Hidden Consumers in Wave-exposed Boulder Beaches: Implications to Trophic Studies in Marine-terrestrial Ecotones

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Abstract

Invertebrate communities and ecological processes are well understood in high-energy sandy beaches, where beach-cast wrack (macrophyte detritus) often accumulates and forms hotspots of nutrient cycling as well as enhancing diversity and driving food webs. Grazing invertebrates play a key role in recycling wrack and facilitating the transfer of nutrients for spatial subsidies across this marine-terrestrial ecotone. Cobble and boulder beaches can also form a prominent feature of wave-exposed coasts and accumulate wrack, yet we know far less about the invertebrates in these beaches and their possible role for recycling wrack. Here, we determine the biomass of detrital macrophytes on, and embedded in, the boulder matrix, as well as the density and biomass of macroinvertebrates in high-energy, boulder beaches in south-eastern New Zealand. We use these data to compare densities and biomass of wrack and invertebrates with published data for sandy beaches to examine the possible importance of these understudied coastal habitats in recycling wrack and facilitating trophic subsidies. The biomass of beach-cast macroalgae exceeded 100 g DW $0.1m^{-2}$ on boulder beaches, where the kelps *Durvillaea* spp. and *Macrocystis pyrifera* were the main forms of wrack on both types of beaches. This was comparable to many other sandy beaches across the globe. However, the total biomass of invertebrates on boulder beaches in our study was higher than that reported for sandy beaches in the region and across the globe, while densities were similar or higher than those found on sandy beaches. Like sandy beaches across the globe, amphipods were abundant on boulder beaches, however, the relatively large gastropod *Diloma nigerrimum* was particularly dominant in this habitat. With its known high grazing rates, combined with high densities and biomass, this grazer is likely to play a disproportionately important role in the processing of beach-cast kelp and a key role in transferring nutrients back into the ocean or to adjacent terrestrial food webs.

Introduction

Shoreline ecotones provide a transition zone between land and sea, where ecological functions support biodiversity and productivity in both terrestrial and marine environments. Organic matter is often deposited in large quantities along shorelines (e.g. Griffiths et al. 1983; Orr et al. 2005; Mateo, 2010), where it can enhance biodiversity and secondary production through the provision of nutrients and food resources in this marine-terrestrial ecotone (Polis et al. 1997), as well as return bioavailable nutrients to adjacent marine waters (Colombini et al. 2002). Our understanding of the ecological functions of beach ecotones is mainly based on sandy-beach systems (see Schlacher et al. 2008). The deposition of macroalgal and/or seagrass detritus (known as “wrack”) in these systems can support a high diversity and density of invertebrates comprising a mixture of marine and terrestrial species (e.g. Colombini et al. 2002; Jedrzejczak 2002; Ince et al. 2007), particularly representing grazers such as amphipods and isopods (Griffiths et al. 1983; Pennings et al. 2000; Crawley and Hyndes 2007). These grazers also often exhibit a preference for kelp (species from the orders Laminariales and Fucales) as a food source (Pennings et al. 2000; Dugan et al. 2003; Crawley and Hyndes 2007), indicating that kelp in particular plays a pivotal role in driving secondary production in this ecotone. These consumers, along with insects such as flies and beetles, provide important ecological roles through breaking down detritus for nutrient recycling and forming vectors for the transfer of organic material to adjacent ecosystems (Hyndes et al. 2014).

The complex three-dimensional structure provided by cobble or boulder habitats has been shown to contain highly diverse and abundant fauna (Chapman 2002, 2005; Le Hir and Hily 2005; Kuklinski and Bader 2006; Yakovis et al. 2008; Grzelak and Kuklinski 2010). However, the focus on these habitats has been on broad assemblage structure in relatively wave-sheltered intertidal or subtidal environments, rather than wave-exposed shoreline habitats where wrack accumulates. Disturbance through wave energy and sand deposition reduces the biodiversity of boulder fields (McGuinness 1987a, b), suggesting that cobbles and boulders on high-energy beaches may contain a lower diversity of invertebrates than similar habitats in more sheltered environments. However, the high retention of detrital kelp within the structure of cobble beaches (Orr et al. 2005) could promote a greater diversity and density/biomass of grazers, and therefore form an important vector for the transfer of nutrients derived from kelp to terrestrial or adjacent marine ecosystems. Our understanding of the ecology of these systems is poor, despite their presence across most, if not all, continents (Oak 1984; Rios and Mutschke 1999; Orr et al. 2005; Le Hir and Hily 2005; Irvine et al. 2006; Banks and Skilleter 2007; Harris et al. 2013; Naderloo et al. 2013).

In this study, we aimed to determine the biomass of beach-cast wrack and the densities and biomass of macroinvertebrates in cobble/boulder beaches in a high wave-energy environment where kelp detritus is known to accumulate, and compare the findings to published studies of sandy beaches in similar settings. We examined this in the coastal region of southern New Zealand, where boulder beaches are a prominent feature of the high wave-energy coastline (Morton 2004). We focused on wrack and macroinvertebrates in areas of the beach where wrack is visible and absent to determine whether material is bound in the boulder matrix. We then discuss our results in the context of existing published data from the region and elsewhere across the globe for both sandy and cobble/boulder beaches. Since detritivores (often termed “mesograzers” in beach systems) dominate the macroinvertebrates (see above), we have focused on this functional group. This has allowed us to discuss the role of mesograzers/detritivores in processing beach-cast wrack and forming vectors for the transfer of nutrients from stranded drift material to other ecosystems.

Methods

Our study was undertaken along the wave-exposed coastline of north Otago in south-eastern New Zealand, where cobble or boulder beaches are common. The kelp *Macrocystis pyrifera* [Laminariales] and *Durvillaea* spp. [Fucales] form a major component of the wrack along sandy-beach shorelines (Suarez et al. 2015) and detrital wrack has been observed on cobble or boulder beaches in the region. Furthermore, a range of gastropod species has been observed in cobble or boulder beaches, but they have not been quantified (Morton, 2004). Three beach sites comprising a mixture of cobble and/or boulders (Figure 1) were selected for this study (Seconds 45° 54’54.91”S, 170° 29’13.23”E; Puketeraki 45° 39’17.72”S, 170° 39’10.95”E; Boulder 45° 38’23.61”S, 170° 40’18.89”E). We use the term “boulder beaches” to simplify the text. All sites had a predominantly easterly aspect and were therefore exposed to ocean swells tending SE to NE, with a mean swell height ranging between 0.64 and 1.03 m in October and 0.55 and 1.21 m in November 2010 (SOM Table 1). Maximum swell height ranged from 3.4 and 4.5 m in October 2010 and 1.4 to 1.7 m in November 2010. The site “Seconds” tended to have higher mean wave height than the other sites (SOM Table 1).

Sampling was conducted from the 16th to 19th of November, 2010, on beaches that comprised beach-cast wrack that was dominated by kelp. At each site, 0.1 m^2 quadrats were positioned haphazardly along the mean high-water mark, with five quadrats positioned in patches where large kelp (*Durvillaea* spp. and/or *Macrocystis pyrifera*) were visibly stranded, and five quadrats positioned in areas visibly free of kelp wrack that were at least 5 m away from patches of kelp. “Kelp” treatment was included in the design to determine if the visible presence of beach-cast kelp represented the amount of kelp detritus on the beach. Large cobbles or boulders (>10 cm diameter) were then individually removed from the quadrat, and biological material was picked from each boulder and transferred to a plastic bag. Gravel and all organic material were removed and transferred to the plastic bag until a base of firm sand was reached (typically ~ 10-30 cm depth). All samples were transported to the laboratory where they were stored frozen (-20 °C) until processing.

In the laboratory, samples were thawed then individually picked by hand to separate macroinvertebrates from sediment and wrack. Once fauna and flora were identified to the lowest possible taxonomic level, individuals of each faunal taxon were counted, and then blotted wet mass for samples of each taxon of fauna and flora were measured. Samples were then dried at 60°C until a constant weight was reached, which was recorded. Since juvenile amphipods were numerous and difficult to identify, the total number and biomass of amphipods were recorded and the proportion of species within Hyalidae and Talitridae was estimated.

Total densities and biomass of grazers, as well as densities and biomass of the most dominant taxa, were tested across kelp treatment (2 levels; fixed factor) and sites (3 levels; random factor). Data were tested for homogeneity of variance using Levene’s test, and normality using Shapriro-Wilk test. Where homogeneity or normality did not result, data were log-transformed.

To compare biomass of kelp and biomass and density of grazers/detritivores in our boulder beaches to those in other similar beaches and sandy beaches, we examined and extracted published data based on searches in Clarivate Web of Knowledge and Elsevier Scopus using the terms (“beach*” OR “shore”) AND (“wrack” OR “beach-cast”OR “allochthonous”). For consistency with the metrics used in the current study, data extraction was restricted to those studies in which data were either provided or could be converted to biomass and/or abundances per m^2. Since most studies provided wrack biomass as wet weight, we converted our dry weight data to wet weight based on dry weight to wet weight ratios measured during the study.

Results

Where wrack was visible at the surface, the kelps *Durvillaea* spp. were either the only or dominant form of beach-cast material, contributing 78-100% of the wrack (Table 1). The kelp *Macrocystis pyrifera* was the next most dominant form of wrack, contributing 0-11% to the biomass of wrack. The remaining wrack mainly comprised other brown algae, along with some red algae (Table 1). In comparison, *Durvillaea* spp. were almost absent from areas where wrack was absent on the surface, while *M. pyrifera* and other brown algae were present but in smaller amounts. Red algae were generally present in small quantities in areas where wrack was visible and absent on the surface (Table 1), and was typically found at the base of the boulders. Total biomass of beach-cast wrack was approximately 100 g DW 0.1 m^{-2} when beach-cast wrack was visibly present in the surface, and 1-2 orders of magnitude less when wrack was not visible on the surface (0.2-28 g DW 0.1 m^{-2}; Figure 2A).

The macroinvertebrates found in the boulder beaches were dominated by grazers or detritivores (Table 3). Focusing on grazers/detritivores (here on termed grazers), total grazer density and biomass differed when macroalgae was visibly present or absent on the beach surface ($p<0.05$, Table 2). However, mean densities and biomass exceeded 100 ind. and 100 g DW 0.1 m^{-2}, respectively, regardless of whether or not wrack was visible on the beach surface (Figure 2B, E). In patches where wrack was visible, total grazer densities exceeded 1,000 ind. 0.1 m^{-2} while biomass was around 1,000 g DW 0.1 m^{-2}.

Amphipods were the most numerous macroinvertebrate present in the boulder beaches (Table 3), and were typically found at the base of the boulders. Approximately 80% belonged to the family Hyalidae. The trochid gastropod *Diloma nigerrimum* was also highly abundant and was present in high biomass, while the ellobiid gastropod *Marinula filholi* was also relatively abundant. The densities and biomass of amphipods did not differ between areas with the visible presence or absence of wrack (Table 2). The mean density of amphipods ranged from 31 to 6,343 ind. 0.1 m^{-2}, while biomass ranged from 0.07 to 13.6 g DW 0.1 m^{-2} (Figure 2C, F). In comparison, the densities and biomass of *D. nigerrimum* differed when beach-cast macroalgae was visibly present or absence, with mean densities and biomass ranging between 1,037 and 9,240 ind. 0.1 m^{-2}, and 688 and 2,721 g DW 0.1 m^{-2}, respectively, where wrack was visible, and ranging between 192 and 3,137 ind. 0.1 m^{-2}, and 119 and 1,372 g DW 0.1 m^{-2}, respectively, where wrack was visibly absent (Figure 2D, G). Since the soft tissue to total biomass ratio for this gastropod was 0.95, biomass of soft tissue ranged from 113 to 2,585 g DW 0.1 m^{-2}.

Discussion

Our ecological understanding of wave-exposed beaches is typically based on sandy beaches (Dugan et al. 2003; Jaramillo, 2006; Ince et al. 2007; Duarte et al. 2010; Olabarria et al. 2010; MacMillan and Quijón 2012), but here we show that cobble and boulder beaches in a wave-exposed environment house exceptionally high densities and biomass of mesograzers that rival sandy beaches. Given their presence along shorelines of various regions across the globe (e.g. Le Hir and Hily 2005; Banks and Skilleter 2007; Naderloo et al. 2013), it is surprising that our understanding of these beaches remains poorly understood in the framework of western science. The high amount of drift kelps that become stranded in cobble or boulder beaches (current study; Orr et al. 2005) suggests that the grazing assemblages in this habitat are likely to play a major role in processing beach-cast kelp and transferring its nutrients to terrestrial systems or returning bio-available nutrients to marine ecosystems. While we recognize that our study has limited temporal coverage, we argue that this shoreline ecotone appears to provide a hotspot of nutrient recycling via grazers or detrivores and requires far greater research effort to understand its role in these processes.

The combined densities of mesograzers in boulder beaches in our study exceeded those reported for mesograzers on sandy beaches in the region, and far exceeded densities of mesograzers reported on sandy beaches elsewhere across the globe (Table 4). Supporting our results, amphipod densities are also high in gravel/cobble beaches in north-eastern USA (Behbehani and Croker 1982). However, the full extent of the value of boulder beaches as a habitat for mesograzers is demonstrated by their biomass, which was far higher on boulder beaches sampled in this study, compared to those reported for sandy beaches in the region (>10kg vs 12 g DW m^{-2}; Table 4). This largely reflects the presence of the gastropod *D. nigerrimum*, which is likely to benefit from the greater heterogeneity of the boulder beaches through larger interstitial spaces and presence of hard substrata (Le Hir and Hily 2005), and the high biomass of stranded kelp, its preferred food source (Quintanilla-Ahumada et al. 2018).

The high biomass of particularly kelp on the boulder beach surface would reflect the sporadic inputs of this detrital material over the tidal and storm cycles. While our study was restricted to a short timeframe, it coincided with a period of high biomass on some nearby sandy beaches (Suárez et al. 2015). Unlike sandy beaches, the greater interstitial spaces among the larger grain size of cobbles and boulders are more effective at trapping and retaining large wrack particles (Behbehani and Croker 1982; Orr et al. 2005). This is supported by studies examining the long-term retention of oil on beaches exposed to oil spills from the crash of the Exxon Valdez in 1989. Monitoring of boulder beaches affected by the spill found that oil was surprisingly well retained in the matrix of the beaches despite the intermittently high-energy nature of the environment and apparent mobility of boulders and gravels (Hayes and Michel 1999; Irvine et al. 2006). This pattern of retention was explained by surface boulders acting to “armour” underlying sediment from wave forces, thus leading to a high level of oil retention in the sediment matrix. This “boundary layer” would allow detritus particles to be retained, and at least partly explain the presence of kelp and other macroalgae within the cobble/boulder matrix, as shown by the presence of macroalgae in areas where wrack was absent at the surface. This would allow detritus to be retained for longer periods than on high-energy, sandy beaches, but further research is required to confirm this. Greater retention, and the movement of boulders during strong surges (pers. obs.), could enhance the physical and microbial breakdown of macroalgal particles within the boulder matrix, and facilitate consumption by grazers.

Like semi-aquatic amphipod species in sandy-beach ecosystems across the globe (e.g. Crawley and Hyndes 2007; Lastra et al. 2008; Duarte et al. 2010), including *B. quoyana* in the study region (Suárez-Jiménez et al. 2017), the gastropod *D. nigerrimum* displays a feeding preference for kelp (Quintanilla-Ahumada et al. 2018). This preference, combined with the high grazing rates and high densities of this mesograzer, would result in a high capacity to process beach-cast kelp in this shoreline system. In Chile, *D. nigerrimum* consumes over 600 mg WW kelp ind.$^{-1}$.day^{-1} (Quintanilla-Ahumada et al. 2018) compared to 15 mg WW kelp ind.$^{-1}$.day^{-1} by *B. quoyana* on sandy beaches in our study region (Suárez-Jiménez et al. 2017). This difference partly reflects the increase in feeding rates of marine mesograzers with increasing body size (Ruesink, 2000). The biomass we observed for *D. nigerrimum* in the boulder beaches was three orders of magnitude greater than those recorded for *B. quoyana* on sandy beaches in the region (see Table 4). Even at maximum densities for *B. quoyana* on sandy beaches, the biomass we recorded for *D. nigerrimum* in boulder beaches far exceed those of amphipods on sandy beaches (see Table 4). The difference could be even higher if amphipods were included, but their role in consuming kelp is unknown. It is worth noting that a high proportion of the amphipods found in the boulders belonged to Hyalidae. Since these amphipods have been shown to display preferences for green or red algae (Taylor and Steinberg 2005), and they occurred at the base of the boulder matrix where red algae accumulated (Pers. obs), it is possible that they were consuming red algae.

Our study highlights the need to consider cobble and boulder beaches when determining the capacity of beaches to process beach-cast macrophytes. The high biomass of mesograzers in wave-exposed boulder beaches in our study is consistent with the results of a meta-analysis by Ricciardi and Bourget (1999), who showed that boulder habitats contain 10-100 times the biomass of macroinvertebrates than sandy and rocky shore habitats in sheltered environments. Our results suggest that the differences may be even greater between boulder and sandy beaches in wave-exposed coasts. Macroalgae can be cast in large quantities onto cobble and boulder beaches on wave-exposed coasts in others regions (Orr et al. 2005). Furthermore, gastropod grazers such as *Diloma* species are distributed widely in the intertidal zone across the globe (Donald et al. 2011), and exhibit far greater consumption rates on kelp (Quintanilla-Ahumada et al. 2018) than amphipods whose consumption rates range up to 46 mg WW ind.$^{-1}$.day^{-1} (Duarte et al. 2008, 2010; McMillan and Quijón 2012; Poore et al. 2013; Suárez-Jiménez et al. 2017; Michaud et al. 2019). It is therefore plausible that this pattern occurs in other cobble or boulder beaches that are distributed across the globe (Rios and Mutschke 1999; Orr et al. 2005; Le Hir and Hily 2005; Banks and Skilleter 2007; Harris et al. 2013, Naderloo et al. 2013). Invertebrates inhabiting wave-exposed cobble or boulder beaches tend to be inconspicuous, which may partly explain the paucity of studies on those communities, but our study suggests they could play a disproportionate role in the processing of beach-cast macroalgae compared to sandy beaches, and are likely to play an important role in the transfer of that material through marine (Crawley et al. 2009) and terrestrial (Polis and Hurd 1996; Mellbrand et al. 2011) food webs as well returning nutrients back into the ocean. A broader and more comprehensive understanding of their role is particularly relevant given their susceptibility to long-term impacts from oil spills (Irvine et al. 2006) and the vulnerability of shoreline systems to coastal armouring (Dugan et al. 2008) and rising sea levels (Vitousek et al. 2017).

Declarations

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Author contributions: GH and RM conceived and designed the study, while all authors were involved with the field collections. RS and DR processed that samples. GH wrote the paper, while RM, RS and DR provided feedback and edited the manuscript.

Data availability: Data will be placed in the ECU data repository on acceptace of the manuscript.

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Tables

Table 1. Total biomass (grams dry weight) and percentage contribution of the different forms of macroalgae in cobbles or boulders where wrack was visibly present or absent on the beach surface.

	Wrack visible		**Wrack not visible**	
	Biomass	**%**	**Biomass**	**%**
Phaeophyceae				
Durvillaea spp.	5686	93.6	<1	0.3
Macrocystis pyrifera	200	3.3	76	39.9
Halopteris spp.	2.5	0.0	<1	0.3
Padina sp.	1	0.0	1	0.5
Carpophyllum spp.	9	0.1	12	6.3
Cystophora spp.	1	0.0	2	1.0
Margineriella spp.	39	0.6	39	20.5
Xiphophora spp.	28	0.5	24	12.6
Landsburgia spp.	15	0.2	6.5	3.4
Desmarestia spp.	10	0.2	<1	0.3
Phaeophyceae spp.	19	0.3	4	2.1
Chlorophyta				
Chlorophyta spp.	2.1	0.0	1.5	0.8
Rhodophyta				
Adamsiella spp.	1.5	0.0	3.6	1.9
Gigartina spp.	0	0.0	0	0.0
Rhodophyta spp.	28.5	0.5	19.5	10.2
Alistmatales				
Zostera sp.	0.5	0.0	0	0.0
Unidentified detritus	29.4	0.5	0	0.0

Table 2. Two-way ANOVA results for biomass of beach-cast macroalgae, and densities and biomass of amphipods and *Diloma* in the boulder habitat. # = Log10(x+1), ^ = Sqrt, * = did not meet normality or homogeneity of variance requirements.

Variable	**Treatment (df = 1)**			**Site (df = 2)**			**Treatment x Site (df =2)**			**Residual**
	MS	**F**	**P**	**MS**	**F**	**P**	**MS**	**F**	**P**	**MS**
Macroalgal biomass$^{\#,*}$	12.8	46.1	0.021	2.0	7.3	0.121	0.3	2.7	0.085	2.0
Total grazer density$^{\#}$	4.1	18.5	0.050	3.2	14.5	0.064	0.2	1.7	0.199	3.2
Total grazer biomass$^{\wedge}$	2774.1	38.8	0.025	1738.9	24.3	0.039	71.4	0.5	0.640	71.4
Amphipod density$^{\#,*}$	3.0	6.1	0.131	4.1	8.5	0.106	0.5	1.16	0.332	0.5
Amphipod biomass$^{\#,*}$	0.8	0.7	0.481	4.0	3.9	0.205	1.0	2.7	0.086	1.0
Diloma density$^{\wedge}$	2878.5	33.3	0.029	1629.3	18.9	0.050	86.3	0.4	0.665	86.3
Diloma biomass$^{\wedge}$	2763.6	38.0	0.025	1738.2	23.9	0.040	72.7	0.5	0.639	0.5

Table 3. Total abundance and biomass (grams DW) of the different grazer species collected at cobble and boulder beaches, with details of taxonomy and functional group.

Species	Class: Family	Functional feeding group	Numbers	Biomass
Amphipods*	Malacostraca: Hyalidae & Talitridae	Grazer/detritivore	42097	92.1
Diloma nigerrimum	Gastropoda: Trochidae	Grazer/detritivore	39198	32039.7
Unidentified *Turbinidae*	Gastropoda: Turbinidae	Grazer/detritivore	80	8.1
Marinula filholi	Gastropoda: Ellobiidae	Grazer/detritivore	640	49.7
Chiton	Polyplacophora	Grazer	1	0.02
Macrophalmus hirtipes	Malacostraca: Macrophthalmaidae	Grazer/detritivore	17	16.8
Micrelenchus sp.	Gastropoda: Trochidae	Grazer/detritivore	1	0.05
Gastropod	Gastropoda	Grazer/detritivore	6	1.5
Scutuloidea maculata	Isopoda: Sphaeromatidae	Grazer/detritivore	71	1.3
Isopod	Isopoda	Grazer/detritivore	172	0.1
Limpet	Gastropoda: Patellogastropoda	Grazer	12	0.10
Insect larval	Insecta	Unknown	59	0.2
Pyura pachydermatina	Ascidiacea: Pyuridae	Suspension	3	15.8
Oligochaete	Oligochaeta	Unknown	32	0.4

*Based on adults, at least 80% were Hyalidae, while the remaining 20% were Talitridae. Juveniles were numerous and difficult to identify.

Table 4. Mean and range of wrack biomass and grazer density and biomass for different forms of wrack and different raxa of grazers recorded in different forms of wave-exposed beaches in different regions, based on extracted data from published papers. Note: papers were only included if biomass of wrack was provided in wet weight (WW).m^{-2}, and biomass or density data for consumers were provided in dry weight DW.m^{-2} and numbers of inividuals.m^{-2}, respectively. Wrack biomass data from the current study were converted to wet weights, since this was the most common metric used for the variable in published studies.

Beach type	Form of wrack	Kelp biomass (kg WW.m^{-2}) Mean (range)	Grazer type	Species	Grazer density (ind.m^{-2}) Mean (range)	Grazer biomass (g DW.m^{-2}) Mean (range)	Region	Reference
Cobbles/boulders	Kelp wrack	3.1 (<01-9.1)	Amphipod		13,966 (314-63,430)	30.5 (0.7-136.6)	New Zealand	This study
Cobbles/boulders	Kelp wrack	3.1 (<01-9.1)	Gastropod	*Diloma nigerrimum*	12,795 (1,156-28,936)	10,298 (1,186-27,207)	New Zealand	This study
Course sand/cobble	Macroalgae and seagrass	18.7 (0.7-59.3)	Amphipod	*Orchestia platensis*	32,724 (225-122,000)		USA	Behbehani & Croker (1982)
Sand	Kelp	12.5 (7.3-18.1)	Amphipod	*Orchestoidea tuberculata*	4,603 (0-30,370)		Chile	Jaramillo (2006)
Sand	Kelp	12.5 (7.3-18.1)	Isopod	*Tylos spinulosus*	695 (54-1429)		Chile	Jaramillo (2006)
Sand	Bare sand (adjacent to kelp wrack)	0	Amphipod	*Balorchestia quoyana*	683 (0-2,120)	1 .5 (0.0-7.3)	New Zealand	Marsden (1991)
Sand	Kelp wrack	6.4 (1.5-15.3)	Amphipod	*Balorchestia quoyana*	17,450 (173-69,737)	11.9 (3.1-20.1)	New Zealand	Marsden (1991)
Sand	Macroalgae (mainly kelp)	4.0 (0.10-18.1)					New Zealand	Suarez et al. (2015)
Sand	Macroalgae and seagrass	0.1 (<0.1 – 0.2)					USA (south)	Morrow et al. (2014)
Sand	Macroalgae	<0.1					Spain/Portugal	Marques et al. (2003)
Sand	Macroalgae and seagrass	0.1					Spain/Portugal	Gomez et al. (2013)
Sand	Macroalgae and seagrass		Amphipod		6.5 (0.2-14.7)		Australia (west)	Ince et al. (2007)
Sand	Macroalgae and seagrass		Amphipod	*Allorchestes compressa*	24,332 (0-144,144)		Australia (west)	McLachlan (1985)
Sand	Seagrass		Amphipod		24,182		Africa (east)	Ochieng & Erftemeijer (1999)
Sand	Seagrass		Isopod		1,823		Africa (east)	Ochieng & Erftemeijer (1999)
Sand	Macroalgae		Amphipod	*Tylos europaeus*	102 (0-487)		Portugal	Goncalces & Marques (2011)

	Talorchestia brito *Talitrus saltator*

Figures

Figure 1

Photos representing the: (A) habitat structure of a cobble/boulder beach; (B) kelp stranded on the beach; and (C) the gastropod Diloma nigerrimum aggregating on stranded kelp on a cobble beach in the South Island of New Zealand.

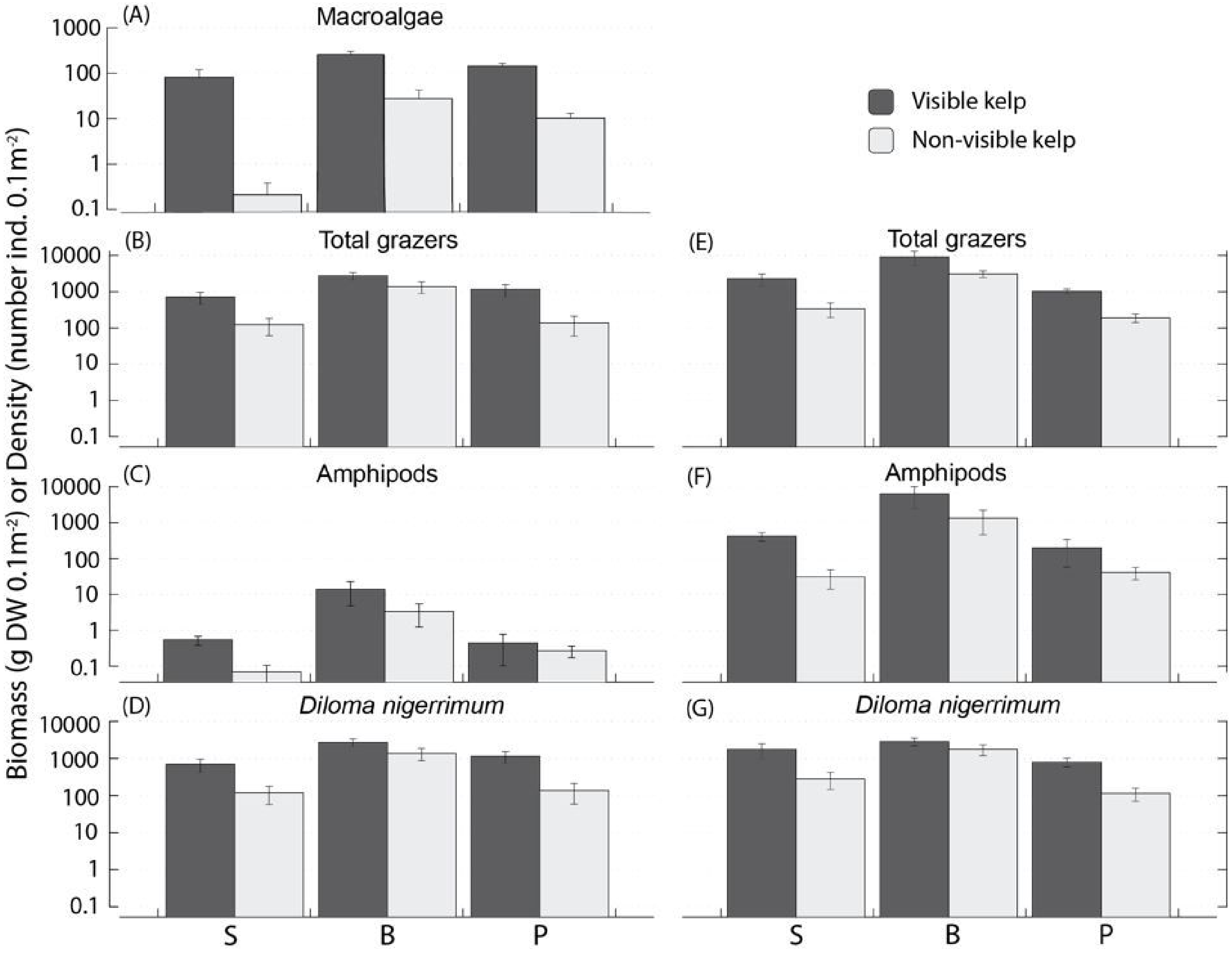

Figure 2

Mean biomass (g dry weight 0.1m-2, +SE) of: (A) beach-cast macroalgae; (B) all grazers; (C) amphipods; and (D) the gastropod Diloma nigerrimum; and mean densities (number of individuals 0.1m-2, +SE) of (E) all grazers; (F) amphipods; and (G) the gastropod Diloma nigerrimum in patches with (“visible kelp”) and without (“non-visible kelp”) wrack on the surface of cobble/boulder beaches (termed “boulder”) in southern New Zealand. S = Seconds, B = Boulder, P = Puketeraki.

Supplementary Files

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- SOMTable1.docx