Histeridae), ground beetles (Carabidae), and spiders occupy the wrack to feed on other insects including larvae (Colombini & Chelazzi, 2003) which feed on dune vegetation, brown and red algae (Ince *et al.* 2007).

Macrofaunal species have been found to occupy wrack within 3 days of it being washed ashore, but different species have an optimal abundance at different stages of succession (Griffiths & Stenton-Dozey, 1981; Inglis, 1989; Olabarria *et al.* 2007). Dipteran flies, amphipods and isopods have been found to be abundant within 3 days of the kelp being washed ashore, in contrast to the coleopteran species, such as staphylinid beetles, which are most abundant at later stages of decomposition (Griffiths & Stenton-Dozey, 1981; Inglis, 1989; Colombini *et al.* 2000; Jedrzejczak, 2002b). The trends seen in the succession of washed-up seaweed by beach macrofauna have been suggested to be due to biological requirements and predator-prey relationships. For instance, amphipods require a moist environment to survive (MacIntyre, 1963), hence their high abundance at early stages of succession (Griffiths & Stenton-Dozey, 1981; Inglis, 1989; Jedrzejczak, 2002b), whereas coleopteran beetles occupy later stages as they prefer older, drier seaweed (Griffiths & Stenton-Dozey, 1981; Colombini *et al.* 2000).

Aim

This study was designed to examine the pattern of succession of the macrofaunal community associated with transplanted samples of *D. antarctica* to test for seasonality in taxonomic composition, and differences in the abundance and biomass of adult and juvenile amphipod stages.

Hypotheses

1. Macrofaunal abundance and biomass will change over time and will differ between taxonomic groups.
2. The pattern of colonization of *D. antarctica* will differ between seasons.
3. The abundance and biomass will differ between juvenile and adult amphipods.

2.2. Methods

2.2.1 Study site

The study site, Victory Beach, is a wave-exposed, east-facing sandy beach on the Otago Peninsula, on the east coast of the South Island, New Zealand (Fig. 2.1). At a length of 3.5 km it is the longest sandy beach on the Peninsula, and is backed by 2 km of sandflats and dunes (up to 10 meters high) that run the length of the beach (Johnson, 1992; Bishop & Hamel, 1993; Wilson, 2004). Highest erosion is on the southern dunes, and decreases northward along the beach (Fig. 2.2) (personal obs.).

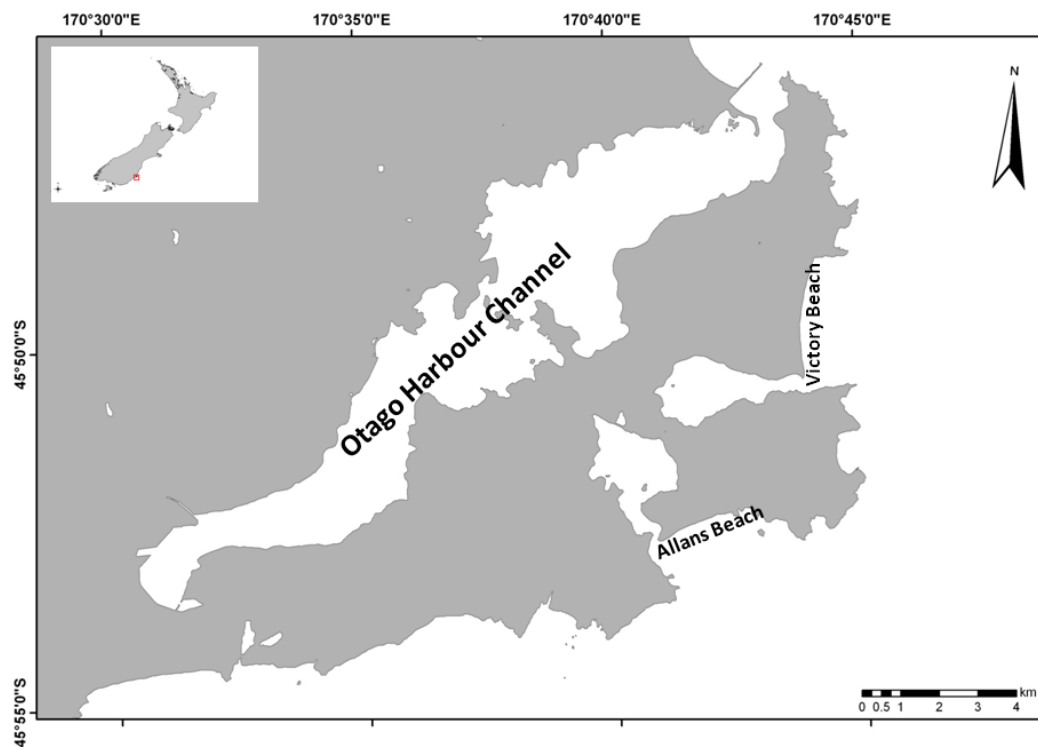


Figure 2.1 Location of Victory Beach and Allans Beach on the Otago Peninsula, New Zealand.

Victory Beach backs on to the Okia Reserve, a 213-hectare reserve that was purchased in 1991 by the Yellow-Eyed Penguin Trust and the Dunedin City Council (O.R.M.P., 1998). It is home to a range of amphibian, reptile, bird and mammal species including the yellow-eyed penguin (*Megadyptes antipodes*) and the New Zealand Hooker sea lion (*Phocartos hookeri*) (O.R.M.P., 1998). The vegetation ranges from kowhai (*Sophora spp.*), mahoe (*Melicytus ramiflorus*), New Zealand flax (*Phormium spp.*) to introduced species such as marram grass (*Ammophila arenaria*) and lupins which dominate the sand dunes (Johnson, 1992;

DOC, 2003). The area is of historic value as there is evidence of Maori settlement within the reserve and within Papanui Inlet, the entrance to which is at the south end of Victory Beach (Hamel, 2001; DOC, 2003). It is also a popular site for tourists.

Physical Characteristics

New Zealand is characterised by semi-diurnal tides and the tidal range is 1-2 metres (Stanton *et al.*, 2001). On average, swells off the coast of New Zealand have a mean height of three metres (Laing, 2000). Breaking waves four metres in height have been observed for sandy beaches on the coast of Otago (Garden, 2005). Victory beach faces due east and so is exposed to any easterly wind or swell (Fig. 2.3). After a storm the dunes on the southern end were observed to have eroded back significantly (Fig. 2.2) (author's observation). Easterly and southerly swell may refract around Papanui headland, concentrating along the sandy southern end (Fig. 2.3). With no headland to stabilize the dunes, the southern end is prone to high erosion.

Sediments on Otago sandy beaches are derived from the Clutha River (Carter & Carter, 1986). There is no published data on sediment grain size for Victory Beach, but the mean sediment grain size for neighbouring sandy beaches (Allans Beach and Warrington Beach) is 125 μ m (3 ϕ), which after Brown & McLachlan (1990), is classified as very fine sand (Dufour unpublished data, 2007).

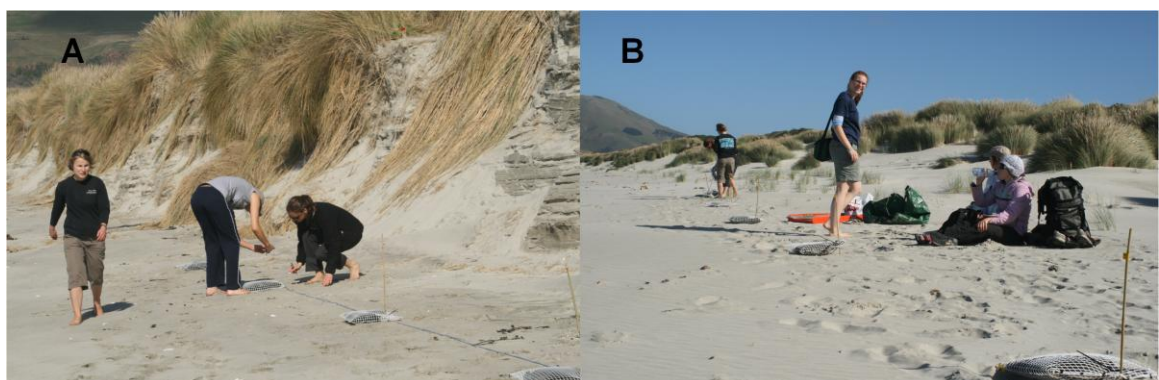


Figure 2.2 Photo of the sand dunes at the southern (A) and northern (B) end of Victory Beach. The field workers illustrate the relative size of the dunes in each photo (author's photo).

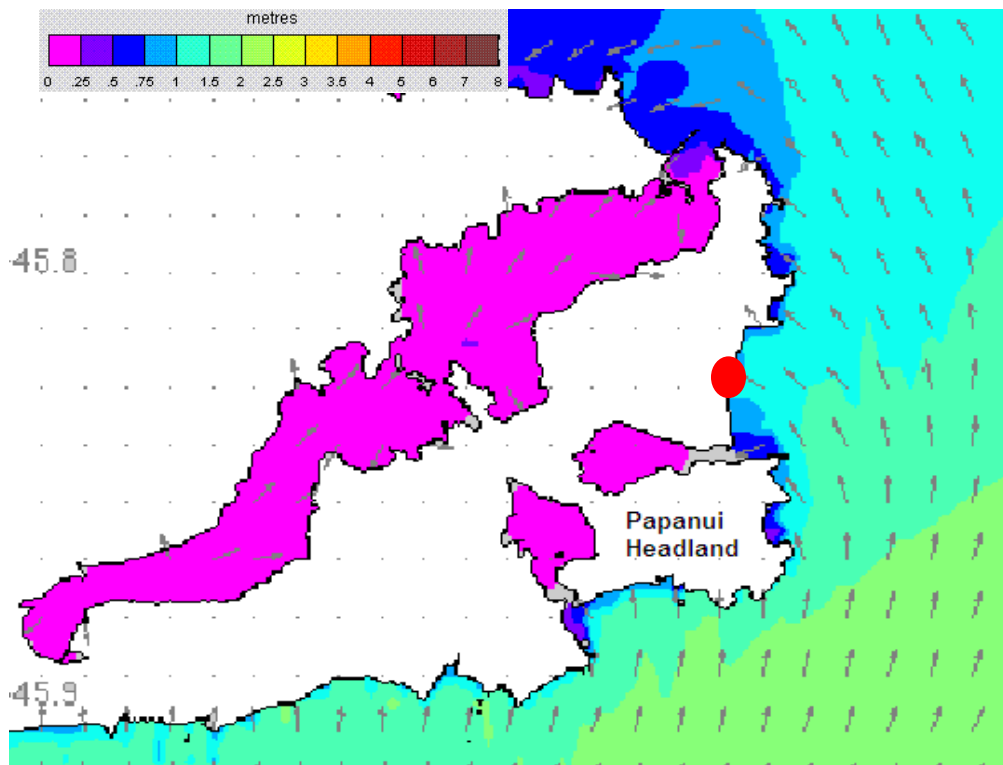


Figure 2.3 Map showing wave height (metres) and direction of swell associated with the Otago Peninsula and Victory Beach (red circle) for the 26th of March at 07h00 (swellmap.com, March 2009).

2.2.2 Kelp sample preparation

Fresh *D. antarctica* was collected from Allans Beach, on the Otago Peninsula, one day prior to placing samples out on Victory Beach (Fig. 2.1). Kelp was removed by prising the holdfast from the rock using a hammer and chisel. At the laboratory the kelp was rinsed in seawater to remove any macrofauna before being blotted dry. Trellis mesh bags (37 cm x 38 cm) with 1 cm x 1 cm holes were filled with 1 kg $\pm$ 0.1 kg wet weight *D. antarctica* fronds, and placed in a seawater holding tank until deployment in the field (within at least 12 hours).

2.2.3 Fieldwork

In late autumn (6th April-5th May) and winter (21nd June-20th July) 2008, four sites, each 24 m x 4 m, were randomly selected across the entire length of Victory Beach but separated by a minimum of a 100 m (Fig 2.4). All sites were cleared of visible detritus prior to placing the mesh bags of *D. antarctica*.

At each site, six kelp samples were placed at 4 m intervals (to prevent interaction of macrofauna between kelp samples) along a 20 m transect that ran parallel to the upper shore (the edge of terrestrial vegetation) (Fig 2.5). To prevent the kelp bags being washed away, bamboo stakes were placed at least 40 cm into the sand via holes in the mesh bags and secured with cable ties.

On Day 1, 3, 6, 10, 20 and 30, kelp samples were collected at random and were placed rapidly, along with any sand that was covering the kelp samples, into plastic bags and taken to the laboratory.



Figure 2.4 Location of the four sampling sites (A, B, C, D) along Victory Beach, Otago Peninsula (Google Earth: accessed 22nd of October, 2010).

2.2.4 Laboratory analysis

Species Abundance

Kelp samples were frozen at -20°C for a minimum of 48 hours to euthanise associated macrofauna. Kelp samples were thawed for at least 2 hours at 15°C and sieved on a 1 mm mesh, along with any associated sand, to extract macrofauna. Macrofauna were preserved in

40% isopropanol (IPA), and identified to the lowest taxonomic level possible and counted under a dissecting microscope. Amphipods were separated into adult and juveniles to analyse abundance and biomass for autumn and winter.

Macrofaunal biomass

Macrofaunal samples were rinsed in freshwater to remove excess IPA and placed onto coffee filters which had been oven dried at 60° C and weighed (g). Samples were oven dried at 59°C for a minimum of 3 days, transferred to a desiccator for 1 hour, and weighed to the nearest 0.001g. The filter dry-weight was deducted from the overall dry-weight of the macrofauna and filter paper to obtain the dry weight of the macrofauna.



Figure 2.5 *Durvillaea antarctica* mesh bags at 4 m intervals along a 20 m transect line across the upper shore of Victory Beach, Otago Peninsula (author's photo).

2.2.5 Statistical analysis

Faunal abundance and biomass were expressed as percentages of total abundance and biomass associated with kelp samples, and analysed using a three-way ANOVA (General Linear Model) in Minitab 14. Two-way ANOVA was carried out on the abundance and biomass of individual taxonomic groups, and of adult and juvenile amphipods, to determine individual trends between seasons and sampling days. Data were checked for homogeneity of variance using Levene's test, and $\log_{10}(n+1)$ transformed when required. Species with an abundance of ten or fewer (over both sampling periods) were not included in the statistical analysis.

2.3. Results

2.3.1 Abundance between species

Twenty macroinvertebrate taxa were found to be associated with the samples of *D. antarctica* during autumn and winter (Table 2.1). The major taxonomic groups associated with the community succession of *D. antarctica* samples comprised Amphipoda, Staphylinidae, other Coleoptera and Diptera, which made up 99.9% of total macrofaunal abundance (Table 2.2). Amphipoda made up 74-96% of total faunal abundance during both sampling periods, except on days 20 and 30 in autumn when its abundance accounted for 68% and 31% of total abundance respectively (Table 2.2). Other Coleoptera, which made up 0-4% of total faunal abundance in autumn and 0% of total faunal abundance in winter, had the lowest abundance of all four taxa (Table 2.2). A post-hoc test showed that abundance of Amphipoda was significantly greater than that of the three other taxa, while the abundances of Staphylinidae and Diptera were both significantly more abundant than the abundance of other Coleoptera, but their abundances were not significantly different to each other (Tukey's test, p -value < 0.01) (Table 2.2).

Autumn tended to have a higher overall total abundance than winter, but a three-way ANOVA showed there was no significant difference in abundance between seasons (F -value= 3.68, p -value= 0.057) (Fig. 2.6). There was, however, a significant difference between days (F -value= 15.98, p -value< 0.001), and an interaction effect between season, day and species (F -value= 2.05, p -value= 0.016). A post-hoc test using day as a factor showed that abundance on day 1 was significantly lower than for all other sampling days, while abundance on day 3 was significantly different to days 10, 20 and 30 (Tukey's test, p -value < 0.02).

2.3.2 Biomass between species

Total biomass was primarily composed of Amphipoda (53-98% in autumn and 92-98% in winter), whereas on average the other three main taxonomic groups made up less than 10% of total biomass (Table 2.2). A post-hoc test showed that the biomass of Staphylinidae, other Coleoptera and Diptera were not significantly different (Tamahane's test, p -value> 0.05), but all were significantly different to Amphipoda which had the highest biomass across both sampling periods (Tamahane's test, p -value <0.001) (Table 2.2).

Table 2.1 Total abundance (number and % of total community) and biomass (dry weight (g) and % of total community) of individual taxonomic groups associated with samples of *Durvillaea antarctica* on Victory Beach, Otago Peninsula. Autumn and winter numbers are the pooled samples over all sampling dates. n/a-not applicable because too low to quantify, dash-absent from samples.

Taxa	Total no.		% of community		Total biomass (g)		% of community	
	autumn	winter	autumn	winter	autumn	winter	autumn	winter
Amphipoda								
<i>Bellorchestia quoyana</i>	11699	9138	73.62	85.04	38.9	16.7	87.30	96.81
Coleoptera								
Staphylinidae	1961	1134	12.34	10.55	1.13	0.4	2.54	2.32
<i>Blediotrogus guttiger</i>								
<i>Macralymma punctiventre</i>								
Other Coleoptera								
Tenebrionidae	181	2	1.14	0.02	n/a	n/a	n/a	n/a
<i>Chaerodes trachyscelides</i>								
<i>C. trachyscelides</i> larvae	29	4	0.18	0.04	n/a	n/a	n/a	n/a
Curculionidae	4	6	0.03	0.06	n/a	n/a	n/a	n/a
<i>Aphela algarum</i>								
Coccinellidae	1	-	0.01	-	n/a	n/a	n/a	n/a
Scarabaeidae	1	-	0.01	-	n/a	n/a	n/a	n/a
Total	216	12	1.36	0.11	2.61	0.02	5.86	0.12
Diptera								
Mycetophilidae	359	337	2.26	3.14	n/a	n/a	n/a	n/a
pupa	146	54	0.92	0.5	n/a	n/a	n/a	n/a
Coelopidae	9	34	0.06	0.32	n/a	n/a	n/a	n/a
Sphaeroceridae pupae	342	30	2.15	0.28	n/a	n/a	n/a	n/a
Muscidae	1	-	0.01	-	n/a	n/a	n/a	n/a
Nematocera	-	1	-	0.01	n/a	n/a	n/a	n/a
Therevidae	-	1	-	0.01	n/a	n/a	n/a	n/a
Unknown pupa <i>sp</i>	22	-	0.14	-	n/a	n/a	n/a	n/a
Total	879	457	5.53	4.26	1.8	0.17	4.04	0.99
Other								
Isopoda	13	2	0.08	0.02	n/a	n/a	n/a	n/a
Decapoda	5	1	0.03	0.01	n/a	n/a	n/a	n/a
Diplopoda	-	1	-	0.01	n/a	n/a	n/a	n/a
Hymenoptera	-	1	-	0.01	n/a	n/a	n/a	n/a
Formicidae	-	1	-	0.01	n/a	n/a	n/a	n/a
Heteroptera	1	-	0.01	-	n/a	n/a	n/a	n/a
Arachnida	1	-	0.01	-	n/a	n/a	n/a	n/a
Total	20	5	0.13	0.06	0.12	0.007	0.27	0.04

Table 2.2 Mean abundance (% of total abundance, $\pm$ S.E) and biomass (% total biomass, $\pm$ S.E) of the four major taxonomic groups associated with samples of *Durvillaea antarctica*, over a 30-day sampling period during autumn (day 1-20, n=4; day 30, n=3) and winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008.

Day		<i>Amphipoda</i>		<i>Staphylinidae</i>		<i>Other Coleoptera</i>		<i>Diptera</i>	
		autumn	winter	autumn	winter	autumn	winter	autumn	winter
1	abundance	79 $\pm$ 18.16	84 $\pm$ 20.14	2 $\pm$ 1.64	2 $\pm$ 0.34	1 $\pm$ 0.40	0 $\pm$ 0.34	17 $\pm$ 6.51	13 $\pm$ 5.37
	biomass	96 $\pm$ 19.85	93 $\pm$ 14.17	1 $\pm$ 0.47	0 $\pm$ 0.28	1 $\pm$ 0.78	1 $\pm$ 1.36	2 $\pm$ 1.95	6 $\pm$ 3.77
3	abundance	96 $\pm$ 29.10	78 $\pm$ 16.44	2 $\pm$ 1.12	5 $\pm$ 2.14	0 $\pm$ 0.05	0 $\pm$ 0.15	2 $\pm$ 1.25	17 $\pm$ 11.01
	biomass	98 $\pm$ 36.22	92 $\pm$ 21.47	1 $\pm$ 0.63	1 $\pm$ 0.31	0 $\pm$ 0.00	0 $\pm$ 0.07	1 $\pm$ 0.25	6 $\pm$ 4.59
6	abundance	91 $\pm$ 31.11	91 $\pm$ 20.71	8 $\pm$ 3.78	4 $\pm$ 2.65	0 $\pm$ 0.07	0 $\pm$ 0.04	1 $\pm$ 0.40	5 $\pm$ 0.58
	biomass	98 $\pm$ 41.08	98 $\pm$ 36.48	1 $\pm$ 0.36	1 $\pm$ 0.52	0 $\pm$ 0.22	0 $\pm$ 0.09	0 $\pm$ 0.10	1 $\pm$ 0.43
10	abundance	74 $\pm$ 22.98	86 $\pm$ 30.36	16 $\pm$ 8.24	13 $\pm$ 7.22	3 $\pm$ 2.23	0 $\pm$ 0.06	7 $\pm$ 2.80	2 $\pm$ 0.66
	biomass	83 $\pm$ 27.48	96 $\pm$ 32.08	3 $\pm$ 1.73	3 $\pm$ 1.55	13 $\pm$ 10.84	0 $\pm$ 0.05	1 $\pm$ 0.22	1 $\pm$ 0.42
20	abundance	68 $\pm$ 25.36	74 $\pm$ 31.08	26 $\pm$ 14.94	23 $\pm$ 9.41	4 $\pm$ 3.35	0 $\pm$ 0.18	2 $\pm$ 0.49	3 $\pm$ 1.69
	biomass	78 $\pm$ 17.01	97 $\pm$ 28.61	4 $\pm$ 2.16	3 $\pm$ 2.13	17 $\pm$ 15.76	0 $\pm$ 0.03	1 $\pm$ 0.37	0 $\pm$ 0.15
30	abundance	31 $\pm$ 19.41	88 $\pm$ 61.40	31 $\pm$ 15.07	8 $\pm$ 2.89	1 $\pm$ 0.24	0 $\pm$ 0.06	38 $\pm$ 18.20	4 $\pm$ 3.01
	biomass	53 $\pm$ 15.13	97 $\pm$ 42.10	8 $\pm$ 3.61	2 $\pm$ 0.13	2 $\pm$ 0.89	0 $\pm$ 0.55	37 $\pm$ 25.74	1 $\pm$ 0.55

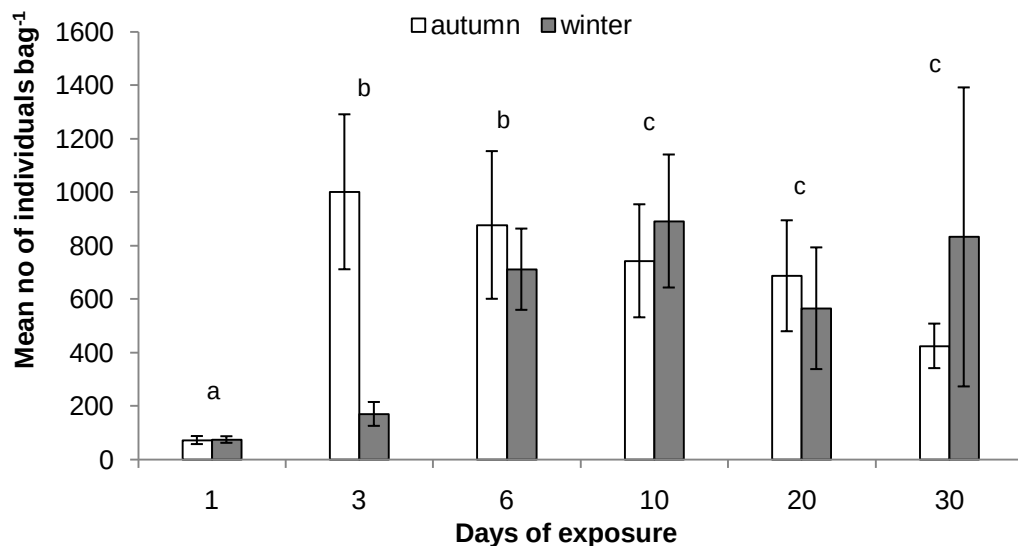


Figure 2.6 Mean ($\pm$ S.E) macrofauna abundance associated with samples of *Durvillaea antarctica* over a 30-day sampling period during autumn (day 1-20, n=4; day 30, n=3) and winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach. Dissimilar letters indicate significant differences between sampling days.

A three-way ANOVA on log biomass showed there was a significant difference among days of exposure (F-value= 4.41, p-value= 0.001). However, Tamahane's post-hoc test did not show significant differences between sampling days. Macrofaunal biomass appeared to increase until day 10 after which it leveled off for the remainder of the sampling period (Fig 2.7). For instance, day 1 had the lowest average total biomass of 0.34 g in autumn and 0.07 g in winter, while day 3 and 6 appeared to have the highest mean macrofaunal biomass in autumn (2.81 g and 2.92 g respectively) (Fig 2.7).

The average total faunal biomass was also significantly different between autumn and winter (F-value= 11.39, p-value= 0.001) (Table 2.2). Autumn had a higher average macrofaunal biomass than winter over the whole sampling period (e.g. on day 6 the average total macrofauna biomass was 2.92 g in autumn and 0.80 g in winter) except for day 30 where macrofaunal biomass appeared to be highest in winter (Fig 2.7). Three-way ANOVA also showed significant interaction effects between species within seasons (F-value= 3.04, p-value= 0.031), between species within days (F-value= 2.80, p-value= 0.001) and between species within days and within seasons (F-value= 3.07, p-value< 0.001), but no significant interaction between day within seasons (F-value= 1.55, p-value= 0.178).

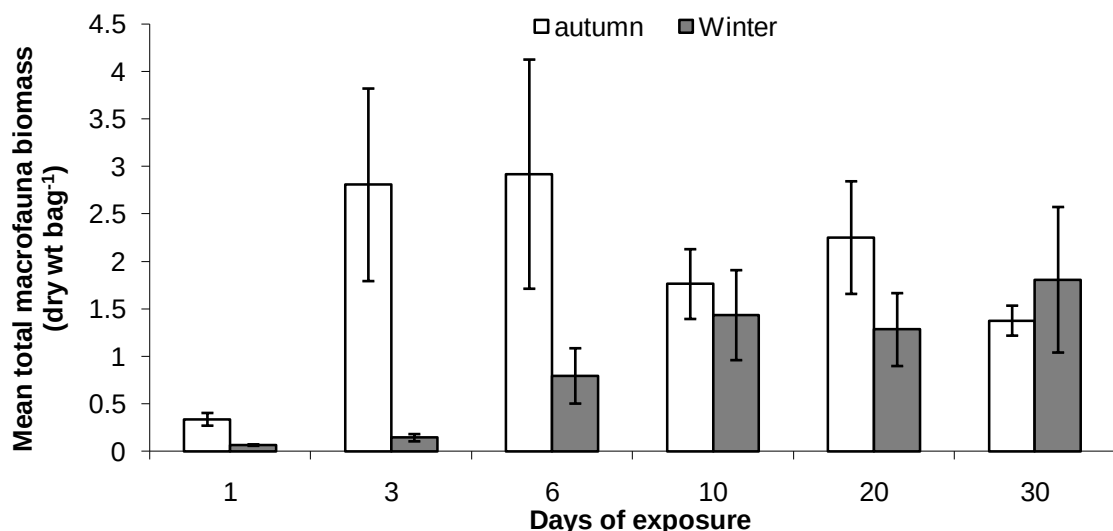


Figure 2.7 Mean ($\pm$ S.E) macrofauna biomass (g) associated with samples of *Durvillaea antarctica* over a 30-day sampling period during autumn (day 1-20, n=4; day 30, n=3) and winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach.

2.3.3 Abundance within species

All four taxonomic groups were present after one day of exposure (Fig. 2.8). Subsequently, some species appeared to decrease in abundance, while others increased with days of exposure. For instance, Amphipoda abundance was lowest on day 1 compared to days 3 and 6 (Tukey's test, $p\text{-value} < 0.04$), while Staphylinidae abundance was highest on day 20 in contrast to average abundance of days 1 and 3 of sampling (Tukey's test, $p\text{-value} < 0.04$). Diptera and other Coleoptera appeared to be more abundant after ten days of sampling; however, there was no significant difference in abundance between days (ANOVA, $p\text{-value} > 0.05$).

There was no seasonal difference in abundance for each of the four major taxonomic groups (two-way ANOVA, $p\text{-value} > 0.05$) (Fig 2.8). There was, however, a significant interaction effect between season and days for Amphipoda ($F\text{-value} = 2.66$, $p\text{-value} = 0.040$) and Diptera ($F\text{-value} = 2.60$, $p\text{-value} = 0.04$).

2.3.4 Biomass within species

Similar trends to abundance distribution are seen in the average biomass of the four major taxonomic groups, where Staphylinidae, other Coleoptera and Diptera biomass appeared to increase with increasing time of exposure, whereas Amphipoda biomass decreased over time in autumn (day 3, 2.76 g - day 30, 0.73 g) and increased over time in winter (day 1, 0.06 g - day 30, 1.75 g) (Fig 2.9). The biomass of all taxonomic groups, except other Coleoptera, differed significantly between days of sampling and between seasons, where autumn sampling showed on average a higher biomass than winter (two-way ANOVA, $p\text{-value} < 0.05$) (Fig 2.9). Amphipoda biomass was lowest on day 1 which differed significantly to that of days 6, 10 and 20 (Tukey's test, $p\text{-value} < 0.03$) (Fig 2.9a). Staphylinidae biomass appeared to increase after day 6, whereas Diptera biomass appeared to be constant throughout both sampling periods until day 30 (in autumn) where it reached its highest average biomass of 0.50 g (Fig 2.9b and 2.9c). However, post-hoc tests showed no detectable differences between days for Staphylinidae and Diptera (Tamahane's test, $p\text{-value} > 0.05$).

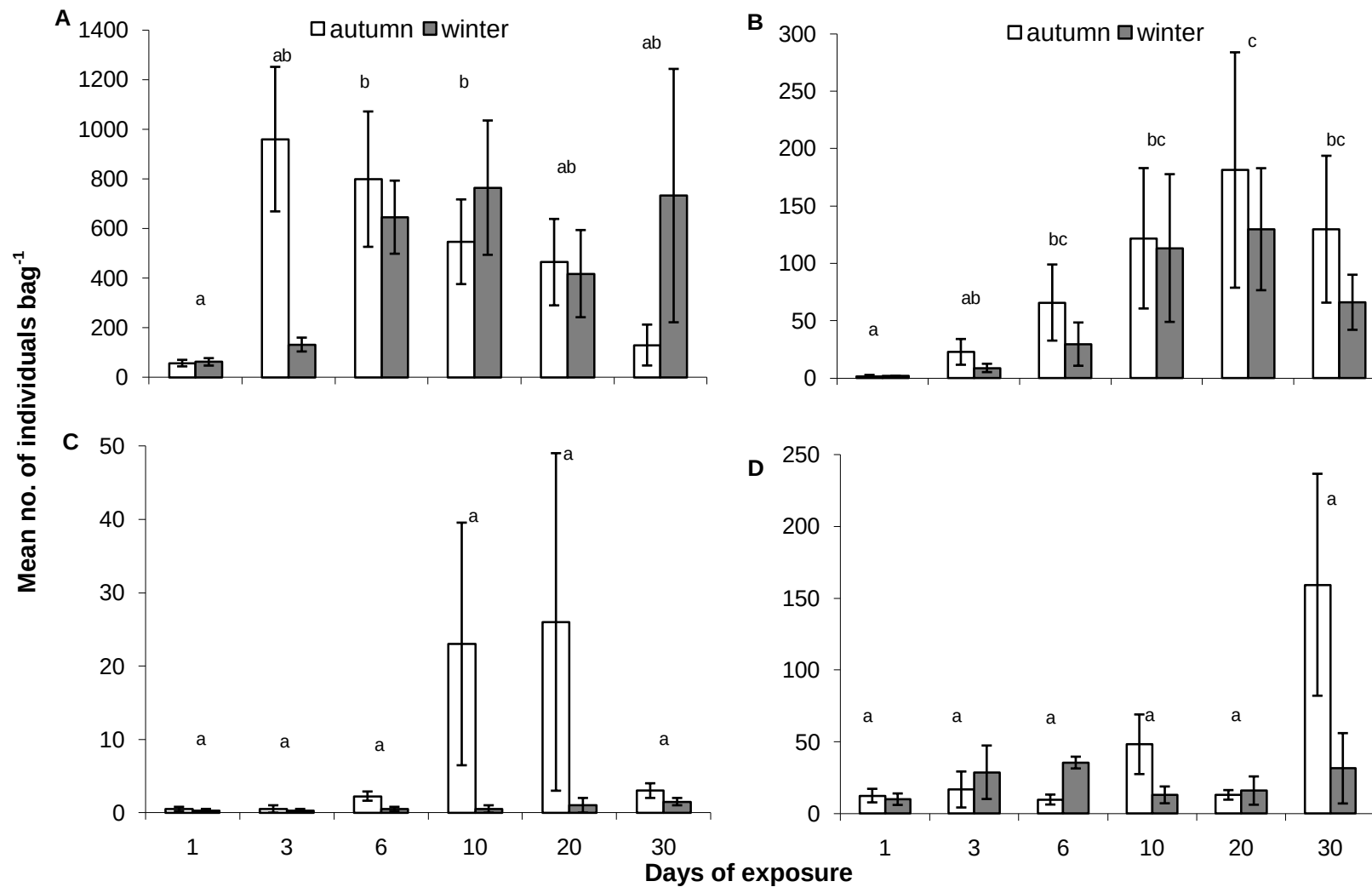


Figure 2.8 Mean number ($\pm$ S.E.) of (A) Amphipoda, (B) Staphylinidae, (C) other Coleoptera, and (D) Diptera (per kelp sample) over a sampling period of 30 days during autumn (day 1-20, $n=4$; day 30, $n=3$) and winter (day 1-10, $n=4$; day 20, $n=3$; day 30, $n=2$) 2008, on Victory Beach. Significant differences between sampling days are denoted by dissimilar letters.

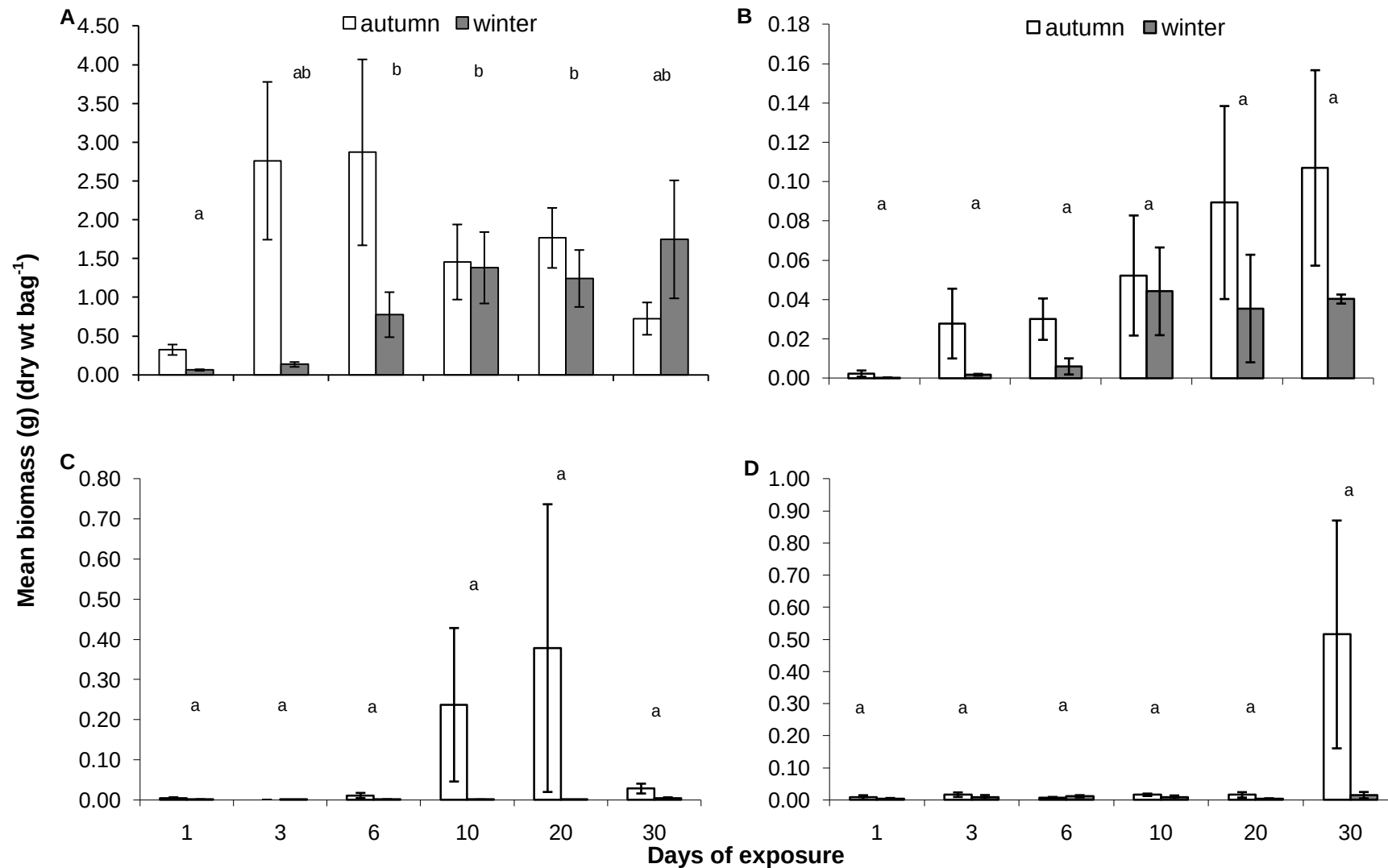


Figure 2.9 Mean biomass (g) ($\pm$ S.E) of (A) Amphipoda, (B) Staphylinidae, (C) other Coleoptera, and (D) Diptera (per kelp sample) over a sampling period of 30 days during autumn (day 1-20, n=4; day 30, n=3) and winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach. Significant differences between sampling days are denoted by dissimilar letters

2.3.5 Adult and juvenile

Both juvenile and adult talitrid amphipods occupied samples of *D. antarctica* from day 1 of exposure (Fig. 2.10 & 2.11). On average, juveniles made up a higher percentage of the total macrofaunal abundance than adults. For instance, on day 3 (in autumn) 80% of the total macrofaunal abundance consisted of juveniles, whereas adults comprised 16% of total macrofaunal abundance (Table 2.3). An alternative pattern is seen in adult and juvenile biomass where adults made up 48-87% of total macrofaunal biomass over autumn and winter sampling periods, whereas juvenile biomass was 9-50% of total macrofaunal biomass (Table 2.3).

Table 2.3 Mean adult and juvenile Amphipoda abundance (individuals per kelp sample, $\pm$ S.E) and biomass (g) associated with samples of *Durvillaea antarctica* over a 30-day sampling period in summer (day 1-20, n=4; day 30, n=3) and winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach, Otago Peninsula. The percentage of adult and juvenile amphipods within the total macrofauna community is also listed (% per kelp sample, $\pm$ S.E).

	Day	No. of individuals		% of total abundance		Biomass (g)		% of total biomass	
		autumn	winter	autumn	winter	autumn	winter	autumn	winter
adult	1	28	9	38 $\pm$ 6.08	11 $\pm$ 2.29	0.29	0.02	87 $\pm$ 22.82	35 $\pm$ 9.22
	3	157	19	16 $\pm$ 5.45	11 $\pm$ 3.25	2.11	0.07	75 $\pm$ 27.69	49 $\pm$ 12.34
	6	209	160	24 $\pm$ 10.12	23 $\pm$ 8.97	2.41	0.42	83 $\pm$ 34.53	53 $\pm$ 27.81
	10	93	122	12 $\pm$ 3.60	14 $\pm$ 4.24	1.21	0.66	69 $\pm$ 25.77	46 $\pm$ 15.67
	20	142	116	21 $\pm$ 8.86	20 $\pm$ 1.58	1.55	0.94	68 $\pm$ 20.27	73 $\pm$ 21.41
	30	49	178	12 $\pm$ 3.60	21 $\pm$ 8.54	0.67	1.08	48 $\pm$ 12.62	60 $\pm$ 15.08
juvenile	1	30	54	41 $\pm$ 21.73	72 $\pm$ 19.04	0.03	0.04	9 $\pm$ 5.03	58 $\pm$ 11.63
	3	803	113	80 $\pm$ 24.98	66 $\pm$ 13.76	0.65	0.06	23 $\pm$ 9.82	43 $\pm$ 11.50
	6	590	485	67 $\pm$ 21.70	68 $\pm$ 14.63	0.46	0.35	16 $\pm$ 6.88	44 $\pm$ 10.69
	10	454	643	61 $\pm$ 19.47	72 $\pm$ 26.70	0.25	0.72	14 $\pm$ 4.00	50 $\pm$ 18.02
	20	322	302	47 $\pm$ 24.26	54 $\pm$ 30.40	0.22	0.3	9 $\pm$ 4.82	24 $\pm$ 18.74
	30	81	555	19 $\pm$ 16.46	67 $\pm$ 52.86	0.06	0.67	4 $\pm$ 4.32	37 $\pm$ 27.02

Abundance

There was a significant difference between days of exposure in juvenile abundance (F-value= 7.35, p-value< 0.001) and adult abundance (F-value= 6.46, p-value< 0.001), but there were no significant differences found in adult (F-value= 1.02, p-value= 0.319) and juvenile abundance (F-value= 1.46, p-value= 0.236) between seasons. Both juvenile and adult abundance were lowest on day 1 of sampling (Tukey's test, p-value <0.05) (Fig 2.10). For example, in autumn, juvenile abundance reached an average of 30 individuals (41.2% of total macrofauna abundance) on day 1 and increased to 803 individuals (80.1% of total macrofauna abundance) on day 3 (Table 2.3). Post-hoc tests on adult Talitridae showed that day 1 abundance was

significantly lower than abundance on days 6, 10, 20 and 30 (Tukey's test: p -value <0.05), while post-hoc tests on juvenile Talitridae showed that day 1 had significantly lower abundance than days 3, 6, 10 and 20 (Tukey's test: p -value <0.05) (Table 2.3 & Fig 2.10).

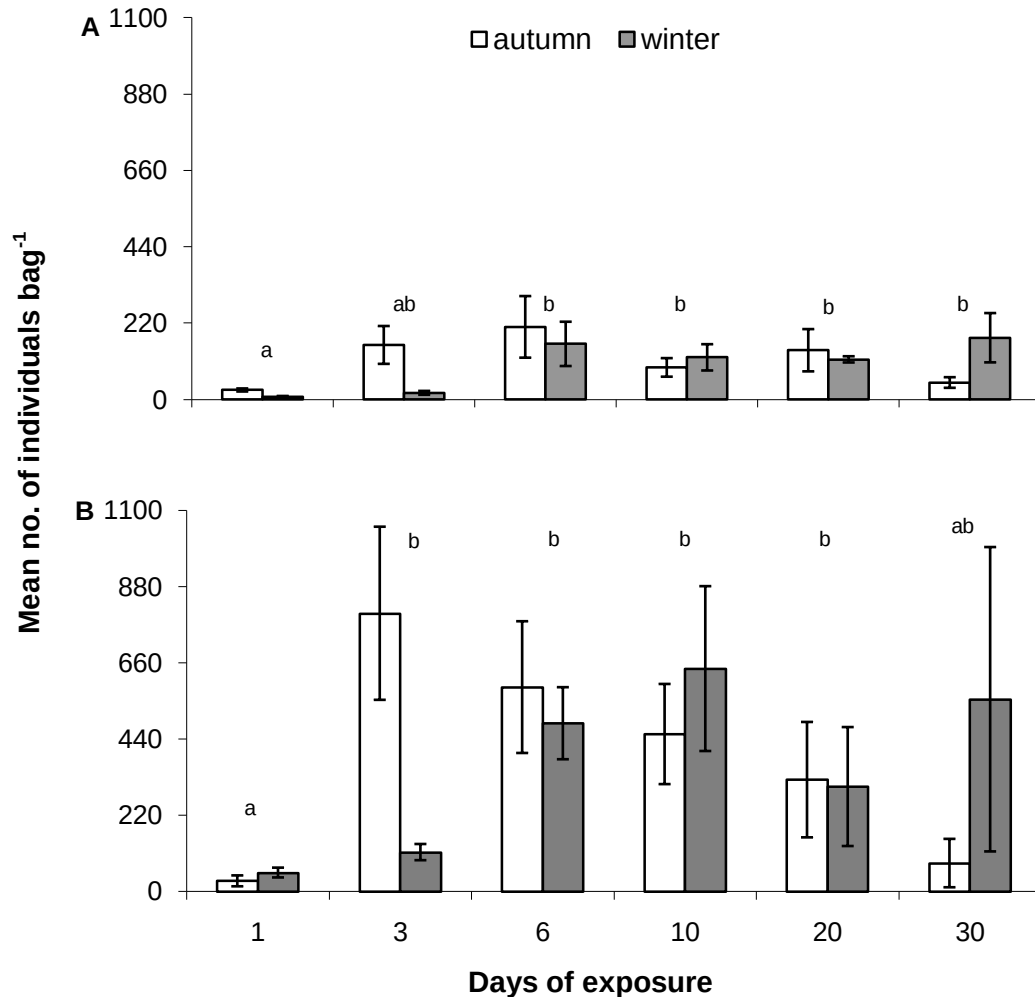


Figure 2.10 Mean ($\pm$ S.E) adult (A) and juvenile (B) Talitridae abundance associated with samples of *Durvillaea antarctica* over a 30-day sampling period in autumn (day 1-20, $n=4$; day 30, $n=3$) and winter (day 1-10, $n=4$; day 20, $n=3$; day 30, $n=2$) 2008, on Victory Beach. Dissimilar letters denote significant differences between days of exposure.

Biomass

Biomass of juvenile talitrids showed no significant difference between seasons (F -value= 0.71, p -value= 0.405) nor between days of exposure (F -value= 2.50, p -value= 0.051). However, there was a significant difference in juvenile biomass between days within seasons (F -value= 3.29, p -value= 0.017). On day 3 in autumn, juveniles reached their greatest biomass (0.65 g) and made up 23% of total macrofaunal biomass, whereas in winter the highest

juvenile biomass was found on Day 10 of sampling (0.72 g) and made up 50% of total macrofaunal biomass (Fig 2.11b & Table 2.3). Adult biomass differed significantly between seasons (F-value= 10.52, p-value= 0.003) and between days of exposure (F-value= 2.74, p-value= 0.036). Autumn had a higher adult biomass than winter throughout the sampling period, except for day 30 where winter (1.078 g) appeared to be higher than autumn (0.67 g) (Fig 2.11a). Adult biomass appeared to increase during the early stages of exposure (around day 6) and then level off after day 10, whereas biomass appeared to fluctuate slightly (between 0.60 g - 1.50 g) between the last days of sampling (Fig 2.11a). However, a post-hoc test showed that day 20 (1.55 g in summer, 0.94 g in winter) was the only sampling day to have a higher adult biomass than that found on day 1 (0.30 g in summer, 0.02g in winter) (Tamahane's test: p-value= 0.041) (Fig 2.11a).

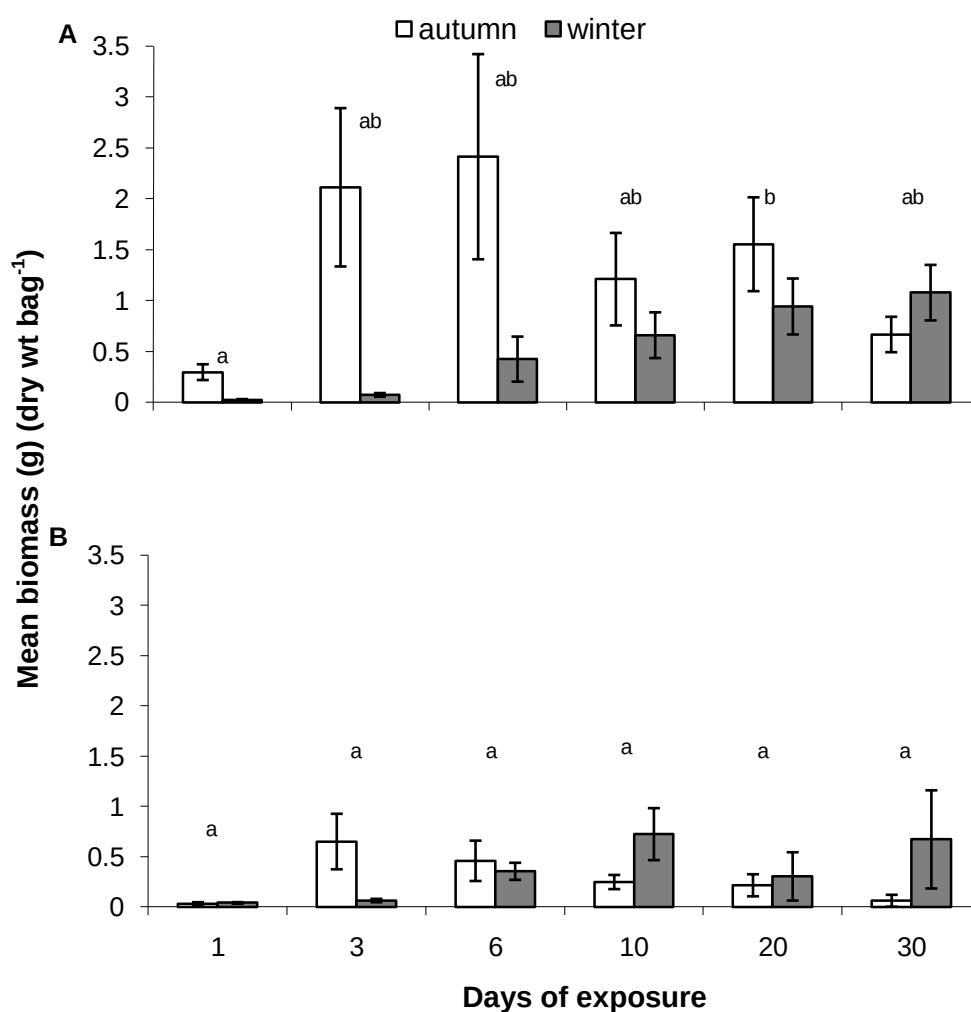


Figure 2.11 Mean ($\pm$ S.E) adult (A) and juvenile (B) Talitridae biomass (g) associated with samples of *Durvillaea antarctica* over a 30-day sampling period in autumn (day 1-20, n=4; day 30, n=3) and winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach. Dissimilar letters denote significant differences between days of exposure.

2.4. Discussion

2.4.1 Macrofauna community

The macrofaunal community associated with samples of stranded *D. antarctica* comprised a total of 20 taxa. These included the talitrid amphipod *Bellorchestia quoyana* (formerly known as *Bellorchestia quoyana*), Diptera such as the kelp fly (Coelopidae), species of isopod, arachnid, and diplopod, and coleopteran species including the tenebrionid *Chaerodes trachyscelides* and the staphylinid species *Blediotrogus guttiger* and *Macralymma punctiventre* (Table 2.1). The talitrid amphipod, dipteran, staphylinid beetle and other coleopteran species composed 99.9% of the total macrofaunal abundance associated with *D. antarctica* (during both autumn and winter sampling periods). Previous studies on the succession of macrofauna on washed-up kelp have shown similar findings where a small fraction of the species associated with the kelp samples make up a large percentage of the community. The amphipod *Orchestia platensis* and the oligochaetes *Enchytraeus* made up 86% of the macroinvertebrate community at four New Hampshire beaches (Behbehani & Croker, 1982). Similarly, in a study carried out in Spain, 5 of the 53 species identified accounted for 77% of the total macrofauna community (Olabarria *et al.* 2007), while 6 of the 22 macrofaunal species associated with samples of *M. pyrifera*, on Pegasus Bay (Canterbury, New Zealand), accounted for 93% of the total macrofaunal community (Inglis, 1989).

In this study *B. quoyana* dominated samples of *D. antarctica*, accounting for 31-96% of the total macrofaunal abundance, and 53-98% of the total macrofaunal biomass during both sampling periods (Table 2.2). *B. quoyana* has been found to be a key consumer of stranded kelp and its presence can be detected by circular holes on the blades of kelp (Inglis, 1989). These holes were found in abundance on samples of *D. antarctica* (authors obs.), suggesting that washed up kelp provides an important food source for *B. quoyana* on Victory Beach, off the Otago Peninsula. Previous studies have also shown the macrofaunal community of washed-up kelp to be dominated by amphipods. The amphipod *Talorchestia martensii* accounted for 89% of total macrofauna community associated with wrack on Sar Uanle (Indian Ocean) (Colombini *et al.* 2000), *Orchestia platensis* accounted for 50% of the community abundance and 81% of community biomass across three New Hampshire habitats (Behbehani & Croker, 1982), and in Peru the macroinvertebrate biomass was dominated by the amphipod *Transorchestia chiliensis* (average biomass of 48 mg bag⁻¹ of *Ulva*) (Catenazzi & Donnelly, 2007). Conversely, in a New Zealand study Inglis (1989) found dipteran flies

were the major component of the macrofaunal community associated with samples of *M. pyrifera*. The difference in findings may in part be due to the different collection methods of the kelp samples from the field. Inglis (1989) used insecticide which ensured all wrack-associated fauna, including flying insects, did not escape when kelp bags were transferred into plastic bags.

2.4.2 Macrofauna succession

Previous studies have found dipteran, amphipod and coleopteran species to colonise wrack within the first few days of being washed ashore (Dobson, 1974; Inglis, 1989; Chown, 1996; Catenazzi & Donnelly, 2007; Olabarria *et al.* 2007; Garrido *et al.* 2008). In this study the four main taxonomic groups, associated with *D. antarctica*, colonized samples within day 1 of exposure, where the average abundance and biomass for each taxon was at its lowest. The succession associated with stranded kelp has been found to vary among species and over time (Inglis, 1989; Jedrzejczak, 2002b; Catenazzi & Donnelly, 2007; Olabarria *et al.* 2007; Garrido *et al.* 2008).

Amphipods are key colonisers of beach-cast algae (Griffiths & Stenton-Dozey, 1981; Behbehani & Croker, 1982, Marsden 1991b; Colombini *et al.* 2000). In this study amphipods were most abundant during the early stages of succession (day 3 and 6 of exposure) while staphylinid beetles (*Blediotrogus guttiger* and *Macralymma punctiventre*) occupied the wrack during later stages, peaking in abundance on day 20 of exposure. Inglis (1989) obtained similar findings where *B. quoyana* reached its highest abundance within the first 3 days of sampling, while staphylinid beetles (*Bledius* spp.) were most abundant on day 18 of sampling. Species composition has been found to change over time possibly due to the decay and desiccation of organic matter on sandy beaches (Catenazzi & Donnelly, 2007; Ince *et al.* 2007). This may explain the early colonisation of *D. antarctica* by the talitrid amphipod, which requires a moist environment to thrive (Marsden, 1991a), whilst carnivorous coleopteran species are late colonisers as they prefer older, drier wrack (Griffiths & Stenton-Dozey, 1981; Colombini *et al.* 2000) where there is an abundance of prey. Alternatively, the decrease in amphipod biomass and abundance overtime may be a means of avoiding the influx of carnivorous staphylinid beetles, which prey on other invertebrates (Klimaszewski *et al.*, 1996).

Dipteran and other Coleoptera abundance and biomass appeared to increase over time; however, this trend was not statistically significant ($p\text{-value} > 0.05$). This was unexpected as other studies have found the abundance and biomass of coleopteran beetles, dipteran adults and larvae on washed-up kelp to change significantly over time (Inglis, 1989; Chown, 1996; Hodge & Arthur, 1997; Catenazzi & Donnelly, 2007; Garrido *et al.* 2008). These findings were based on studies that either solely investigated dipteran or coleopteran assemblages (Chown, 1996; Hodge & Arthur, 1997; Garrido *et al.* 2008), or the sampling method included the collection of meiofauna and associated larval stages (Inglis, 1989; Catenazzi & Donnelly, 2007) that were too small to be extracted by 1-mm mesh sieves (Inglis, 1989; Chown, 1996). Adult flies use the kelp to breed and lay their eggs (Catenazzi & Donnelly, 2007).

In this study the biomass of Diptera differed significantly between sampling days, with highest biomass occurring during later stages. The change in dipteran biomass over time may be attributed to the hatching of newly laid eggs into pupae and then adults. For instance, in a study on dipteran assemblages on the north-east coast of England, adult abundance peaked at the beginning and end of the wrack cycle, while the adults found during later stages were the offspring of adults that originally colonized the fresh cast-up wrack (Hodge & Arthur, 1997).

2.4.3 Seasonal changes

Previous research has shown a significant difference in macrofaunal abundance between summer and winter months (Behbehani & Croker, 1982; Persson, 1999), where summer had the highest abundance. The availability of washed-up wrack varies seasonally (Marsden, 1991a) and in turn influences the numbers of individual macrofauna (Griffiths & Stenton-Dozey, 1981; Behbehani & Croker, 1982; Ince *et al.* 2007; Olabarria *et al.* 2007; Garrido *et al.* 2008). For instance, Behbehani & Croker (1982) showed that the abundance of *Orchestia platensis* decreased as the amount of available wrack decreased from summer to winter.

This study was carried out during autumn (April-May) and winter (June-July); however, the amount of wrack was kept consistent between seasons. Any differences in biomass and/or abundance observed between seasons must, therefore, be attributed to environmental differences rather than kelp availability. All four taxa (Amphipoda, Staphylinidae, other Coleoptera and Diptera) showed no seasonal difference in abundance, but displayed a

seasonal difference in biomass. All common taxa, except other Coleoptera, displayed higher average biomass during autumn. Higher biomass indicates species recruitment, a higher number of individuals and/or that individuals are growing (Behbehani & Croker, 1982; Persson, 1999). The latter is the most probable scenario, as there was no significant difference in abundance between seasons. Air temperature differed between sampling seasons with mean values 12.4°C for autumn and 8.3°C for winter (wharf data from Otago University, 2008), and may be a contributing factor to seasonal differences in observed biomass. However, further investigation into the particular effects of temperature and other environmental factors on the succession of macrofauna on washed up wrack need to be conducted to examine such influences.

2.4.4 Adult and juvenile Talitridae

Durvillaea antarctica is important as food and/or refuge for adult and juvenile talitrid amphipods (*B. quoyana*) on Victory Beach. Both adults and juveniles were present throughout autumn and winter sampling (Fig. 2.10 & 2.11). Similar findings were found for a population of *B. quoyana* on another New Zealand sandy beach receiving a low input of washed up debris, where both adults and juveniles were present throughout the year (Marsden, 1991b). The early colonisation of both adults and juveniles indicates that both groups are primary colonisers of fresh washed up kelp; nonetheless, Marsden (1991a) found *B. quoyana* juveniles to have a stronger association with fresh debris. On average, juveniles made up more than 50% of total macrofauna abundance whereas adults accounted on average for more than 60% of total macrofauna biomass. Only adult biomass differed significantly between autumn and winter sampling, with winter harbouring lower adult biomass.

Summary

- The macrofaunal community associated with stranded *D. antarctica* on Victory Beach consisted of similar species previously found on other beaches in New Zealand and around the world.
- Similar to other studies, *B. quoyana* is a key coloniser of stranded kelp wrack on Victory Beach. Its abundance decreased as the abundance of staphylinid beetles increased over time due to the change in the kelps characteristics.

- There was no seasonal difference in abundance of the four major taxonomic groups (Amphipoda, Staphylinidae, other Coleoptera and Diptera).
- Seasonal differences in macrofaunal biomass, excluding coleopteran biomass, are attributed to factors other than the amount of washed up detritus onto the upper shores. This requires further research.



Field assistants setting out mesh bags along transect that was set 2 metres away from dunes (edge of where vegetation stopped) along Victory Beach, Otago Peninsula (author's photos).

3.1. Introduction

3.1.1 Macrofauna distribution

The macrofauna of sandy beaches increases in abundance and diversity down the shore, where the fauna in the upper shore is influenced by dune vegetation and washed-up wrack (Brown & McLachlan, 1990; Colombini & Chelazzi, 2003; Dugan *et al.* 2003). For instance, De La Huz & Lastra (2008), who sampled 20 beaches on the north-west coast of Spain, found that the mean total macrofaunal abundance ranged between 176 and 2183 individuals per metre within the intertidal zone and the mean total abundance ranged between 6 and 2960 individuals in the supratidal zone. Previous studies have shown that the upper shore of beaches is dominated by semi-terrestrial species, while marine species thrive in the intertidal zone (James & Fairweather, 1996; De La Huz & Lastra, 2008). In Catherine Hill Bay, New South Wales (Australia), two species of isopods dominated core samples taken on the upper shores, while a glycerid polychaete, a species of amphipod, bivalve and cumacean dominated the intertidal zone (James & Fairweather, 1996). In comparison, a study by Olabarria *et al.* (2007) found core samples on the upper shores of O' Vilar beach (Spain) to be dominated by *Phaleria cadaverina*, a coleopteran species. The tenebrionid beetle *Phalerisida maculata*, the talitrid amphipod *Orchestia tuberculata* and the oniscid isopod *Tylos spinulosus*, which are all burrowing species, have also been reported to dominate the upper shores (Jaramillo *et al.* 2003).

3.1.2 Influence of kelp on macrofauna distribution

Physical factors shape the faunal community of the intertidal zone while the upper shore macrofaunal community is influenced by other factors such as kelp deposition and human disturbance (Dugan *et al.* 2003; Jaramillo *et al.* 2006; De La Huz & Lastra 2008). Algal material washed up onto the shores acts as a food source (Dugan *et al.* 2003) and as a refuge from predators (Inglis, 1989; Colombini *et al.* 2000) for the beach macroinvertebrates. The density and biomass of wrack deposited onto the upper shores is known to directly impact the species richness, abundance and biomass of macroinvertebrates on beaches (Dugan *et al.* 2000; Jaramillo *et al.* 2006). This has been demonstrated by previous studies that investigated the species richness and the macrofaunal abundance on high-wrack versus low-wrack beaches (Ince *et al.* 2007), and on groomed versus ungroomed beaches (Dugan *et al.* 2000; Deidun *et al.* 2009). In south-western Australia the mean faunal abundance on high-wrack beaches

(mean volume of 0.27-1.07 m³ wrack m⁻²) was 20-291 and 0.5-3.5 individuals 0.64 m⁻² compared to the mean abundance of 0-3 and 0-0.1 individuals 0.64 m⁻² on the low-wrack (mean volume 0.00-0.09 m³ wrack m⁻²) beaches (Ince *et al.*, 2007). Similarly, Olabarria *et al.* (2007), who studied the effect of different patch sizes of kelp within O' Vilar beach (an exposed beach in Spain), showed that large patches (0.49 m²; 5 kg $\pm$ 50 g wet weight) of wrack overall had a higher number of individuals and species than small patches (0.09 m²; 1kg $\pm$ 50 g wet weight) of washed up-kelp.

Fauna present in low numbers or even absent from upper shores in response to a lack of stranded kelp, include Coleoptera, gastropod, talitrid amphipod, tylid isopod, dipteran and polychaete species (Dugan *et al.* 2000; Jaramillo *et al.*, 2006; Deidun *et al.* 2009). Staphylinid beetles and the gastropod *Truncatella subcylindrica* were absent from groomed beaches of the Maltese Islands. Further, Diptera, coleopteran larvae, isopod *Spelaeoniscus vallettai* and *Chaetophiloscia elongata*, and the polychaete *Ophelia bicornis* were present in low numbers on the groomed beaches (Deidun *et al.* 2009). For instance, there was a total of 43 coleopteran larvae on ungroomed beaches compared to 10 larvae on groomed beaches. The opposite applies where some species dominate and thrive in areas where there is a lack of wrack. For instance isopod *Idotea* spp. and the tenebrionid beetle *Phaleria acuminata* have been found only on beaches where grooming occurred (Deidun *et al.* 2009). This may be attributed to the lack of predators and/or competition from species that rely on wrack for their survival.

Talitrid amphipods, staphylinid beetles and Diptera, such as species of Mycetophilidae, are commonly found on stranded *D. antarctica* on Victory Beach, Otago Peninsula (Chapter 2). Talitrid amphipods are known for their burrowing behaviour (McIntyre, 1963; Morton & Miller, 1968); therefore these faunal species are predicted to be present in high abundance in sediment directly under washed-up kelp. Since previous studies have found stranded kelp to directly enhance the abundance and diversity of beach fauna it is also predicted that the fauna in core samples obtained at a distance from the kelp will be less abundant or absent.

Aim

To study the effects of washed-up wrack on the abundance and distribution of macrofauna within the upper shore of a sandy beach on the Otago Peninsula.

Hypotheses

1. Faunal abundance will decrease with increasing distance from samples of *D. antarctica*.
2. Faunal abundance in core samples will differ over time and between seasons.
3. Marine species will be more abundant directly under kelp samples (0 metre), whilst insect species will be more abundant in core samples taken 1 metre from *D. antarctica* samples.
4. Adult and juvenile amphipod abundance will be highest in cores taken directly under kelp.

3.2. Methods

3.2.1 Fieldwork

Kelp samples were experimentally placed at random within four sites along the upper shore of Victory Beach (described in Chapter 2 Methods). Core samples were obtained at each of the four sampling sites during autumn (6th April to 5th May) and winter (21st June to 22nd July) 2008.

A core of 10 cm diameter (78.5 cm²) taken to a depth of 10 cm was used to extract macrofauna directly under the kelp (0 m), at 0.5 m and 1 m away from the kelp on days 1, 3, 6, 10, 20 and 30. To reduce edge effects, core samples at 0 m were obtained in the centre of where the kelp sample lay (Olabarria *et al.*, 2007). Core samples were sieved on a 1 mm mesh, preserved in 40% isopropanol (IPA) and taken back to the laboratory to be identified.

3.2.2 Laboratory analysis

Individuals were identified to the lowest taxonomic level possible and counted under a dissecting microscope. Fauna were classified to order level for statistical analysis.

3.2.3 Statistical analysis

Faunal abundance was expressed as a percentage of total abundance associated with distance (0, 0.5 and 1 m) from the kelp sample, and analysed using a three-way ANOVA (General Linear Model) in Minitab 14, with season, day of exposure and core distance as factors. Data were checked for homogeneity of variance using Levene's test and log₁₀ (n+1) transformed when required. Taxa with a total abundance of 10 or fewer over the whole sampling period were not included in the statistical analysis.

3.3. Results

3.3.1 Total macrofauna abundance and distribution

Core samples taken directly under kelp (0 m) had higher mean macrofaunal abundance for both seasons than those taken 0.5 and 1 m away (Fig. 3.1) (F-value 46.13, p-value<0.001). For instance, overall mean abundance was 14 individuals core⁻¹ (78.5 cm²) at 0 m, 3 individuals core⁻¹ (78.5 cm²) at 0.5 m and 2 individuals core⁻¹ (78.5 cm²) at 1 m. Season and days of exposure did not show significant differences in faunal abundance (season, F-value 0.17, p-value 0.681; day, F-value 2.27, p-value 0.054).

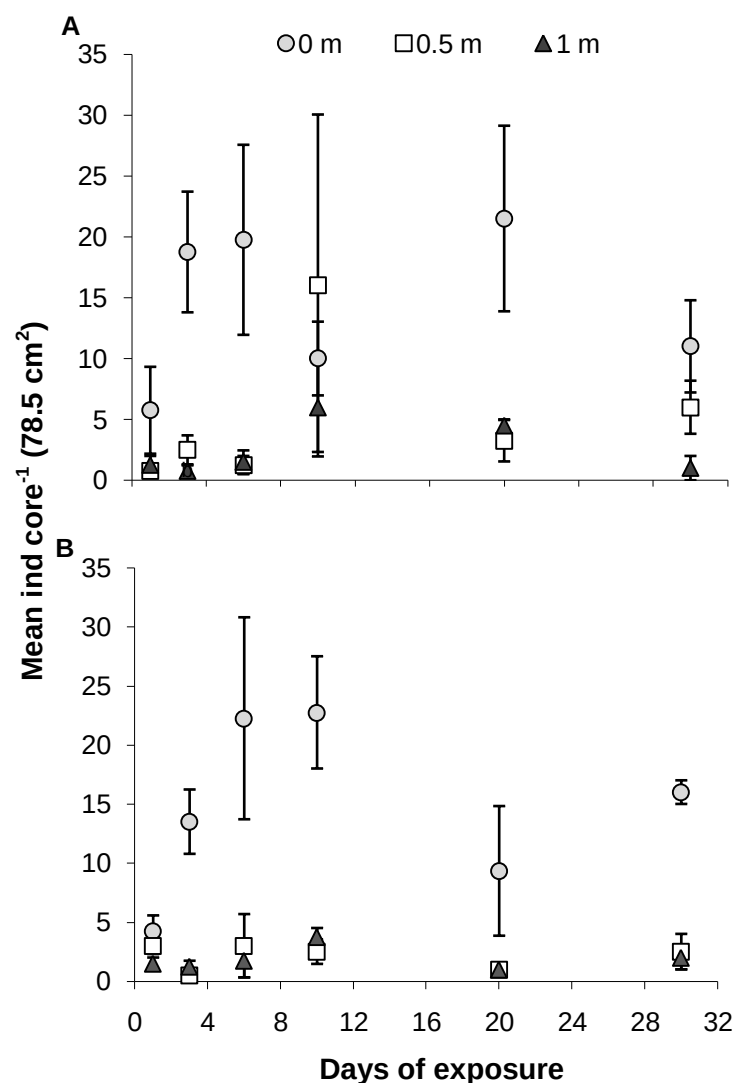


Figure 3.1 Mean macrofaunal abundance ($\pm$ S.E) per core sample (78.5 cm²) taken at 0, 0.5 and 1 m intervals from *Durvillaea antarctica* during (A) autumn (day 1-20, n=4; day 30, n=3) and (B) winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach, Otago Peninsula.

3.3.2 Individual faunal abundance and distribution

The macrofaunal community was dominated by amphipods, their total abundance ranging between 48-78% of total number of individuals in autumn and 63-90% in winter, whereas each of the three remaining major taxa contributed less than 40% of the total community within each core distance for both seasons (Table 3.1). Macrofaunal community at 0 m was dominated by amphipods (74% in autumn and 90% in winter), followed by Coleoptera (23% in autumn and 6% in winter). Isopods and Diptera were the least abundant taxonomic groups at 0 m, but their total abundance increased as the distance from the kelp sample increased. For instance, isopods made up 1.5% of the community in autumn and 1% of the community in winter, but at 1 m their abundance made up 36% of the community in autumn and 18% of the community in winter (Table 3.1).

Table 3.1 Total abundance (number and % of total community) of the four main taxonomic groups found at 0, 0.5 and 1 m from samples of *Durvillaea antarctica* on Victory Beach, Otago Peninsula. Autumn and winter numbers are the pooled samples over all sampling dates.

Taxa	Core	Total number		% of the community	
		autumn	winter	autumn	winter
Amphipoda	0	247	279	73.7	89.7
	0.5	86	28	77.5	63.6
	1	30	25	48.4	62.5
Isopoda	0	5	3	1.5	1.0
	0.5	6	2	5.4	4.6
	1	22	7	35.5	17.5
Coleoptera	0	77	18	23.0	5.8
	0.5	9	3	8.1	6.8
	1	8	1	12.9	2.5
Diptera	0	6	9	1.8	2.9
	0.5	8	11	7.2	25.0
	1	2	6	3.2	15.0

Isopods and Diptera did not show significant differences in abundance as a response to seasons, days of exposure and core samples (p-value > 0.05) (see Appendix, Table A.4, Fig. A.1 & A.2). Amphipod and coleopteran abundance was highest in cores taken directly under kelp (0 m) (Tamahane's test, p-value <0.001). Amphipod and coleopteran abundance in 0.5 and 1 m cores averaged 0 throughout both sampling periods and showed no statistical differences in abundance (Tamahane's test, p-value > 0.05) (Fig 3.2 & 3.3). Amphipod abundance differed significantly between days of exposure (F-value 3.35, p-value 0.008) (Fig.

3.2). Abundance appeared to increase gradually from day 1 to day 6 of exposure and then decrease from day 10 to day 30 of exposure, but a post-hoc test did not detect significant differences between sampling days (Tamahane's test, p -value > 0.05). There was no significant difference in coleopteran abundance between days of exposure, but their abundance differed significantly between seasons; an abundance of 7 individuals core^{-1} (78.5 cm^2) in autumn was the highest mean number of individuals in comparison to the maximum of 3 individuals core^{-1} (78.5 cm^2) in winter (F-value, 6.92, p -value 0.01) (Fig. 3.3).

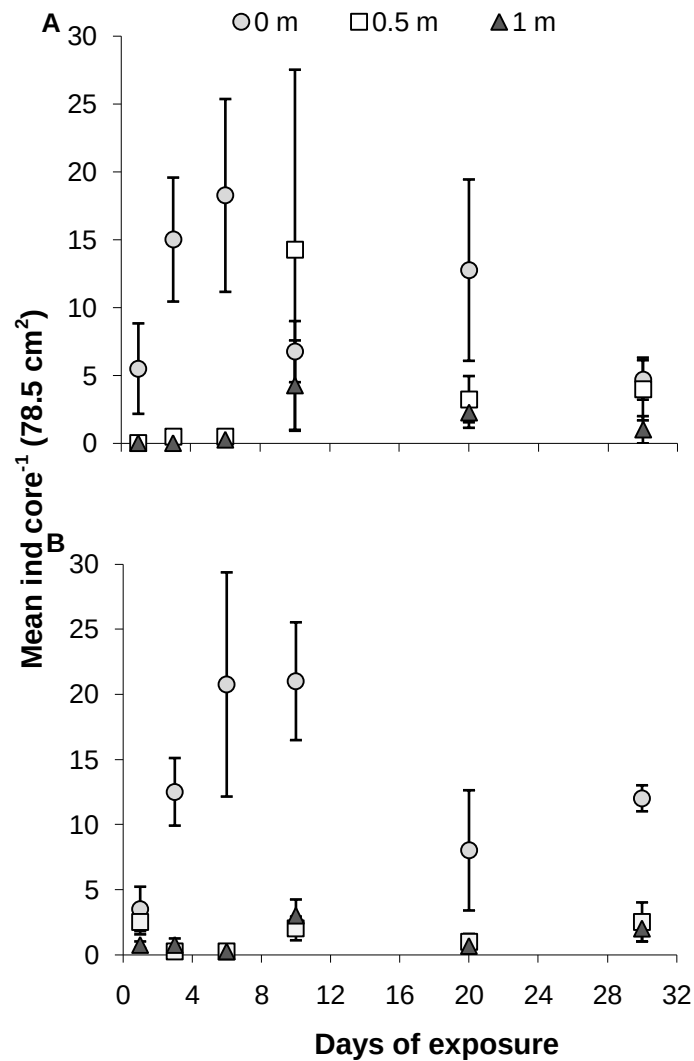


Figure 3.2 Mean amphipod abundance ($\pm$ S.E.) per core sample (78.5 cm^2) taken at 0, 0.5 and 1 m intervals from *Durvillaea antarctica* during (A) autumn (day 1-20, $n=4$; day 30, $n=3$) and (B) winter (day 1-10, $n=4$; day 20, $n=3$; day 30, $n=2$) 2008, on Victory Beach, Otago Peninsula.

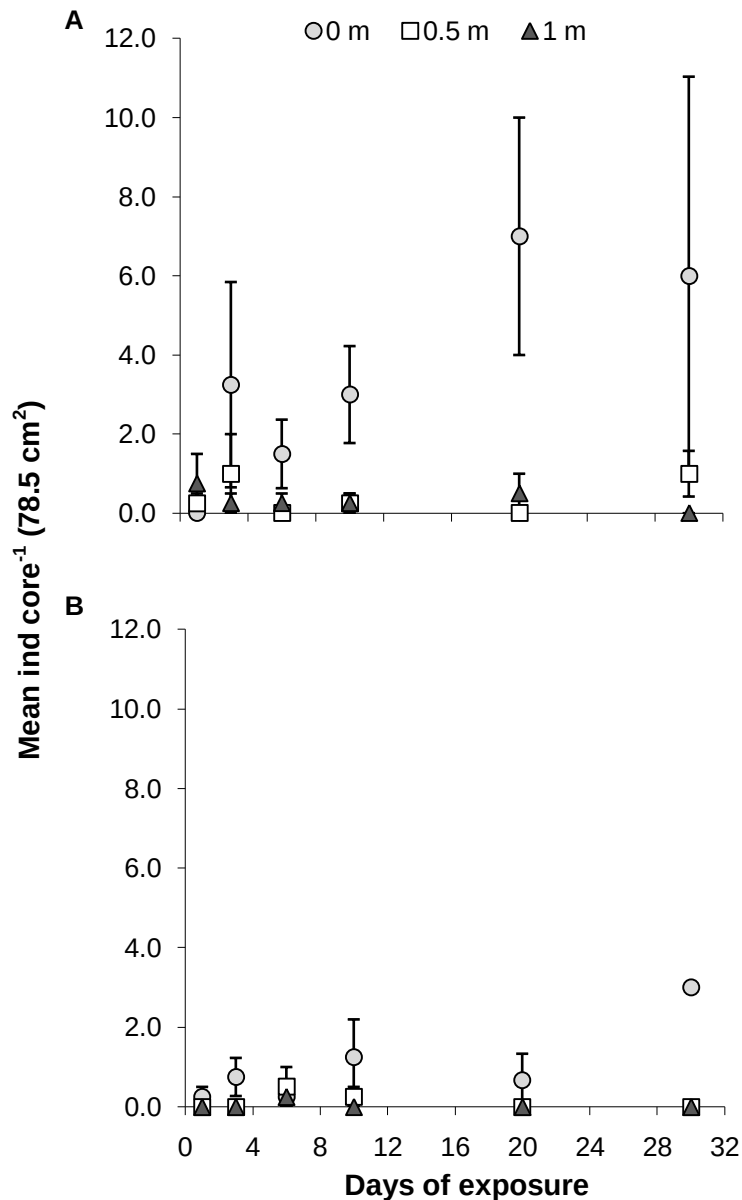


Figure 3.3 Mean coleopteran abundance ($\pm$ S.E) per core sample (78.5cm²) taken at 0, 0.5 and 1 m intervals from *Durvillaea antarctica* during (A) autumn (day 1-20, n=4; day 30, n=3) and (B) winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach, Otago Peninsula.

3.3.3 Adult and juvenile amphipod abundance and distribution

Adult abundance did not vary significantly between seasons or days of exposure (p-value >0.05). The mean number of adult amphipods differed significantly between core samples (F-value 114.91, p-value <0.001) with the highest abundance directly under the kelp (0 m) (Tamahane's test, p-value <0.001); however, there was no significant difference in abundance between 0.5 and 1 m from the kelp (Tamahane's test, p-value < 0.05) (Fig. 3.4). For instance, mean abundance at 0 m ranged between 6-17 individuals core⁻¹ (78.5 cm²) in autumn and 2-

17 individuals core⁻¹ (78.5 cm²) in winter, whereas mean abundance at 0.5 and 1 m ranged between 0-6 individuals core⁻¹ (78.5 cm²) (Fig. 3.4). Adult amphipod abundance also showed significant interaction effect between day and core (F-value 2.80, p-value 0.004), and between season, day and core (F-value 1.99, 0.042).

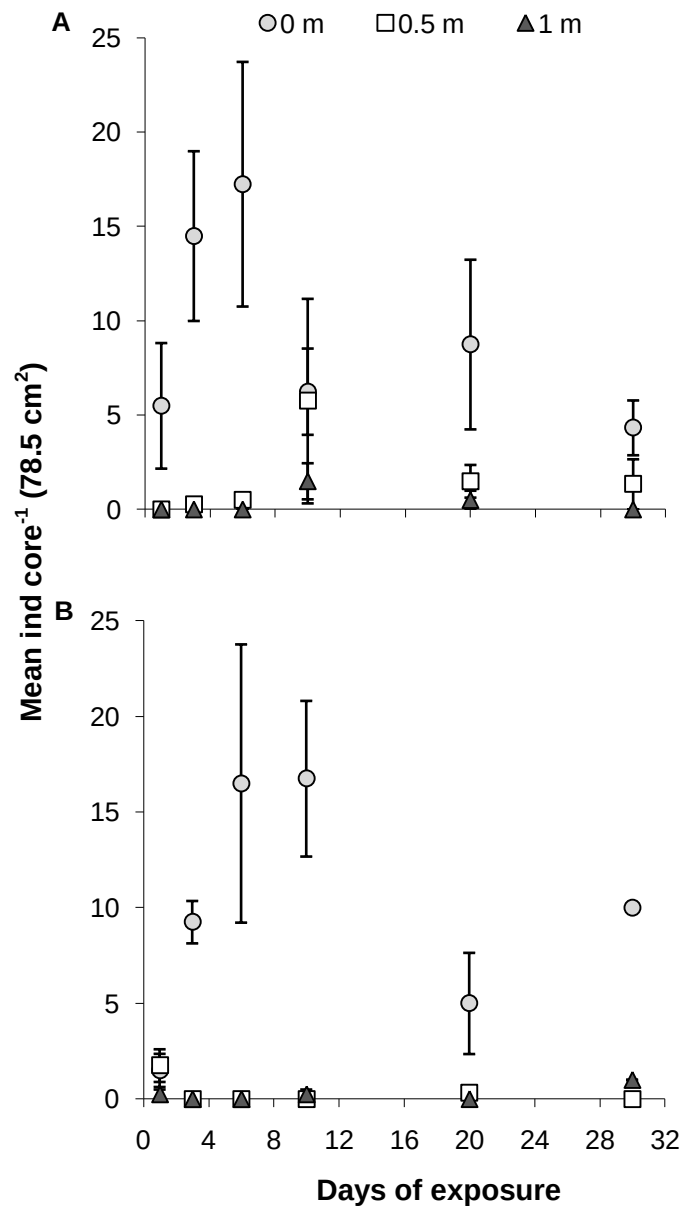


Figure 3.4 Mean adult amphipod abundance ($\pm$ S.E) per core sample (78.5cm²) taken at 0, 0.5 and 1 m intervals from *Durvillaea antarctica* during (A) autumn (day 1-20, n=4; day 30, n=3) and (B) winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach, Otago Peninsula.

Juvenile abundance differed significantly between seasons and days of exposure (p-value <0.05), but there was no significant difference between core samples taken at 0, 0.5 and 1 m from the kelp (F-value 3.05, p-value 0.052). Juveniles, with a mean abundance of 2 individuals core⁻¹ (78.5 cm²), were most abundant throughout the winter sampling period (F-value 5.74, p-value 0.019) (Fig 3.5). Juvenile core abundance remained low until day 10, when it doubled and appeared to decrease for the remainder of the sampling period. A post-hoc test using day as a factor found only day 10 and day 1 to be significantly different in abundance (Tamahane's test, p-value 0.029) (Fig. 3.5).

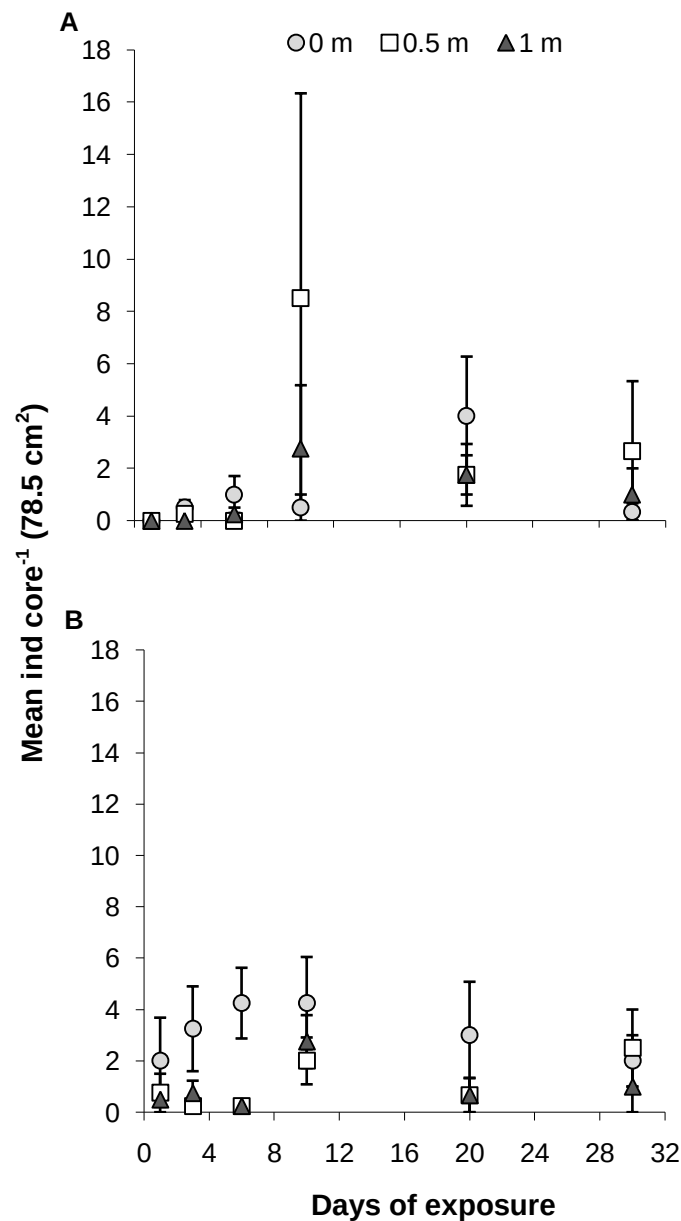


Figure 3.5 Mean juvenile amphipod abundance (±S.E) per core sample (78.5cm²) taken at 0, 0.5 and 1 m intervals from *Durvillaea antarctica* during (A) autumn (day 1-20, n=4; day 30, n=3) and (B) winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach, Otago Peninsula.

3.4. Discussion

3.4.1. Macrofauna

The sediment of the upper shore of Victory Beach is inhabited by the talitrid amphipod *Bellorchestia quoyana*, Coleoptera including the tenebrionid *Chaerodes trachyscelides*, the isopod *Scyphax ornatus*, and mycetophilid Diptera. The predominance of arthropod species on the upper shore of Victory Beach agrees with previous studies (e.g. James & Fairweather, 1996; Stephenson, 1998; Jaramillo *et al.*, 2003; Rodil *et al.*, 2008). For instance, in a study, carried out on Wainui Beach (Gisborne), *C. trachyscelides*, *B. quoyana* and *S. ornatus* were also found to dominate the upper shore (Stephenson, 1993; Stephenson, 1998). On Victory Beach the highest macrofaunal density was, as predicted, found in sediment taken directly under samples of *D. antarctica*, in contrast to that found in bare sediment. This indicates the likely importance of stranded organic material in supporting macrofaunal populations on Victory Beach.

3.4.2. Individual trends

Bellorchestia quoyana was the most abundant taxon, contributing to more than 50% of total macrofaunal abundance in both sampling periods, while the remaining taxa made up less than 40% of the total macrofaunal abundance. As well as dominating core samples, *B. quoyana* was the most abundant species associated with samples of stranded *D. antarctica* on Victory Beach (see Chapter 2). The high abundance of *B. quoyana* seen in both core and kelp samples agrees with a previous study by Olabarria *et al.* (2007), where the dominant taxa in kelp samples also dominated bare sand samples, in this case the tenebrionid beetle dominated the upper shore of O' Vilar (Spain).

When comparing faunal abundances at different distances from the stranded kelp, total abundance for Isopoda and Diptera were found to increase with increasing distance, whereas coleopteran and amphipod abundances were highest in sediment directly under the kelp. This suggests that stranded *D. antarctica* on Victory Beach influences faunal species that are primary consumers of stranded kelp. In this study, Coleoptera primarily consisted of the flightless sand burrowing tenebrionid *C. trachyscelides* and, like *B. quoyana*, its adults and larvae feed on stranded algae (MacIntyre, 1963; Harris, 1991). By contrast, staphylinid beetles dominated the samples of stranded kelp (see Chapter 2). In this study staphylinids

were either absent or present in small numbers in the core samples. This may be because staphylinids are predators and/or scavengers that are known to occupy stranded kelp to feed on other macroinvertebrates (Colombini & Chelazzi, 2003).

Coleoptera and Amphipoda were the only taxa that showed a significant difference in abundance and, as predicted, were most abundant directly under stranded kelp. The low abundance or absence of talitrid amphipods and Coleoptera (mainly tenebrionids) in bare sand cores, compared to abundance directly under stranded kelp, agrees with finding from previous studies that have found macrofaunal species to be directly influenced by stranded macrophytes (Brown & McLachlan, 1990; Marsden 1991a; Dugan et al., 2000; Colombini & Chelazzi, 2003; Dugan *et al.*, 2003; Ince *et al.*, 2007; Deidun *et al.*, 2009). Marsden (1991a), who studied the density and biomass of talitrid amphipods as a response to stranded material on Brighton Beach (Canterbury), New Zealand, found the average amphipod abundance to be highest where there was stranded material, in comparison to areas with bare sand. The same was found for populations of *B. quoyana* and *C. trachyscelides* on Wainui Beach (North Island of New Zealand), where both taxa were most abundant under stranded algae, with mean abundances of 16 and 33 individuals m⁻² respectively (Stephenson, 1993).

In this study, mean amphipod abundance was 673 individuals m⁻² over both sampling periods, whereas mean coleopteran abundance was 178 individuals m⁻² in autumn and 51 individuals m⁻² in winter. Coleoptera was the only taxon that differed significantly in abundance between seasons. This seasonal difference in abundance may be as a result of a seaward migration during colder periods, similar to that seen in *Eurynebria complanata* and *Phaleria acuminate* (Colombini *et al.*, 2002). This migratory behaviour has been suggested to be a response to the changes in the distribution of stranded material along the shore, or a response to microclimatic changes (Marsden, 1991a, 1991b; Colombini *et al.*, 1994; Fallaci *et al.*, 1999; Colombini *et al.*, 2002), or as a preference for soft sand to facilitate burrowing (Craig, 1973). This study used samples of *D. antarctica*, which has been found to be more abundant on New Zealand shores during winter (Marsden, 1991a). This may suggest that the low coleopteran abundance on Victory Beach during winter may be a response to changes in microclimatic conditions rather than the seasonal variation in the input of stranded organic material. The mean air temperature recorded on the Otago Peninsula was 12.4°C and 8.3°C in winter (wharf data from Otago University, 2008). Further research needs to be undertaken to identify what factor(s) causes seasonal variations in coleopteran abundance, especially core sampling in

summer and spring to identify whether higher temperatures result in higher abundance of beetles.

3.4.3. Adult and juvenile talitrid abundance

The talitrid amphipod *B. quoyana* is a primary consumer of freshly deposited *Macrocystis pyrifera* and *D. antarctica* on the shores of New Zealand beaches (MacIntyre, 1963; Inglis, 1989; Marsden 1991a, 1991b). Talitrid amphipods are early colonisers of washed-up kelp (Griffiths & Stenton-Dozey, 1981; Inglis 1989; see Chapter 2) and their abundance is influenced by the presence of stranded organic material (Griffiths & Stenton-Dozey, 1981; Inglis, 1989; Marsden, 1991a; Colombini *et al.*, 2002; Jedrzejczak, 2002b). The abundance and biomass of both male and female adult, and juvenile talitrid amphipods, are known to be related to washed-up organic material (Craig, 1973; Marsden, 1991a). In this study, only adults were influenced by the presence of *D. antarctica* samples, where their abundance was highest in cores taken directly under the kelp. Juveniles, on the other hand, were not found to be influenced by the presence of stranded material, but rather by the length of time the drift kelp had been on the shore and the time of year the sampling took place. These findings agree with those of Marsden (1991a) who studied the distribution of *B. quoyana* on Brighton Beach, New Zealand, where juveniles were most common in bare sand and tended to be distributed more seaward than the adults. The seaward distribution seen in talitrid juveniles is suggested to be a behavioural adaptation to avoid desiccation (Colombini *et al.*, 2002). Juveniles on Brighton Beach, Canterbury, were distributed between 10-15 m from the dunes during April and May, while in June and July they occupied sand between 3-10 m from the dunes. The lower abundance of juveniles seen in autumn compared to winter on Victory Beach may be because the transect in this study was set out at 2 m from the dune, thus excluding juvenile talitrid amphipods and any other fauna found in the intertidal zone. This study focused on the impact of stranded kelp on the macrofaunal community on the upper shore only. It would be of interest to investigate the ecological impact of stranded *D. antarctica* on the macrofauna at all tidal levels on Victory Beach, on the Otago Peninsula.

Summary

- Stranded *D. antarctica* influenced the abundance of macrofauna on the upper shore of Victory Beach.

- *Bellorchestia quoyana* was the most abundant species in bare sediment and in sediment directly under the kelp.
- Isopoda and Diptera did not show any significant differences in abundance for season, days of exposure, and distance from stranded kelp.
- Amphipoda and Coleoptera were directly influenced by the presence of stranded kelp.
- The time of year that sampling took place influenced only Coleoptera, where its abundance was highest in autumn.
- The period of time the kelp had been stranded on the shore influenced only talitrid amphipods. Separate analysis of variance showed that juvenile, not adult, abundance changed with days of exposure, whereas adults were mainly influenced by the presence of kelp.
- Stranded kelp impacted the abundance and distribution of macrofaunal species on Victory Beach. Further study is recommended to examine the patterns of distribution found during spring and summer, and to investigate whether those patterns are similar or different to those seen in this study.
- For any future study, it is recommended that shore level and macrophyte cover are taken into account to test whether seasonal differences in abundance for Coleoptera and juvenile amphipods are a result of changes in the microclimate or changes in the input of stranded material.

Chapter 4 Decay rate and elemental analysis of
Durvillaea antarctica, on an exposed sandy
beach.



Stranded *Durvillaea antarctica* on Victory Beach, Otago Peninsula (author's photo).

4.1. Introduction

4.1.1 Ecological impact of kelp

The accumulation of stranded kelp acts as an important source of nutrients (Rice & Tenore, 1981; Mateo, 2010; Olabarria *et al.*, 2010) for primary consumers on sandy shores, where primary productivity is low (Chown, 1996; Pennings *et al.*, 2000; Lastra *et al.*, 2008). The decomposition of such kelp is controlled by a range of factors, such as: microorganisms (Fenchel, 1969), weather conditions (Chown, 1996), wave action and tidal currents (Orr *et al.*, 2005), oxygen availability and macrofaunal species (Rice & Tenore, 1981; Zimmer 2002, 2004; Lastra *et al.*, 2008). Nutrients, such as carbon, nitrogen and phosphorus, are released to the surrounding sediments as a result of kelp decomposition (Hanisak, 1993). This nutrient enrichment is beneficial to certain taxa (Posey *et al.*, 1999; Bolam *et al.*, 2000; Rossi & Underwood, 2002; Olabarria *et al.*, 2010). The isopod *Ligia palasii*, for instance, was found to consume up to 50% more of kelp samples enriched in organic matter than that of the control samples (Pennings *et al.*, 2000). Furthermore, the abundance of some taxa, such as capitellid, orbinid and nereidid polychaetes, oligochaetes, and gammarid amphipods, was found to increase in areas where wrack was added (Bolam *et al.*, 2000; Rossi & Underwood, 2002).

Not all taxa, however, exhibit a positive response to such nutrient enrichment (Bolam *et al.*, 2000; Rossi & Underwood, 2002; Olabarria *et al.*, 2010). For example, the abundance of gammarid and urogastrid amphipods did not differ significantly between wrack and control sites, but did change as a function of shore level and beach type (Rossi & Underwood, 2002). Additionally, Bolam *et al.* (2000) found a decrease in the abundance of the spionid polychaete *Pygospio elegans* as a response to the green alga *Enteromorpha prolifera* in the intertidal area of a sandflat. Variations in the responses of individual taxa to the addition of wrack may be attributed to the different ways that wrack is utilized among taxa, i.e. as food and / or shelter, and whether the wrack is on the surface or buried in the sediment (Rossi & Underwood, 2002). For example, kelp that is buried will provide nutrients for the benthos (Rossi, 2006), but will not be directly available to grazers (Rossi, 2007), such as talitrid amphipods, which use kelp as a food source on the surface (Inglis, 1989). Environmental factors (Knox, 2001; Rodil *et al.*, 2007), chemical composition of sediments (Posey *et al.* 1999; Norkko *et al.* 2000; Colombini & Chelazzi, 2003; Posey *et al.*, 2006; Olabarria *et al.*, 2010) and prey-predator relationships (Griffiths & Stenton-Dozey, 1981; Norkko, 1998; Colombini *et al.*, 2000; Posey *et al.* 2006) also influence the macrofaunal community structure. The macrofaunal response to

stranded kelp is, therefore, complex and variable (Rossi & Underwood 2002; Olabarria *et al.*, 2010).

Previous research has demonstrated that kelp degradation is influenced by macrofauna, as well as other physical and biological factors previously mentioned. Stranded kelp is fragmented by herbivores (Zimmer, 2002, 2004), such as acalypterate flies, *Paractora trichosterna* and *Antrops truncipennis*, which accounted for weight losses of 20 and 23% respectively in protected and exposed beds of dry kelp over a 49-day sampling period in the Sub-Antarctic island of South Georgia (Chown, 1996). Conversely, the decomposition of stranded *Macrocystis pyrifera* was not influenced by faunal species in a New Zealand study, but by abiotic leaching and microorganisms (Inglis, 1989) that process the high-fibre, low-nitrogen material into a high nutritive product for macroinvertebrates (Rice & Tenore, 1981; Knox, 2001). Variations in the decomposition rate between these studies can also be explained by the different kelp species used in the study. Mews *et al.* (2006) demonstrated that the presence of herbivores did not impact the decomposition rate of *Fucus* spp. but did influence the breakdown of *Ulva* spp., *Macrocystis integrifolia* and *Nereocystis luetkeana*.

4.1.2 Kelp decomposition

The lifecycle, position on the intertidal zone, nutritional value, water content, microbial activity and defense mechanisms vary among species of kelp (Enriquez *et al.*, 1993; Pennings *et al.*, 2000; Fourqurean & Schrlau, 2003; Orr *et al.*, 2005). These differences cause variable rates of decomposition among species (Rice & Tenore, 1981; Smith & Foreman, 1984; Pennings *et al.*, 2000; Fourqurean & Schrlau, 2003). Over a sampling period of 150 days, for instance, decomposing red algae lost up to 65% of their organic content in contrast to brown seaweeds which lost up to 40% of their organic content (Rice & Tenore, 1981). The changes in organic matter reflect the changes occurring to the carbon and nitrogen content during decomposition. For example, carbon content may decrease through respiration by microorganisms (Fourqurean & Schrlau, 2003), while nitrogen compounds can be exported or imported, resulting in the C:N ratio in decaying seaweed to either decrease or increase overtime (Rice & Tenore, 1981; Pennings *et al.*, 2000). For example, the C:N ratio of the brown seaweeds *Sargassum* (33.3 ± 0.3 in fresh and 35.5 ± 0.4 in wrack) and *Spatoglossum* (18.8 ± 1.0 in fresh and 18.1 ± 0.9 in wrack) was found to decrease over time, whereas the red

seaweeds *Gracilaria* and *Hypnea* exported nitrogen resulting in an increase in the C:N ratio (Rice & Tenore, 1981). As a result, the nutrient content of stranded seaweeds will not only depend on the type of species stranded but also on the time the kelp has been decomposing.

As a food source, stranded kelp is not only rich in organic matter but also provides a high content of free water (MacIntyre, 1963). The initial water content of brown seaweeds has been found to range between 75-90% for freshly deposited seaweeds and 12-23% in aged seaweeds (Pennings *et al.* 2000). The water content of deposited kelp decreases over time (Griffiths & Stenton-Dozey, 1981; Pennings *et al.* 2000) as it dries due to sun and wind exposure (Ochieng & Erftemeijer, 1999). Water availability is especially important, for instance, to crustaceans occupying the highly saline environments of the upper shore (MacIntyre, 1963), and for the decomposition rate of stranded kelp (Alkemade & Van Rijswijk, 1993). The water content of stranded seaweed has been suggested to influence the decomposition rate, where stranded seaweed with higher water content has a higher decomposition rate (Newell *et al.*, 1985; Alkemade & Van Rijswijk, 1993). Findings by Newell *et al.* (1985) explain the slower decay rate seen in dried kelp, where samples of salt-marsh material with less than 15% water content could not be synthesized by microorganisms due to inefficient bacterial respiration.

The rate of decomposition can be determined by measuring the weight loss of stranded kelp, resulting from the microbial degradation of the organic matter (Valiela *et al.*, 1985) and consumption by macrofauna (Griffiths & Stenton-Dozey, 1981; Lastra *et al.*, 2008). On a sandy beach in Canterbury (New Zealand) the brown seaweed *Macrocystis pyrifera* reached 50% of its original dry weight after 18 days of exposure. The size of the kelp deposits influences the rate of decomposition. Griffiths & Stenton-Dozey (1981) found larger deposits were lost at a faster rate than single plants on the coast of South Africa, whereas Olabarria *et al.* (2007) showed larger patches had a slower rate of decomposition on an exposed beach in Spain; but in all studies the initial loss was rapid. The different outcomes seen between these studies may be explained by the different environmental and/or biological factors that affect the decomposition rate and the different species of kelp used in the studies. For instance, grazers are responsible for the decay of kelp in some studies (Griffiths & Stenton-Dozey, 1981; Chown, 1996), and not in others (Inglis, 1989) due to the presence or absence of defense mechanisms against grazers in the species of kelp used (Pennings *et al.*, 2000). Such defense mechanisms include phenolic compounds which make kelp unpalatable to

macrofauna, hence other food sources (such as aged kelp) lacking these compounds will be preferred as they do not require detoxification (Pennings *et al.*, 2000).

Aim

The objective of this study was to investigate the decomposition rate of *D. antarctica* on an exposed beach on the south-east coast of New Zealand, by firstly analysing: (1) water content and weight loss, (2) carbon and nitrogen content, and (3) the C:N ratio over a 30-day sampling period during autumn and winter; and, secondly, to understand the influence of: (1) moisture content, (2) weight loss and (3) the ratio of C:N on the abundance and biomass of total macrofauna. To this end a number of specific hypotheses were posed.

Hypotheses

1. Initial dry weight of *D. antarctica* remaining will decrease over time.
2. Moisture content of *D. antarctica* will decrease as weight loss of *D. antarctica* increases.
3. Moisture content will influence the macrofaunal abundance associated with samples of *D. antarctica*.
4. The initial dry weight of *D. antarctica* remaining will influence the abundance of the associated macrofaunal community.
5. Carbon content will decrease and nitrogen content will increase over the sampling period, thus changing the C: N ratio.
6. The C:N ratio will influence the total macrofaunal abundance and biomass associated with *D. antarctica* on Victory Beach.
7. Changes in the initial dry weight remaining of *D. antarctica* will influence changes in the nutrient content of the kelp.

4.2. Methods

4.2.1 Field work

Kelp samples were collected in autumn and winter 2008 after 1, 3, 6, 10, 20 and 30 days of exposure, on Victory Beach, as per methods outlined in Chapter 2. In the laboratory, kelp samples were rinsed in freshwater to remove sand and associated fauna, blotted dry, weighed (to the nearest 0.01 g), and placed in the drying oven at 60°C for 5 days. The samples were then re-weighed to determine their moisture content. Decomposition rate was measured by calculating the initial dry weight remaining upon collection.

4.2.2 Laboratory analysis

To determine carbon and nitrogen content, dry kelp samples were ground to a fine powder. Subsamples of 2-3 mg of fine powder were analysed for percentage of organic carbon and nitrogen content using a Carlo Erba Elemental Analyser EA 1108. This was carried out by the Campbell Macroanalytical Laboratory at the University of Otago. The ratio of C:N for *D. antarctica* was then calculated.

4.2.3 Statistical analysis

Two-way ANOVA tests were carried out for the following responses in SPSS 15: the percentage of original dry weight, percentage of moisture loss, the percentage of carbon and nitrogen and the ratio of C:N. Data were checked for homogeneity of variance using Levene's test, and $\log_{10}(n+1)$ transformed when required. To determine if changes in the C:N ratio of *D. antarctica* varied with the total macrofaunal abundance and biomass, a multiple regression analysis was carried out using Minitab 14.

4.3. Results

4.3.1 Kelp weight and moisture loss

Both the weight and moisture loss of *D. antarctica* differed significantly between seasons and days of exposure (p -value < 0.05). The mean initial kelp dry weight remaining ranged between 42-67% in autumn and 55-71% in winter (Fig. 4.1). The mean moisture content of kelp ranged between 57-66% in autumn and 71-81% in winter (Fig. 4.2). The mean initial dry weight remaining and the mean moisture content were lowest during autumn sampling. For instance, on day 6 of exposure there was 48% of the original kelp weight remaining in autumn compared to 66% remaining in winter (Fig. 4.1). On the same day, the mean percentage of moisture remaining was 62% in autumn and 71% in winter (Fig. 4.2).

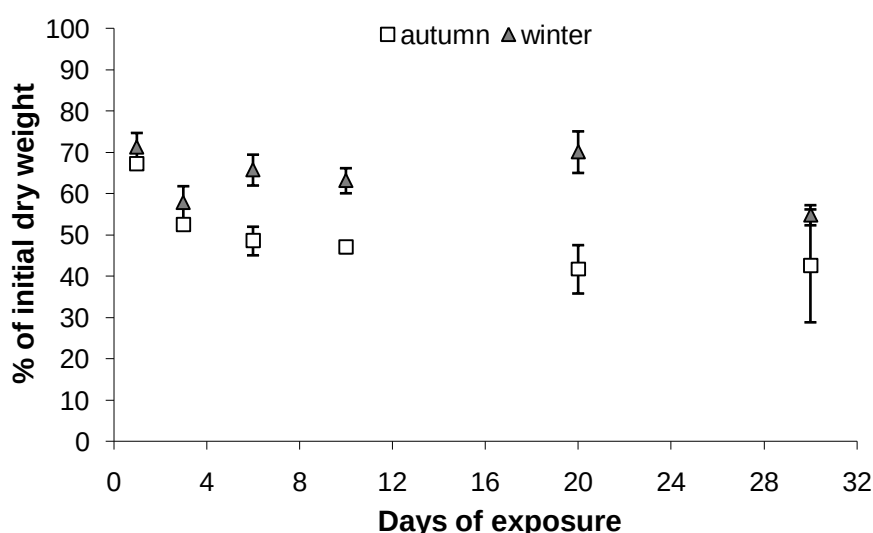


Figure 4.1 Changes in the mean percentage of initial dry weight ($\pm$ S.E) during a sampling period of 30 days in autumn (day 1-20: $n=4$, day 30: $n=3$) and winter (day 1-10: $n=4$, day 20: $n=3$, day 30: $n=2$) on Victory Beach, on the Otago Peninsula.

A Tamahane's post-hoc test on days of exposure showed that the mean weight loss differed significantly between day 1 and day 3 of sampling. On day 3 the kelp samples had lost half of their initial weight (p -value 0.003) (Fig. 4.1). The mean percentage of moisture content also appeared to decrease gradually over time, except for sampling on day 20, where the moisture content for both autumn (67%) and winter (81%) was higher than that for day 1 (66% in autumn and 74% in winter) (Fig. 4.2). An ANOVA showed mean moisture content to differ significantly between days (F -value 4.82, p -value 0.002). Tamahane post-hoc tests, however, could not detect differences (p -value > 0.05) (Fig. 4.2).

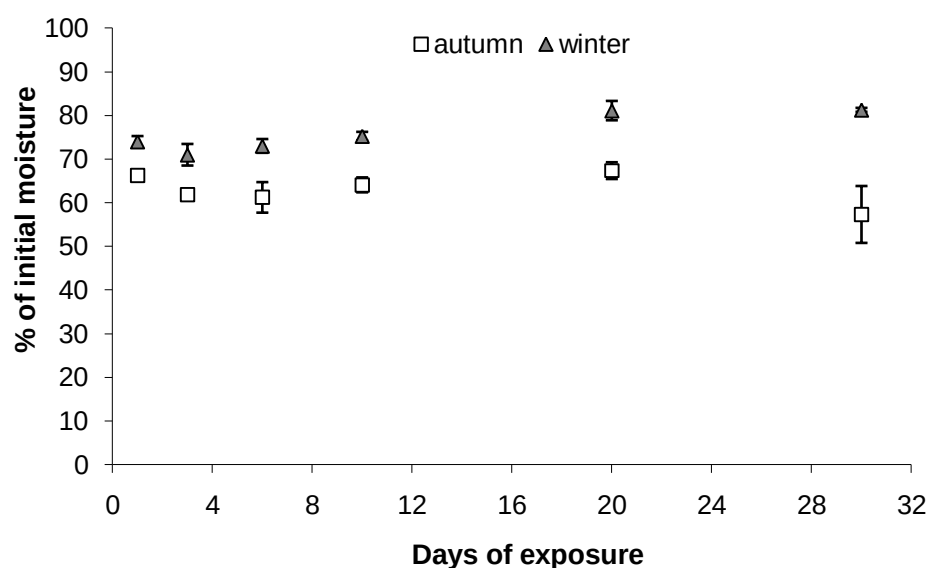


Figure 4.2 Percentage of initial moisture ($\pm$ S.E) over a sampling period of 30 days in autumn (day 1-20: n=4, day 30: n=3) and winter (day 1-10: n=4, day 20: n=3, day 30: n=2) on Victory Beach, on the Otago Peninsula.

The R^2 value of 43% suggests there is a linear relationship between the water content and the decomposition rate of *D. antarctica*. Kelp samples with a high percentage of initial weight remaining had a higher percentage of water. For example, a sample with 77% of initial dry weight had a water content of 75% (Fig. 4.3). In contrast, a sample with 44% of the initial dry weight had 62% water (Fig. 4.3). A linear regression analysis showed that changes in decomposition rate caused significant changes in the water content values (Table 4.1). The following equation can be used to determine the percentage of water in *D. antarctica* samples:

$$\% \text{ moisture} = 45.5 + 0.410(\text{initial dry weight})$$

Table 4.1 Linear regression analysis for the moisture content as a response to initial weight remaining in kelp samples, on Victory Beach, 2008. Significant p-values are shown in bold.

Predictor	coef	S.E. coef	T	p-value
Constant	45.55	4.254	10.71	<0.001
Initial dry weight	0.41	0.073	5.64	<0.001

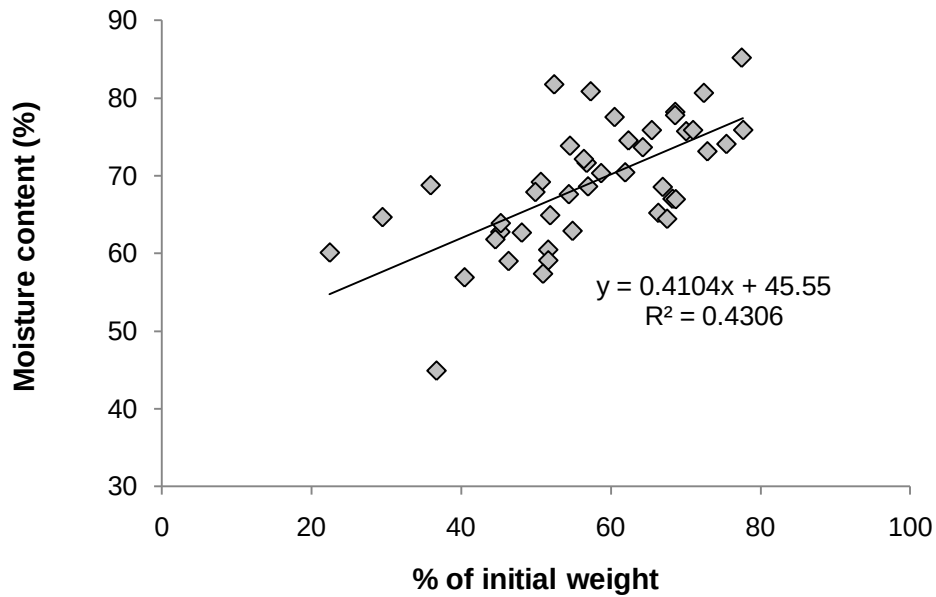


Figure 4.3 Relationship between initial dry weight (%) remaining in *D. antarctica* samples (n = 44) and its water content (%) after a given period of time on Victory Beach, 2008.

Relationship with macrofaunal community

Moisture content of *D. antarctica* appeared to influence the total macrofaunal biomass associated with samples, whereas moisture content and total macrofaunal abundance demonstrated no relationship. As the moisture content increased, the total biomass decreased. For instance, a sample with 85% water had a biomass of 0.54 g in contrast to a sample with 69% water and a biomass of 2.88 g. A linear regression analysis, however, showed values of moisture content did not influence changes in the total macrofaunal abundance ($R^2 = 0.00$, p-value = 0.889) or changes in log biomass ($R^2 = 0.045$, p-value = 0.164).

Initial weight remaining, on the other hand, significantly influenced changes in the values of total macrofaunal log abundance ($R^2 = 0.16$, p-value = 0.008) and macrofaunal log biomass ($R^2 = 0.21$, p-value < 0.01) (Table 4.2 & 4.3). The following regression equations can be used to determine (a) the total abundance and (b) biomass for a given percentage of initial dry weight:

$$(a) \text{ Log abundance} = 3.39 - 0.015 (\% \text{ of initial dry weight}),$$

$$(b) \text{ Log biomass} = 0.781 - 0.008 (\% \text{ initial dry weight}).$$

These equations indicate that the relationships are negative, where log biomass and log macrofaunal abundance decreased with increasing initial weight of *D. antarctica* remaining (Fig. 4.4 & 4.5). For example, a sample with 77% initial dry weight had 476 individuals (log abundance of 2.7) and a log biomass of 0.538. In comparison, a sample with only 62% of initial dry weight remaining had 882 individuals (log abundance of 2.9) and a log biomass of 0.969. Both relationships are, however, very weak as indicated by the low R^2 value of 16% for log abundance and 21% for log biomass (p-value <0.05).

Table 4.2 Linear regression analysis for macrofaunal log abundance as a response to initial weight remaining in kelp samples, on Victory Beach, 2008. Significant p-values are shown in bold.

Predictor	coef	S.E. coef	T	p-value
Constant	3.394	0.306	11.09	< 0.001
Initial dry weight	-0.015	0.005	-2.79	0.008

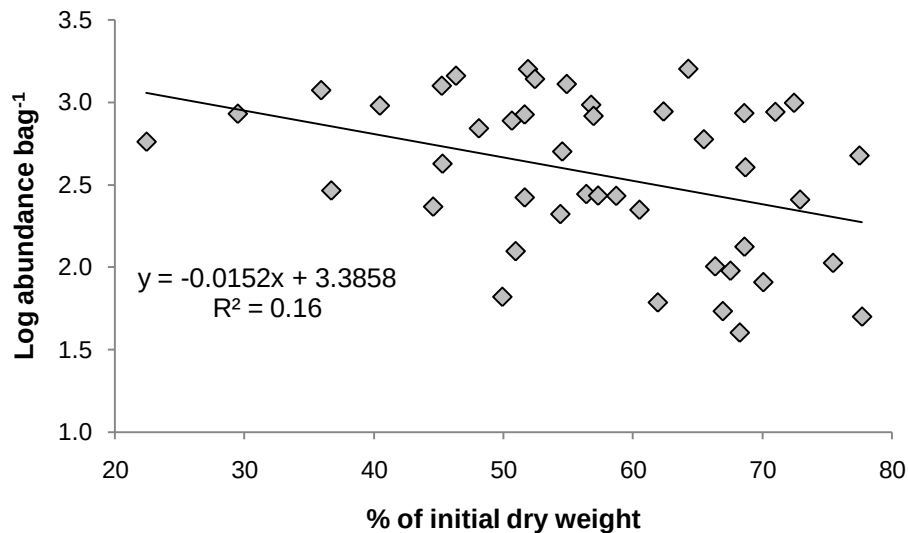


Figure 4.4 Relationship between the initial dry weight (%) of *Durvillaea antarctica* and macrofaunal log abundance associated with samples on Victory Beach, during autumn (n = 23) and winter 2008 (n = 21).

Table 4.3 Linear regression analysis for log biomass as a response to initial weight remaining in kelp samples, on Victory Beach, 2008. Significant p-values are shown in bold.

Predictor	coef	S.E. coef	T	p-value
Constant	0.781	0.142	5.5	< 0.001
Initial dry weight	-0.008	0.002	-3.32	0.002

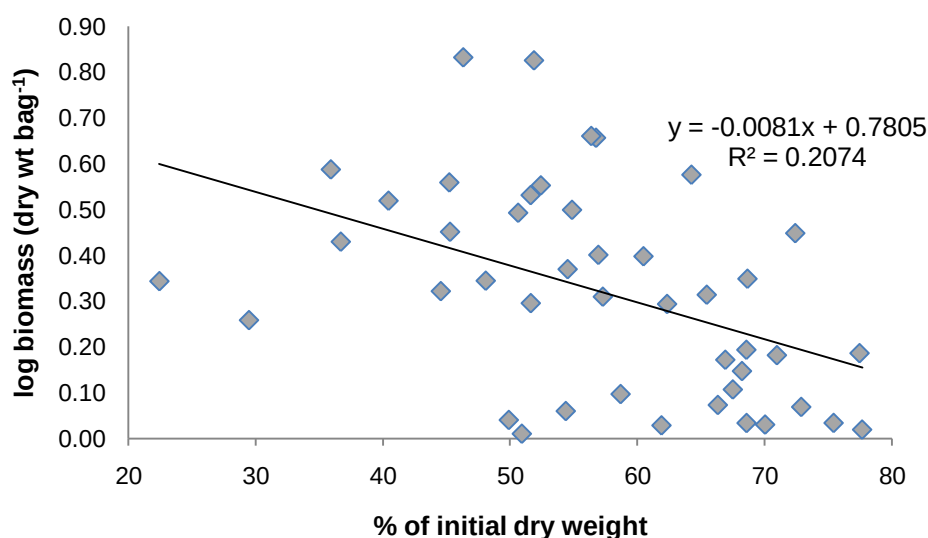


Figure 4.5 Relationship between the initial dry weight (%) of *Durvillaea antarctica* and log macrofaunal biomass associated with samples on Victory Beach, during autumn (n = 23) and winter (n = 21) 2008.

4.3.2 Organic content

The mean percentage of organic carbon in *D. antarctica* samples ranged between 22.1-34.5% in autumn and 23.0-33.1% in winter. The mean percentage of nitrogen ranged between 0.78-1.14% in autumn and 0.84-1.26% in winter. There was no significant difference between seasons or days of exposure for mean percentage of nitrogen (p-value > 0.05, see Appendix). Percentage of carbon did not vary between autumn and winter (F-value 0.78, p-value 0.383), but there was a significant interaction effect between seasons and days of exposure (F-value 2.89, p-value 0.029). The percentage of carbon was found to decrease as the time of exposure increased (F-value 14.24, p-value < 0.001) (Fig. 4.6). A post-hoc test on days of exposure as a factor showed no significant results, but the carbon content appeared to decrease gradually until day 10, when it then dropped more steeply from about 30% to about 25% at the end of the sampling period (Fig. 4.6).

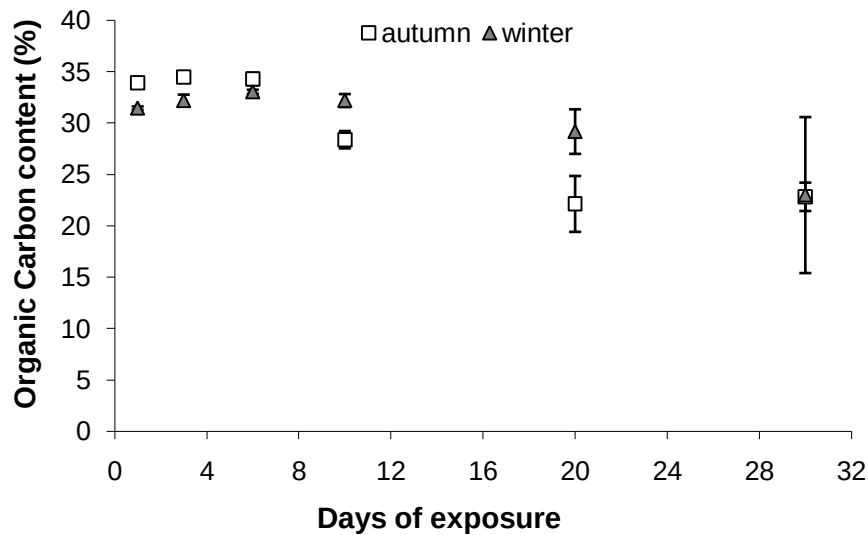


Figure 4.6 Changes in the mean percentage of organic carbon ($\pm$ S.E) over a 30-day period during autumn (day 1-20: n=4, day 30: n=3) and winter (day 1-10: n=4, day 20: n=3, day 30: n=2) on Victory Beach, on the Otago Peninsula

Ratio of carbon to nitrogen

The C:N ratio of stranded *D. antarctica* was not found to differ significantly between seasons or days of exposure (ANOVA: p-value > 0.05). A multiple regression analysis showed, however, that total macrofaunal abundance was influenced by changes in the values of C:N and the period of time the kelp had been stranded ($R^2 = 0.44$, p-value < 0.05), but not by the time of year sampling took place ($R^2 = 0.25$, p-value > 0.05) (Table 4.4).

The following regression equation can be used to determine the total number of individuals associated with samples of stranded *D. antarctica*:

$$\text{Log abundance} = 0.625 + 0.020 (\text{season}) + 0.153 (\text{day}) + 0.0480 (\text{C:N})$$

This relationship, however, is very weak as shown by the low R^2 value of 44%. The variable of interest for this study was the C:N of *D. antarctica*. Figure 4.7 depicts the linear relationship between C:N and the total macrofaunal abundance, where C:N increases with total macrofaunal abundance.

The total macrofaunal log biomass associated with samples of *D. antarctica* was not found to be influenced by changes in the C:N content of the kelp (R^2 -value 0.37, p-value = 0.599). It was, however, influenced by the time of year and the period of time the kelp had been stranded on the shore (R^2 -value 0.37, p-value < 0.05) (Table 4.5). The low R^2 value suggests that only 35% of the variance is explained by the regression equation (log biomass = $0.026 - 0.170(\text{season}) + 0.059(\text{day}) + 0.004(\text{C:N})$).

Table 4.4 Multiple regression analysis for macrofaunal log abundance as a response to seasons (autumn, winter), days of exposure (1, 3, 6, 10, 20, 30) and the C: N content in kelp samples on Victory Beach, 2008. Significant p-values are shown in bold.

Predictor	coef	S.E. coef	T	p-value
Constant	0.625	0.543	1.15	0.256
Season	0.020	0.116	0.17	0.864
Day	0.153	0.034	4.50	<0.001
C:N	0.048	0.015	3.14	0.003

Table 4.5 Multiple regression analysis for macrofaunal log biomass as a response to seasons (autumn, winter), days of exposure (1, 3, 6, 10, 20, 30) and the C:N content in kelp samples on Victory Beach, 2008. Significant p-values are shown in bold.

Predictor	coef	S.E. coef	T	p-value
Constant	0.256	0.275	0.93	0.357
Season	-0.167	0.059	-2.88	0.006
Day	0.059	0.017	3.44	0.001
C:N	0.004	0.008	0.53	0.599

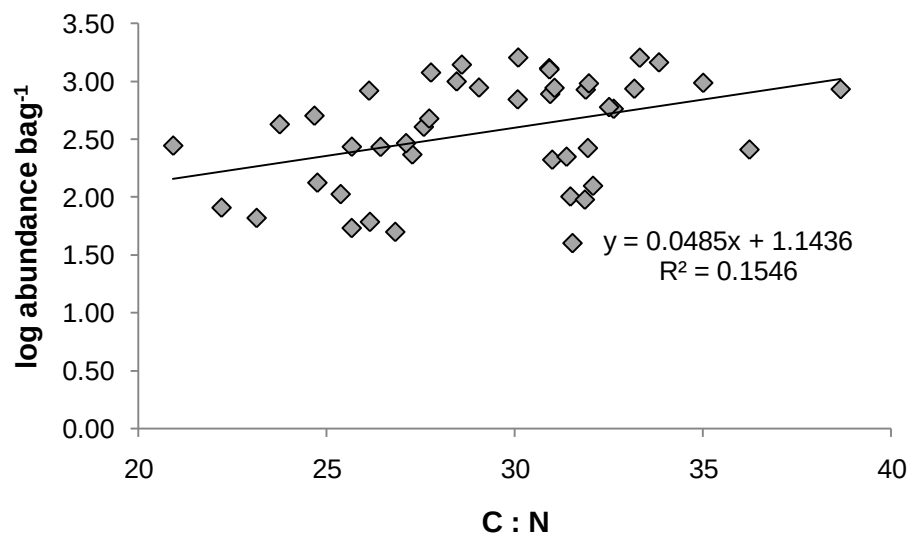


Figure 4.7 The relationship between the ratio of carbon to nitrogen and the total macrofauna abundance associated with samples of *D. antarctica* on Victory Beach, over a 30-day sampling period in autumn (n = 23) and winter (n = 21) 2008.

Relationship between organic matter and decomposition rate

The C:N ratio did not vary with changes in values of initial dry weight (%) ($R^2=0.045$, p -value= 0.167). Carbon and nitrogen content, however, showed a significant response to variations in initial dry weight of *D. antarctica*, where percentage of both carbon and nitrogen increased with increasing percentage of initial dry weight remaining (p -value <0.05) (Table 4.6 & 4.7). A sample with 75% initial weight remaining, for instance, had 31.5% carbon and 1.24% nitrogen; in contrast, a sample with only 36% initial dry weight remaining contained 20.1% and 0.74% respectively (Fig. 4.8 & Fig. 4.9). The following two equations can be used to estimate (a) percentage of carbon and (b) percentage of nitrogen:

$$(a) \text{ Carbon} = 22.42 + 0.137 (\text{initial dry weight}),$$

$$(b) \text{ Nitrogen} = 0.677 + 0.006 (\text{initial dry weight}).$$

These linear relationships, however, are very weak as the R^2 values for both nitrogen and carbon were less than 20% (Fig. 4.8 & 4.9).

Table 4.6 Linear regression analysis for the carbon content as a response to initial weight remaining in kelp samples, on Victory Beach, 2008. Significant p -values are shown in bold.

Predictor	coef	S.E. coef	T	p-value
Constant	22.424	3.314	6.77	< 0.001
Initial dry weight	0.137	0.057	2.42	0.021

Table 4.7 Linear regression analysis for the nitrogen content as a response to initial weight remaining in kelp samples, on Victory Beach, 2008. Significant p -values are shown in bold.

Predictor	coef	S.E. coef	T	p-value
Constant	0.677	0.121	5.62	< 0.001
Initial dry weight	0.006	0.002	3.11	0.003

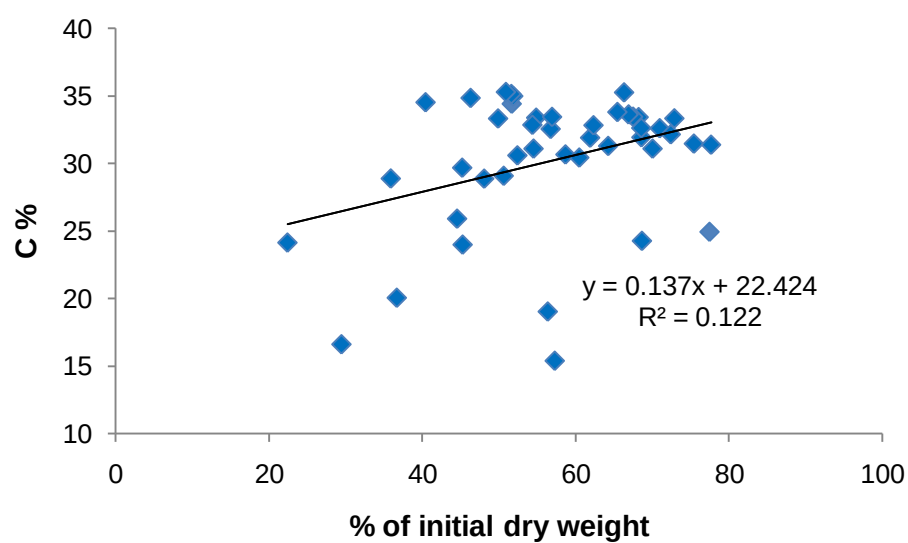


Figure 4.8 Relationship between organic carbon (%) content and the initial dry weight of *Durvillaea antarctica* remaining after a given amount of time stranded on Victory Beach (2008). R^2 values and regression equations are shown in bold beneath data plots.

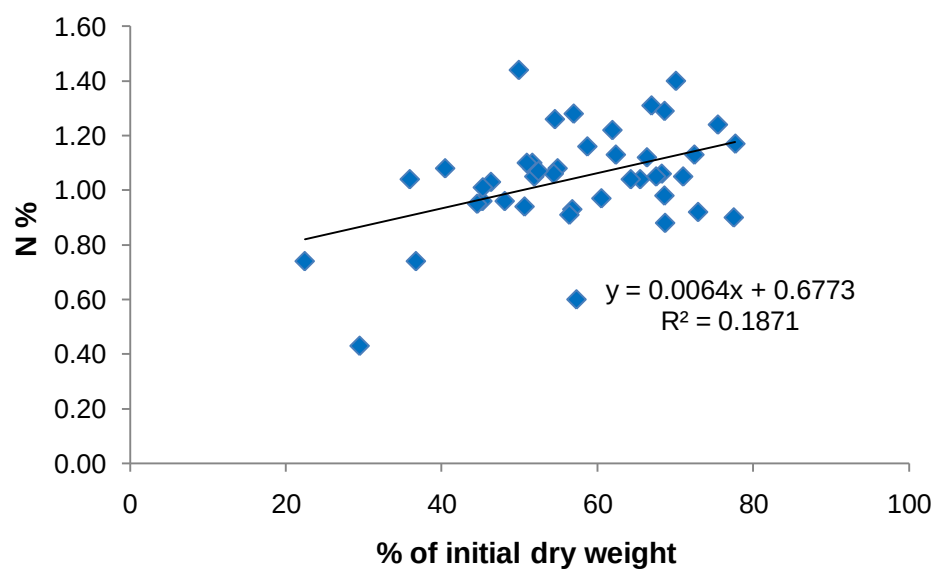


Figure 4.9 Relationship between organic nitrogen (%) content and the initial dry weight of *Durvillaea antarctica* remaining after a given amount of time stranded on Victory Beach (2008). R^2 values and regression equations are shown in bold beneath data plots.

4.4. Discussion

4.4.1. Kelp decomposition

The decomposition rate and the moisture content of *D. antarctica* stranded on an exposed sandy beach in southeastern New Zealand were found to decrease over 30-day sampling period and to differ between autumn and winter sampling. Percentage of initial dry weight remaining ranged between 42 - 67% in autumn and 55 - 71% in winter. *D. antarctica* reached 42% of initial dry weight within 20 days of sampling during autumn. Inglis (1989) has shown a similar decomposition rate for the brown kelp *Macrocystis pyrifera* where it reached 41% of its initial dry weight within 18 days of exposure on Pegasus Bay, a moderately exposed sandy beach on the east coast of New Zealand. The similarities in the rate of decomposition of stranded macroalgae between the present study and that of Inglis (1989) may be due to the fact that both studies were carried out during autumn and on the east coast of the South Island, New Zealand. Environmental conditions for the studies, including temperature, humidity and wind exposure were, therefore, similar.

Temperature affects the decomposition rate of stranded macrophytes, where higher temperatures result in a higher rate of decomposition (Hanisak, 1993; Mateo & Romero, 1996; Jedrzejczak, 2002a; Lastra *et al.*, 2008). For instance, *Zostera* stranded on sandy shores of Poland decomposed at a faster rate during spring/summer than during autumn/winter (Jedrzejczak, 2002a). Thus, on Hel Great Beach (one of the three beaches sampled) bags lost 34-100% of total biomass of *Zostera* in spring/summer and 12-71% in autumn/winter. The average air temperature was 12.4°C in autumn and 8.3°C in winter for the present study. Cooler temperatures in winter resulted in a slower decay rate and moisture loss than in autumn, hence the decomposition rate and moisture loss of *D. antarctica* on Victory Beach is influenced by temperature. Warmer temperatures may influence the decomposition rate of stranded kelp by subsequently increasing consumption rate of primary consumers. For instance, the talitrid amphipod *Talitrus saltator* consumed a greater amount of stranded *Saccorhiza polyschides* at 20°C and 15°C than at 10°C (Lastra *et al.* 2008). Warmer temperatures in autumn could have resulted in a faster feeding rate on *D. antarctica* by *Bellorchestia quoyana*. Future research needs to be carried out to determine if temperature directly affects the feeding rate of *B. quoyana* inhabiting Victory Beach.

Macrofaunal community

The decomposition of *D. antarctica* followed an approximately negative linear relationship, similar to that reported by Inglis (1989) for *M. pyrifera* in Pegasus Bay. Previous studies suggest that such linear rates of decomposition show that kelp is broken down by microorganism rather than by primary consumers (Inglis, 1989; Jedrzejczak, 2002a). If primary consumers accounted for the decomposition rate of stranded seaweed there would have been a rapid decline at the start of sampling (Griffiths & Stenton-Dozey, 1981) and a significant relationship between increased initial weight remaining and macrofaunal abundance and biomass. The macrofaunal community, however, was negatively correlated to the decomposition rate of *D. antarctica*. Fresh kelp (with a higher percentage of initial dry weight and higher water content) contained a lower macrofaunal abundance and biomass than older wrack (with a low water content and a lower amount of initial dry weight remaining). This suggests that the macrofaunal community on Victory Beach prefers older drier seaweed. This was unexpected as crustaceans were the main taxon associated with stranded *D. antarctica* and require moisture for their excretions (see Chapter 2) (MacIntyre, 1963).

The lack of a significant correlation between moisture content and macrofaunal abundance and biomass further suggests moisture content is not an important factor for the macrofaunal community associated with stranded kelp on Victory beach. Preference for older drier seaweed suggests that the presence of defense compounds could be more important than the moisture content of the stranded seaweeds for the macrofaunal community of Victory Beach. Defense compounds have been found to decrease significantly over time making the seaweed more palatable to consumers (Pennings *et al.*, 2000; Rothäusler & Thiel, 2006). For instance, the amphipod *Parhyalella ruffoi* preferred older samples of the kelp *Lessonia nigrescens* which had a reduced content of defense compounds (Rothäusler & Thiel, 2006). Defense compounds, however, do not always influence the consumption of macroalgae by consumers. For instance, fresh samples of *D. antarctica* were found to contain a phlorotannin concentration of 1.8% of dry weight, which did not influence the consumption rate of *D. antarctica* by the talitrid amphipod *Orchestoidea tuberculata* (Duarte *et al.*, 2010). Further research is required to determine if defense compounds influence the consumption rate of *D. antarctica* by the talitrid amphipod *B. quoyana*, a primary consumer on Victory Beach.

4.4.2 Organic content

The carbon content ranged between 22.1 - 34.5% in autumn and 23.0 - 33.1% in winter, while nitrogen content ranged between 0.78 - 1.14% in autumn and 0.84 - 1.26% in winter. These findings range within concentrations found for seaweeds in previous studies (Mateo & Romero, 1996; Poore & Steinberg, 1999; Pennings *et al.* 2000; Hemmi & Jormalainen, 2002). For instance, Poore & Steinberg (1999) sampled eight species of brown seaweeds and showed that carbon content ranged between 14 - 32% while nitrogen content ranged between 0.7 - 2.3% in fresh samples. The C:N ratio for *D. antarctica* ranged between 21 and 38 for both autumn and winter. These findings indicate a food source that is deficient (C:N > 20) in nitrogen (Barile *et al.*, 2004).

Percentage of organic carbon significantly differed between days of exposure, where it decreased over time. Percentage of nitrogen and the C:N ratio, however, did not differ significantly over time or between seasons. This was unexpected as previous research has shown the C:N ratio of brown seaweeds to change over time due to the increase in nitrogen within the samples resulting from bacterial nitrification (Rice & Tenore, 1981), or C:N decreases indirectly due to grazing on microorganisms by meiofaunal and macrofaunal species (Pascal *et al.*, 2008). In this 30-day study period there was no clear pattern in the ratio of C:N, which agrees with the findings of McLeod (unpublished data) who measured the C:N ratio of *D. antarctica* and *Ecklonia* on the upper shore of Warrington Beach, southeastern New Zealand, for a period of 16-22 days. The lack of significant differences in C:N ratio over time may be due to the short sampling period of both studies. The decomposition rate can vary from weeks to months depending on the species of macrophyte in question, and due to variations in bacterial activity between species (Enriquez *et al.*, 1993). Rossi & Underwood (2002) suggested that increasing length of time could produce a significant change in the kelps' characteristics and the associated macrofaunal assemblages.

Macrofaunal assemblage

The total macrofaunal abundance was affected by both the ratio of C:N and by the length of time the seaweed had been stranded. Total macrofaunal abundance increased with increasing C:N ratio. The positive correlation between macrofaunal abundance and C:N ratio indicates the macrofaunal community prefers an environment which is low in nitrogen and/or high in carbon. This was unexpected as previous research has shown herbivores to select nitrogen-

rich macroalgae (Yates & Peckol, 1993; Jiménez *et al.*, 1996; Cruz-Rivera & Hay, 2000; Barile *et al.*, 2004; Duarte *et al.*, 2010). Not all species prefer a nutrient-rich environment (Newell & Field, 1983; Bolam *et al.*, 2000; Jormalainen *et al.*, 2001; Rossi & Underwood, 2002; Rossi, 2003). For instance, the tube-building amphipod *Ampithoe longimana* did not discriminate between high and low quality food types. On the other hand the mobile, non-tube-building amphipods, *Gammarus mucronatus* and *Elasmopus levis*, preferred food sources that were high in protein, nitrogen and total carbon (Cruz-Rivera & Hay, 2000). The macrofaunal community on the upper shore of Victory Beach, therefore, depends on sources of available carbon rather than nitrogen.

The total macrofaunal biomass was not influenced by the C:N but rather by the time of year sampling took place and how long the kelp had been stranded. The lack of relationship between C:N ratio and macrofaunal biomass was unexpected because growth and/or reproduction are significantly influenced by the nutritional content of macroalgae (Duffy & Hay, 1991; Hemmi & Jormalainen, 2002; Barile *et al.*, 2004; Duarte *et al.*, 2010). For example, the talitrid amphipod *Orchestoidea tuberculata* was found to have a higher growth rate when fed on *D. antarctica*, containing the highest percentage of protein and carbohydrate content, than individuals fed on *Lessonia nigrescens* and *M. pyrifera* (Duarte *et al.*, 2010). Harriague & Albertelli (2007) have shown different aspects of the macrofaunal community to be influenced by different components of the organic matter. For instance, macrofaunal abundance was significantly influenced by the protein:carbohydrate ratio, whereas species richness and species numbers were significantly correlated to the protein content, carbohydrate content, phaeopigments and chlorophyll *a* concentration. In the present study, the significant relationship between macrofaunal biomass and the period of time the kelp had been stranded could be as a result of kelp components other than the ratio of C:N, such as the overall protein content, carbohydrate content or the concentration of defense compounds. Further research should investigate other kelp components mentioned and their relationships to macrofaunal abundance and biomass to determine if these factors influence macrofaunal assemblages on Victory Beach.

4.4.3 Relationship between organic content and decomposition rate

The percentage of carbon and nitrogen was significantly correlated to the amount of dry weight remaining. This suggests that as samples of stranded *D. antarctica* decompose there is a loss of nitrogen and carbon from the kelp. This agrees with previous research which has found significant correlations between the organic content and the amount of kelp remaining (Rice & Tenore, 1981; Enriquez *et al.*, 1993). For instance, Enriquez *et al.* (1993), who studied the decomposition rates of algae and plant species, found the decomposition rate to be strongly correlated with the nitrogen and phosphorus content, and weakly correlated with the concentration of carbon. In this study, the relationship between the dry weight remaining and the carbon and nitrogen content was very weak. The percentage of carbon and nitrogen decreased as the amount of kelp remaining decreased. These findings suggest that as the kelp decomposes it dries up and causes the cell contents, such as the organic matter, to be lost through leaching (Ochieng & Erftemeijer, 1999).

Summary

- Stranded kelp is an important food source for macrofaunal species on exposed shores.
- The decomposition rate and moisture loss of *D. antarctica* decreased over time and were slower during winter, suggesting temperature influences the decomposition of *D. antarctica*.
- The macrofaunal community on Victory Beach is not influenced by moisture content but by the C:N ratio and possibly by the presence of defense compounds in the stranded kelp.
- Percentage carbon varied temporally but not between seasons. The percentage of nitrogen did not differ between days of exposure or between seasons. Both nitrogen and carbon, however, were influenced by variations in the dry weight remaining, suggesting that organic matter is lost through leaching.
- The C:N ratio did not change significantly over time or between seasons possibly due to the short 30-day sampling period.

Chapter 5 General Discussion



Victory Beach, a southern New Zealand exposed sandy beach (author's photo).

5.1 The role of stranded *Durvillaea antarctica*

In temperate regions, food webs of exposed sandy shore have been found to be supported by marine subsidies (Brown & McLachlan, 1990; Dugan *et al.*, 2003; Colombini & Chelazzi., 2003; Lastra *et al.*, 2008). Stranded *D. antarctica* in the present study is shown to be ecologically important to marine and terrestrial macroinvertebrate species on the upper shore of Victory Beach, an exposed sandy beach on the southeastern coast of New Zealand. Twelve taxa of invertebrates were identified (to the lowest taxonomic level possible) on samples of *D. antarctica*, four of which were significantly abundant throughout a 30-day sampling period in autumn and winter, namely Talitridae, Staphylinidae, other Coleoptera, and Diptera. Within a day of being stranded the kelp was colonized by these four major taxonomic groups, and the talitrid amphipod *Bellorchestia quoyana* was identified as the most common macrofaunal invertebrate in terms of abundance and biomass. Overall, the percentage abundance of *B. quoyana* was at least 5 times higher, and its percentage biomass was at least 12 times higher than the percentage abundance and biomass of Staphylinidae, other Coleoptera and Diptera (see Fig. 5.1).

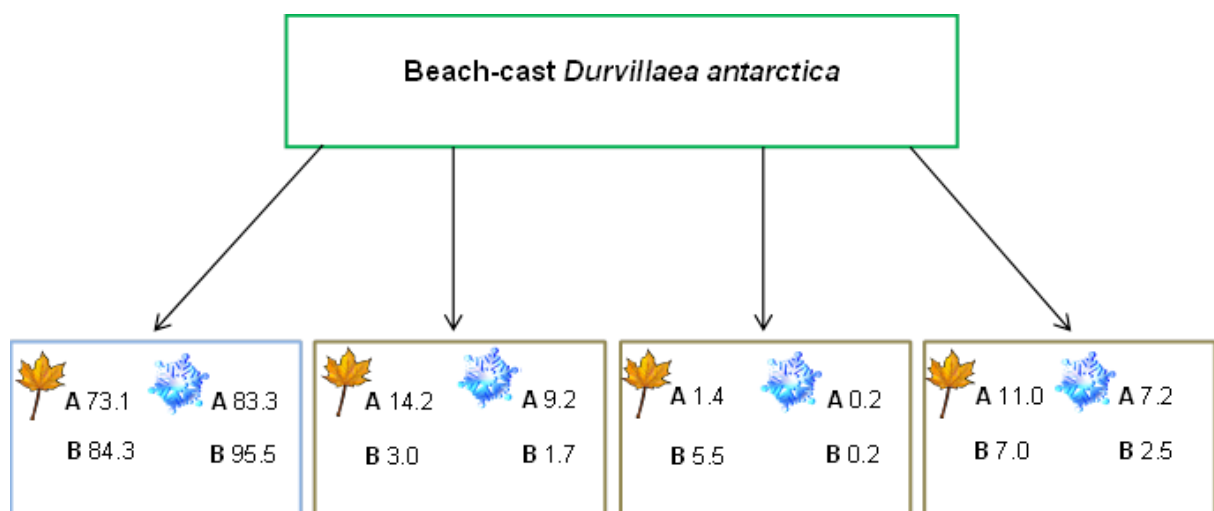


Figure 5.1 Summarised findings of the mean percentage abundance (A) and mean percentage biomass (B) of the four major taxonomic groups found within samples of stranded *D. antarctica* over a 30 day sampling period on the upper shore of Victory Beach. Autumn findings are represented by a leaf and winter findings by a snowflake.

Bellorchestia quoyana is a common sandhopper found on the upper shore of New Zealand sandy beaches (Morton & Miller, 1968; Inglis 1989). It is a primary consumer of stranded

detritus (MacIntyre, 1963; Inglis, 1989; Jedrzejczak, 2002b; Lastra *et al.*, 2008) and its distribution is closely associated with beach-cast macrophytes (Marsden, 1991a). For instance, on Pegasus Bay (Canterbury, New Zealand) *B. quoyana* was more abundant in core samples associated with *Macrocystis pyrifera* (437.1 individuals m⁻²) than in bare sand (15.3 individuals m⁻²). Similarly, the present study showed *B. quoyana* dominated sediment samples where its abundance was 3-74 times higher directly beneath the kelp, 3-16 times higher at 0.5 m and 1-27 times higher at 1 m, than the mean abundance of Coleoptera, Diptera and Isopoda. Overall, *B. quoyana* preferred to burrow in sediments directly under stranded kelp. Its abundance in sediments directly under *D. antarctica* was at least 1.2 times higher than that found in bare sediment (refer to Fig. 5.2).

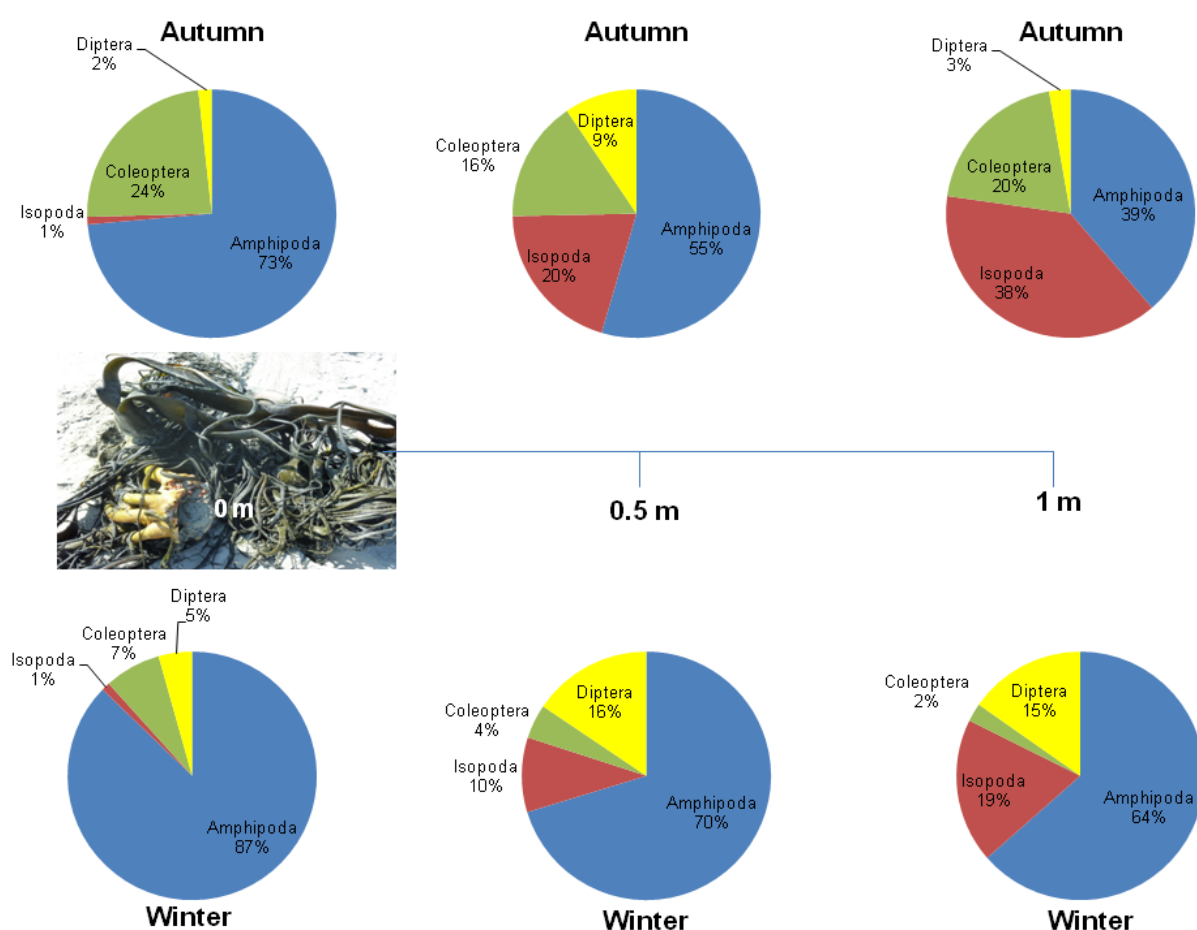


Figure 5.2 Summarised findings of the overall mean percentage core abundance of the four major taxonomic groups at 0, 0.5 and 1 metre from samples of *D. antarctica* during a 30-day sampling period on the upper shore of Victory Beach.

The presence of circular holes with a diameter of 1-5mm in seaweed can be used to identify whether talitrid amphipods feed on stranded macrophytes (Inglis, 1989; Jedrzejczak, 2002b). On a sandy beach off the coast of Poland, for instance, *Zostera marina* had an abundance of circular holes in coarse mesh bags where *Talitrus saltator* was present in high numbers, whereas circular holes were absent on *Z. marina* in small sized mesh (0.05 mm and 0.48µm) which had a low abundance of *T. saltator* (Jedrzejczak, 2002b). Similar holes were identified in aged samples of *D. antarctica* suggesting *B. quoyana* is a dominant consumer of *D. antarctica* on Victory Beach. Adult and juvenile distribution in the present study suggests different age groups are influenced by different factors. For instance, adults were influenced by the presence of stranded *D. antarctica*, whereby their abundance decreased with increasing distance from the primary food source. Abundance of juveniles in sediments, on the other hand, varied between seasons and the length of time the kelp had been stranded. Juveniles were most abundant in winter and their abundance peaked within 10 days of sampling and then appeared to decrease as the kelp progressively decayed. These findings are at odds with a study by Marsden (1991b) who found juvenile recruitment of *B. quoyana* to occur year round, except in winter. Higher juvenile abundance in the present study may instead reflect the vertical distribution of juveniles. For instance, Marsden (1991a) found the distribution of juveniles to differ between seasons. In autumn juveniles were concentrated between 10-15 m from the dunes but only 3-10 m from the dunes in winter. The sample sites in the present study were set 3 m away from the dunes, hence, lower abundances of juveniles in autumn were possibly due to the seaward movement of juveniles.

In the present study, adult and juvenile abundance within kelp did not differ significantly between seasons but adult biomass was significantly higher in autumn than winter. The average biomass of Staphylinidae and Diptera was also significantly higher in autumn than winter, suggesting individuals have a faster growth rate during autumn (see Fig. 5.1). Previous research has shown seasonal variations in wrack input to influence seasonal differences in macrofaunal assemblages (Griffiths & Stenton-Dozey, 1981; Behbehani & Croker, 1982; Ince *et al.*, 2007; Olabarria *et al.*, 2007; Garrido *et al.*, 2008). In the present study, the amount of wrack was kept consistent across seasons suggesting other factors, such as environmental variables, are affecting the biomass of amphipods, staphylinid and dipteran species. Previous research has shown temperature to influence the feeding rate and growth rate of macrofaunal species, such as the talitrid amphipod *T. saltator* (Marques *et al.*, 2003; Lastra *et al.*, 2008). The mean autumn temperature was 12.4°C and mean winter temperature was 8.3°C for the

present study. The higher biomass of adult amphipods in autumn on Victory Beach suggests individuals grow faster in autumn than in winter. Future research needs to examine the influence of temperature on feeding rates and growth rates of wrack-associated macrofauna to determine its impact on the growth rate of macrofaunal species within New Zealand sandy beaches.

5.2 Chemical composition of *D. antarctica*

Stranded macrophytes act as a source of nutrients (such as, carbon, nitrogen and phosphorus) (Rice & Tenore, 1981; Poore & Steinberg, 1999; Rossi & Underwood, 2002; Mateo, 2010; Olabarria *et al.*, 2010) for primary consumers on sandy shores (Chown, 1996; Pennings *et al.*, 2000; Hemmi & Jormalainen, 2002; Lastra *et al.*, 2008). The nutritional value of a kelp species can be measured by the content of carbon, nitrogen and the C: N ratio. The percentage of carbon and the percentage of nitrogen for *D. antarctica* ranged between 0.78-1.26% and 22-35% respectively. This agrees with previous research where the percentage of nitrogen ranged between 0.72-2.13% for nine species of stranded macrophytes on the Pacific Northwest of North America (Pennings *et al.*, 2000). Also, Hemmi & Jormalainen (2002) tested the nutritional value of apical and basal sections of the brown alga *Fucus vesiculosus* off the southwest coast of Finland and found a mean carbon content of 35.9-36.3% (apical section) and 36.3-37.3% (basal section), and mean nitrogen content of 2.01-2.06% (apical section) and 1.32-1.33% (basal section); whilst the litter of the seagrass *Posidonia oceanica* planted in a subtidal zone off the coast of Spain had a mean carbon content of 30.5-31.8% and mean nitrogen content of 0.73-0.85% (Mateo & Romero, 1996)

The C:N ratio ranged between 21 and 38 for both autumn and winter sampling. These findings agree with previous research (Rice & Tenore, 1981; Poore & Steinberg, 1999; Pennings *et al.*, 2000; McLeod, unpublished data). For instance, the mean C:N ratio for fresh and aged *D. antarctica* was 48 and 47, respectively, and 21 and 28 for fresh and aged samples of *Ecklonia* during a sampling period of 16-22 days on Warrington Beach, southeastern New Zealand (McLeod, unpublished data). Similar to this study, McLeod (unpublished data) found that the C:N ratio was not significantly different between days of exposure, which may be due to the short sampling period of 30 days or less. The C:N ratio was positively correlated to the total macrofaunal abundance ($R^2 = 0.44$, $p\text{-value} < 0.05$), where macrofaunal abundance

increased as the carbon content increased and the nitrogen content decreased, suggesting the macrofaunal community on Victory Beach prefer a food source rich in carbon rather than nitrogen. This agrees with previous research on the amphipod *Peramphithoe parmerong* (Poore & Steinberg, 1999), *Melagorchestia californiana* and *Traskorchestia traskiana*, and the isopod *Ligia pallasii* (Pennings *et al.*, 2000), where these herbivores did not show a preference for a nitrogen-rich food. These herbivores select plant hosts based on the content of defence compounds, where decreased concentrations make the wrack more palatable (Poore & Steinberg, 1999; Pennings *et al.*, 2000). The macrofaunal community associated with stranded *D. antarctica* increased with decreasing amount of kelp remaining suggesting that they prefer aged kelp over fresh. It is recommended that future research investigates the content of defence compounds in fresh and aged kelp samples to determine whether it influences macrofaunal assemblages associated with stranded *D. antarctica*, on New Zealand sandy shores.

5.3 Implications of findings

The presence of both marine and terrestrial taxa, such as staphylinid, coleopteran and dipteran species, within this study demonstrates the importance of *D. antarctica* in the marine-terrestrial interface. The low number of individuals and the low biomass seen in early stages of decomposition suggest *D. antarctica* is used as a shelter at the beginning of decomposition, but as the decomposition rate increases (hence, the less initial weight remaining) the kelp is likely used as a food source by the macrofauna of Victory Beach. The staphylinids *Blediotrogus guttiger* and *Macralymma punctiventre* colonised *D. antarctica* and were present throughout the 30-day sampling period in autumn and winter, where their mean abundance was 14% and 9% of total abundance respectively (Fig. 5.1). Both staphylinid species are known to feed on decaying material in terrestrial and marine habitats, and *M. punctiventre* also preys on other invertebrates (Klimaszewski *et al.*, 1996). Both species of staphylinids were rarely found in sediment samples within the upper shore of Victory Beach. For instance, Staphylinidae made up 29% of total coleopteran abundance for pooled samples. The majority of Coleoptera consisted of *Chaerodes trachyscelides* which comprised 59% of total coleopteran abundance. The difference in abundance in sediment samples could be explained by the different morphologies between these two taxonomic groups. *Chaerodes trachyscelides*

is a tenebrionid beetle highly specialized for burrowing in sand (Harris, 1991), whereas staphylinid species lack obvious adaptations for sand-burrowing (Harris, pers. comm., 2009).

Harvesting of seaweed

The results of the present study show the importance of washed-up wrack for invertebrate communities in terms of shelter and as a food source. Harvesting and/or beach cleaning could, therefore, significantly depress species richness and abundance on New Zealand sandy shores. Seaweeds are harvested for multiple reasons, such as: pharmaceuticals, agricultural products, for food and agar production (Chapman & Chapman, 1980). In some areas, mainly highly populated beaches in the North Island of New Zealand, cast-up seaweeds are removed for aesthetic purposes (beach grooming) (Zemke-White *et al.*, 2005). In New Zealand, commercial harvesting of beach-cast seaweed started in the 1940s when the supply of agar from Japan ceased (Schiel & Nelson, 1990). Since then, it has been used by mussel farmers, paua farmers, for fertilizers and still for agar extraction (Schiel & Nelson, 1990; Zemke-White *et al.*, 2005). The Ministry of Fisheries established fishing permits for the collection of attached seaweeds (since 1971) (Luxton & Courtney, 1987) and for unattached free-floating seaweeds (since 1996), but not for the collection of beach-cast seaweed due to the long-established industry of agar production (Hurd *et al.*, 2004). The collection of beach-cast seaweed was restricted to certain areas until 2009 when the Ministry of Fisheries extended the allowable area for harvest (www.fish.govt.nz/en-nz, accessed October 2010).

Brown & McLachlan (2002), in a review of threats faced by sandy shores, concluded that beach cleaning was likely to have a detrimental effect on the ecosystem due to the importance of stranded kelp in the food web, especially on exposed shores where primary productivity may be limited. Previous studies have shown the negative impact of the removal of stranded kelp (grooming) on the species richness, abundance and biomass of meiofaunal and macrofaunal communities (Lavery *et al.* 1999; Dugan *et al.*, 2003; Malm *et al.*, 2004; De La Huz *et al.*, 2005; Gheskiere *et al.*, 2006; Deidun *et al.*, 2009). For instance, a study based on 15 exposed sandy beaches on the southern Californian coast found the removal of stranded macrophytes to significantly depress the diversity, abundance and biomass of macrofaunal species (Dugan *et al.*, 2003). Deidun *et al.* (2009) found different macrofaunal species respond to the removal of kelp in different ways. For instance, in a study on three groomed and three ungroomed beaches on the Maltese Islands, the amphipod *Orchestia stephensi* had a similar abundance in groomed and ungroomed sites, whereas Staphylinidae and the

grastropod *Truncatella subcylindrica* were abundant on ungroomed beaches, but absent on groomed beaches. Like other talitrid amphipods, *O. stephensi* is capable of burrowing up to a depth of 10 cm within sand (Deidun *et al.*, 2009). As previously mentioned, staphylinids were abundant within *D. antarctica* but not in sediment samples due to the lack of specialised burrowing mechanisms. Therefore, the harvesting of beach-cast seaweed on New Zealand shores poses a greater threat to the survival of some macrofaunal species as they have no means of avoiding the process by which beach-cast seaweed is removed.

Species occupying the upper shore are considered most affected by the removal of stranded seaweed, especially talitrid amphipods which rely on kelp for food and shelter (Brown & McLachlan, 2002; Dugan *et al.*, 2003; Lastra *et al.*, 2008). As previously mentioned, in the present study stranded *D. antarctica* directly enhanced the abundance of the talitrid amphipod and Coleoptera within sand. Avian predators forage on stranded macrophytes and their associated macroinvertebrate species (Dugan *et al.*, 2000; Dugan *et al.*, 2003; Speybroeck *et al.*, 2008). For instance, the abundance of two plover species *Pluvialis squatarola* and *Charadrius alexandrinus nivosus* were positively correlated to the abundance and species richness of wrack-associated macrofauna across 15 beaches off the Californian Coast (Dugan *et al.*, 2003). It is, therefore, important to expand research concerning the ecological impact of beach-cast seaweed on the abundance of primary as well as secondary consumers within New Zealand's upper shores, as any increase in harvesting has the potential to negatively affect native species higher up the food chain, such as the tui (*Prosthemadera novaeseelandiae*) and the Auckland banded dotterel (*Charadrius bicinctus exilis*) which are known to feed on wrack-associated macroinvertebrates (Pierce, 1980; Daniel, 1982).

5.4 Limitations

Isopods were rarely found within *D. antarctica* and their abundance within sediments appeared to increase with increasing distance from the source of food. Previous related studies have also found isopods to be lacking as a common taxonomic group associated with stranded macrophytes on the upper shore (Griffiths & Stenton-Dozey, 1981; Inglis 1989; Jędrzejczak, 2002b). These studies focused on the macrofaunal colonisation of wrack over time, and used a given wet weight (0.5– 1 kg) of kelp within each sample bag, similar to the 1 kg wet weight of *D. antarctica* used for the present study. Other studies, however, that investigated the

relationship of wrack patch size and macrofaunal abundance and biomass, showed isopods to be a dominant taxon (Colombini *et al.*, 2000; Dugan *et al.*, 2003; Ince *et al.*, 2007; Olabarria *et al.*, 2007). For instance, the isopod *T. europaeus* made up 1.4% of the total macrofaunal community (across all patch sizes [1 kg, 3 kg and 5 kg] and sites) associated with wrack on an exposed beach in Spain (Olabarria *et al.*, 2007). The sample size used for this study is considered a small patch size which would cover an area of 0.09 m² (Olabarria *et al.*, 2007). As previously mentioned, macrofaunal communities are controlled by the amount of wrack available, where high macrofaunal densities are supported by high macrophyte biomass (Lavery *et al.* 1999; Dugan *et al.*, 2003; Malm *et al.*, 2004; De La Huz *et al.*, 2005; Gheskiere *et al.*, 2006; Deidun *et al.*, 2009). The absence of isopods in samples of *D. antarctica* within the present study may be due to the sample size. Future studies should therefore aim to test the effect of patch size on the abundance and biomass of macrofaunal species within New Zealand sandy shores, further emphasizing the need to control the amount of kelp harvested within New Zealand.

An alternative explanation for the low abundance of isopods on the upper shore of Victory Beach may be the variable activity patterns demonstrated by different species. Activity patterns differ between species as a response to humidity, sand temperature, sand moisture (Fallaci *et al.*, 1999; Jaramillo *et al.*, 2003), circadian rhythm, moon phases and tidal fluctuations (Fallaci *et al.*, 1996; Colombini *et al.*, 2000; Yannicelli *et al.*, 2001; Jaramillo *et al.*, 2003; Lastra *et al.*, 2010). Isopods are nocturnal scavengers, actively foraging on stranded wrack and other macroinvertebrates at night (Fallaci *et al.*, 1996; Jaramillo *et al.*, 2003). For instance, *T. europaeus* is highly active between 1800 - 0600 h, and in summer months its mean daily activity peaks at 2200 h (Fallaci *et al.*, 1996). Sampling for the present study was limited to daylight hours, therefore the abundance and biomass of species that forage at night, such as isopods, were perhaps not adequately assessed.

5.5 Conclusions and future recommendations

This research investigated the chemical composition and colonisation of stranded *D. antarctica* by macrofaunal species on the upper shore of Victory Beach, an exposed sandy beach on the southeast coast of New Zealand. The presence of *D. antarctica* enhanced the abundance of some species (the common sandhopper *B. quoyana* and Staphylinidae) but not others (Diptera and Isopoda), suggesting some taxonomic groups are more vulnerable to the

removal of wrack than others. A recommendation for future study is to carry out sampling during both night and day to take into account different activity levels of different macrofaunal species, as stranded *D. antarctica* could be inhabited by different species depending on time of day.

Meiofauna inhabiting the upper shore are also important colonisers of stranded kelp (Behbehani & Croker, 1982; Inglis, 1989; Jędrzejczak, 2002b). For instance, the meiofaunal community associated with stranded *M. pyrifera* on the upper shore of Pegasus Bay (Canterbury, New Zealand) comprised nematodes (85%), Acarina (5.7%), dipteran larvae (4.8%), enchytraeid oligochaetes (2.9%) and Collembola (1.4%) (Inglis, 1989). The present study focused on the influence of stranded kelp on the abundance and biomass of wrack-associated macrofauna, hence the holes within the mesh bags (1 cm x 1 cm) were too large to capture meiofaunal species. A future recommendation is to use mesh size (e.g. 48µm) that allow meiofaunal species to remain in samples when kelp-associated fauna is extracted, so that their abundance can be quantified.

Beach grooming and/or seaweed harvesting has been implicated as one of the main management concerns for the future of the ecology of sandy shores (Brown & McLachlan, 2002). Wrack is important to macrofaunal and meiofaunal species throughout the intertidal zone (Marsden, 1990a; Dugan *et al.*, 2003; Rodriguez *et al.*, 2003; Harriague *et al.*, 2006), including the supralittoral zone where the marine-terrestrial boundary lies (Griffiths & Stenton-Dozey, 1981; Inglis, 1989; Jędrzejczak, 2002b; Olabarria *et al.*, 2007). Publications concerning the role of stranded wrack on macrofaunal species within New Zealand sandy shores are limited to those of Inglis (1989) and Marsden (1991a). Kirkman & Kendrick (1997) stated that understanding the ecological significance of beach-cast seaweed in sandy beach food webs is essential for determining the effects of its removal on the community structure of associated fauna, especially for native New Zealand bird and reptiles which are under threat (Kirkman & Kendrick, 1997). The present study contributes to the available information on the significant role of stranded seaweed in sandy shore foodwebs.

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Appendix

Table A.1. Summary of three-way ANOVA analysis for total macrofauna abundance and total macrofaunal biomass, considering the effects of season (autumn and winter), days of exposure (day 1, 3, 6, 10, 20 and 30), and species as factors. Significant results are indicated by bold p-values. df- degrees of freedom; MS- Mean Square

	Source	df	MS	F-value	p-value
Total macrofauna abundance (ind bag⁻¹)	Season (A)	1	0.67	3.68	0.057
	Day (B)	5	2.909	15.98	< 0.001
	Species (C)	3	30.415	167.05	<0.001
	A x B	5	0.122	0.67	0.647
	A x C	3	0.336	1.84	0.142
	B x C	15	0.583	3.2	<0.001
	A x B x C	15	0.374	2.05	0.016
Total macrofauna biomass (dry wt bag⁻¹)	Season (A)	1	0.102	11.39	0.001
	Day (B)	5	0.039	4.41	0.001
	Species (C)	3	0.846	94.86	<0.001
	A x B	5	0.014	1.55	0.178
	A x C	3	0.027	3.04	0.031
	B x C	15	0.025	2.8	0.001
	A x B x C	15	0.027	3.07	<0.001

Table A.2. Summary of two-way ANOVA analysis for individual faunal abundance, and adult and juvenile amphipod responses, considering the effects of season (autumn and winter) and days of exposure (day 1, 3, 6, 10, 20 and 30) as factors. Significant results are indicated by bold p-values. df- degrees of freedom; MS- Mean Square

	Source	df	MS	F-value	p-value
Amphipoda abundance (ind bag⁻¹)	Season (A)	1	11952	0.08	0.773
	Day (B)	5	436654	3.09	0.022
	A x B	5	376285	2.66	0.04
Adult abundance (ind bag⁻¹)	Season (A)	1	0.712	1.02	0.319
	Day (B)	5	4.493	6.46	< 0.001
	A x B	5	2.269	3.26	0.017
Juvenile abundance (ind bag⁻¹)	Season (A)	1	1.848	1.46	0.236
	Day (B)	5	9.313	7.35	< 0.001
	A x B	5	3.301	2.60	0.044
Staphylinidae abundance (ind bag⁻¹)	Season (A)	1	0.049	0.16	0.69
	Day (B)	5	2.835	9.39	<0.001
	A x B	5	0.104	0.34	0.882
other Coleoptera abundance (ind bag⁻¹)	Season (A)	1	768.8	2.54	0.12
	Day (B)	5	268.7	0.89	0.5
	A x B	5	256.1	0.85	0.526
Diptera abundance (ind bag⁻¹)	Season (A)	1	0.088	0.49	0.488
	Day (B)	5	0.369	2.07	0.096
	A x B	5	0.464	2.6	0.044

Table A.3. Summary of two-way ANOVA analysis for individual faunal biomass, and adult and juvenile amphipod responses, considering the effects of season (autumn and winter) and days of exposure (day 1, 3, 6, 10, 20 and 30) as factors. Significant results are indicated by bold p-values. df- degrees of freedom; MS- Mean Square.

	Source	df	MS	F-value	p-value
Amphipoda biomass (g dry wt bag⁻¹)	Season (A)	1	0.162	5.64	0.024
	Day (B)	5	0.104	3.63	0.01
	A x B	5	0.087	3.04	0.023
Adult biomass (g dry wt bag⁻¹)	Season (A)	1	0.266	10.52	0.003
	Day (B)	5	0.069	2.74	0.036
	A x B	5	0.057	2.27	0.071
Juvenile biomass (g dry wt bag⁻¹)	Season (A)	1	0.006	0.71	0.405
	Day (B)	5	0.02	2.5	0.051
	A x B	5	0.026	3.29	0.017
Staphylinidae biomass (g dry wt bag⁻¹)	Season (A)	1	0.002	4.24	0.048
	Day (B)	5	0.001	2.56	0.044
	A x B	5	<0.001	0.43	0.825
other Coleoptera biomass (g dry wt bag⁻¹)	Season (A)	1	0.124	2.01	0.166
	Day (B)	5	0.046	0.74	0.599
	A x B	5	0.046	0.75	0.595
Diptera biomass (dry wt bag⁻¹)	Season (A)	1	0.008	4.23	0.048
	Day (B)	5	0.005	2.82	0.032
	A x B	5	0.005	2.58	0.045

Table A.4. Summary of three-way ANOVA analysis for total macrofauna, adult and juvenile amphipod and individual faunal responses, considering the effects of season (autumn and winter), days of exposure (day 1, 3, 6, 10, 20 and 30), and core samples (0, 0.5 and 1 meter) as factors. Significant results are indicated by bold p-values. df-degrees of freedom; MS- Mean Square.

	Source	df	MS	F-value	p-value
Macrofaunal abundance (ind core⁻¹ (78.5cm²))	Season (A)	1	0.022	0.17	0.681
	Day (B)	5	0.294	2.27	0.054
	Core (C)	2	5.985	46.13	<0.001
	A x B	5	0.225	1.74	0.134
	A x C	2	0.059	0.45	0.636
	B x C	10	0.169	1.31	0.238
	A x B x C	10	0.087	0.67	0.747
Amphipoda abundance (ind core⁻¹ (78.5cm²))	Season (A)	1	0.631	0.55	0.461
	Day (B)	5	0.383	3.35	0.008
	Core (C)	2	6.554	57.33	<0.001
	A x B	5	0.151	1.32	0.262
	A x C	2	0.05	0.44	0.649
	B x C	10	0.231	2.02	0.039
	A x B x C	10	0.098	0.86	0.574

Table A.4 contd.

	Source	df	MS	F-value	p-value
Adult abundance (ind core⁻¹ (78.5cm²))	Season (A)	1	0.039	0.53	0.465
	Day (B)	5	0.14	1.92	0.098
	Core (C)	2	8.402	114.91	<0.001
	A x B	5	0.059	0.81	0.543
	A x C	2	0.053	0.73	0.487
	B x C	10	0.204	2.80	0.004
	A x B x C	10	0.146	1.99	0.042
Juvenile abundance (ind core⁻¹ (78.5cm²))	Season (A)	1	0.532	5.74	0.019
	Day (B)	5	0.337	3.63	0.005
	Core (C)	2	0.283	3.05	0.052
	A x B	5	0.096	1.03	0.403
	A x C	2	0.271	2.92	0.059
	B x C	10	0.086	0.93	0.511
	A x B x C	10	0.027	0.29	0.981
Coleoptera abundance (ind core⁻¹ (78.5cm²))	Season (A)	1	0.385	6.92	0.01
	Day (B)	5	0.078	1.40	0.231
	Core (C)	2	1.01	18.15	<0.001
	A x B	5	0.029	0.53	0.753
	A x C	2	0.058	1.05	0.355
	B x C	10	0.093	1.68	0.097
	A x B x C	10	0.05	0.89	0.542
Diptera abundance (ind core⁻¹ (785cm³))	Season (A)	1	0.015	0.56	0.456
	Day (B)	5	0.034	1.30	0.271
	Core (C)	2	0.06	2.26	0.11
	A x B	5	0.054	2.02	0.082
	A x C	2	0.017	0.64	0.532
	B x C	10	0.02	0.76	0.669
	A x B x C	10	0.011	0.43	0.929
Isopoda abundance (ind core⁻¹ (785cm³))	Season (A)	1	0.095	2.56	0.113
	Day (B)	5	0.029	0.77	0.571
	Core (C)	2	0.47	1.26	0.288
	A x B	5	0.004	0.11	0.99
	A x C	2	0.014	0.38	0.684
	B x C	10	0.017	0.46	0.914
	A x B x C	10	0.011	0.29	0.981

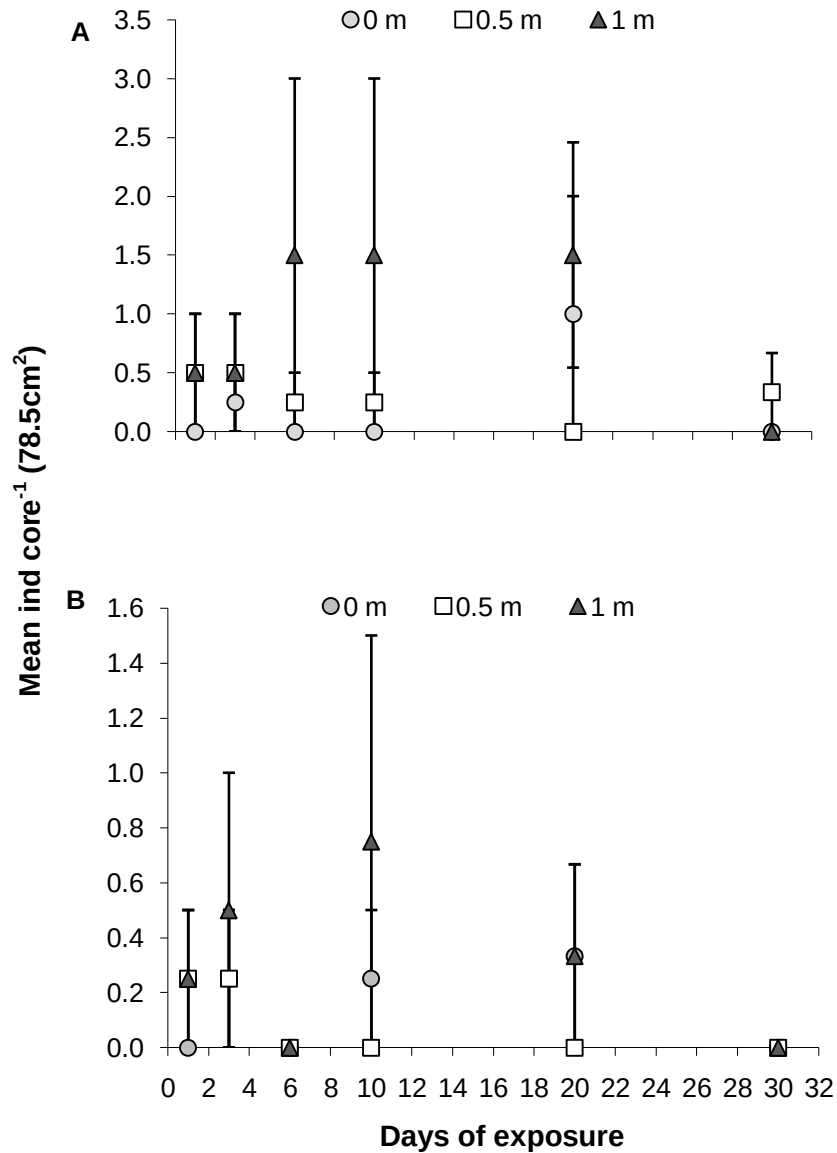


Figure A.1. Mean Isopoda abundance ($\pm$ S.E) per core sample (78.5 cm²) taken at 0, 0.5 and 1 m intervals from washed up *Durvillaea antarctica* during (A) autumn (day 1-20, n=4; day 30, n=3) and (B) winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach, Otago Peninsula.

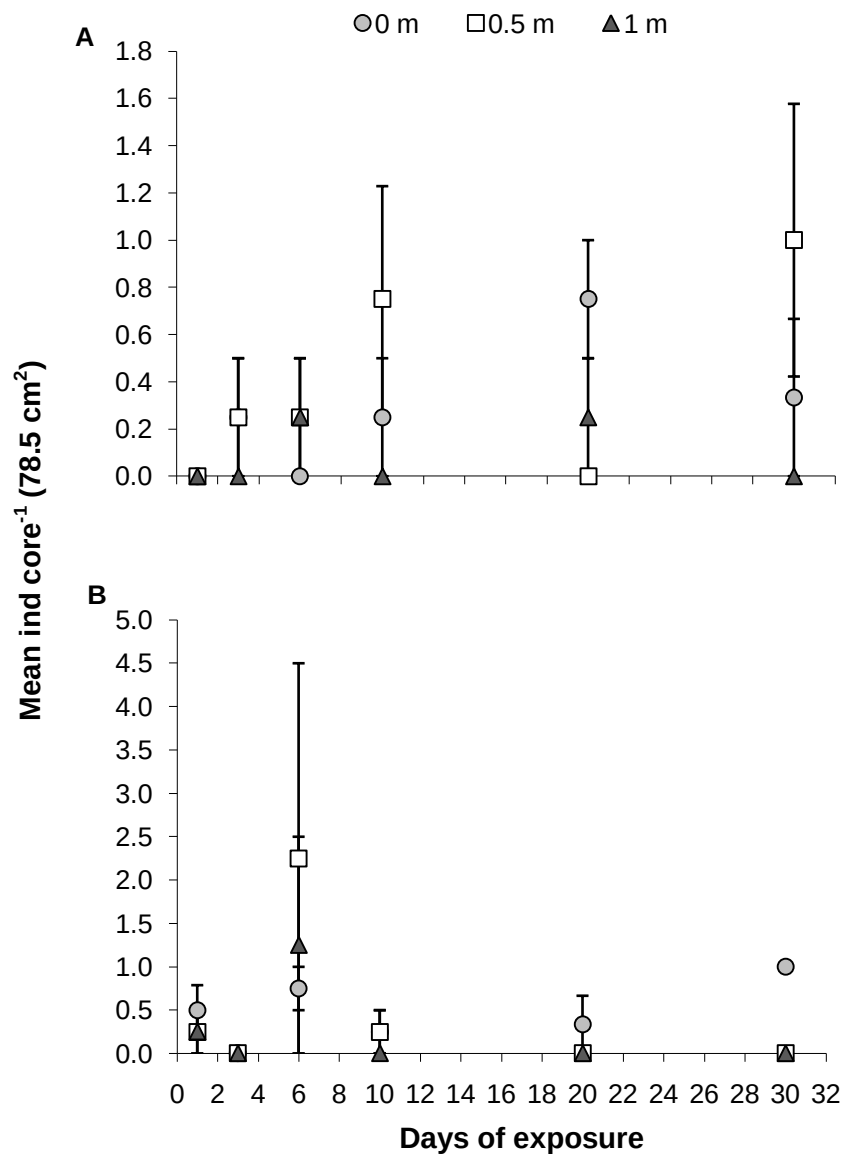


Figure A.2. Mean Diptera abundance ($\pm$ S.E) per core sample (78.5 cm²) taken at 0, 0.5 and 1 m intervals from washed up *Durvillaea antarctica* during (A) autumn (day 1-20, n=4; day 30, n=3) and (B) winter (day 1-10, n=4; day 20, n=3; day 30, n=2) 2008, on Victory Beach, Otago.

Table A.5. Summary of two-way ANOVA analysis for initial weight loss (%), moisture loss (%), organic Carbon and Nitrogen content (%), C : N ratio, considering the effects of season (autumn and winter), and days of exposure (day 1, 3, 6, 10, 20 and 30) as factors. Significant results are indicated by bold p-values. df-degrees of freedom; MS- Mean Square.

	Source	df	MS	F-value	p-value
Initial weight loss	Season (A)	1	2032.386	26.10	< 0.001
	Day (B)	5	316.078	4.06	0.006
	A x B	5	146.591	1.88	0.125
Moisture loss	Season (A)	1	1079.576	20.84	< 0.001
	Day (B)	5	249.876	4.82	0.002
	A x B	5	109.136	2.11	0.09
Organic Carbon	Season (A)	1	6.837	0.78	0.383
	Day (B)	5	124.205	14.23	< 0.001
	A x B	5	25.25	2.89	0.029
Organice Nitrogen	Season (A)	1	0.018	0.78	0.384
	Day (B)	5	0.018	0.77	0.578
	A x B	5	0.018	0.77	0.578
C : N ratio	Season (A)	1	53.63	4.26	0.047
	Day (B)	5	18.36	1.46	0.231
	A x B	5	14.96	1.19	0.337

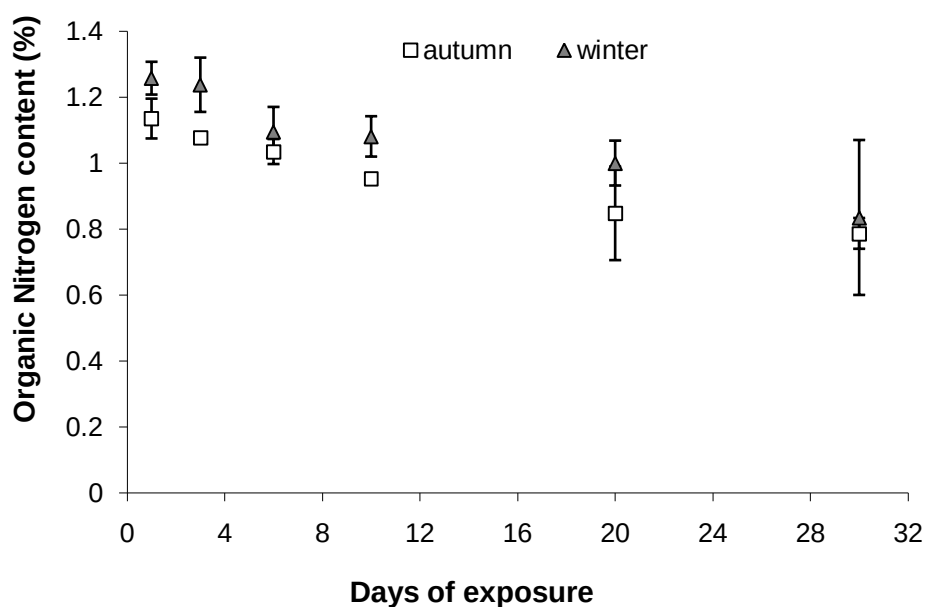


Figure A.3. Changes in the mean percentage of organic Nitrogen ($\pm$ S.E) over a 30-day period during autumn (day 1-20: n=4, day 30: n=3) and winter (day 1-10: n=4, day 20: n=3, day 30: n=2) on Victory Beach, off the Otago Peninsula.

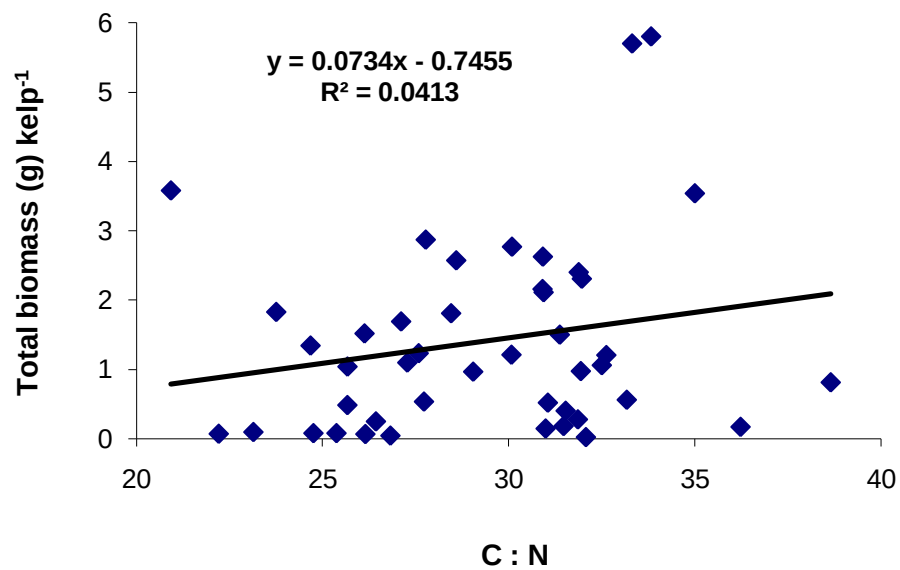


Figure A.4. The relationship between the ratio of Carbon to Nitrogen and the total macrofauna biomass associated with samples of *D. antarctica* on Victory Beach, over a 30-day sampling period in autumn (day 1-20: n=4, day 30: n=3) and winter (day 1-10: n=4, day 20: n=3, day 30: n=2).

Table A.6 Raw data for macrofaunal abundance associated with *Durvillaea antarctica* samples during autumn, 2008.

Day	Site	Talitridae adult	Talitridae juvenile	Isopoda	Decapoda	Staphilinidae	other Coleoptera	Diptera	Arachnida
1	A	27	0	0	0	1	0	12	0
1	B	20	48	0	0	5	1	26	1
1	C	23	65	1	0	0	0	6	0
1	D	40	7	0	0	0	1	6	0
3	A	159	663	0	0	18	0	0	0
3	B	307	1234	0	0	55	0	0	0
3	C	111	1158	2	0	15	2	8	0
3	D	52	156	0	0	3	0	54	0
6	A	139	693	0	0	119	2	5	0
6	B	257	573	0	0	127	4	8	0
6	C	429	1004	0	0	14	2	6	0
6	D	12	88	0	0	3	1	19	0
10	A	147	789	0	0	258	4	67	0
10	B	98	374	0	0	192	14	98	0
10	C	19	103	0	1	25	72	13	0
10	D	106	550	1	3	12	2	7	0
20	A	86	89	0	0	234	3	13	0
20	B	320	398	0	0	449	5	5	0
20	C	48	762	2	0	36	1	6	0
20	D	114	40	0	0	6	95	21	0
30	A	20	6	0	0	140	1	125	0
30	B	72	221	0	0	235	4	46	0
30	D	55	17	1	0	14	4	301	0

Table A.7 Raw data for macrofaunal abundance associated with *Durvillaea antarctica* samples during winter, 2008.

Day	Site	Talitridae adult	Talitridae juvenile	Isopoda	Decapoda	Bivalvia	Staphilinidae	other Coleoptera	Diptera	Fromicidae	Diplopoda
1	A	8	90	0	0	0	2	0	6	0	0
1	B	10	43	0	0	0	2	0	6	0	0
1	C	4	23	0	0	0	1	0	22	0	0
1	D	12	60	0	0	0	2	1	6	0	0
3	A	20	157	0	0	0	14	1	18	0	0
3	B	33	138	0	0	0	16	0	84	0	0
3	C	18	107	0	0	0	2	0	7	0	0
3	D	6	50	0	0	0	3	0	6	0	1
6	A	18	189	0	0	0	25	0	25	0	0
6	B	89	661	0	0	0	84	1	42	0	0
6	C	248	590	0	0	0	1	1	42	0	0
6	D	286	501	0	1	0	8	0	33	0	0
10	A	53	484	0	0	0	301	0	24	0	0
10	B	78	405	0	0	0	93	0	22	0	0
10	C	224	1351	0	0	0	26	0	1	0	0
10	D	131	332	1	0	0	33	2	5	0	0
20	A	98	214	1	0	1	125	3	35	0	0
20	B	127	634	0	0	0	224	0	11	0	0
20	C	122	59	0	0	0	40	0	2	0	0
30	A	107	115	0	0	0	42	2	7	0	0
30	B	249	994	0	0	0	90	1	56	1	0

Table A.8 Raw data for macrofaunal biomass (g) associated with *Durvillaea antarctica* samples during autumn, 2008. Note: some taxa have no record for biomass as they were too small to be weighed.

Day	Site	Talitridae adult	Talitridae juvenile	Staphilinidae	other Coleoptera	Diptera
1	A	0.374	0.000	0.003	0.000	0.028
1	B	0.133	0.032	0.007	0.011	0.003
1	C	0.202	0.077	0.000	0.000	0.002
1	D	0.471	0.010	0.000	0.006	0.001
3	A	1.993	0.365	0.008	0.000	0.034
3	B	4.340	1.340	0.020	0.000	0.000
3	C	1.230	0.820	0.080	0.000	0.020
3	D	0.884	0.077	0.003	0.000	0.013
6	A	1.771	0.452	0.049	0.025	0.011
6	B	3.080	0.400	0.040	0.020	0.000
6	C	4.780	0.980	0.030	0.000	0.012
6	D	0.019	0.003	0.001	0.000	0.004
10	A	2.132	0.322	0.139	0.025	0.008
10	B	1.786	0.190	0.048	0.079	0.012
10	C	0.170	0.080	0.020	0.810	0.020
10	D	0.747	0.398	0.002	0.036	0.025
20	A	1.550	0.060	0.150	0.030	0.040
20	B	2.398	0.231	0.196	0.031	0.016
20	C	0.270	0.520	0.010	0.000	0.005
20	D	1.990	0.050	0.002	1.454	0.003
30	A	0.318	0.001	0.168	0.004	1.202
30	B	0.827	0.180	0.145	0.040	0.015
30	D	0.851	0.002	0.008	0.042	0.331

Table A.9 Raw data for macrofaunal biomass (g) associated with *Durvillaea antarctica* samples during winter, 2008. Note: some taxa have no record for biomass as they were too small to be weighed.

Day	Site	Talitridae adult	Talitridae juvenile	Isopoda	Diplopoda	Staphilinidae	other Coleoptera	Diptera
1	A	0.024	0.057	0.000	0.000	0.000	0.000	0.002
1	B	0.041	0.027	0.000	0.000	0.001	0.000	0.002
1	C	0.010	0.025	0.000	0.000	0.000	0.000	0.011
1	D	0.021	0.049	0.000	0.000	0.000	0.004	0.000
3	A	0.064	0.077	0.000	0.000	0.002	0.000	0.005
3	B	0.123	0.098	0.000	0.000	0.003	0.000	0.029
3	C	0.061	0.019	0.000	0.000	0.001	0.000	0.002
3	D	0.038	0.060	0.000	0.001	0.001	0.000	0.000
6	A	0.041	0.120	0.000	0.000	0.006	0.000	0.007
6	B	0.155	0.337	0.000	0.000	0.018	0.002	0.010
6	C	0.466	0.492	0.000	0.000	0.000	0.003	0.008
6	D	1.030	0.467	0.000	0.000	0.001	0.000	0.022
10	A	0.167	0.335	0.000	0.000	0.057	0.000	0.004
10	B	0.433	0.614	0.000	0.000	0.014	0.000	0.002
10	C	1.187	1.481	0.000	0.000	0.102	0.000	0.000
10	D	0.845	0.467	0.003	0.000	0.004	0.003	0.026
20	A	0.469	0.052	0.002	0.000	0.009	0.001	0.007
20	B	0.932	0.785	0.000	0.000	0.090	0.000	0.004
20	C	1.421	0.074	0.000	0.000	0.007	0.000	0.000
30	A	0.804	0.184	0.000	0.000	0.043	0.007	0.005
30	B	1.349	1.160	0.000	0.000	0.038	0.001	0.025