Tidal range and recovery from the impacts of mechanical beach grooming

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A B S T R A C T

Mechanical grooming to remove litter and wrack from sandy beaches reduces strandline biodiversity. The impact of tidal range on recovery rates of strandline ecosystems after grooming has not been examined to date, even though tidal range is known to affect the spatial and temporal patterns of seaweed. We compared taxon richness of macroinvertebrates that occur all year round at 104 sites on two coastlines at similar latitudes in Northern Europe that have pronounced differences in tidal range. Macroinvertebrate taxon richness was positively correlated with algae depth on both groomed and ungroomed beaches but was lower on groomed beaches. This was the case even in the off season despite wrack depths returning to similar levels found on ungroomed beaches. These impacts of grooming which extend into the winter offseason where found to be higher on beaches with a lower tidal range. We suggest this is likely to be because in areas with little tidal variation, irregular and unpredictable storm events are likely to be the predominant source of new wrack deposits. Our results suggest it is particularly important that management strategies to mitigate the impacts of grooming are adopted in areas with low tidal range.

1. Introduction

Cumulative pressures on the world's coastlines are putting beaches at risk from a variety of anthropogenic and natural impacts. Anthropogenic pressures include residential, recreational, agricultural and commercial use of coastal land and near shore waters (Nordstrom, 2003; Davenport and Davenport, 2006). These pressures are predicted to heighten as the proportion of the human population living near the coast increases (Brown and McLachlan, 2002; Schlacher et al., 2007, 2008; Defeo et al., 2009). Physical processes such as beach erosion and accretion, freshwater transport, sediment transport and flooding, coupled with these increasing anthropogenic pressures, can substantially reduce the ecosystem services provided by beaches (Schlacher et al., 2007). It is becoming apparent that the need to act on these anthropogenic pressures is an urgent undertaking (Brown and McLachlan, 2002; Defeo et al., 2009). An increase in sea level rise has been reported globally over the last century (Meehl et al., 2007). This rise is inevitably going to increase beach erosion and landward retreat of shorelines, which will in turn lead to extensive habitat loss, particularly on beaches where human development halts natural inland migration of the shoreline (Feagin et al., 2005). The protection of beaches and sand dunes is becoming ever more critical as a defence against rising sea levels.

Conflicts between the needs of recreational users and the requirements of organisms that inhabit beaches presents a particularly difficult problem in developing a sustainable solution that accommodates both (Nordstrom, 2003; McLachlan et al., 2013; Kelly, 2016). Many beach managers adopt mechanical grooming to remove seaweed and litter from beaches and prevent unpleasant odours from decaying wrack reducing the attractiveness of a beach to tourists. However beached wrack plays a key role in a number of key shoreline processes (Dugan et al., 2003; Nordstrom et al., 2012; Kelly, 2014, 2016), such as remineralisation of nutrients, the formation and maintenance of dune systems and providing a viable habitat for coastal flora and fauna.

A number of studies have investigated the impacts of grooming (Davenport and Davenport, 2006; Defeo et al., 2009; Kelly, 2014). In California grooming resulted in a nine-fold reduction in wrack cover (Dugan and Hubbard, 2010). The loss of wrack results in the loss of habitat and resources for a large number of species including crabs (Tewfik et al., 2016) and shorebirds (Schlacher et al., 2017). For example in Wales grooming was found to reduce the overall abundance and diversity of strandline-related species (Llewellyn and Shackley,

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1996). Grooming has been found to impact talitrid amphipod populations in Italy (Fanini et al., 2005). Studies have shown grooming is associated with low strandline macroinvertebrate diversity in California (Dugan et al., 2003) and Scotland (Gilburn, 2012), with depth of wrack being identified as the most important determinant of biodiversity in the latter study. Wrack provides food and shelter for macroinvertebrates such as amphipods, dipteran larvae and scavenger beetles which in turn provide food for shorebirds (Brown and McLachlan, 2002; Ince et al., 2007; Olabarria et al., 2007; Lastra et al., 2008; Defeo et al., 2009; Gonçalves and Marques, 2011).

The impacts of beach grooming also extend beyond the strandline. The abundance and richness of coastal plants were fifteen and three times lower adjacent to groomed beaches in California (Dugan and Hubbard, 2010). These reductions are likely to be occurring as the strandline facilitates nutrient remineralisation (Maun, 1994) and enhances the growth of dune plants (Williams and Feagin, 2010). This also explains why another study where groomed material was redeposited elsewhere on a beach did not detect any substantive impact (Morton et al., 2015) as remineralisation will not have been majorly affected.

Studies investigating the impacts of beach grooming have already identified substantial ecological impacts. However, these studies have not investigated how environmental factors might have synergistic or antagonistic effects together with grooming. Considering the importance of strandlines to conservation and ecosystem services and the conflict with recreational users it is essential for the development of successful management strategies to determine whether environmental factors do interact with grooming. Tidal range is one factor that potentially could be of considerable significance. Beaches with higher tidal ranges could receive larger deposits of beached wrack and as a consequence might recover from the impacts of grooming more quickly. Ince et al. (2007) recorded higher macroinvertebrate abundance levels from beaches with high wrack inputs than from those with smaller inputs. By contrast, areas with little or no tidal range might be largely dependent on unpredictable storm events for replenishing stocks of beached wrack removed by grooming. The aim of this study was to determine how the impacts of grooming on strandline macroinvertebrate biodiversity vary between two stretches of coastline with similar latitude but with very different tidal ranges in Scotland and Sweden by comparing the taxon richness of the community at beaches both within and outside of the grooming season.

2. Materials and methods

2.1. Study regions

The study was carried along the coastlines of Eastern Scotland and Western Sweden. Both coastlines have many beaches were mechanical grooming is carried out at least once a week during the summer months. The location of the Scottish beaches sites ranged from Inverboyndie (57.669834N and −2.546297E) to Barns Ness (55.987167N and −2.451667E). The Swedish beaches were located between Apelviken (57.083448N and 12.256786E) and Kåseberga (55.399386N and 12.978539E). The tidal regime in Sweden varies from 10 to 40 cm in the Skagerrak, 5–20 cm in the Kattegat to 0 cm in the Baltic (Leppäranta and Myrberg, 2009). By contrast the Scottish coastline has a tidal range between about 4 and 5 m (UK Hydrographic Office). Salinity also varies between the two coastlines and is so highly correlated with tidal range that only tidal range was included in the study.

2.2. Sampling design

The study sites were 104 sections of beach, 44 in Scotland and 60 in Sweden. Where only a section of the beach was groomed a site was chosen within both the groomed and ungroomed sections. However, where the entirety of a beach was groomed then the next nearest

ungroomed beach was selected to generate an equal number of groomed and ungroomed sections of beach. All beaches were visited during both the summer grooming season and also during the winter offseason. This allowed for seasonal differences to be observed at the same beach.

The depth of the wrack was measured at various points to establish the maximum depth of wrack present at each site. Each section of beach was then sampled for a period of 10 min where organisms were observed and identified to taxon level *in situ*. The method for sampling involved searching for strandline macroinvertebrates in, on or under the wrack starting at the point of maximum depth. Patches of wrack at all zones on the beach from the high water springs down to the swash zone were searched which resulted in wrack beds of different ages and stages of desiccation being covered. Each beach was sampled once during the grooming season (June–August) and once during the off season (October–February).

2.3. Study organisms

Taxon richness was used as a biodiversity indicator of the fauna inhabiting the stranded seaweed as this has been shown to be an efficient surrogate for species richness generally (Williams and Gaston, 1994; Balmford et al., 1996) and in the context of strandlines (Gilburn, 2012). Using this simple measure means that large numbers of sites can be included in the study. The eight taxa chosen in the surveys were used as they the most commonly found on beaches throughout the UK and Sweden, are a diverse selection of organisms with different niches within the strandline environment and have successfully be used as an indicator of the impact of grooming on macroinvertebrate strandline communities (Gilburn, 2012). Furthermore all these taxa can be found both within and outside the grooming season. Six of the taxa were assessed at the family level, one, mesostigmata mites, was assessed at the level of order and one taxon, oligochaetes, to the level of sub-class. The eight taxonomic groups used were: 1) Diptera - Coelopidae (*Coelopa frigida* and *Coelopa pilipes*); 2) Diptera - Sepsidae (*Orygma luctuosum*); 3) Diptera - Anthomyiidae (*Fucellia maritim*a); 4) Diptera - Sphaeroceridae (*Thoracochaeta zosterae*); 5) Coleoptera - Staphylinidae – (*Cafius xantholoma* and *Aleochara algarum*); 6) Amphipoda - Talitridae (of three genera *Talitrus*, *Talorchestia* and *Orchestia*); 7) Mesostigmata (*Parasitus kempersi* and *Thinoseuis fucicola*); and 8) Oligochaete.

2.4. Data analysis

Statistical analyses were undertaken using R version 3.2.2 (R Core Team, 2015). The lm4 (Bates et al., 2015) and MuMIn (Barton, 2015) packages were used for statistical analysis, whilst ggplot2 (Wickham, 2009) and the effects package (Fox, 2003) were used for graphics. We performed a series of Generalised Linear Mixed-Effects Models (GLMMs) with binomial distribution and logit link (Zuur et al., 2009). We ran models using presence/absence of each of the eight taxa as the response variable with 'site' included in all models as a random (grouping) factor to quantify both within and between site variance. The following predictor variables were included in the starting model: log tidal range, aspect, exposure, Longitude, Latitude, grooming season (a factor with two levels: winter or summer), grooming status (a factor with two levels: ungroomed or groomed) and log algae depth. Models were compared and the best model selected using an information theoretic approach (Akaike Information Criteria, AIC, Burnham and Anderson, 2014). Akaike weights give the probability that a model is the best model, given the data and the set of candidate models (Burnham and Anderson, 2014). Salinity was excluded from the model due to its high level of collinearity with tidal range which resulted in excessively high variance inflation factors. A better model was generated using tidal range than salinity. All two-way interactions between significant variables were explored and a three-way interaction between tidal range, grooming status and season to determine whether

Table 1

Model parameter estimates for the fixed effects from a GLMM of taxon richness with binomial distribution and log link. (The intercept in this case is showing the coefficient for ungroomed beaches in winter).

Fixed Effects:	Estimate	Std. Error	z value	P
Intercept	−3.17	0.70	−4.56	< .001
Grooming	−0.69	0.19	−3.62	< .001
Season (Summer)	1.84	0.51	3.61	< .001
Tidal range	−0.76	0.15	−5.05	< .001
Algae depth	1.48	0.14	10.28	< .001
Grooming × Season	−0.90	0.30	−3.01	.003
Grooming × Tidal range	1.40	1.10	1.44	.149
Season × Tidal range	−0.21	0.11	−2.00	.045
Season × Algal depth	−0.37	0.17	−2.20	.028
Tidal Range × Algal depth	0.31	0.05	6.86	< .001
Grooming × Season × Tidal range	−0.35	0.15	−2.36	.018

tidal range affects the impacts of grooming between seasons. A further linear model was performed with algae depth with the same response variables with the exception of algae depth itself.

3. Results

3.1. Taxon richness

The GLMM did not retain the predictor variables aspect, exposure, longitude or latitude. Taxon richness was found to be positively associated with the depth of wrack present and negatively associated tidal range (Table 1). The model also suggested that grooming was having a strong negative impact on taxon richness and predicted more species should be present in summer. Several interactions involving all four variables also affected taxon richness (Table 1). No interaction was found between grooming and algal depth suggesting that the same pattern of association is present between algal depth and taxon richness on both groomed and ungroomed beaches (Fig. 1). There was a strong interaction between grooming and season with groomed beaches having particularly low diversity during the grooming season (Fig. 2).

We detected an interaction between season and tidal range with taxon richness decreasing with tidal range in summer and increasing with tidal range in winter (Fig. 3). There was also a three-way interaction between grooming, season and tidal range. The difference in taxon richness between summer and winter on groomed beaches is strongly associated with tidal range with little difference between summer and winter on beaches with low tidal and large differences on beaches with high tidal range (Fig. 3). There was also a highly significant positive interaction between tidal range and algal depth in their
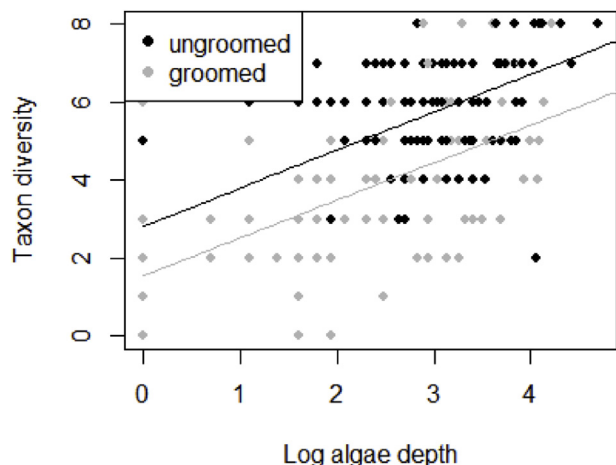

Fig. 1. Association between taxon diversity and algae depth on groomed and ungroomed beaches.
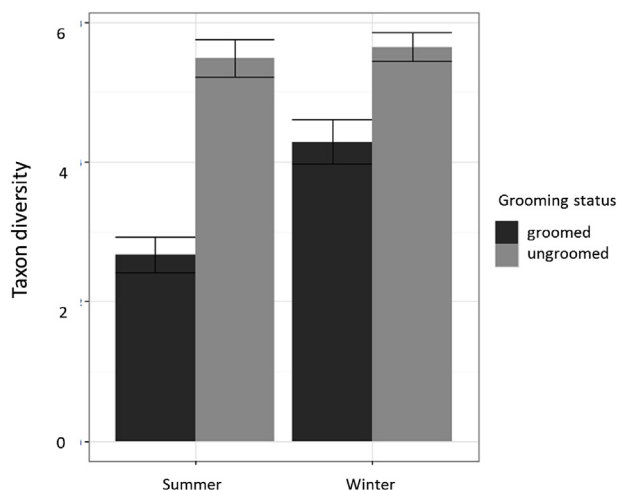

Fig. 2. Effect of both season and grooming status on mean taxon diversity. Error bars represent standard error.
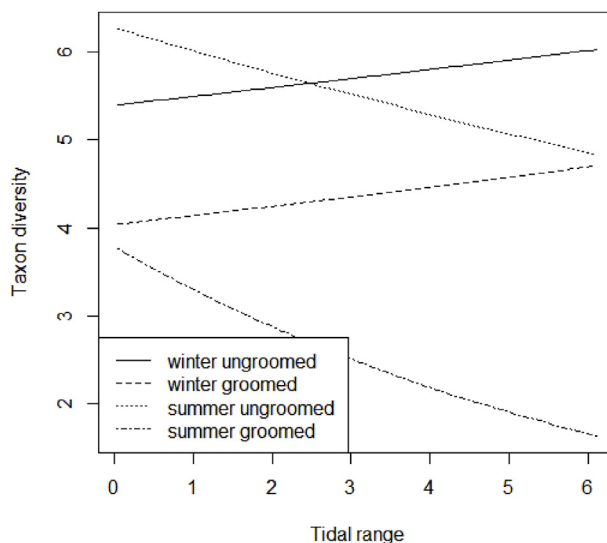

Fig. 3. Interaction plot showing the effect on taxon diversity of interactions between tidal range, grooming status and season (summer or winter).

impacts on taxon richness, with the depth of algae being associated with more pronounced increases in taxon richness in areas with higher tidal range.

3.2. Algal depth

Algal depth was highly positively associated with taxon richness (Table 1). A linear model of algal depth only retained grooming status and season (Table 2). Wrack beds were deeper during the winter (Fig. 4). There was also a significant interaction term between grooming status and season (Fig. 5) with groomed beaches having

Table 2

Model parameter estimates for a linear model estimating algae depth during on sandy beaches. The intercept is showing the coefficient for ungroomed beaches in winter. Numbers in Bold are significant at P < 0.05.

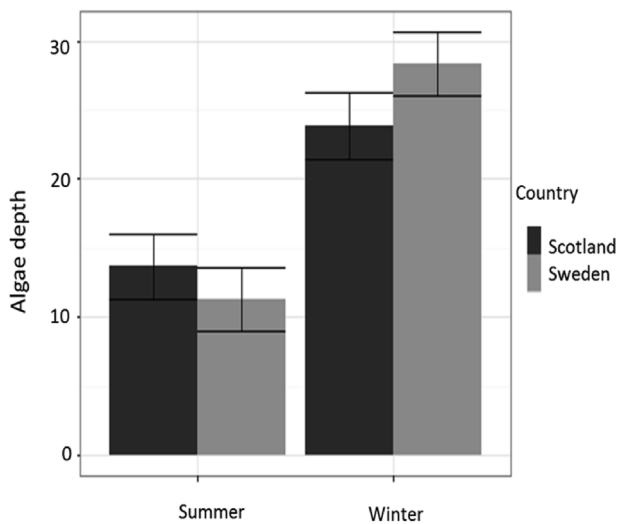| Coefficients:	Estimate	Std. Error	z value	P
Intercept	3.16	0.12	26.17	**< .001**
Grooming	−0.24	0.17	−1.40	.160
Season (Summer)	−0.68	0.17	−4.02	**< .001**
Grooming × Season	−1.17	0.24	−4.78	**< .001**

Fig. 4. Differences in algae depth in Scotland and Sweden during winter and summer.
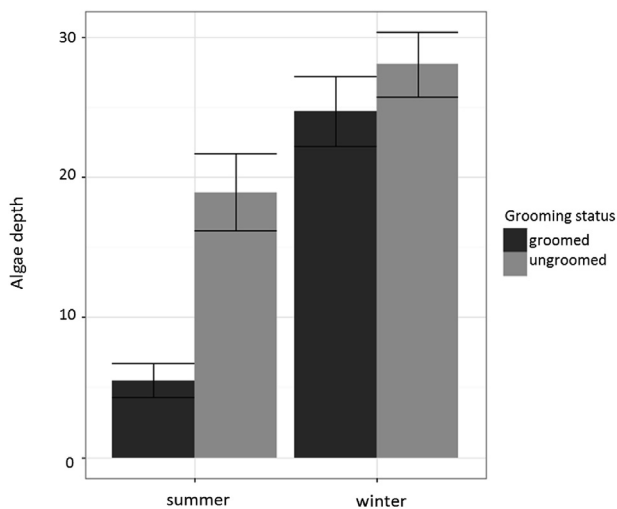

Fig. 5. Plot showing the effect of grooming season and grooming status on algae depth.

relatively low depths of wrack during the grooming season but not during winter.

4. Discussion

Our study shows that mechanical beach grooming on beaches in both Scotland and Sweden is having a marked effect on the strandline macroinvertebrate community. We also reveal that the level of macroinvertebrate diversity on a beach is being predominantly determined by the depth of wrack deposits and the impacts of grooming on this community likely occur largely as a result of reducing the depth of wrack. We show that the rate of recovery from that impact is associated with the tidal range at a beach which will affect the replenishment rate of wrack which has major implications for beach management.

4.1. Grooming and macroinvertebrate taxon richness

Our model revealed that several factors, grooming, season, algae depth and tidal range are all associated with macroinvertebrate taxon richness. Diversity was highly significantly lower on groomed beaches and the impacts of grooming on diversity were significantly greater during the grooming season suggesting that some recovery does occur of taxon richness during the winter off season. The rate of recovery on groomed beaches was found to be strongly associated with tidal range

with substantial recovery of diversity occurring on beaches with high tidal range but little on beaches with low tidal range. This could be as a result of wrack deposits being more rapidly replaced on beaches with high tidal range during spring high tides. Beaches will low tidal ranges tended to be more brackish and around the Baltic the deposits also contain a high proportion of eelgrass (Mossbauer et al., 2012) whereas deposits on higher tidal range beaches which are predominantly consist of macroalgae.

The taxa included in the study were chosen because they occur all year around. No difference was found in the level of macroinvertebrate richness between summer and winter on ungroomed beaches which confirms our choice of study organisms. Previous studies have found differences between summer and winter (Gonçalves and Marques, 2011). Including those taxa that are less commonly or not found in would have been much less informative about the impacts of grooming and the subsequent recovery period during the off season.

Fewer taxa were found on groomed beaches on both seasons suggesting that the impacts of grooming extend into the winter off season. A previous study has shown that grooming reduces macroinvertebrate richness during the summer grooming season in Scotland (Gilburn, 2012) but our study is the first to report a similar effect in Sweden and the first to report that the impacts of grooming extend into the winter in both Scotland and Sweden. A previous study in Sweden found no impact on littoral macroinvertebrates (Malm et al., 2004) but did not consider strandline macroinvertebrates. This study was also conducted further into the Baltic Sea where wrackbeds predominantly consist of eelgrass (Mossbauer et al., 2012) which provides a much less useful resource for many strandline taxa for example species such as coelopids are not found due to the lack of brown algae within the deposits. So the likely difference in the two studies is that ours was restricted to those parts of Sweden where deep wrackbeds occur and only considered species that inhabit the wrack and which therefore are most likely to be impacted by beach grooming. Our study also found that depth of algae was a key factor in determining macroinvertebrate diversity with more taxa found on beaches with deeper deposits of wrack. The low levels of wrack around the Baltic are therefore likely to have resulted in lower levels of macroinvertebrate diversity prior to grooming.

It should be noted that tourist beaches are inevitably more likely to be subjected to mechanical grooming. Tourists can damage coastal environments (Davenport and Davenport, 2006) by trampling dunes or using recreational vehicles. However, tourists do tend to actively avoid deposits of wrack due to their unpleasant odour and associated invertebrates. Indeed this is major factor in why many local authorities engage in mechanical grooming, therefore we consider it unlikely that the tourists have directly contributed to the loss of strandline biodiversity. Consequently any impacts of tourism are likely to be indirect through encouraging the use of mechanical grooming.

4.2. Grooming and depth of algal deposits

The maximum depth of algae at a beach was found to be an important determinant of taxon richness at both groomed and ungroomed beaches. The relationship between algal depth and diversity was the same for both groomed and ungroomed beaches although the level of diversity was lower on groomed beaches at each depth. This could suggest either additional negative impacts of grooming unrelated to the depth seaweed, for example disturbance or removal of sand, or a time lag before recovery from grooming occurs once seaweed has been redeposited upon a groomed beach.

The maximum depth of algae at a beach was found to higher in winter than summer on both groomed and un groomed beaches. On ungroomed beaches this is likely to be due to storms depositing more seaweed during winter than summer. On groomed beaches, the cessation of grooming during winter will allow the wrack deposits to start to accumulate to more natural depths. There was more than a three-fold difference in maximum algal depth between groomed and ungroomed

beaches during the summer but little difference by the winter off season showing that seaweed does reaccumulate. However, the lower levels of macroinvertebrate diversity on groomed beaches in winter, particularly in areas with low tidal range, suggests that in addition to replenishment of wrack, macroinvertebrate communities also suggests need time to recover from grooming events.

Tidal range did not seem to impact the amount of seaweed found on beaches in either summer or winter. This seems to conflict with the finding that diversity on beaches with lower tidal range seems to recover more slowly. However, beaches with higher tidal range are likely to get regular deposits of fresh wrack whereas beaches with lower tidal range might have to wait for irregular storm events for a large deposit of wrack.

4.3. Long-term impacts

Sandy beach processes operate over the long-term and our study just considered two snapshots in time, one in the grooming season and one in the off-season. It has been suggested that because of the complex nature of processes at sandy beaches that long term studies should be carried out. However, such studies are likely to be spatially limited in terms of the number of beaches that they could include in the study. We temporally-limiting our study by only sampling each beach twice consequently we were able to include over 100 beaches across several different coastlines with different tidal ranges and aspects. The strong patterns of association we found show that this strategy has been successful in highlighting clear patterns and impacts of grooming although it should be noted that our study was not conducted blind as the data would have been collected in the knowledge of the management programme present at each. This is an issue that is not really possible to avoid as even if naïve data collectors were employed there would still be evidence eof mechanical grooming such as tractor marks and lack of seaweed, and at some sites collections of raked seaweed that would have made a truly blind study unfeasible. The strong associations we found between grooming, tidal range, algal depth and season are also unlikely to be have to be generated by external confounding factors considering the large spatial scale of our study. It should also be noted that grooming had been occurring over many consecutive seasons at most of the beaches included in the study so the lower diversity at groomed beaches both in summer and winter are likely to have included longer-term impacts from repeated grooming events over many years.

4.4. Management implications

We show that tidal range has a major impact on recovery rates on groomed beaches, it is possible for managers to use this information and tailor their policies to try and minimise the impacts of grooming. In Sweden, where tidal range is low macro-invertebrate communities take longer to recover. This is likely because these beaches must wait until a storm event to receive fresh inputs of wrack. Rather than being removed the seaweed could be transported to a more suitable area of the beach where it is less likely to be considered a nuisance by the public and where it can naturally decompose to recycle nutrients into both dune and marine environments. In Scotland littering laws would prevent councils from moving wrack from one part of a beach to another if it contained any litter which is likely in most deposits. In Sweden grooming is carried out by each local municipality (or kommun) and a small number of kommuns already carry out this practice. If it was made more widespread then it substantially help mitigate or even remove the impacts of grooming by avoiding the removal of any material from the beach (Morton et al., 2015). Indeed gathering several thin strands of wrack and redepositing it in a deeper pile at one end of the beach might even improve the environment for most beach macro-invertebrates as our study and others have found that algae depth is a key factor in determining diversity.

On beaches where it is not practical to move the seaweed to one end, for example on small beaches or beaches where the entire beach is likely to be used, then managers could be encouraged to only groom the lower part of the beach (Kelly, 2016). This could be particularly effective on beaches with higher tidal ranges and consequently more stratification of deposits up the beach. The lower part of the beach is where most recreational activities occur so this would enable some wrack and macro-invertebrates to remain whilst minimising the impact of beach users (Kelly, 2016).

References

Balmford, A., Green, M.J.B., Murray, M.G., 1996. Using higher-taxon richness as a surrogate for species richness: I. Regional Tests. Proc. R. Soc. Lond. B Biol. Sci. 263, 1267–1274.

Barton, K., 2015. MuMIn: Multi-Model Inference. R package Version 1.15.1. http://CRAN.R-project.org/package=MuMIn.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. http://dx.doi.org/10.18637/jss.v067.i01.

Brown, A.C., McLachlan, A., 2002. Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. Environ. Conserv. 29, 62–77.

Burnham, K.P., Anderson, D.R., 2014. Multimodel inference: understanding AIC and BIC in model selection. Socio. Meth. Res. 33, 261–304.

Davenport, J., Davenport, J.L., 2006. The impact of tourism and personal leisure transport on coastal environments: a review. Estuar. Coast. Shelf Sci. 67, 280–292.

Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M., Scapini, F., 2009. Threats to sandy beach ecosystems: a review. Estuar. Coast. Shelf Sci. 81, 1–12.

Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuar. Coast. Shelf Sci. 58, 25–40.

Dugan, J.E., Hubbard, D.M., 2010. Loss of coastal strand habitat in Southern California: the role of beach grooming. Estuar. Coasts 33, 67–77.

Fanini, L., Cantarini, C.M., Scapini, F., 2005. Relationships between the dynamics of two Talitrus saltator populations and the impact of activities linked to tourism. Oceanologia 47, 93–112.

Feagin, R.A., Sherman, D.J., Grant, W.E., 2005. Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. Front. Ecol. Environ. 3, 359–364.

Fox, J., 2003. Effect displays in R for generalised linear models. J. Stat. Softw. 8, 1–27.

Gilburn, A.S., 2012. Mechanical grooming and beach awards status are associated with low strandline biodiversity in Scotland. Estuar. Coast. Shelf Sci. 107, 81–88.

Gonçalves, S.C., Marques, J.C., 2011. The effects of season and wrack subsidy on the community functioning of exposed sandy beaches. Estuar. Coast. Shelf Sci. 95, 165–177.

Ince, R., Hyndes, G.A., Lavery, P.S., Vanderklift, M.A., 2007. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. Estuar. Coast. Shelf Sci. 74, 77–86.

Kelly, J.F., 2014. Effects of human activities (raking, scraping, off-road vehicles) and natural resource protections on the spatial distribution of beach vegetation and related shoreline features in New Jersey. J. Coast. Conserv. 18, 383–398.

Kelly, J.F., 2016. Assessing the spatial compatibility of recreational activities with beach vegetation and wrack in New Jersey: prospects for compromise management. Ocean Coast. Manag. 123, 9–17.

Lastra, M., Page, H.M., Dugan, J.E., Hubbard, D.M., Rodil, I.F., 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. Mar. Biol. 154, 163–174.

Llewellyn, P.J., Shackley, S.E., 1996. The effects of mechanical beach-cleaning on invertebrate populations. Br. Wildl. 7 (3), 147–155.

Leppäranta, Myrberg, 2009. Oceanography of the Baltic Sea. Springer-Praxis, Heidelberg, Germany 378p.

Malm, T., Råberg, S., Fell, S., Carlsson, P., 2004. Effects of beach cast cleaning on beach quality, microbial food web, and littoral macrofaunal biodiversity. Estuar. Coast. Shelf Sci. 60, 339–347.

Maun, M.A., 1994. Adaptation's enhancing survival and establishment of seedlings on coastal dune systems. Vegetatio 111 (1), 59–70.

McLachlan, A., Defeo, O., Jaramillo, E., Short, A.D., 2013. Sandy beach conservation and recreation: guidelines for optimising management strategies for multipurpose use. Ocean Coast. Manag. 71, 256–268.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J., Zhao, Z.-C., 2007. Global climate projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Avery, K.B., Tignor, M., Miller, H.L. (Eds.), The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of

the Intergovernmental Panel on Climate. Cambridge University Press, Cambridge, United Kingdom, pp. 747–845.

Morton, J.K., Ward, E.J., de Berg, K.C., 2015. Potential small- and large-scale effects of mechanical beach cleaning on biological assemblages of exposed sandy beaches receiving low inputs of beach-cast macroalgae. Estuar. Coasts 38, 2083–2100.

Mossbauer, M., Haller, I., Dahlke, S., Schernewski, G., 2012. Management of stranded eelgrass and macroalgae along the German Baltic coastline. Ocean Coast. Manag. 57, 1–9.

Nordstrom, K.F., 2003. Restoring naturally functioning beaches and dunes on developed coasts using compromise management solutions: an agenda for action. In: Dallmeyer, D. (Ed.), Values at Sea: Ethics for the Marine Environment. University of Georgia Press, Athens, Georgia, pp. 204–229.

Nordstrom, K.F., Jackson, N.L., Freestone, L., Korotky, K.H., Puleo, A., 2012. Effects of beach raking and sand fences on dune dimensions and morphology. Geomorphology 179, 106–115.

Olabarria, C., Lastra, M., Garrido, J., 2007. Succession of macrofauna on macroalgal wrack of an exposed sandy beach: effects of patch size and site. Mar. Environ. Res. 63, 19–40.

R Core Team, 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Schlacher, T.A., Dugan, J., Schoeman, D.S., Lastra, M., Jones, A., Scapini, F., McLachlan, A., Defeo, O., 2007. Sandy beaches at the brink. Divers. Distrib. 13, 556–560.

Schlacher, T.A., Shoeman, D.S., Dugan, J., Lastra, M., Jones, A., Scapini, F., McLachlan, A., 2008. Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. Mar. Ecol. 29 (S1), 70–90.

Schlacher, T.A., Hutton, B.M., Gilby, B.L., Porch, N., Maguire, G.S., Maslo, B., Connolly, R.M., Olds, A.D., Weston, M.A., 2017. Algal subsidies enhance invertebrate prey for threatened shorebirds: a novel conservation tool on ocean beaches? Estuar. Coast. Shelf Sci. 191, 28–38.

Tewfik, A., Bell, S.S., McCann, K.S., Morrow, K., 2016. Predator diet and trophic position modified with altered habitat morphology. PLoS One 11.

UK Hydrographic office. http://www.ukho.gov.uk/Easytide/easytide/. Last accessed 6/8/17.

Wickham, H., 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Williams, A., Feagin, R., 2010. Sargassum as a natural solution to enhance dune plant growth. Environ. Manag. 46, 738–747.

Williams, P.H., Gaston, K.J., 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? Biol. Conserv. 67 (3), 211–217.

Zuur, A.F., Ieno, E.N., Walker, N.J., Savaliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science & Business Media, New York.