The role of buoyancy in the dispersal of marine plastic debris and the impact of biofouling: does size matter?

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ABSTRACT

Recent studies suggest that a significant proportion of the plastic pollution that enters the sea is disappearing from the surface, despite being less dense than seawater. Observations across size classes show that it is particularly smaller plastics, <5 mm in length, that are susceptible to removal. The dynamics and transport mechanisms that determine the pathways taken by floating marine plastic debris are poorly understood and the processes causing this disappearance of plastic are unknown. A spatial gradient in the size composition of floating litter has also recently been observed by visual at-sea surveys in the South Atlantic Ocean, where smaller plastic litter items are found in greater relative abundance closer to the coast becoming less frequent with increasing distance out to sea. Conversely, larger, more buoyant plastic items were found to be proportionally more abundant at greater distances away from the coastal source. Both the observations of missing microplastic and the apparent spatial gradient evident in the size composition of dispersing litter suggest that size selective mechanisms are removing smaller fragments of plastics from the surface. The nature of these and the whereabouts and ultimate fate of these smaller plastic fragments is unknown.

Two studies were conducted. The first was an empirical investigation to confirm how the size and buoyancy of litter items are influenced by dispersal distances from a point source. Beach littler samples were collected from beaches at increasing distances from a major pollution source: Cape Town in the Western Cape province of South Africa. The size and buoyancy compositions of litter at each distance interval were compared. Mean size and buoyancy increased significantly with increased distance from Cape Town. Mean item volume rose from 5.1 ml to 604 ml. Over 90% of the items recovered closer to Cape Town were in the two lowest buoyancy categories, in contrast to the furthest sampling site, where only 20% of the litter recovered occupied these categories and 55% occupied higher bin ranges. The findings from the beach litter samples were comparable to those of the recent at-sea surveys in the same region and confirmed the spatial gradient in size composition shown by that study.

The second study was an experimental investigation into marine biofouling as a possible explanation for the size-selective sinking of smaller plastics at sea. . The study was conducted *in situ* at the False Bay Yacht Club in Simon's Town in the Western Cape. Samples of high-density and low-density polyethylene plastic of varying thickness were cut into squares of three different sizes, tethered to exposure rails and submerged approximately 10 cm below the surface for a 12-week study period. A subset was removed bi-weekly, their buoyancy

observed and change in dry weight measured. My results showed that both fragment size and material thickness were significant determinants of fouling mass accumulated. Exposure times required for sinking varied from 17 days for the smallest thinnest samples to 66 days for the largest, thickest ones. All sample sizes sank within the study period. Sample volume was a close correlate of time to sinking. Refined versions of these estimates could be scaled by factors such as environmental conditions and proximity to litter inputs, and potentially included into numerical models of floating litter abundance and distribution. Both studies showed that high volume debris items persist longer at the ocean surface.

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GENERAL INTRODUCTION

Plastic has become a ubiquitous pollutant of the world's marine environments and is now recognised as a global threat to marine biodiversity (Carpenter and Smith, 1972; Colton et al., 1974; Holmström, 1975; Ryan, 1988; Gregory, 1991; Goldberg, 1997; Walker, 1997; Winston et al., 1997; Ryan and Gregory, 1997; Galgani et al., 2000, Moore et al., 2001; Barnes, 2002; Derraik, 2002; Barnes et al., 2009; Thompson et al., 2004; 2009; Zarfl et al., 2010). Injury, starvation and death due to entanglement or ingestion of drifting plastic items have been documented in over 250 marine species (Laist, 1997; Cadee, 2002; Sazima et al., 2002; Gregory, 2009; Jacobsen et al., 2010, Schuyler et al., 2013; Provencher et al., 2014). Floating plastic modifies pelagic habitats and presents new pathways for marine alien invasions (Barnes, 2002; Thompson et al., 2005; Barnes et al., 2009; Gregory, 2009) Plastics also pose chemical threats because they absorb waterborne persistent organic pollutants and make them bio-available for ingestion by organisms in potentially toxic concentrations, which can then bio-magnify through the upper trophic levels of the food chain (Mato et al., 2001; Rios and Moore, 2008; Teuten et al., 2009). These threats are expected to become increasingly urgent as the human population and our use of (particularly disposable) plastics continues to grow (Thompson et al., 2009).

Accumulation and dispersal in the marine environment

Plastic pollution enters the sea via a number of pathways, including river runoff, direct deposition of litter on beaches, the discarding and abandonment of fishing gear and dumping or spillages from ships (Pruter 1997; Ryan et al., 2009; Thompson et al., 2009). It persists for years because of its durability (Derraik, 2002; Thompson et al., 2009). Most marine plastic debris (60-64%, Andrady and Neal, 2009; Cozar et al., 2014) is made up of polymers such as polyethylene and polypropylene that are less dense than sea water and are therefore positively buoyant (Andrady, 2011; Reisser et al., 2014). These materials accumulate in high concentrations in enclosed bays and seas and in the five sub-tropical ocean gyres where they converge due to prevailing winds and currents (Moore et al., 2001; Pichel et al., 2007; Martinez et al., 2009; Moret Ferguson et al., 2010, Law et al., 2010,, Eriksen et al., 2013; 2014; Cozar et al., 2014; Ryan, 2014). Over time, buoyant plastics become embrittled due to abrasion and UV exposure (Scott, 1972; Andrady, 1990, 2011; Barnes, 2009) and fragment into progressively smaller pieces known as microplastics (Thompson et al., 2004; Arthur et al., 2009; Barnes, 2009; Andrady, 2011; Cole et al., 2011; Wright et al., 2013).

The dynamics and transport mechanisms that determine the dispersal of floating plastics in the marine environment are poorly understood (Ryan et al., 2009; Reisser et al., 2014). Large-scale distribution patterns, such as the convergence of plastic debris in the sub-tropical gyres, are predicted by oceanographic circulation models. These patterns have been largely corroborated by empirical data from at-sea surface sampling (Lebreton et al., 2012; Maximenko et al., 2012; Van Sebille et al., 2012; Cozar et al., 2014; Eriksen et al., 2014). However, the total quantities of floating debris calculated from these empirical observations are orders of magnitude smaller than the values predicted. Recently published estimates of the actual global load of marine plastic vary. Eriksen et al. (2014) estimate a total weight of 268,940 tons of plastic of all sizes floating on the surface of the world's oceans. Cozar et al. (2014) calculate the global weight of microplastics specifically at between 7,000 and 35,000 tons. This reflects the findings of a regional study conducted in the eastern Pacific that estimated a total load of 21,290 tons of microplastic in that region (Law et al., 2014). Based on comparisons with global production estimates however, these values should lie somewhere between 1 and 30 million tons (Thompson, 2006; Cole et al., 2011, Cozar et al., 2014; Plastics Europe, 2014). This suggests that despite the buoyancy and durability of most plastic materials (Andrady, 2011), substantial quantities are being lost from the ocean surface (Eriksen et al., 2014).

Furthermore, when observed and expected abundance values are compared across size classes, both of the global studies mentioned above report observed abundances of microplastics (<5 mm) significantly lower than expected, especially for items <1mm (Cozar et al., 2014; Eriksen et al., 2014). Again, this is contrary to what would be expected, as the size composition of litter entering marine waters from land-based sources, which account for the majority of litter observed at sea (Ryan, 2013), typically show higher densities of smaller items than larger items (Ryan et al., 2014a; Martins and Sobral, 2011). These findings suggest a spatial gradient between the relative abundances of small and large items of floating debris with increasing distance from shore.

Such a gradient is evident in the findings of other recent studies reporting ship-based observations of floating litter at sea (Ryan, 2013; 2014). These studies show progressively fewer smaller items visible on the ocean surface as distance from coastal waters increases in both the Bay of Bengal (Ryan, 2013) and the South Atlantic Ocean (Ryan, 2014). Similar gradients also appear among the types of litter items observed, with more buoyant items such as empty bottles and polystyrene fragments relatively more abundant further out to sea and

less buoyant items such as food wrappers, appearing to be more prolific nearer to shore. This pattern of debris size and type with distance from shore has not yet been explicitly reported.

Figures 1 and 2 show the results of unpublished data from a subsequent survey of the size composition of floating debris at sea conducted in the same region as Ryan (2014). These data provide further empirical evidence for this pattern, with a high abundance of items of 5cm or smaller observed in coastal and shelf waters compared to a relative paucity of the same size in oceanic waters. The opposite appears to be true in oceanic waters, where larger items occur more frequently (Figure 1).

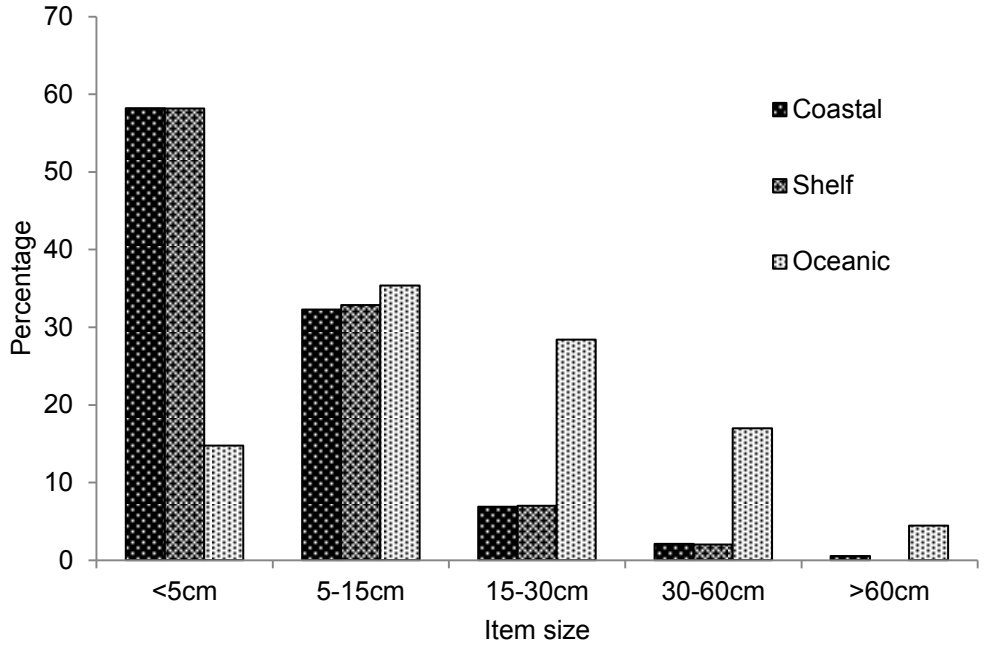


Figure 1: The percentage composition of floating marine litter by litter item size in coastal, shelf and oceanic waters in the South Atlantic Ocean. Data from Ryan (2014), Ryan et al. (2014b) and unpublished surveys of ship-based observations of debris off South Arica. Total observations: $n_{coastal}$ = 399; n_{shelf} = 189; $n_{oceanic}$ = 359.

Similarly, there are striking differences in the types of litter observed in oceanic waters compared to coastal waters (Figure 2), where smaller thinner litter items become less common with increasing distances from shore and very buoyant items, such as empty bottles and polystyrene fragments, become proportionally more abundant further away than they are closer to pollution sources.

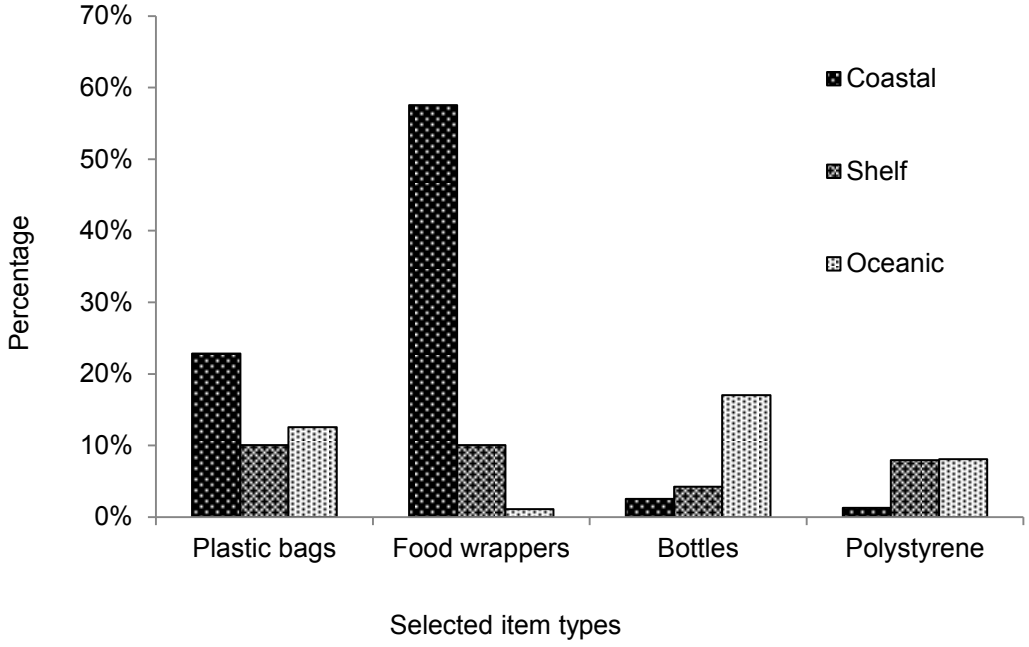


Figure 2: The percentage composition of floating marine litter by litter item type in coastal, shelf and oceanic waters in the South Atlantic Ocean. Data from Ryan (2014), Ryan et al. (2014b) and unpublished surveys of ship-based observations of debris off South Africa. Total observations: n= 947.

My thesis takes these apparent dispersal patterns as its departure point and explores them further. If smaller plastic fragments are being removed from the sea surface, it follows that larger, more buoyant plastics are less susceptible to these mechanisms and are more likely to remain at the sea surface for longer periods. They are also likely to disperse over greater distances than smaller plastics, which is supported by the preliminary observations shown in Figures 1 and 2.

Chapter 1 investigates empirically how litter size and buoyancy influence dispersal distances, to provide further evidence of the effects of the selective sinking out of plastic litter items. This chapter reports the size and buoyancy characteristics of beach litter samples collected at seven different beach sites located at varying distances from a major urban pollution source in the South Atlantic Ocean. It compares the size characteristics of these samples to marine debris observed at sea in the same region. I tested the prediction that smaller, less buoyant plastics are more abundant in litter samples collected close to a pollution source, whereas larger, more buoyant plastics are more likely to dominate samples collected far from their source.

Chapter 2 focuses on the apparent selective removal of microplastics from the sea surface. Several explanations for this have been proposed. These include fragmentation rates that are either much faster (nano-fragmentation, Law et al., 2010) or much slower than those included in current models (Eriksen et al., 2014), near-shore trapping (Isobe et al., 2014), ingestion by marine organisms (Cozar et al., 2014), vertical wind mixing in the upper ocean layer (Kukulka et al., 2012; Reisser et al., 2014), and sinking due to biofouling by algae and other epibiotic organisms (Andrady, 2011; Wright et al., 2013; Cozar et al., 2014). It is also likely that a combination of these physical, chemical and biological processes is responsible.

In this chapter, I investigate one of these mechanisms: marine biofouling and the extent to which it might account for the disappearance of smaller plastic fragments, due to their proportionally larger ratio of surface area to volume. In it, I report an experimental investigation into the effect of fragment size on the rate of biofouling growth and subsequent buoyancy loss of buoyant plastic debris.

The thesis concludes with a brief synthesis that highlights the main findings from each chapter and makes recommendations for further research.

CHAPTER 1

AN EMPIRICAL INVESTIGATION INTO THE SIZE AND BUOYANCY CHARACTERISTICS OF DISPERSED MARINE DEBRIS IN THE SOUTHERN ATLANTIC OCEAN

INTRODUCTION

Our knowledge of the composition and worldwide distribution of marine debris is derived from four main sources: beach litter surveys; at-sea surveys; estimations of debris entering the marine environment (from ships and from river runoff) and the monitoring of interactions between debris and marine wildlife (Rees and Pond, 1995; Ryan et al., 2009). Each type of study has its own set of advantages and drawbacks (Ryan et al., 2009) and findings are often undermined by inconsistencies in data collection methods and data that are not comparable (Ribic, 1996; Velander and Mocogni, 1999; Ryan, 2013). Despite these limitations, reasonably robust data can be collected when sampling techniques are well documented and standardised (Cheshire et al., 2009; Ryan, 2013).

Comparisons between data from at-sea litter surveys and beach litter surveys in the same area are rarely drawn, usually because the different techniques are used to answer different questions and the data are not comparable. Thiel et al. (2013) is one example. Comparisons of this kind are valuable because the two survey types contain different biases. At-sea surveys from boats are complicated by the effects of hydrodynmic processes such as eddy fields, and visual detection surveys are also dependent on weather and light conditions (Ryan, 2013). They are also costly, logistically challenging and skill-dependent (Ryan et al., 2009). These kinds of at-sea surveys however can detect litter over large distances and avoid the interference of local beach dynamics and surrouding land-uses (Ryan, 2013). Beach litter surveys on the other hand are cost-effective, require little in the way of specialised skills or equipment and are more accessible than the open ocean or indeed the seabed (Madzena et al., 1997; Derraik, 2002; Ryan et al., 2009). However, the reliability of data from beach litter surveys can also be compromised by sampling biases. For instance, smaller and buried items are often overlooked (Ryan et al., 2009), beaches with high seaweed accummulation rates show underestimated litter abundances and sampling also tends to be more selective when litter loads are larger (Velander and Mocogni, 1999). By using beach litter surveys to collect data comparable with those compiled from an at-sea survey of floating litter in the same region, I hoped to add weight to the inferences that could be drawn from both.

The use of beach litter surveys to understand marine debris distribution

In addition to providing information about the presence and types of litter in different regions when conducted and reported methodically (Ryan et al., 2009), beach litter surveys have

served as indicators of some important trends in marine debris. These include the prevalence of plastic as a marine pollutant (Gregory and Ryan, 1997), the major sources of marine pollution (Ryan et al., 2009), the distances that buoyant debris can travel and the threat of rafting by alien species (Winston et al., 1997; Barnes et al., 2009). Analysis of beach litter composition can also be useful from a management perspective (Edyvane et al., 2004; Liu et al., 2013). Long-term beach litter surveys conducted in South Australia for example, showed a consistent decline in ship-based debris following the implementation of MARPOL Annex V in 1991, suggesting that compliance enforcement measures were indeed effective in those waters (Edyvane et al., 2004).

Aim of this study

In the present study, the aim was to explore trends in the buoyancy and size characteristics of litter with increased dispersal distance from the same pollution source, to provide support for the patterns shown by a recent at-sea survey conducted in the South Atlantic Ocean (Figures 1 and 2). These suggest that the size and buoyancy composition and characteristics of visible floating marine litter changes with increasing distance from a pollution source. This pattern supports other global data recently reported, that microplastics, approximately <5 mm in size, are selectively disappearing from the sea surface (Cozar et al., 2014; Eriksen et al., 2014). Based on this evidence, I expected to find a higher abundance of smaller items close to a source of marine plastic pollution, with proportional quantities reducing as distance from the source increased. I also expected to find a greater number of larger, more buoyant items further from the source.

The primary means of data collection were beach litter surveys conducted in the Western Cape Province of South Africa and on the island of Tristan da Cunha (Tristan).

Urban beaches are known to reflect marine litter inputs and remote beaches are known to track long-distance litter (Ryan et al., 2009). By contrasting the size and buoyancy composition of marine litter on urban and increasingly remote beaches along a transect, it is possible to draw inferences about the effect of dispersal distance and concomitantly, dispersal time, on the mean size and buoyancy of dispersed debris. It is also possible therefore, to profile the characteristics of the debris that enters marine environments but does not disperse.

STUDY AREA AND METHODS

Beach litter samples were collected from two urban beaches and four remote beaches on the southwestern coast of South Africa's Western Cape Province, at increasing distance intervals from the city of Cape Town (34°S, 18°E; Figure 3, Table 1). These samples were compared in terms of their buoyancy, volume, diameter or maximum length, surface area, mass and thickness. A seventh sample was collected from the islands of Tristan da Cunha (37°S, 12°W) and Gough Island (40°S, 10°W) in the central South Atlantic, approximately 2,800 km west of Cape Town (Ryan, 2013). Cape Town was treated as a singular pollution point source. Urban beaches were located within the metropolitan boundaries of Cape Town. Remote beaches were located at distance intervals of approximately 100 km and 200 km from the city centre in two directions: northwest of the city up the province's western coast, and southeast towards the province's southern coast. One urban beach was selected from each side of the city. This resulted in two comparable coastal profiles, each comprising one urban beach, one intermediate remote beach (100 km) and one distant remote beach (200 km).

Study area

Cape Town is a large urban centre, with the metropolitan area centred on the Cape Peninsula and extending 30 km north along the west coast and east along the northern shores of False Bay. The city is home to more than 3.74 million inhabitants (City of Cape Town, 2012). The city's beaches are characterised by high litter loads, mainly from land-based sources (Ryan et al., 2014a). The coastal waters of the South Atlantic Ocean support heavy commercial shipping around the southern tip of the continent (Lebreton et al., 2012; Ryan, 2014). Cape Town Harbour in Table Bay is a major hub for cargo ships, as well as a stopover point for many foreign fishing fleets that operate in the pelagic waters of the South Atlantic, oil carriers and other smaller commercial and tourism-related shipping activity (National Ports Authority, 2014). Marine litter in this region of the ocean is therefore likely to have both land-based and marine based sources. Tristan is also strongly influenced by land-based debris from South America, given prevailing westerly winds and currents in this region (Ryan et al., 2009; Lebreton et al., 2012).

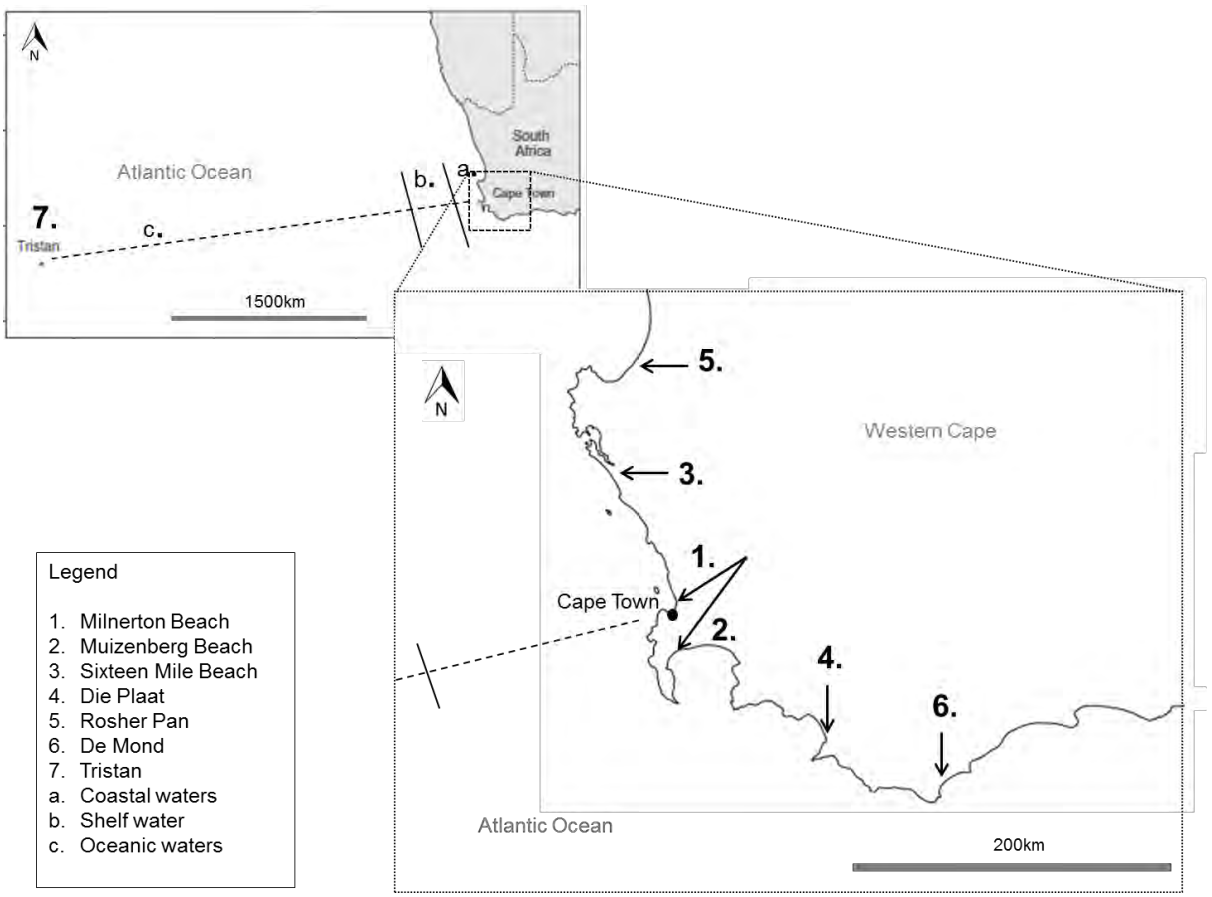


Figure 3: Location of the six beach sampling sites in the Western Cape, South Africa and the seventh at Tristan da Cunha in the South Atlantic Ocean, and the transect line of the at-sea survey conducted between Cape Town and Tristan.

Study design

Beaches were selected based on their location and their physical characteristics. All beaches had a substrate of fine sand, gentle to moderate beach gradients and were over 500 m in length. All were similarly exposed to the sea, with no jetties, breakwaters, tidal pools or rocky outcrops. All were backed by a line of well vegetated dunes. Freshly washed-up litter was collected from each beach during October and November 2014. No prior clean-ups were performed (Ryan et al., 2009) although Milnerton Beach is cleaned daily by municipal workers and would have been cleaned the day before sampling. Sampling at the urban sites took place in the early morning (07:00 - 07:30), before the arrival of most visitors and at various times for the remote beach sites.

Table 1: The seven beach survey sites where litter was sampled during October and November 2014, divided into coastal sets, "West" for the sampling set northwest of Cape Town and "South" for the set southeast of Cape Town, with approximate distances from the Cape Town metropolitan area.

Sample set	Km from CT	Beach	Type of access	Location
West	0	Milnerton	Public, urban beach	Table Bay
West	100	Sixteen Mile	Restricted, protected area	W. Coast Nat Park
West	200	Rocher Pan	Restricted, protected area	Rocher Pan Nature Reserve
South	0	Muizenberg	Public, urban beach	False Bay
South	100	Die Plaat	Restricted, protected area	Walker Bay Nature Reserve
South	200	De Mond	Restricted, protected area	De Mond Nature Reserve
Oceanic	2800	Tristan da Cunha	Restricted, protected island	South Atlantic Ocean

Table 2: Transect lengths sampled and numbers of freshly stranded items collected at each beach

Site	Transect length (m)	Sample size
Urban beaches (0 km)		
West Coast	350	256
South Coast	750	279
Intermediate beaches (100 km)		
West Coast	500	520
South Coast	4,500	186
Remote beaches (200 km)		
West Coast	4,300	180
South Coast	5,200	198
Oceanic beaches on Tristan/Gough (2,800 km)	1,100	150

Sampling was conducted at the highest strand line by either one or two observers. Only litter on wet sand was collected and a lower size limit of 2 mm was applied at all sampling sites, to ensure consistency. All items collected were placed in reinforced refuse bags. Most bottles collected were empty, but if a closed bottle contained water, I recorded the water level of the contents. At the furthest remote beach on the west coast (Rocher Pan), low litter levels resulted in the entire beach being cleaned (although only litter on wet sand was retained from the first visit). This beach was re-visited five days later and a second sample collected of all debris that had accumulated. The minimum sample size aimed for was 200 items, based on

initial estimates of how much variation was expected. This determined the minimum transect length at each site, which ranged from 350 m to 4.3 km due to differences in litter densities. It was not possible to reach this target at the more remote sampling sites because litter densities were too low (Table 2). To assess the composition of litter at a really remote site, litter was also collected on Tristan da Cunha and Gough Islands in the central South Atlantic. The litter on a 1000-m stretch of sand and cobble beach west of Tristan settlement was removed on 10 September 2014. This beach was visited again 20 days later on 30 September 2014, and all accumulated litter collected. A few additional samples of freshly-washed up litter were collected from cobble beaches on Gough Island from 14 to 28 September 2014.

Data measurement

Samples were processed at the laboratory. Each item was washed, dried in a drying oven at 30°C for a minimum of 24 h, and labelled. Plastic sleeves and packets required the longest drying time and in many cases needed to be turned inside out to expose both the interior and exterior surfaces.

Items were classified by their material as either plastic or non-plastic (wood, metal, glass, brick, stone, latex, paperboard, leather or cloth). Following Ryan (2014), they were categorised as follows: packaging (food wrappers, bottles, lids, bags, pressed polystyrene, other wrappers, for example hygiene wrappers, polystyrene lumps, packaging tape, food tubs and containers, and tubes); disposable items (cigarette filters, straws, earbuds, and sucker sticks); fishing-related items (rope, foam, fish tray pieces, floats, reels and other, such as lightsticks); pieces (hard shards and soft fragments of plastic with unidentifiable uses) and personal items(hardware items, toothbrushes, shoe soles and cigarette lighters). Non-plastic items included tins and cans, light bulbs, glass bottles, fragments of wooden items and natural debris. The presence of visible encrusting epibiota was also recorded and broadly classified according to the most common groups found. It was not possible to identify biota to species level.

Samples were weighed using a digital scale accurate to 0.01 g. The material thickness of each item was measured using a micrometer accurate to the nearest 0.01 mm, Vernier callipers, accurate to the nearest 0.1 mm or a ruler accurate to the nearest 1 mm. In instances where the thickness of an item was variable, such as a bottle where the plastic around the main body is thinner than the plastic at the neck, the thickness of the main body was recorded.

The dimensions of each item were measured using a ruler or tape measure. Items were allocated to one of five size classes: a (<5 cm), b (5-15 cm), c, (15-30 cm), d (30-60 cm) and e (>60 cm) to match the protocol used in the at-sea surveys in the same area (Ryan, 2014).

Surface area was estimated based on the approximate shape of the item. Where items were best described as composites of several shapes, their surface areas were calculated as the sum of the surface areas of their component parts. For example, the surface are of a round tub with its lid on was calculated as the sum of the surface area of the cylinder of its main body, plus the surface area of two discs, for its lid and its base. Total surface area contained all surfaces, both inside and out. Volume was calculated by measuring the volume of seawater displaced by each item when fully submerged in a measuring cylinder. Two measures of buoyancy were also recorded using this method of displacement: free-floating buoyancy and submerged buoyancy. Free-floating buoyancy here refers to the buoyant force acting upon the item when it floats on the surface unimpeded, the minimum buoyant force that it would experience floating in natural conditions. This was calculated by measuring the volume of seawater displaced by each item when allowed to float freely and multiplying this by the density of seawater (1.027 $g.cm^{-3}$). Submerged buoyancy refers to the buoyant force acting on the item when its volume is totally submerged and the equivalent volume of water displaced is at a maximum. This would equate to the maximum buoyant force that could act upon the item when submerged in the upper surface ocean layer, where seawater density can be reasonably given as a constant. This was calculated as the item's volume multiplied by the density of seawater.

Seawater was obtained from the laboratory aquaria. Displacements were conducted in measuring cylinders of six different capacities: 10 ml (±0.1ml), 100 ml (±1 ml), 250 ml (±2 ml), 500 ml (±5 ml), 1,000 ml (±10ml) and 2,000 ml (±20 ml). A 3,000 ml beaker and a cylindrical 16-litre tank were used for larger items. Items that were too large for the 16 litre tank were cut or broken into parts and either measured together or successively. Three measures were taken for bottles that were cracked or did not have a lid: water displaced by free floating, water displaced when submerged without being allowed to fill and water displaced filled, after which point most sank.

Statistical analysis

Statistical analyses were performed in the R environment Version 3.1.2 (R Core Team, 2014), using the packages, car v 20-2.2 (Fox and Weisberg, 2011), lme4 v 1.1-7.0 (Bates et al., 2014) and lsmeans v 2.14 (Lenth and Herva, 2014).

The effect of distance from Cape Town on the mean free-floating buoyancy of beach litter items and on various size parameters including volume, maximum length, surface area, thickness and mass was analysed using a generalised linear mixed model (GLMM) to control for possible non-independence of the data, with a negative binomial distribution and a logistic-link function. Measurement values were rounded before fitting the model, which does not accept non-integer values. Residual plots were visually inspected to ensure model assumptions were met.

Each model included distance from Cape Town as a fixed effect and sampling site as a random effect. The significance of the effect of distance on each parameter was analysed according to χ^2 goodness-of-fit tests using the Anova function in the car package (Fox and Weisberg, 2011). The means and 95% confidence intervals for each parameter were calculated using the lsmeans function (Lenth and Herva, 2014) and then back-transformed.

RESULTS

A total of 1,769 litter items was collected, of which 97% were made of plastic. The total mass collected was 23.057 kg. Packaging was by far the most common type of litter, making up 69% of all items collected. Single-use disposable items and fishing-related paraphernalia contributed 9% each to the total while unidentified hard plastic pieces comprised 8% (Table 3).

The proportional abundance of plastic bottles increased with increasing distance from Cape Town from 1% of the total items collected at 0 km, 2% at 100 km, to 10% at 200 km to 37% at 2,800 km. The proportional abundance of large fragments of polystyrene showed a similar overall gradient, although less steep: from 3% at 0 km, 2% at 100 km, 10% at 200 km to 13% at 2,800km (Table 3). Other items that reflected this increase in relative abundance were fishing or shipping-related items such as rope and polyurethane foam fragments, although the trend did not extend all the way to Tristan, where fish tray fragments and floats were the more common fishery items. Food wrappers, including items such as chip packets and chocolate wrappers, were the most abundant items at coastal beaches, and together with cigarette filters and single-use disposable items overall, they decreased in abundance with increasing distance from Cape Town.

Spatial trends in buoyancy and size characteristics

The mean free-floating buoyancy of beach litter differed significantly among litter samples collected from different sampling sites (χ^2=98.01, df=1, p<0.0001) and the mean submerged buoyancy of items showed an even stronger spatial trend (χ^2=150.9, df=1, p<0.0001).

Mean free-floating buoyancy rose 50-fold over the full distance covered by the study, from 5.2 g^{-1} at Cape Town to 15.1 g^{-1} at 100 km, 56.5 g^{-1} at 200 km and 266.2 g^{-1} for the items collected at Tristan (Table 4, Figure 4). Many items such as food wrappers and hard plastic fragments floated just below the water surface when released into the measuring cylinders, such that the volume of water displaced was the same when floating as it was when submerged. The more buoyant items however, with higher volumes and enclosed gases, such as bottles and polystyrene fragments displaced low volumes of water when floating freely and very high volumes when forcibly submerged.

Table 3: The abundance and composition of beach litter collected at sampling sites during September to November 2014.

	0km		100km		200km		2,800km		Total	
	n	%	n	%	n	%	n	%	n	%
Packaging										
Food wrappers	231	43	209	30	49	13	1	1	490	28
Lids and lid rings	36	7	104	15	23	6	11	7	174	10
Bags	11	2	83	12	28	7	0	0	122	7
Bottles	4	1	14	2	37	10	56	37	111	6
Pressed polystyrene	44	8	16	2	43	11	0	0	103	6
Other wrappers	27	5	39	6	12	3	0	0	78	4
Polystyrene	14	3	6	1	38	10	20	13	78	4
Packaging tape	14	3	13	2	6	2	0	0	33	2
Tubs and containers	3	1	9	1	10	3	1	1	23	1
Tubes	0	0	8	1	2	1	1	1	11	1
Total	**384**	**72**	**501**	**71**	**248**	**66**	**90**	**60**	**1223**	**69**
Disposable items										
Cigarette filters	53	10	0	0	4	1	0	0	57	3
Straws	22	4	17	2	6	2	0	0	45	3
Earbuds	2	0	26	4	1	0	1	1	32	2
Sucker sticks	3	1	11	2	1	0	0	0	15	1
Other	2	0	1	0	1	0	1	1	5	0
Total	**83**	**16**	**56**	**8**	**13**	**3**	**2**	**1**	**154**	**9**
Fishing and shipping-related items										
Rope	8	1	30	4	39	10	2	1	79	4
Dense foam	2	0	1	0	18	5	6	4	27	2
Fish tray pieces	2	0	2	0	1	0	10	7	15	1
Floats	0	0	1	0	4	1	9	6	14	1
Reels	3	0	4	1	1	0	0	0	8	0
Other	0	0	3	0	2	1	5	3	10	1
Total	**15**	**0**	**41**	**6**	**65**	**17**	**32**	**21**	**153**	**9**
Pieces										
Large hard fragments	22	4	41	6	16	4	1	1	80	5
Small hard fragments	5	1	43	6	11	3	5	3	64	4
Total	**27**	**5**	**84**	**12**	**27**	**7**	**6**	**4**	**144**	**8**
Personal and household items										
General hardware	0	0	7	1	3	1	3	2	13	1
Toothbrushes	0	0	1	0	2	1	2	1	5	0
Shoe soles	1	0	0	0	0	0	3	2	4	0
Lighters	0	0	1	0	1	0	0	0	2	0
Other	4	1	5	1	2	1	3	2	14	1
Total	**5**	**1**	**14**	**2**	**8**	**2**	**11**	**7**	**38**	**2**
Non-plastic items										
Wooden items	1	0	3	0	6	2	0	0	10	1
Natural debris	0	0	0	0	1	0	5	3	6	0
Tins and cans	2	0	1	0	0	0	1	1	4	0
Glass bottles	0	0	0	0	0	0	2	1	2	0
Light bulbs	0	0	0	0	2	1	0	0	2	0
Other	18	3	6	1	8	2	1	1	33	2
Total	**21**	**4**	**10**	**1**	**17**	**4**	**9**	**6**	**57**	**3**
Grand Total	535	100	706	100	378	100	150	100	1769	100

The distribution profiles of free-floating buoyancy at each distance reflect this trend (Figure 5). Almost 95% of the urban beach samples (0 km) occupy the two smallest buoyancy classes. This proportion decreases only slightly over the first 100 km distance interval to approximately 90% and then more steeply to just over 50% at 200 km, with another 25% of litter items in the next highest class. Conversely, less than 20% of the Tristan sample occupies these low buoyancy values, while the most common items (approximately 55% of the overall sample) are an order of magnitude more buoyant.

The increase in mean volume was strongly significant (χ^2=506.6, df=1, p<0.0001), despite the fact that variation within samples was high (Figure 6). The distribution profiles for volume follow similar patterns to those of free floating buoyancy (Figure 7).

In terms of item length or diameter, litter became increasingly likely to be larger as distance from Cape Town increased (χ^2=9.325, df=1, p=0.002, Figure 8). When grouped into size classes a – e, the proportion of items in size class a, <5 cm, decreased steadily with increasing distance from Cape Town, replaced at each interval by an almost equivalent proportion of items in class size c, 15-30 cm. Maximum proportions at 0 km, 100 km and 200 km were all in class size b, 5-15 cm (Figure 8).

Mean litter mass increased significantly (χ^2=129.74, df=1, p<0.0001) from 1.2 g at Cape Town (0 km), to 4.6 g, 100 km from Cape Town, 10.5 g, 200 km from Cape Town and 100.2 g at Tristan (2,800 km from Cape Town) (Table 4). The material thickness of the litter items also increased significantly overall although the trend was less marked (χ^2=12.966, df=1, p=0.0003) and in fact showed a slight decrease over the first 100-km interval. Mean material thickness changed from 1.5 mm at Cape Town to 1.1 mm at 100 km, 4.1 mm at 200 km and 8.5 mm at 2,800 km (Table 4).

Table 4: Means and 95% confidence intervals for buoyancy and size parameters of beach litter at increasing distance from Cape Town

Dist. (km)	0	100	200	2800
Parameter				
Free-floating buoyancy (g^{-1})				
Mean	5.2	15.1	56.5	266.2
95% CI	3.3 - 8.3	9.6 - 23.7	35.3 - 90.4	135.4 - 525.8
Volume (ml)				
Mean	5.1	16.9	94.7	604.4
95% CI	3.7 - 6.9	11.4 - 24.9	61.3 - 146.2	395.1 - 924.8
Length (mm)				
Mean	97.3	122.8	145.9	178.9
95% CI	76.2 - 124.2	96.3 - 156.7	113.9 - 186.9	125.4 - 255.2
Mass (g)				
Mean	1.2	4.6	10.5	100.2
95% CI	1.0 - 1.5	3.9 - 5.4	8.5 - 13.0	71.7 - 140.1
Material thickness (mm)				
Mean	1.5	1.1	4.1	8.5
95% CI	1.2 - 1.7	0.9 - 1.2	3.3 - 4.8	5.9 - 11.1

Figure 4: Change in mean free-floating buoyancy of beach litter with increasing distance from Cape Town. Error bars show 95% confidence limits. Axes are shown on logarithmic scales; the Cape Town sample (0 km) has been shown as a distance of 1 km to ensure its visibility using this scale.

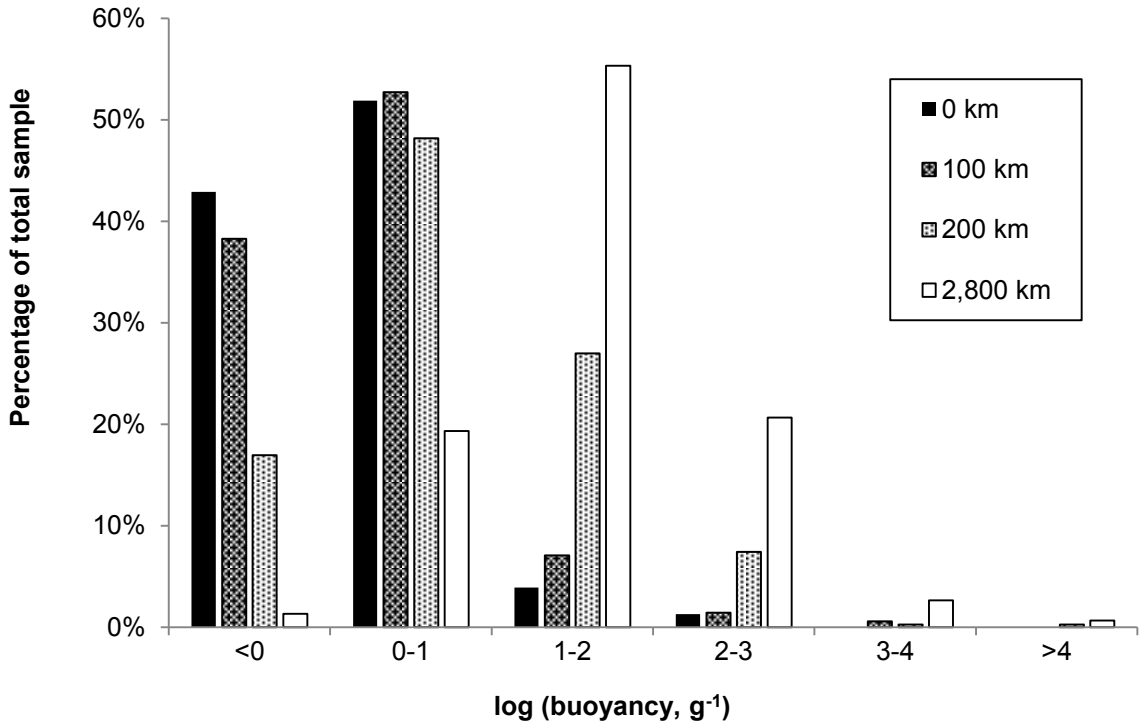


Figure 5. Distribution profiles of free-floating buoyancy of beach litter samples at each distance interval. Total observations: $n_{0\ km}$ = 535; $n_{100\ km}$ = 706; $n_{200\ km}$ = 378; $n_{2,800\ km}$ = 150. Data have been logged

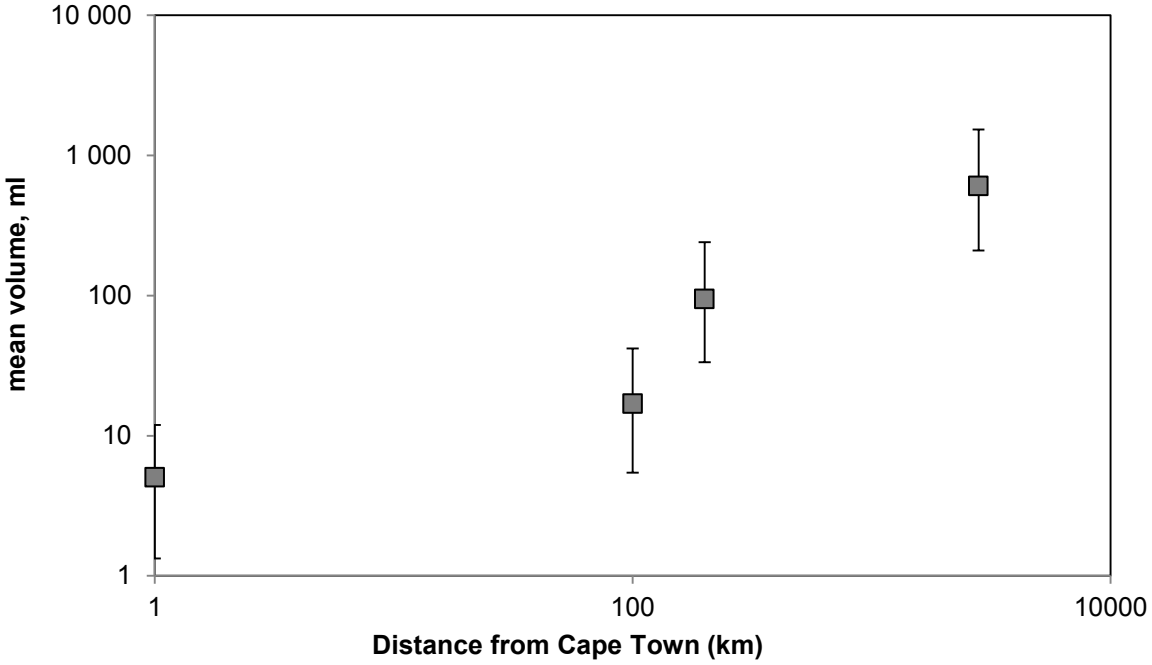


Figure 6: Change in mean volume of beach litter with increasing distance from Cape Town. Error bars show upper and lower 95% confidence limits. Axes are shown on logarithmic scales; the Cape Town sample (0 km) has been shown as a distance of 1 km to ensure its visibility using this scale.

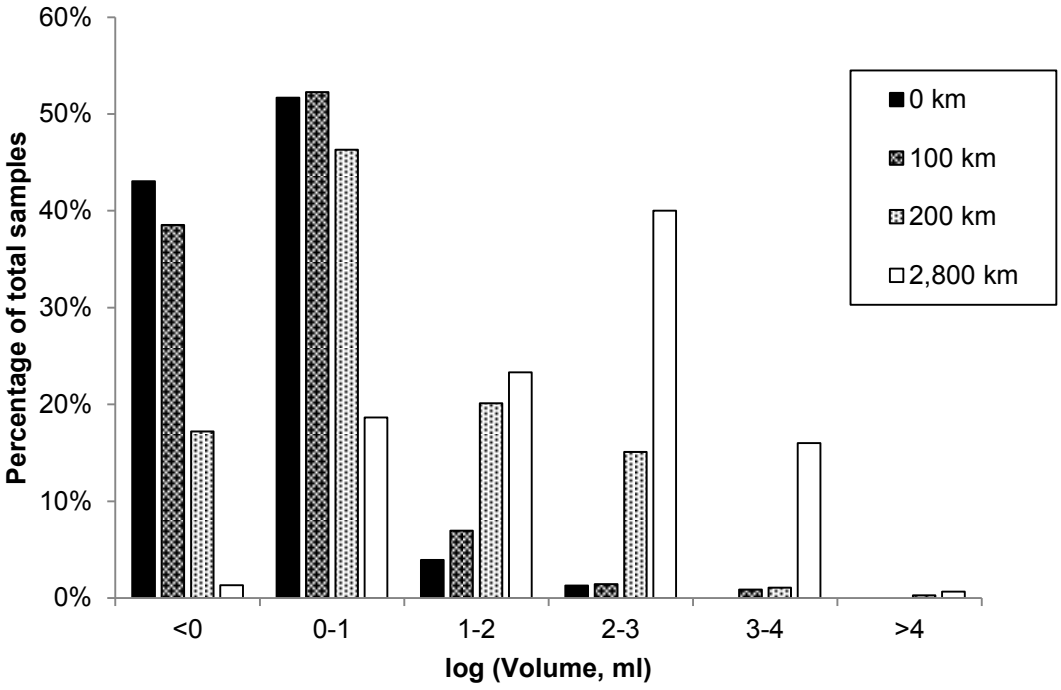


Figure 7: Distribution profiles of volume of beach litter samples at each distance interval. Total observations: $n_{0\ km}$ = 535; $n_{100\ km}$ = 706; $n_{200\ km}$ = 378; $n_{2,800\ km}$ = 150. Data have been logged.

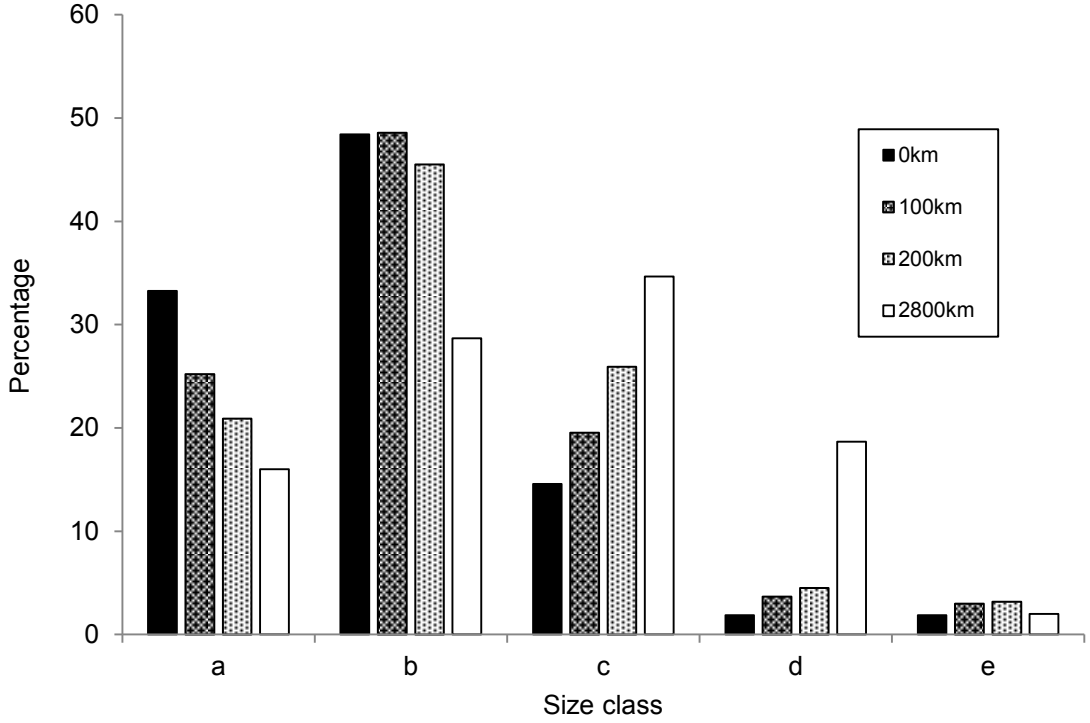


Figure 8: Size composition of beach litter collected binned according to the same size categories used in the at-sea data in Figure 1. Total observations: $n_{0\ km}$ = 535; $n_{100\ km}$ = 706; $n_{200\ km}$ = 378; $n_{2,800\ km}$ = 150.

Epibiota

I recorded six main groups of large encrusting epibionts: algae and algal films; bryozoans; goose barnacles (*Lepas* spp.); other barnacles; mussels and polychaete worms (Tables 5 and 6). There were no clear trends for any species except goose barnacles which increased in frequency with distance from Cape Town. They were observed on 50 items in total, 0% of Cape Town litter, 1% of the 100-km litter, 3% of the 200-km litter and on 21% of the Tristan litter. Algae or algal films were the most common (Table 5) and were present on almost half of the 10-km litter sample (43%), 19% at 200 km and 9% of the items collected at Tristan. After algae, encrusting bryozoans were the most common biota, observed on 68 items, only two of which were items retrieved from Cape Town. Barnacles were less common; observed on approximately 2% of the 100-km and 200-km samples, mussels on 6% of 200-km samples and 5% of Tristan samples (Table 6). Polychaete worm tunnels were on 2% of the samples overall.

Table 5: Percentage of item categories with epibiota

Item category	Algae	Barnacles	Bryozoa	Lepas	Polychaete worms	Mussels	No epibiota	Total
Disposable items	6	0	1	1	0	1	91	100
Fishing related	10	1	5	7	1	4	72	100
Packaging	28	1	4	3	1	3	60	100
Personal and household items	11	0	8	3	3	5	70	100
Pieces	26	2	5	1	1	1	64	100
Non-plastic items	9	0	4	4	0	4	79	100

Table 6: Percentage of items at each distance interval with epibiota

Km from Cape Town	Algae	Barnacles	Bryozoa	Lepas	Polychaete worms	Mussels	No epibiota	Total
0	3	0	0	0	0	1	95	100
100	43	2	3	1	1	1	49	100
200	19	2	8	3	1	6	60	100
2800	9	0	12	21	0	5	52	100

DISCUSSION

The predictions of my study were based on preliminary evidence that the composition and characteristics of visible floating marine litter change the further away one travels from litter source areas. Quantitatively, I predicted that the mean size and buoyancy of beach litter at five remote beaches at increasing distances from Cape Town would be higher than on two urban beaches located within the metroplitan area of the city. The results of my study confirm these predictions for all parameters of size and buoyancy measured: notably mean item volume, free-floating and submerged buoyancy, length, surface area, material thickness and mass all increased significantly as distances to more remote beaches increased. Volume showed particularly pronounced increases with each distance interval and an overall mean 100-fold increase across the full distance between sampling sites. These trends are shown independently in both directions away from Cape Town, up the west coast and towards the south coast. The size distributions of the items I sampled on beaches, in terms of maximum length, were also reflected by the size distribution of floating litter sampled at sea in the same region. My results provide further support to the recent hypothesis put forward (Cozar et al. 2014, Eriksen et al. 2014) that substantial quantities of small plastic particles are lost from the sea surface, and that this phenonemon is not restricted to microplastics. My findings indicate that small macro-debris items also fail to disperse long distances from major land-based sources, especially items made from thin plastic that lack included air pockets, limiting their ability to drift at the surface while supporting biofouling communities.

Trends found by other beach litter surveys

It is widely noted throughout the beach debris literature that comparisons between data are rarely possible because sampling and data classification methodologies are not standardised (Gregory and Ryan 1997; Ryan et al., 2009, Hidalgo-Ruz et al., 2012). This makes it difficult to extract and compare trends from previously published reports, despite the fact that such a multitude of reports is available (Derraik et al., 2002; do Sul and Costa 2007; Ryan et al., 2009).

Similar beach litter studies analysing spatial variations in size compostion of litter are difficult to find. Thiel et al. (2013) studied comparisons in size between beached and coastal debris, but distances involved did not exceed more than ~10km. They found small differences in the diversity of debris type with increasing distance from the shore, noting the debris

became dominated by styrofoam and manufactured wooden items, whereas on shore, it was much more varied (Theil et al., 2013). This reflects the patterns found in my study to some extent, in terms of the increased abundance of polystyrene lumps with distance, but again the short distance intervals used here limit comparisons. Santos et al. (2005) looked at debris composition on non-urban beaches in northwest Brazil and found that plastic bottles were the dominant debris type (35%), which echoes my findings regarding the high dispersability of plastic bottles and polystyrene lumps as the most super-buoyant items. However, the survey site again was a much shorter distance from the nearest city, only 60 km (Santos et al., 2005).

Madzena et al. (1997) was the only study that included a report of size composition profiles at different beach sites. The study reported surface area as an indicator of size in their study of debris at six different beaches along another South African coastline: the Transkei in the Eastern Cape. This study too found different results to mine. The most contaminated beach surveyed by litter density, Coffee Bay, also contained the highest number of large items (>100 cm^2) and the smallest numbers of small items (<1 cm^2). This was opposite to my findings, which found the most contaminated beaches to contain the highest quantities of small pieces with a relative paucity of large items. Again however, these comparisons can only be drawn very coarsly. Coffee Bay is a rural beach site, rather than a major pollution source like Cape Town. Furthermore, the study sampled along three randomly located transects rather than only selecting freshly washed up litter from below the strand line. Since fragmentation is known to be accelerated by beach dynamics (Barnes et al., 2009; Corcoran et al., 2009), standing stock assessments of litter composition are not necessarily indicative of wider trends, making comparisons with findings from other studies difficult.

Of course there are several studies that report the vast distances that items of plastic debris can disperse, giving data on presence and or litter densities on other Antarctic or subantartic islands similarly remote to Tristan (Gregory and Ryan, 1997; Convey et al., 2002; Barnes et al., 2010; Eriksson et al., 2013). But low litter densities and the emphasis on fishing gear make it difficult to extract meaningful comparisons with my results.

Other potential causes for observed trends

Beach litter surveys are at best, simplified snapshots of extremely complex systems (Ryan et al., 2009). Winds, waves, local tidal patterns and currents as well as numbers of beach-goers, nearby land-use and marine activity and regular beach cleanups all influence direct litter

input patterns at different beaches (Corbin and Singh, 1993; Ryan et al., 2009, Ribic et al., 2010; 2012; Martins and Sobral, 2011; Slavin et al., 2012; Ryan et al., 2014a). Longer term factors such as coastal geomorphology also bias the accumulation patterns of debris from offshore (Bowman et al., 1998; Kataoka et al., 2013) and these factors also combine to determine the retention rates of litter on different beaches (Ryan et al., 2014a). These results need to be considered in this context, as various factors could be responsible for the contrasting compositional profiles found. For example, smaller items, such as sweet wrappers and drinks straws that were more common among the urban beach samples are characteristic of the litter being deposited directly on city beaches. Large fragments of polystyrene and larger bottles more common among the remote samples may be more likely to enter the system as shipping and fishing jetsam or as river-borne waste from inland sources closer to those sampling sites. Their relative abundance could in that case be a function of different input sources, rather than differences in the dispersal reach of different sizes or types of litter from the same source. The source of washed up items is difficult to ascertain without using mark-recapture methods that were logistically too challenging with the limited time available for this study. A previous study of litter dispersal in Indonesia concluded that similar items, square polystyrene blocks, found on remote beaches were actually most likely to have been used as packaging in the urban centre of Jakarta and then dispersed, rather than having come from fishing fleets at sea (Willoughby et al., 1997). The remote sites sampled in this study were within 75 km of that city. In this study, where the distances are much greater, it is more difficult to exclude other sources.

While efforts were made to limit the influence of locally deposited litter at the remote sampling beaches by only selecting sites located within protected areas and which therefore did not receive picnickers and recreational beach visitors, there are other possible sources of locally generated litter for which I was not able to control. For the sake of simplicity, Cape Town was treated as the only major land-based pollution point source in the study area. Its influence in terms of litter inputs, was assumed to decrease radially along both coasts with no other land-based influences. While there are no towns equivalent to Cape Town along either coast, there are two significant towns which would influence litter in the area of two of the sampling sites. Saldanha Bay on the west coast is a natural harbour and significant industrial port. It lies approximately 50 km northwest of The Sixteen Mile Beach. While the prevailing large-scale currents would tend to carry floating litter up rather than down the coast, it is not possible to exclude the effect of Saldanha Bay on the composition of the litter sample from

this site (Site 3 on Figure 3). Similarly, the presence of Hermanus, a seasonal tourist town on the south coast near Die Plaat (Site 4 on Figure 3), and other tourism towns along this coast, may have different litter profiles to Cape Town's urban beaches, which may have influenced the remote coastal samples here as well.

Different regional land uses are also known to affect marine litter composition (Corbin and Singh, 1993; Thiel et al., 2013). The inland region southwest of Cape Town, known as the Overberg, supports high levels of agricultural activity, litter from which may well find its way into the regional coastal waters via river runoff.

In addition to differential input patterns, litter that reaches the water needs to overcome various physical barriers before it becomes subject to larger-scale dispersal vectors. Even though the study design aimed to include only items that had washed up and had therefore been exposed to these vectors in the water, wave action and near-shore trapping may prevent less buoyant items from entering major current paths, while more buoyant items have the advantage of being carried over such barriers by wind. A recent study conducted in Japan examining the transport of micro- (<5 mm) and mesoplastics (5-20 mm) in coastal waters (Isobe et al., 2014) found mesoplastics to be more susceptible to near-shore trapping than microplastics, which were found to disperse more widely offshore. The size range described as mesoplastics here captures many of the smaller items that dominated the urban beach samples in this study, so it is possible that some processes of near-shore trapping might be preferentially causing certain size classes to be prevented from leaving inshore waters, biasing their relative abundance among washed up litter on these beaches. Other processes such as vertical wind-mixing in the upper surface layer are known to impact the vertical distribution of buoyant plastic debris (Kukulka et al., 2012). Differential rise velocities of different size plastics when submerged have been shown to make microplastics less susceptible to these processes (Isobe et al., 2014; Reisser et al., 2014). Urban samples may therefore have included many items among the lower size classes that were being recycled at the shoreline and were being prevented from travelling further. Mark-recapture methods have been used to study litter dispersal (Bowman et al., 1998; Kataoka et al., 2013). As mentioned, such methods were not possible in this case due to time limitations, but might have provided more certainty in this regard.

Finally, the sampling methodology used necessitated a lower size limit which excluded items >2 mm in length or diameter. By identifying litter visually, observations are restricted to

washed up debris of meso- and macro-scale size classes. Another sampling methodology could have revealed different patterns. Sieved sediments taken from remote beaches in Hawaii for example found by far the majority of plastics recovered fell into the two smallest size classes: 1–2.8 and 2.8–4.5 mm. Fewer than 10% of the pieces recovered were larger than 4.5 mm in size (McDermid and McMullen, 2004). A similar bias exists in the methodology employed in the at-sea survey that motivated this study. Neuston net sampling, where the minimum sampling size is determined by the net mesh size and can be as low as several μm, has a much lower sampling limit than visual observation from a moving ship (Ryan et al., 2009). This is particularly relevant for the oceanic waters approaching Tristan, which at 37°S, 12°W, lies just south of the South Atlantic gyre (Figure 3) (Ryan, 2014). Based on previous studies of the densities of floating microplastics in other subtropical zones (Moore et al., 2001; Pichel et al., 2007; Moret-Ferguson et al., 2010), it would be expected that the density of microplastics in this region increase, and the sampling methodology used would not capture this.

Comparison with at sea survey data

Pooling the 100- and 200-km coastal samples makes it possible to compare the results of the beach litter study to those found in the survey conducted at sea in the same region, where coastal waters can be compared with the Cape Town urban samples, shelf waters with the results from the 100- and 200-km beach sets, and the Tristan beach sample with the oceanic water findings at sea (Figure 9). My results show a similar spatial pattern to that observed at sea in the same region. The data from both surveys confirm a decrease in abundance of smaller plastics with increasing distance from source. The results are made more robust by the fact that they have been replicated by two different survey methods. Not only does this reveal a new pattern in our knowledge of the dispersal pathways of marine plastic debris, with significant implications for distribution models, but the study also shows the benefits of standardising sampling techniques in this field.

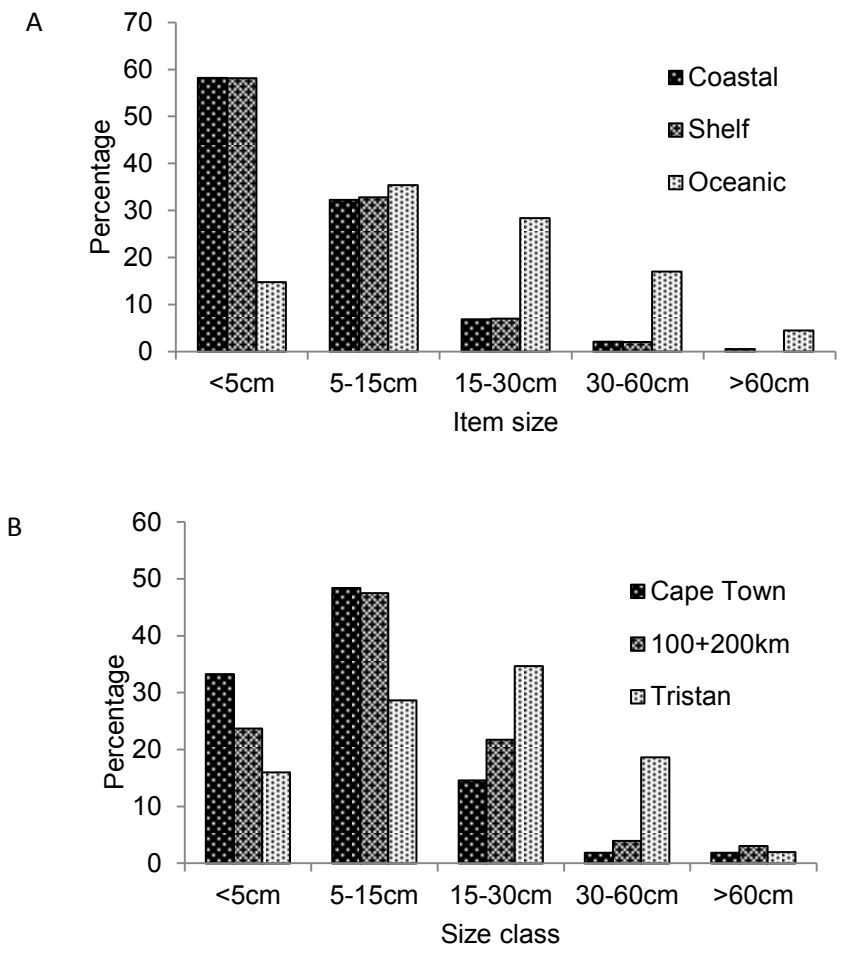


Figure 9: Comparison between (A) at-sea survey and (B) present study showing spatial gradient in size composition with increasing distance from the same pollution source. Total observations: Total observations: $n_{coastal}$ = 399; n_{shelf} = 189; $n_{oceanic}$ = 359, $n_{Cape\ Town}$ = 535; $n_{100+200km}$ = 1,184; $n_{Tristan}$ = 150.

CHAPTER 2

AN EXPERIMENTAL INVESTIGATION INTO THE EFFECT OF FRAGMENT SIZE ON THE RATE OF BUOYANCY LOSS OF MARINE PLASTIC DEBRIS DUE TO BIOFOULING

INTRODUCTION

Biofouling as a ballast for buoyant plastic debris

Evidence of biofouling as a mechanism for the sinking of buoyant plastic debris was first published in 1975, when it was reported that fisherman had recovered plastic bags encrusted in bryozoa from the seafloor of the Skagerrak (Holmström, 1975). Since then, various benthic surveys have revealed that plastic litter is almost as ubiquitous on the seafloor as it is on coastlines, and the proportional debris of plastic is approximately the same as is usually found in beach litter (60-80%) (Gregory and Ryan, 1997; Goldberg, 1997; Hess et al., 1999; Galgani et al., 2000; Katsanevakis et al., 2007; Bergmann and Klages, 2012; Schlining et al., 2013). This proportion is even higher in areas of heavy anthropogenic pressure. Plastic bags have been found to make up 90% of benthic litter in the Mediterranean for example, and overall plastics make up 95% of litter in the seabed sediments of the North Sea, off the Belgian coast (Galgani and Andral, 1998; van Cauwenberghe et al., 2013). Other correlations with marine activity such as heavy fishing have also been identified (Sanchez et al., 2013).

The role of biofouling as the mechanism for sinking has been explicitly identified in some papers (Harms, 1990; Ye and Andrady, 1991; Sanchez et al., 2013) and alluded to in several reviews (Andrady, 2011; Wright et al., 2013; Cozar et al., 2014). However, it has not been specifically identified as a size-selective mechanism for removing smaller litter items from surface waters.

Marine biofouling

Marine biofouling is the colonisation of a solid surface by sessile micro- and macro-organisms in marine environments (Wahl, 1989; Callow and Callow, 2002; Kerr and Cowling, 2003; Zardus et al., 2008; Lobelle and Cunliffe, 2011). Any surface exposed to seawater will undergo fouling and the settlement of fouling organisms on plastic and synthetic polymers in marine environments is well documented, including on beached, sunken or floating plastic debris (Holmström, 1975; Gregory, 1991; 2009; Winston et al., 1997; Moore et al., 2001; Barnes, 2002; 2009; Graham and Thompson, 2009; Ryan et al., 2009; Ryan, 2014). Experimental studies have examined species diversity on plastic substrata, settlement rates and the effects of fouling on material density and biodegradation (Henschel, 1990; Andrady and Pegram, 1989a, Ye and Andrady, 1991; Stevens, 1992; Artham et al., 2009; Lobelle and Cunliffe, 2011). These reports reveal a wide range of taxa

that readily settle on plastic debris, including diatoms, bryozoa, hydrozoa, cirripedia, mollusca, polycheata, ascidia, various algae as well as a 'biofilm' of microscopic organisms (Henschel et al., 1990; Ye and Andrady, 1991; Stevens, 1992; Winston et al., 1997; Gregory, 1978; Barnes, 2002; 2009; Kerr and Cowling, 2003; Gregory, 2009; Thiel and Gutow, 2005; Zardus et al., 2008; Moret-Ferguson et al., 2010;). All of these fouling organisms are negatively buoyant in seawater (Railkin, 2003), raising the density of plastic items and increasing the likelihood of sinking. However, the time taken to reach negative buoyancy is likely to depend on the size of an item (because smaller items have a larger surface area to volume ratio) (Cozar et al., 2014) and its composition (items with trapped air will have much lower densities and thus be able to withstand much greater levels of fouling before sinking.

Timeframes

A diverse and structured fouling community on an immersed substrate takes between one and several weeks to develop (Wahl, 1989). Development follows a sequence of four stages (Wahl, 1989; Kerr and Cowling, 2003). First is the chemical adsorption of dissolved organic molecules to the plastic surface (Wahl, 1989; Kerr and Cowling, 2003). This precipitates the settlement of bacteria, which begins to take place within the first hour of exposure, followed by diatoms and protozoa after approximately a day (Wahl, 1989). This so-called biofilm stimulates the attachment of multicellular organisms, such as algae and invertebrates (Wahl, 1989). Larvae and algal spores are usually present after approximately one week (Lobelle and Cunliffe, 2011), although this can take up to several weeks depending on environmental conditions, including factors such as latitude, season and the biological productivity of the water (Wahl, 1989; Andrady, 2011), as well as the type of plastic (Artham et al., 2009). While the time frames involved in fouling settlement may vary, the order of the settlement sequence is always the same, independent of the species involved, the type of material and the region (Wahl, 1989; Ye and Andrady, 1991).

Ecology of biofouling communities

The bacterial attachment that forms the biological base of the biofilm involves two phases of attachment: adsorption, which is reversible, followed by adhesion, which is not (Kerr and Cowling 2003; Zardus et al., 2008). From as early as this stage, therefore, biofilms become firmly fixed to the substrate surface and are not readily detachable (Kerr and Cowling 2003). Once a fouling community is established, it is subject to the same ecological processes and interactions as any biological community, and it continues to grow and evolve at both the

micro- and macro-level (Wahl 1989). Competition for space is a dominant feature of both intra- and inter-species fouling ecology. Colonisation happens as readily on living surfaces as on inert ones (Wahl 1989). As these macro-organisms grow, many of them, such as barnacles and other sessile crustacea, present new attachment surfaces for other organisms (Wahl 1989). As such the amount of surface area available for settlement on a single artificial surface is not constant, nor is it necessarily a limiting factor to the amount of biomass that surface can accrue (Wahl, 1989, Zardus et al., 2008). However, light can be a limiting factor to the growth of autotrophs. Early field studies found that items that had become negatively buoyant due to fouling underwent rapid defouling when submerged at greater depths and recovered positive buoyancy (Ye and Andrady, 1991). Predation is also an ongoing ecological process that drives fouling community dynamics. Settled communities can be grazed by fish and other predators, reducing the accrued biomass (Holmström, 1975; Reisser et al., 2013).

Implications of size for biofouling and buoyancy

The buoyancy of an object in a medium is a function of the ratio of their respective average densities (measured as total mass per unit volume). For a homogenous object, density is an intrinsic property of the material of which it is composed. In this case, the buoyancy of an object is independent of its volume. However, where items contain entrapped air or other gases, or comprise various materials of different densities, changes in volume result in changes in buoyancy. In these cases, the overall density of the item depends on the ratio of dense to less dense materials. Buoyancy too, is contingent on the ratio of these materials. Since the densities of most fouling organisms are higher than the densities of otherwise buoyant plastics, such as polyethylene (Railkin, 2003; Ye and Andrady, 1991; Lobelle and Cunliffe, 2011), biofouling increases the density of plastic fragments, decreasing their buoyancy.

Why should small pieces sink faster than big pieces?

Small objects have larger surface areas relative to their volume because the ratio of surface area to volume increases as volume decreases (Figure 10). Small objects therefore offer more settlement space to fouling organisms relative to their own volume than large objects. The rate of this loss of buoyancy depends on two factors: the extent of settlement that takes place and the rate of growth of the biomass once settlement has been established.

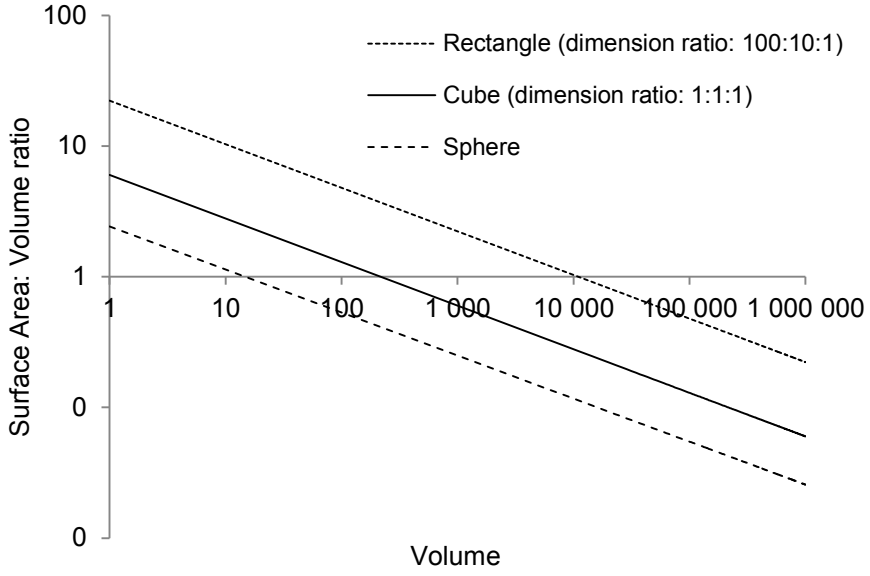


Figure 10: The log transformed relationships between the surface area: volume ratio and volume for different shapes. There is an inverse relationship between volume and surface area: volume ratio. Thus, the smaller an item in terms of its volume, the higher its relative surface area. The surface area, and therefore the surface area to volume ratio are also functions of the shape of an item. The dimensions of the rectangle (100:10:1), which might be approximately proportional to those of a thin plastic film, give the highest surface area: volume ratio for a given volume. A sphere is the most economical shape in terms of surface area.

The latter is a function of the surrounding environmental conditions (Wahl, 1989; Railkin, 2003; Andrady, 2011). But since initial settlement will take place on any solid surface brought into contact with the seawater (Wahl, 1989), the former is believed to be determined largely by the properties of the object's surface, most notably by the amount of surface area relative to its volume available for settlement, and by its surface roughness (Ye and Andrady, 1991; Artham et al., 2009). If biofouling is indeed a significant driver of the disappearance of plastic litter from the ocean surface, it would preferentially remove smaller pieces as a result of their relatively higher surface areas and as such could offer a possible explanation for the paucity of microplastics found at the sea surface (Barnes et al., 2009, Eriksen et al., 2014; Cozar et al., 2014).

It is well known that plastic litter undergoes fouling in marine environments (Ye and Andrady, 1991; Lobelle and Cunliffe, 2011). This study was undertaken to establish the rate at which buoyant plastic materials (high density and low density polyethylene) of different sizes and thicknesses would amass sufficient fouling growth to cause them to sink. I tested the hypothesis that biofouling would cause smaller, thinner plastic fragments to become

negatively buoyant faster than larger, thicker fragments as a result of their higher surface area: volume ratios. I thus test whether biofouling is size-selective as a vertical transport mechanism in the sea. A primary objective was to establish a comparative profile of sinking rates due to biofouling for plastic fragments with different volumes. The results will contribute to our understanding of the distribution and fate of plastics in the sea.

MATERIALS AND METHODS

Study design

Litter exposure trials were conducted from October to December 2014 at the False Bay Yacht Club (34° 11.54'S, 18° 26.05'E), Simon's Town, on the western shore of False Bay, near Cape Town, South Africa (Figure 11). Different size samples of two common plastic pollutants, high-density polyethylene (HDPE) and low-density polyethylene (LDPE) were tethered to exposure rails that were fixed ~20 cm below the water surface underneath a floating dock. This is known as restricted floating exposure, in that samples are allowed to move freely with changing tides and currents, but are vertically restricted to a constant distance from the surface (Ye and Andrady, 1991). Sampling was conducted bi-weekly over a 12-week period. At each sampling interval, a set of replicates was removed for processing and not returned to exposure conditions (destructive sampling).

Marine conditions at study site

Water temperatures in False Bay vary seasonally between 16-19°C in summer (September to March) and 12-14°C in winter (April to August). False Bay experiences strong south-easterly winds in summer and north-westerly winds in winter (Atkins, 1970). The climate is Mediterranean, with most rainfall in winter, between May and September. The surface water characteristics are determined by the predominant wind patterns (Atkins, 1970). South-easterlies bring warm surface water into False Bay from the western Agulhas Bank, whereas in winter, the north-westerly winds create localised upwelling of cold bottom water along False Bay's western and northern shorelines (Van Herweden and Griffiths, 1991).

The club itself is sheltered by a harbour wall to the southeast, part of the adjacent naval base. It has over 250 berths, most of which are occupied by long-term boats, while the remaining berths support a steady turnover of local and international visiting boats . Signs were placed on noticeboards throughout the clubhouse explaining the project, to mitigate the risk of deliberate disturbance by owners and visitors.

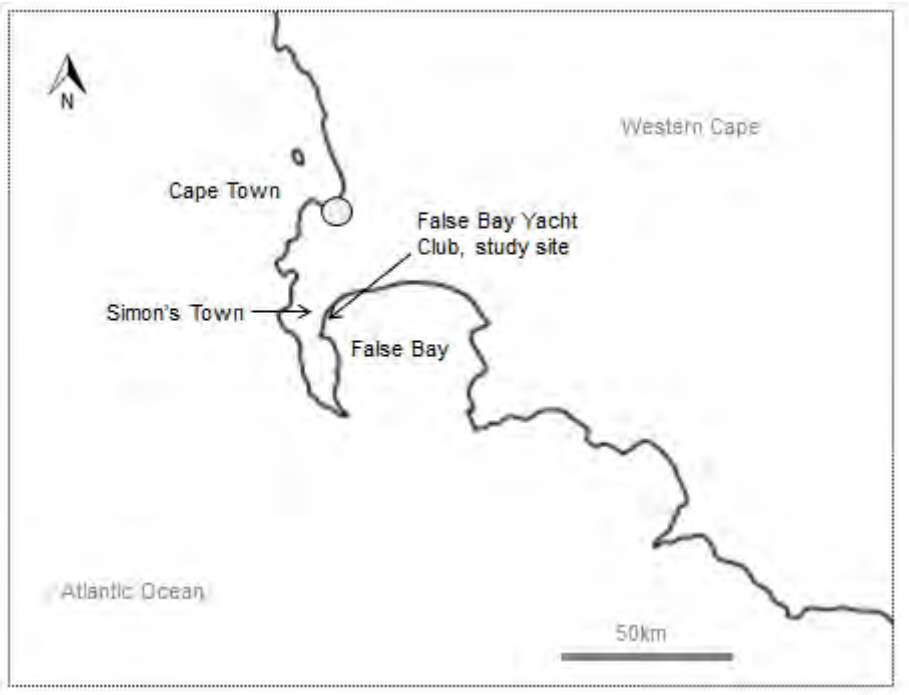


Figure 11: Location of the study site: False Bay Yacht Club, Simon's Town

Study materials

Samples for the experiment were prepared from the two most common forms of polyethylene: HDPE and LDPE. Polyethylene is the most widely produced plastic polymer, with applications in a diverse range of industries, from food packaging and consumer goods to power transmission and electronics (www.plasticseurope.org). HDPE is manufactured at lower pressures and has a more closely packed structure than LDPE, making it stiffer and more inflexible. However, it is still easy to mould, colour and process, and is cheap to produce (www.dynalabcorp.com). It has a melting point of 130°C and a specific gravity of 0.95 (www.dynalabcorp.com). Common applications of HDPE include bottles of fresh produce such as milk or fruit juice, detergent and cosmetic bottles, buckets, fish trays and crates (www.plasticsinfo.co.za). LDPE is manufactured at higher pressures, and its polymer chains are more branched and less closely packed, making it elastic, flexible and cheap. LDPE has a lower specific gravity than HDPE (0.92) and a lower melting point (120°C) (www.dynalabcorp.com). It is most commonly found in the form of plastic bags, including waste bin liners, refuse bags, grocery bags and cling wrap (www.plasticsinfo.co.za).

Size and thickness selection

I used three thicknesses of HDPE: 4; 1 and 0.5 mm, and two thicknesses of LDPE: 0.2 and 0.1 mm. These thicknesses were selected to capture a representative spectrum of thicknesses of debris items. The LDPE and the 0.5 mm HDPE sheets were clear or translucent, while the 1- and 4-mm HDPE sheets were more opaque, with opacity increasing with thickness. The 4- and 1-mm HDPE and the 0.2- and 0.1-mm LDPE sheets were obtained from plastics wholesalers. The 0.5-mm HDPE sheets were cut from the flat surfaces of 2-l juice bottles, as it was not possible to find HDPE thinner than 1 mm available in sheet form. Surface roughness can increase fouling rates (Kerr and Cowling, 2003). The surfaces of all of the samples were all comparably smooth, with the exception of the 0.5-mm samples, which were smooth but had a slightly undulating texture.

I cut squares of three different sizes from each thickness: 5x5 mm (small), 9x9 mm (medium) and 50x50 mm (large). The lower limit was determined by practical considerations of tethering; it represents the upper size limit of particles considered to be microplastics (Wright et al., 2013; Eriksen et al., 2014; Isobe et al., 2014; Reisser et al., 2014). The medium size (9x9 mm) was selected to give an approximately linear decrease in surface area: volume ratio between successive sizes within each thickness. The resulting surface areas, volumes, and surface area: volume ratios for each sample size with each thickness of material are shown in Table 7.

Sample preparation

A total of 90 replicates of each size-thickness combination was prepared, allowing 15 of each to be removed at each sampling interval. The three thinnest samples were cut using a sharp kitchen knife, the 1-mm HDPE samples with a guillotine, and the 4-mm HDPE sheet with a band saw. I pierced a hole in a corner of each sample using a safety pin or a small drill with a 1-mm diameter drill bit for the two thickest samples. All samples were labelled individually using a black permanent marker. I assigned each full sampling set a number from 1 to 6, and each of the 15 replicates within each size thickness combination a letter of the alphabet from A to O. The initial mass of each replicate was measured with a digital scale accurate to 0.1 mg.

Table 7: Summary of the dimensions and mean masses of the 15 sample size-thickness combinations in order of decreasing surface area: volume ratios

Material	Thickness (mm)	Size mm)	S. area (mm^2)	Vol (mm^3)	SA: Vol	Mean mass (g)	CV	N
LDPE	0.1	5	51	2.5	20.4	0.0023	0.13043	57
LDPE	0.1	9	164	8.1	20.22	0.0079	0.07595	65
LDPE	0.1	50	5 010	250	20.04	0.229	0.07249	64
LDPE	0.2	5	52	5	10.4	0.0054	0.87037	62
LDPE	0.2	9	166	16.2	10.22	0.0151	0.05960	67
LDPE	0.2	50	5 020	500	10.04	0.4807	0.03391	66
HDPE	0.5	5	55	12.5	4.4	0.0177	0.11864	67
HDPE	0.5	9	171	40.5	4.22	0.0312	0.14423	64
HDPE	0.5	50	5 050	1 250	4.04	1.0246	0.12200	60
HDPE	1	5	60	25	2.4	0.0325	0.07692	69
HDPE	1	9	180	81	2.22	0.0938	0.04584	71
HDPE	1	50	5 100	2 500	2.04	2.5699	0.03393	68
HDPE	4	5	90	100	0.9	0.0985	0.08731	74
HDPE	4	9	234	324	0.72	0.3193	0.08675	74
HDPE	4	50	5 400	10 000	0.54	9.3607	0.01526	58

Deployment

The samples were tethered in random order to long rails made of polyvinyl chloride (PVC), using 0.2 mm diameter fishing line approximately 50 mm long (Figure 12). The position of each sample along the rail was recorded. Deployment took place on 7 and 9 October 2014. Rails were deployed in successive berths underneath the same dock, approximately 100 mm below the surface (Figure 13).

Figure 12: A selection of the samples tethered to the exposure rails before deployment

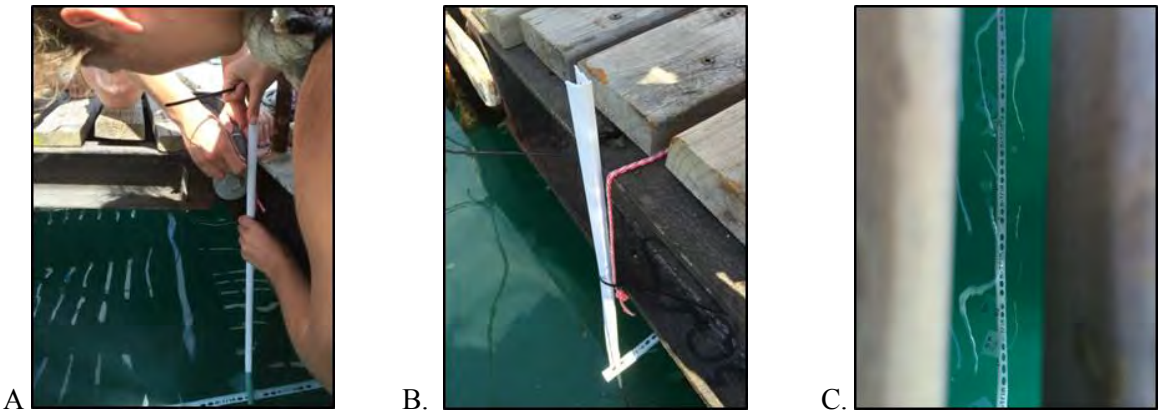


Figure 13: Attaching one of the sample rails to one side of the dock (A), a sample rail fixed in place (B), and one of the sample rails visible through the slats of the dock (C).

Data collection and measurement

Samples were retrieved at two-week intervals over 12 weeks between 21 October and 30 December 2014. By roughly halfway through the study period the rails became heavily fouled, so at the six week sampling interval I cleaned all remaining rails with a nailbrush to remove growth from the rails without dislodging the remaining samples.

After being removed from the water, samples were kept in trays filled with seawater and handled with forceps and scissors. I was careful when I cut the tethering line to separate the settlement attached to the line from the settlement attached to the sample. Samples damaged while removing the line were discarded. Each sample was placed in a glass tank filled with seawater, agitated to ensure that all epibionts were attached, and buoyancy assessed visually as either float or sink (Reisser et al., 2014). Neutral buoyancy was counted as floating.

For each sample, I measured the following parameters: buoyancy, percentage cover of surfaces and edges by epibionts, average and maximum height of growth and the position of thickest growth on the sample surface. Community composition was also assessed visually. As such, only macro-colonisers identifiable without the use of a microscope were able to be recorded. Epibiont cover was classified as 'clear', 'sparse', 'thick' or 'high' and the percentage of each type of cover was estimated visually. Cover was defined as clear if there was no visible cover. 'Sparse' cover was flat and sporadic, or an algal film or thin layer of cover that was visible. 'Thick' cover referred to any mat of cover whether high or flat that completely concealed the sample's surface. 'High' cover referred to structured, three dimensional growth. I combined thick and high cover in the final analysis, which I termed 'heavy' cover.

After inspection, samples were transported in sampling trays to the laboratory, where they were placed in drying ovens at 30°C for 24 hours. Thereafter, dry weights were measured with a digital scale accurate to 0.001 g.

Statistical analysis

All statistical analyses were conducted in the R environment, Version 3.1.2 (R Core Team, 2014). Factors influencing the percentage change in dry mass were analysed using a Generalised Linear Model with negative binomial distribution and a log-link function (glm.nb). Values for the percentage changes in dry mass were rounded before fitting the model, as logistic link functions require integer input values. The parameters included in the global model were surface area, material thickness and the number of weeks of exposure, together with interaction terms for these factors. Visual inspection of residual plots revealed one observation of unusually high leverage. This was a small (5x5 mm) 0.1-mm LDPE sample with unusually high cover of the hydroid, *Tubularia warrenii,* at Week 6, which resulted in a 90-fold increase in dry weight, from 0.0023 g to 0.208 g. The next highest increase in dry weight at this interval was 35-fold. Removing this data point led to no difference in the model outcomes but improved residual fits. I therefore excluded this sample to enhance the reliability of the model (e.g. Cunningham et al., 2013).

Nested possible best fit models were compared using the dredge function in MuMIn v 1.12.1 (Barton, 2010). All models with similar AIC values ($\Delta AIC < 2$) were considered, but models with more parameters were discarded in favour of simpler models, to avoid unnecessary complexity (Arnold, 2010). The relative significance of each parameter in the final model

was calculated using the ANOVA function in the car package v 2.1-22 (Fox and Weisberg, 2011). Residual plots were examined to ensure model assumptions had been met. The effect of the interaction term was examined visually using the effects package v 3.0-3 (Fox, 2003). Estimates presented for each of the parameters as model outcomes and their confidence intervals were back transformed exponentially.

I used the package lsmeans v 2.1.4 (Lenth and Herva, 2014) to compare differences in mean change in dry mass between different surface areas and thicknesses at each sampling interval. I subdivided the data by week and modelled each subset individually, with week and the size-week interaction term removed from the model. Estimates were back transformed exponentially. I tested the fit of the model on the subset data by comparing the least squares means produced to the arithmetic means of the data, calculated using the plyr package v 1.8.1 (Wickham, 2011). I also used the ANOVA function to compare the mean changes in dry mass accumulated across two sampling sets, both exposed to fouling for two weeks but deployed at different times during the study, to investigate the effect of seasonality on the rate of biomass accumulation.

Buoyancy was modelled as a probability using logistic regression (Generalised Linear Model, family=binomial). Data were subdivided over each combination of size and thickness. An individual logistic regression was performed on each subset, modelling the binary variable 'float or sink' against week. Deviance residuals were checked for each model and significance values were found using the ANOVA function. The inflection point of each curve, at which probability of sinking = 0.5, and resultant estimates for number of days to sink were calculated as:

$$P_{sink}(0.5) = |intercept| / |co\text{-}efficient|$$

$$Estimated\ days\ to\ sink = 7\{P_{sink}(0.5)\}$$

The log functions contained in the model outputs mutually cancel one another in the first calculation and as such, there was no need to back transform these parameters.

RESULTS

Of the 1,350 samples deployed, I retrieved 986 (73%). More samples were lost from the sets measured at weeks 8 and 12 than at the other sampling intervals, but there was no consistent bias with respect to the size or thickness of samples lost (Appendix 1).

Surface cover

Cover was approximately evenly divided between sparse and heavy cover (high + thick) at two weeks, but heavy cover steadily rose during the first half of the study, and then stabilised at around 70% for all sample sizes from Week 10 (Figure 14). Large samples displayed consistently more sparse cover than small and medium samples and correspondingly less high and thick cover but these trends began to disappear around Week 8 and by Week 12, cover percentages were comparable across sizes. Similarly, medium-sized samples showed slightly more sparse and slightly less high and thick cover than small samples, but again these differences were clearer during the first half of the study period, and tapered off towards the end (Figure 14). Even though cover demonstrably increased, a small but steady percentage of cover on all sizes remained clear. This varied between approximately 10 and 20%. Settlement occurred preferentially on or near the corners and rough edges of the samples. The thickest growth was located on an edge rather than a flat area of the surface in 81%, 86% and 85% of small, medium and large samples respectively. Epibiont cover along sample edges averaged between 60 and 80% for all sizes. It was frequently evident that the side of the sample downstream of the water flow had little settlement while the other three edges were thickly covered. This pattern was qualitatively distinguishable across all sample sizes.

Maximum height of growth recorded during the study was 160 mm. This was recorded twice, on a large, 1-mm thick HDPE sample at Week 8 and a large 0.5-mm thick HDPE sample at Week 12. Similar heights were not unusual on small and medium samples, however, or on the thinner LDPE samples. The highest growth observed on small and medium samples was 110 mm at Week 12 and 100 mm at Week 10, respectively. The highest growth found on 0.1-mm thick LDPE was 125 mm on a large sample at Week 8 (Appendix 2a). Average height of growth ranged between 1 and 9 mm for small samples, 1 and 13 mm for medium samples and 0 and 24 mm for large samples from the beginning to the end of the study period (Appendix 2b)

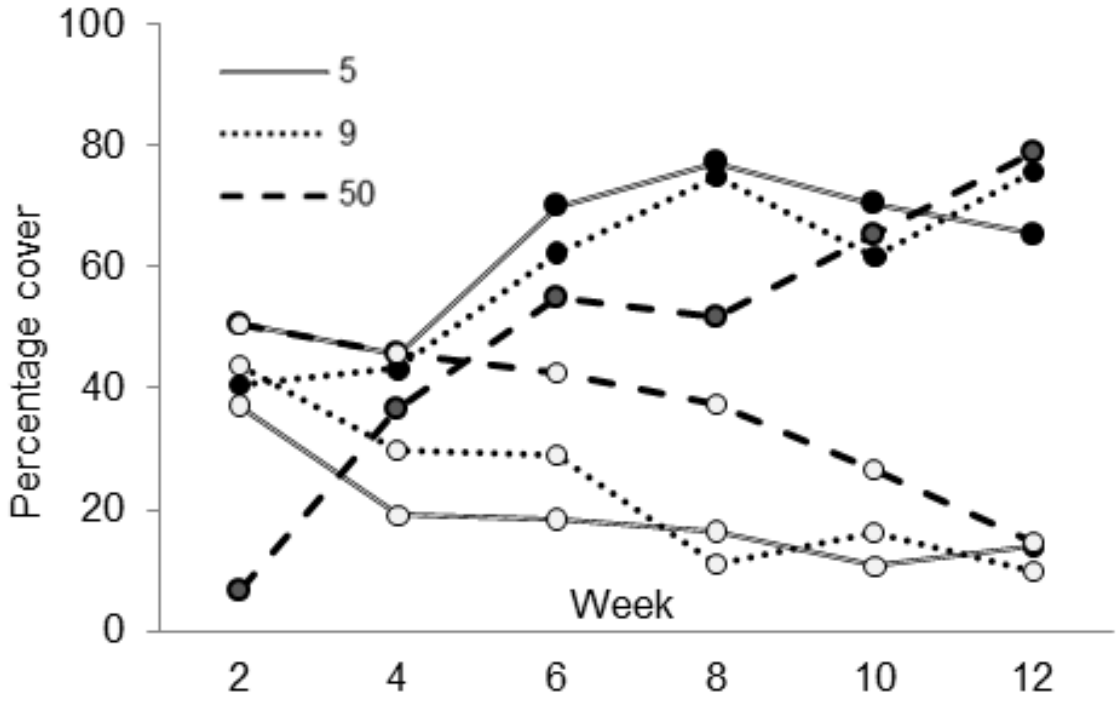


Figure 14: Change in average percentages of heavy cover (closed circles) and average percentage of sparse cover (open circles) for each size class over the 12-week study period.

Epibiotic community development and succession

The taxonomic groups visibly responsible for the greatest proportional weight gains were red and green algae, hydroids, barnacles, bryozoans, mussels and ascidians. Other common organisms observed were amphipods, copepods and tanaids; nudibranch egg sacs were found on several samples and small anemones had begun to appear by the end of the sampling period. Different groups appeared at different stages and dominated settlement at different times. Visible settlement was evident from two weeks, when nearly all samples had developed sparse cover of diatoms and green algal fouling communities. At Week 4, settlement was dominated by the hydroid, *Tubularia warreni.* Complex, three-dimensional fouling assemblages become prominent around Week 6 (Figure 14). Barnacles were observed on two samples at Week 2, and became steadily more common. Similarly, the bryozoan, *Bugula neritina,* was occasionally present from Week 2, in small, isolated tufts, but by Week 6, colonies had become much more developed and in the second half of the study period it was one of the most dominant foulants recorded. The presence of mussel spat also accelerated buoyancy loss. It only appeared at Week 8 and was extremely common thereafter. Other significant individual foulants were various species of ascidians, and the bryozoan, *Cryptosula pallasiana*, both of which were common on the final sample set (Week 12).

Heavy individual organisms, such as barnacles, showed no selection preferences based on the size of the samples. For example, throughout the experiment, barnacles were recorded on 47 small samples, 66 medium samples and 60 large samples.

Proportional change in dry mass

Mean changes in dry mass varied greatly but were consistently several orders of magnitude higher for smaller, thinner samples than for larger, thicker samples (Figure 15). By the end of the study period, mean change in mass after exposure ranged from a 58-fold increase (95% CI=25–102) for the smallest, thinnest pieces to just a 66% increase (95% CI=34-138%) for the largest, thickest pieces (Appendix 4).

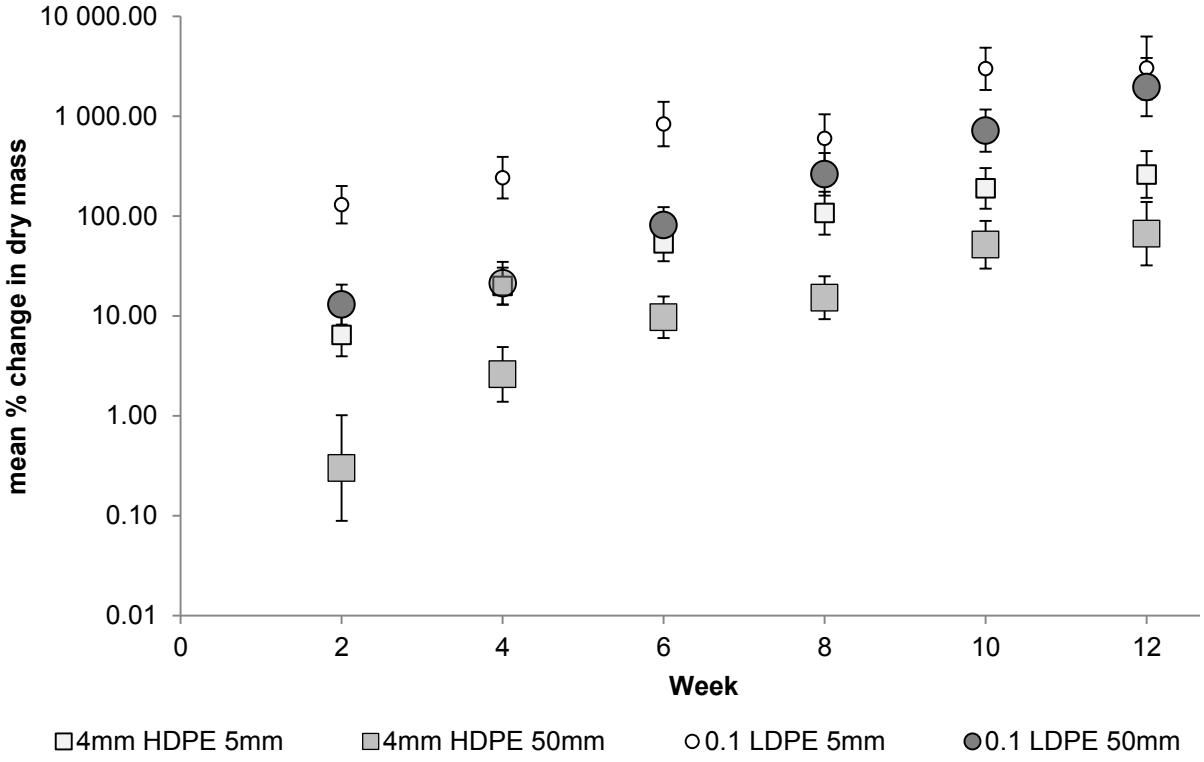


Figure 15: Log-transformed mean percentage changes in dry mass over 12 weeks for the four extreme size thickness categories. Error bars show 95% confidence intervals.

The best fit GLM to explain proportional change in dry mass included sample size, thickness, number of weeks of exposure and an interaction term between size and number of weeks (Table 8).

Table 8: Top five models for percentage change in dry mass, with chosen model in bold

Parameters	df	logLik	AICc	ΔAIC	weight
Size + thickness + week + size*week	**6**	**-5676.43**	**11364.9**	**0**	**0.439**
Size + thickness + week + size*week + thickness*week	7	-5675.9	11365.9	0.97	0.271
Size + thickness + week + size*thickness + size*week	7	-5676.33	11366.8	1.82	0.176
Size + thickness + week + size*thickness + size*week + thickness*week	8	-5675.77	11367.7	2.74	0.112
Size + thickness + week	5	-5683.63	11377.3	12.38	0.001

*Global model formula: Size + thickness + week + size*thickness + size*week + thickness*week, logLik= log(likelihood), N=985 observations*

Material thickness had a significant positive effect (χ^2 =572.5, df=1, p<0.0001), with a 1 mm increase in thickness leading to a 56% increase in mean dry mass (Table 9). Sample size had a similar effect (χ^2 =453.6, df=1, p<0.0001), but was only significant for the first 10 weeks of the study. By week 12 there were few significant differences between sizes (Table 10). Variance increased throughout the study period and was particularly high at Week 12 (SD=2,713). Plots of the mean proportional change in dry mass show large differences in mean mass change between large and small sizes at the early stages, but these differences diminish as the exposure time increases (Figure 15, Table 10). There was little effect of increasing size from 5 to 9 mm, but increasing to 50 mm samples typically was significant (Table 10).

Table 9: Factors affecting change in dry mass with 95% confidence intervals

Parameter	Estimate	2.5% CI	95% CI
Intercept	34.013	27.346	42.513
Thickness	0.561	0.539	0.584
Week	1.491	1.449	1.535
Size	0.949	0.942	0.957
Size*week	1.002	1.001	1.003

Table 10: Significance values of the differences between the mean change in dry mass for each size comparison

		Week					
Thickness	**Size contrasts**	**2**	**4**	**6**	**8**	**10**	**12**
0.1mm	small: medium	-	-	-	-	-	-
0.1mm	small: large	***	***	***	-	**	-
0.1mm	medium: large	*	*	***	*	***	-
0.2mm	small: medium	-	-	-	-	-	*
0.2mm	small: large	***	***	***	***	*	***
0.2mm	medium: large	***	**	***	***	***	-
0.5mm	small: medium	-	-	-	-	-	-
0.5mm	small: large	*	**	**	***	***	-
0.5mm	medium: large	***	***	*	***	***	*
1.0mm	small: medium	-	-	-	-	-	-
1.0mm	small: large	**	***	*	***	***	-
1.0mm	medium: large	-	***	*	**	**	-
4.0mm	small: medium	-	-	-	**	-	-
4.0mm	small: large	**	***	***	***	**	*
4.0mm	medium: large	*	-	*	-	*	*

*- >0.01 * <0.01 **<0.001 ***<0.0001*

Buoyancy

All three sizes of all five thicknesses were negatively buoyant by the end of the 12-week study period, with only six individual samples still positively or neutrally buoyant at the final sampling interval: one small 0.2mm LDPE sample, one medium 0.5mm and one medium 1mm HDPE sample and three 4mm HDPE samples: one each of the small, medium and large size classes respectively. The first samples to sink were the small samples of the thinnest material (0.1mm LDPE), with six of the recovered samples already sinking by the first two week interval. After six weeks of fouling exposure, the majority of small and medium samples across all thicknesses were negatively buoyant. The large samples only began to lose buoyancy at Week 6, and the majority of them were negatively buoyant by eight weeks (Figure 16).

P_{sink} (0.5) times ranged from 17.4 (χ^2=12.309, df=1, p<0.0001) to 66.3 days of fouling exposure (χ^2=29.461, df=1, p<0.0001) across the full spectrum of size-thickness categories (Table 11).

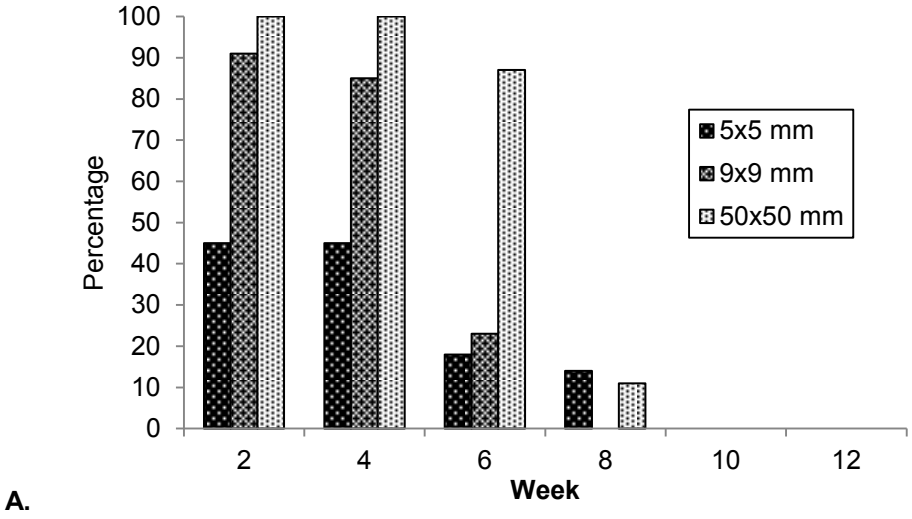
Within the smallest size class, estimated 50% sink times increased dramatically between the thinnest sample (17 d) and thickest sample (49 d), but were roughly constant for the three intermediate thickness values (39-42 d). For the medium and large size class, sink times

increased modestly (9 mm) or were constant (50 mm) with thickness for the 0.1 to 0.5 mm-thick samples, then increased more strongly to 1.0 and 4.0 mm samples (Column 10, Table 11).

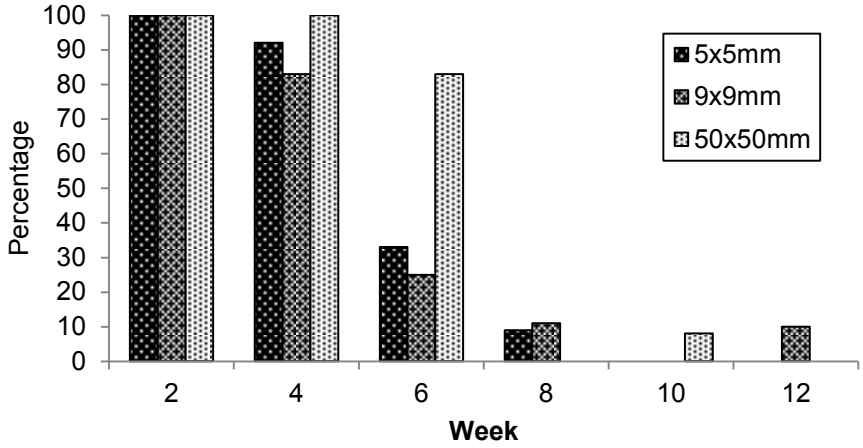
Within each thickness category, the intervals in sample size correlate approximately with linear increases in surface area to volume ratios (Column 2, Table 11). I thus expected the differences in sink times between successive sizes of each thickness to be approximately equal. This is not reflected consistently in the results (Column 10, Table 11). The intervals between sink times within the thinnest (0.1 mm) and thickest materials were comparatively linear, with large step increases between the sizes: 17 days for the small sizes; 35 days for the medium and 49 days for the large sizes of the thinnest LDPE (0.1 mm). For the thickest material (4 mm), the small sizes required 49 exposure days, the medium, 58 days and the large, 66 days. However, the 0.2 mm thicknesses showed a decrease in sink time between the small and medium sizes: from 42 days for the small samples to 39 days for the medium samples. The exposure time required for the large sizes was significantly higher (50.2 d). A strikingly similar pattern emerged from the 0.5 mm thickness. The small and medium sizes here show sink times that are almost equal (40 days), whereas the large samples require an additional 9 days (Figure 16, values combined). The penultimate sample thickness (1 mm), displays more spread between sizes: the small, medium and large size within this thickness require fouling exposure periods of 39, 45 and 62 days, respectively..

Table 11: Logistic regression models for buoyancy as a binary response for each size-thickness combination

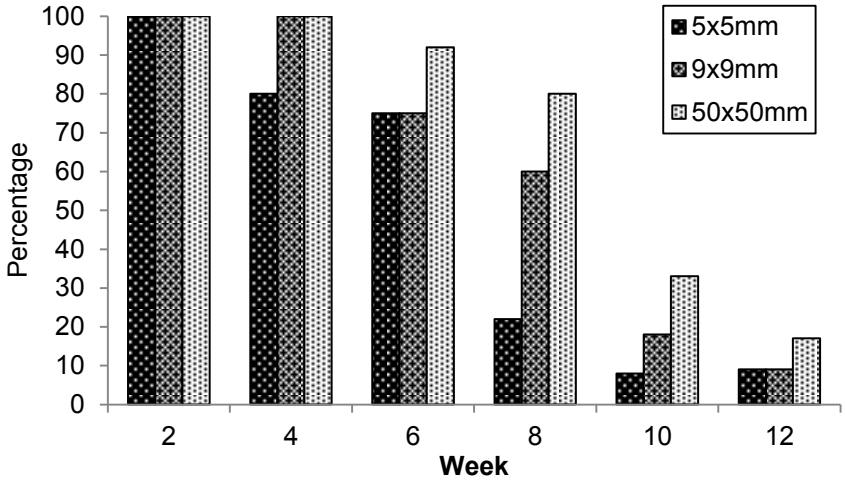
Thickness, size, mm)	SA: Vol	Intercept	SE	Co-efficient	SE	χ^2	p value	Inflection $P_{sink}(0.5)$	Sin rat (days
0.1,5	20.40	1.028	0.7334	-0.414	0.1441	12.309	<0.0001	2.483	17.
0.1,9	20.22	5.854	1.6044	-1.1688	0.3093	51.648	<0.0001	5.009	35.
0.1,50	20.04	14.157	4.1239	-2.04	0.6118	69.553	<0.0001	6.940	48.
0.2,5	10.40	3.359	0.8496	-0.5643	0.133	33.046	<0.0001	5.953	41.
0.2,9	10.22	9.323	2.988	-1.674	0.515	64.802	<0.0001	5.569	39.
0.2,50	10.04	12.236	3.389	-1.707	0.4781	69.271	<0.0001	7.168	50.
0.5,5	4.40	7.382	2.0569	-1.3004	0.3518	60.575	<0.0001	5.677	39.
0.5,9	4.22	4.675	1.239	-0.827	0.2044	42.436	<0.0001	5.653	39.
0.5,50	4.04	9.884	2.7581	-1.4212	0.3997	59.633	<0.0001	6.955	48.
1.0,5	2.40	10.064	3.0793	-1.81	0.5414	70.227	<0.0001	5.560	38.
1.0,9	2.22	4.221	0.979	-0.6632	0.1457	41.428	<0.0001	6.365	44.
1.0,50	2.04	14.268	4.2778	-1.6047	0.4697	68.66	<0.0001	8.891	62.
4.0,5	0.90	4.504	0.9877	-0.6468	0.1392	42.616	<0.0001	6.964	48.
4.0,9	0.72	5.991	1.283	-0.7287	0.1578	45.814	<0.0001	8.221	57.
4.0,50	0.54	7.623	2.034	-0.8051	0.2241	29.461	<0.0001	9.468	66.



A.



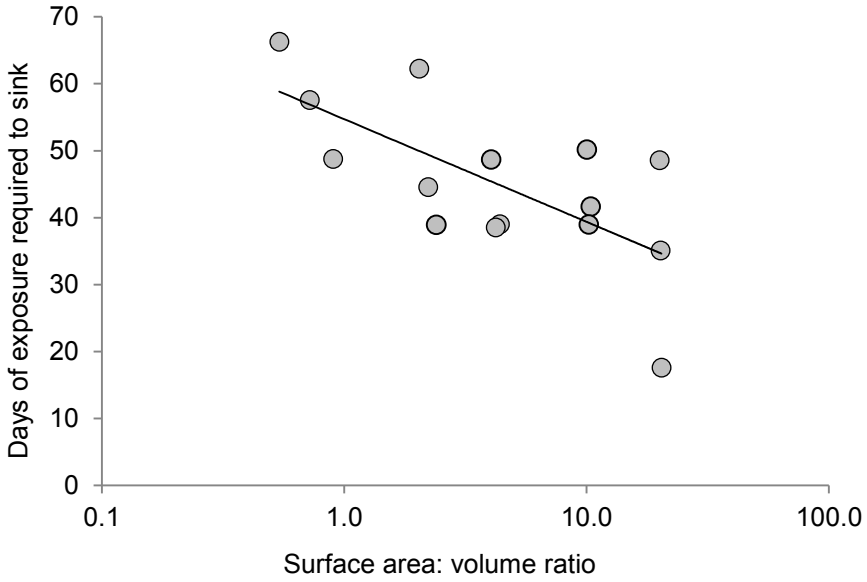
B.



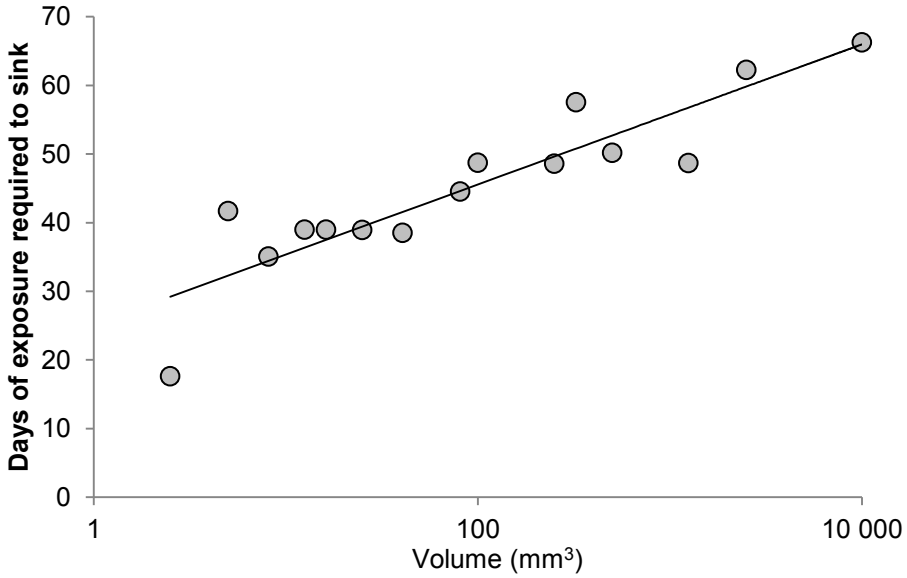
C.

Figure 16: Percentage of samples of each size class still floating at each sampling interval for (A) the thinnest LDPE, 0.1 mm; (B) the medium thickness HDPE, 0.5 mm and (C) the thickest HDPE, 4 mm. N for each size class and thickness given in Appendix 1.

I expected to find an approximately linear relationship between the number of days of exposure required to sink and the surface area: volume ratio of each sample size class. This was not the case (R^2=0.46, Figure 17A). Instead, I found that the pattern of days to sinking was much more closely correlated with sample volume (R^2=0.81, Figure 17B).



A.



B.

Figure 17: Days of exposure required to sink for each combination of size and thickness shown in order of increasing surface area: volume ratios (A, R^2 = 0.46.) and increasing volume (B, R^2 = 0.81)

DISCUSSION

This study is the first experimental investigation into the relationship between the fragment size of buoyant plastics and the rate of buoyancy loss due to biofouling in marine environments. It also provides the first measurements of the periods of fouling required for buoyant plastics to sink from the surface. Furthermore, the results show that these periods appear to be more closely determined by the volume of the plastic than by its surface area to volume ratio. The study also confirms the importance of surface roughness as a factor of fouling settlement rates, as rougher edges consistently supported the densest and highest patches of epibiont growth.

Several previous studies have shown that settlement by fouling organisms sufficiently reduces the buoyancy of plastic debris to cause it to sink (Ye and Andrady, 1991; Lobelle and Cunliffe, 2011). Ye and Andrady (1991) related higher fouling rates of debris with higher relative surface areas but did not specifically investigate the timescales of buoyancy loss for different sized fragments of the same material. Cozar et al. (2014) suggested the possibility of a relationship between buoyancy loss due to fouling and plastic fragment size, as a result of the higher surface area to volume ratios of smaller items, but again this was not explicitly tested. Furthermore, while there were clear differences between the thicknesses at the respective extremes of the sample range, there was almost no difference in settlement growth across the three intermediate thicknesses: 0.2 mm LDPE, 0.5 mm HDPE and 1 mm HDPE. That the rate of proportional change in growth was almost indiscernible between the 0.2 mm LDPE and the 0.5 mm HDPE is noteworthy because the LDPE was soft and flexible and the 0.5 mm HDPE was more rigid. Material stiffness thus appeared not to be a significant factor for the rate of fouling growth in this case.

The community of fouling organisms observed in this experiment was similar to those reported in other fouling studies (Henschel and Branch, 1991; Ye and Andrady, 1991; Bravo et al., 2011) with bryozoans, barnacles, mussels and ascidians responsible for the largest percentage weight gains during the study period. These are also frequently reported on beached or benthic debris in other areas of the world (Winston et al., 1997; Barnes, 2002). Many of the species found are known to be invasive, such as the bryozoan, *Bugula neritina,* and the hydroid, *Tubularia warreni* (Henschel and Branch, 1991), and the presence of these and other invasive species is consistent with the environment of a marina or harbour. The

presence or absence of different specific organisms was also responsible for the high variability that characterised the results.

These results are the first experimental results of their kind and should therefore be considered preliminary. Biofouling is a highly complex phenomenon (Callow and Callow, 2002; Artham et al., 2009) and rates of biofouling are extremely context-specific. They are influenced by environmental conditions such as season, latitude, geographic location, water temperature and nutrient levels (Wahl, 1989; Melo and Bott, 1997; Callow and Callow, 2002), the velocity and turbulence of the surrounding water flow (Melo and Bott, 1997) as well as the surface properties of the substrate, such as surface energy and surface roughness (Absalom et al., 1983; Kerr and Cowling, 2003). Predictions of the dispersal pathways of marine plastic once it has accrued sufficient fouling biomass to become negatively buoyant are complicated by the fact that many of these factors do not remain constant. Fouling colonies would have access to less light and be exposed to lower water temperature as they sank. A previous study conducted in the same area as the current experiment showed significant differences in the community composition and species richness of fouling communities on substrates placed at depths differing by just 10 m (10- and 20 m; Henschel and Branch, 1991). Higher temperatures are associated with higher fouling rates and water temperatures approaching 40°C have been found to be optimal for biofilm development (Melo and Bott, 1997). Loss of light and decreased temperature, together with the presence of predators and grazers, would therefore be likely to result in higher mortality and consequently, the detachment of biomass. This process of defouling has been shown to occur at depths of 50 m (Ye and Andrady, 1991). Defouling would have the opposite effect on buoyancy to that of fouling and defouled debris is believed to then rise again within the water column, although this hypothesis has never been tested (Ye and Andrady, 1991). Depending on the period of such a cycle of fouling and defouling, other factors such as season (Artham et al., 2009) or horizontal dispersal to another location would also impact the track of this hypothesised cycle.

There are other positive and negative feedbacks between fouling rates and the factors that influence them. For example, fouling is known to affect the physicochemical properties of the settled material, such as the hydrophobicity, or surface tension of the substrate, as well as its surface roughness (Artham et al., 2009; Lobelle and Cunliffe, 2011). Both HDPE and LDPE have been shown to undergo biodegradation within three months when exposed to fouling, which affects these surface properties (Artham et al., 2009) and surface roughness is also

increased as a result of predation and grazing on the adhered fouling community (Reisser et al., 2013). But as mentioned, the properties of surface tension (of both the substrate and the settling organisms) and surface roughness are themselves critical determinants of biofilm adhesion rates (Absalom et al., 1983; Wahl, 1989; Kerr and Cowling, 2003). Higher surface tension makes surfaces more hydrophobic and such surfaces tend to favour fouling initially, but prolonged fouling can then begin to reduce surface tension as the adhered biofilm smoothes the micro-topography of the surface (Artham et al., 2009; Bravo et al., 2011). Increased surface roughness also favours fouling while fouling in turn, enhances roughness (Artham et al., 2009). These feedbacks would be subject to the combination of other factors that determine fouling and this would make them difficult to model.

Floating stability has also been shown to influence early fouling community succession (Thiel and Gutow, 2005; Bravo et al., 2011). Super- buoyant items that are less stable when afloat, such as polystyrene fragments, were found to persist at the surface for over 100 days while other less buoyant items sank due to the fouling biomass they accumulated within that period (Bravo et al., 2011). Whether the random and erratic behaviour of free floating polystyrene would ever allow it to become sufficiently fouled to sink out from the surface has not yet been tested, but it seems likely that were this to occur, a slight loss of buoyancy would facilitate accelerated fouling, so that fouling rates and rates of further buoyancy loss would be different depending on the object's position at the surface.

The study conducted by Bravo et al. (2011) is the first experimental study to my knowledge that examined fouling rates on sample items that were allowed to float freely. Most fouling field studies are conducted using samples that are tethered in some way (Ye and Andrady, 1991; Artham et al., 2009, Lobelle and Cunliffe, 2011). This aspect of the study design, as well as the fact that the samples were kept in a fixed location, might have produced systemic biases in the results.

Fouling of debris drifting untethered at the surface of oceanic waters would almost certainly occur at different rates to those found here. Firstly, the environmental conditions of the present study and the nature of the study site were consistently favourable to higher rates of fouling. The biological productivity in the water is high and there are multiple underwater surfaces in close proximity to one another, all of which support established fouling communities. Secondly, unlike the samples in this study, floating fragments would move with the surrounding flow and thus offer less resistance to the hydrodynamic processes that deliver

larvae to fouling surfaces. The obvious experimental challenges of observing the fouling rates of free-floating items of this size have prevented studies of this nature to date. There are several studies on other kinds of materials however, that show a positive relationship between the amount of resistance to flow given by a surface, for example by its orientation relative to flow direction, and the rate at which fouling communities develop thereon (Glasby, 2001; Glasby and Connell ,2001; Schmidt et al., 2004; Rittschof et al., 2007).

It is also unclear how turbulence and wave action affect the adhesion of fouling larvae onto untethered, suspended items. Fast moving water typically delivers more larvae onto a surface, but also creates high-velocity gradients and shear stresses over the surface that are likely to re-suspend larvae (Koehl, 2007). Most studies have found that fouling rates are higher in lower velocity environments (Melo and Bott, 1997) but for floating items the relative velocity of the surrounding water would be significantly less because the item would be travelling with it. There are no conclusive studies to my knowledge on the implications of this relative movement. Some species of hydroids, barnacles and bryozoans have been shown to adhere better in such environments while others fare less well, with differences in adhesion evident even among species of the same groups (Koehl, 2007). Some studies report higher levels of fouling in less sheltered, higher energy environments (Langhamer et al., 2009) but again these are for fixed structures that resist flow, rather than for floating items. Using a study design that involved free floating items in some form of cage at the surface of the sea, similar to the design used by Bravo et al., (2011) for larger items, would be a very useful step towards more reliable estimates of sinking times in open water.

Extending these results to microplastics

There is increasing concern over the impact of the smallest size category of plastic known as microplastics (Thompson et al., 2004; Andrady, 2011; Cole et al., 2013; Wright et al., 2013). There is no consensus yet in the literature on the definition of microplastics in terms of their upper and lower size limits. Some authors reserve the classification to plastics of microscopic proportions, between 0.05 and 0.5 mm (Gregory and Andrady, 2003; Andrady, 2011) while others more commonly use 4- or 5 mm as the upper limit (Arthur et al., 2009; Ng and Obbard, 2006; Fossi et al., 2012; Hidalgo-Ruz et al., 2012; Isobe et al., 2014). Microscopic plastics are an important category because they present a unique set of environmental challenges based on their small size. They are potentially bio-available for ingestion by a different range of marine fauna to macro-debris (Barnes et al., 2009, Fossi et al., 2012; Cole

et al., 2013), they are difficult to observe and they pose a particularly strong threat as a vehicle for leached chemical toxins into the food web (Mato et al., 2001; Ryan et al., 2009; Teuten et al., 2009).The microplastic waste stream is also more difficult to regulate. Not only do microplastics abound in the marine environment due to natural processes of fragmentation that act upon larger debris items (Barnes et al., 2009; Andrady, 2011), they also enter the system directly as primary microplastics, in the form of microscopic plastic particles produced as granules for cosmetic face washes, exfoliants and other household detergents (Fendell and Sewell, 2009). These are washed away into sewerage systems and accumulate in the environment unseen. The inclusion of microplastics into any model of plastic debris behaviour at sea would therefore be an important advantage in our attempts at understanding and mitigating these challenges.

Since my study focussed on size, it is important to consider whether my results could be applied to plastics of smaller diameter than the 5-mm minimum diameter used in the experiment, i.e. whether smaller microplastics would become negatively buoyant in less time than the 5-mm samples tested here. Answering this question accurately would require a combined investigation into surface physics and microbiology that is beyond the scope of this study. From the available literature however, it does seem that the fouling of plastics at the μm scale is likely to occur. Microscopic particles of an organic nature are known to act as substrate for fouling bacteria (Meso and Bott, 1997) and there is no reason why synthetic polymer particles of this size would not. Furthermore, it seems that it would be possible to model fouling rates on microplastics, based on knowledge of the sizes and surface tensions of possible fouling bacteria and the material used. The response of fouling to different surface properties is recognised to be a physical one determined by the relationship of surface properties between the fouling and the substrate (Absalom et al., 1983; Kerr and Cowling, 2003). In Kerr and Cowling (2003), the authors investigated the effect of surface roughness on the settlement of bacteria that were between 0.5 and 1.5 μm along their maximum axes. The roughness values tested were between approximately 5 and 35 nm and the results showed an unexpected peak in settlement for roughness values around 10 nm that was not evident either side of that value. They suggest that this could be the roughness with surface imperfections of just the right size for the extra-cellular substance that bacteria produce that generates part of the biofilm. This suggests that items of 5- or 50 μm could still possess microscopic surface characteristics that favour fouling. On the other hand, a potential minimum size threshold to the relevance of these results could come from the inability of

crustaceous macro-foulers, such as barnacles, to foul microplastics. While these and similar macro-organisms settled on the smallest size samples of 5 mm, it does not follow that they would be able to colonise surfaces much smaller than this. The presence of barnacles on smaller plastics was a strong determinant of negative buoyancy and without their influence in the system, the timescales to sinking observed might not have been the same. On the other hand, the comparatively low volume and high surface area to volume ratio of microplastics might make them more susceptible to quick sinking without the influence of these larger organisms. Further research is required in this area.

The pattern of sinking timescales and proportional change in mass for the different sizes of samples were more closely correlated with sample volume than with their surface area: volume ratios. This suggests that it is not how much surface area is available for settlement that is the most important determinant of the rate of sinking in terms of the properties of the materials, but the quantity of buoyancy that needs to be overcome. The size intervals for this experiment were specifically selected to produce linear increases in surface area to volume ratios within each thickness. The results of my study however, suggest that the relative surface area of an item is not the best determinant of the rate at which it is likely to be weighed down by fouling. Instead, the findings point to the importance of the volume of an item, which is directly proportional to its buoyancy in seawater, as a significant determinant of longevity at the surface even under conditions of heavy fouling exposure. This echoes the empirical results found in the study described in Chapter 2.

Doomed to the seabed?

Fouled debris is not necessarily entombed on the seabed (Goldberg, 1997); it may return to higher levels in the water column, and support further cycles of fouling, sinking, defouling and rising again. The fact that debris items will become fouled therefore does not mean that they are destined for the seafloor. Rather, this knowledge opens the possibility that they could be anywhere within the water column. Refined versions of the timescales of buoyancy loss found in this study could be scaled by factors such as environmental conditions and proximity to litter inputs, and potentially included as correctional terms into numerical models of floating litter abundance and distribution. Whether or not this is possible in the near future, the results are still of value because they show that positively buoyant plastic litter that enters the ocean does not necessarily remain at the surface for as long as previously believed.

SYNTHESIS AND CONCLUSIONS

Summary of study and findings

My study confirms that the mean size of marine litter increases with distance from a pollution source. I measured various parameters of size, including maximum length, volume and mass as well as the buoyancy of items both floating and submerged. For all parameters, there were striking increases with increased distance. Changes in composition were equally evident. The most abundant items close to source were smaller items. These are progressively less evident with increased distance. Larger items become progressively more frequent.

These patterns from beach litter surveys reflect the same gradients observed in plastic floating on the surface. Changes in proportional abundance of different types of items illustrate the trend that items that remain longest at the surface are larger and more buoyant. Bottles and polystyrene lumps were small contributors to overall litter samples close to shore but dominated litter at remote distances.

These findings support the hypothesis of size selective mechanisms removing smaller plastics, including microplastics from the surface (Cozar et al., 2014; Eriksen et al., 2014). They further suggest that plastic items of different sizes have different dispersal pathways, with larger, super buoyant items dispersing further horizontally on the surface, and the trajectories of smaller items determined by a more complex combination of mechanisms, many of which are operating beneath the ocean surface.

Moving from empirical patterns to experimental investigation into one of the potential mechanisms that has been suggested, I exposed different sizes of two common buoyant plastic debris types, HDPE and LDPE to biofouling by marine organisms and was able to show that plastic fragments of different size persist at the surface for different time periods. Small thin fragments, at the current upper limit of microplastics classifications (5 mm) but at the lowest end of my sample size spectrum, were weighed down sufficiently after 17 days of exposure. The larger thicker pieces, the largest of which were 4 mm thick and 50 x 50 mm in area, maintained positive buoyancy for over two months, despite exposure to the same heavy levels of fouling.

These results reflected those found empirically in Chapter 1, that large size and high buoyancy are requirements for plastic items to remain at the surface for long periods of time, which enables long dispersal distances. The presence of dense encrusting epibiota on many of

the items collected with the remote sample sets indicate that biofouling is indeed acting on larger, buoyant items in the marine environment. But like the larger samples tested in the experiment, these have sufficient buoyancy to overcome the ballasting effect of such heavy epibiotic settlement. The longer items are at sea, where they are continuously exposed to fouling, the more this buoyancy is reduced, and so the relative abundance of the most super-buoyant items such as empty bottles and lumps of polystyrene or marine foam increases.

Applications

While physical processes such as vertical wind mixing and other hydrodynamic factors are increasingly in numerical models of plastic abundance estimation, biological effects are rarely incorporated. Accounting for the effects of fouling on smaller items might go some way to further improving the capability of these models. My results could present a starting point, scaled to relevant environmental factors and subject to further tests. Including such a term would be particularly relevant in coastal waters, where fouling rates are likely to be higher due to higher concentrations of established sessile communities and the relative abundances of smaller plastics, shown in Chapter 1.

Recommendations for further research

The problem of marine plastic pollution is becoming an increasingly urgent environmental concern, but we are hampered in our efforts to mitigate it by our poor understanding of the behaviour of this type of debris once it reaches the sea. These results shed new light on how the size of a debris fragment might influence its dispersal and on the importance of considering biological processes such as biofouling, when attempting to map that dispersal. My experimental results could easily be improved upon by testing fouling effects on untethered samples in different energy environments. Such a study would be difficult to conduct, but might provide more realistic estimates of the rate of buoyancy loss. Another important step illustrated by this study is the urgent need to standardise litter sampling techniques for all different types of litter surveys in order to make data more universally meaningful.. Based on the fact that both studies suggest that a significant proportion of buoyant plastic debris does not persist at the surface, there is also a need to encourage further empirical studies of litter on the seabed and in the mid-column, in order to build up more accurate profiles of plastic distribution. Again, such surveys are logistically and financially more difficult than the beach surveys conducted here, but they might be the best way to provide more much-needed clues to the final destination of our plastic waste.

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APPENDICES

Appendix 1: Sample sizes retrieved for each size-thickness category at each sampling interval

Thickness / Size	Week 2	4	6	8	10	12	Total
0.1mm							
5	11	11	11	7	11	6	57
9	11	13	13	8	11	9	65
50	11	11	15	9	11	7	64
0.2mm							
5	11	14	10	5	12	10	62
9	12	11	14	11	10	9	67
50	10	11	15	9	12	9	66
0.5mm							
5	11	12	12	11	11	10	67
9	9	12	12	9	12	10	64
50	7	12	12	8	12	9	60
1mm							
5	10	15	12	10	13	9	69
9	10	15	13	10	13	10	71
50	8	18	8	9	12	13	68
4mm							
5	11	15	16	9	12	11	74
9	11	15	16	10	11	11	74
50	10	10	13	10	9	6	58
Total	**153**	**195**	**192**	**135**	**172**	**139**	**986**

Appendix 2a: Maximum fouling growth (mm) observed for each size-thickness combination

Thickness	Week					
Size	**2**	**4**	**6**	**8**	**10**	**12**
0.1mm						
5	8	25	50	30	60	35
9	5	25	35	30	96	50
50	6	22	60	80	125	75
0.2mm						
5	6	23	30	34	84	53
9	8	30	52	55	35	50
50	6	72	74	70	100	70
0.5mm						
5	6	35	32	40	72	31
9	8	35	50	72	90	52
50	5	30	82	125	80	160
1mm						
5	6	28	34	45	60	50
9	8	52	70	30	75	40
50	5	52	100	160	100	110
4mm						
5	6	25	50	50	65	110
9	7	50	60	60	100	85
50	5	45	100	60	120	140

Appendix 2b: Average fouling (mm) observed for each size-thickness combination

Thickness	**Week**					
Size	**2**	**4**	**6**	**8**	**10**	**12**
0.1mm						
5	1	3	7	4	5	7
9	1	2	7	6	12	12
50	0	2	7	12	12	25
0.2mm						
5	1	3	1	9	3	13
9	1	3	8	10	6	12
50	0	2	6	10	13	21
0.5mm						
5	1	3	8	6	9	7
9	1	5	7	12	13	14
50	1	2	13	14	11	24
1mm						
5	1	3	7	10	5	7
9	1	6	10	5	6	15
50	0	3	13	19	12	24
4mm						
5	1	6	8	6	8	9
9	1	5	12	7	12	13
50	0	6	14	10	19	24

Appendix 3: The percentages of samples that sank at each sampling interval

Thickness	Size	Week					
		2	4	6	8	10	12
0.1mm	5	55	55	82	86	100	100
0.1mm	9	9	15	77	100	100	100
0.1mm	50	0	0	13	89	100	100
0.2mm	5	9	21	50	100	92	90
0.2mm	9	0	9	64	100	100	100
0.2mm	50	0	0	13	78	100	100
0.5mm	5	0	8	67	91	100	100
0.5mm	9	0	17	75	89	100	90
0.5mm	50	0	0	17	100	92	100
1.0mm	5	0	7	67	100	100	100
1.0mm	9	0	13	46	100	85	90
1.0mm	50	0	0	0	22	83	100
4.0mm	5	0	20	25	78	92	91
4.0mm	9	0	0	25	40	82	91
4.0mm	50	0	0	8	20	67	83

Appendix 4: Mean change in dry mass for each sample size at each sampling interval

Thickness Size	Week					
0.1	**2**	**4**	**6**	**8**	**10**	**12**
5	129.9	241.7	1582.7	596.5	2977	3035
9	50.6	89.9	738.2	768.4	3416	4093
50	13.0	21.3	80.9	261.4	716	1947
0.2						
5	33.3	107.7	252.5	1736.1	844	5795
9	31.8	51.1	319.2	718.6	1344	1809
50	5.2	9.2	39.1	115.5	306	754
0.5						
5	16.5	39.6	196.0	287.3	738	853
9	31.1	67.4	161.5	389.3	1003	1237
50	3.2	7.7	38.0	66.9	149	379
1						
5	13.3	27.0	90.0	184.4	461	430
9	7.3	19.7	89.2	123.3	295	391
50	1.4	4.0	16.6	36.3	97	173
4						
5	6.5	20.1	53.4	106.9	190	261
9	5.0	6.1	34.4	32.5	163	275
50	0.5	2.5	9.8	15.2	52	67