The impact of potting for crustaceans on temperate rocky reef habitats: implications for management

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ABSTRACT

Multi-use marine protected areas (MPAs) are increasingly designated towards achieving global conservation targets. To develop effective management, the impact of permitted activities must be understood. Potting for shellfish occurs on temperate rocky reefs globally with impact not fully quantified. This UK-based study used underwater video to quantify (a) benthic condition of rocky reefs, (b) mechanisms of potting interaction and (c) true footprint of potting. Assemblages in static gear areas were more indicative of a healthy reef than those in mixed gear areas. Damage was recorded during pot hauling, but the area of damage was not the entire pot haul path. 25-30 % of individuals were damaged (commonly through tissue abrasion) or removed. Notably, damage occurred to some long-lived, slow growing taxa raising concerns over impacts. Potting is more destructive than previously thought and

managers must balance ecology with social and economic considerations to determine what level of impact is acceptable.

HIGHLIGHTS

- Impacts of potting on UK temperate rocky reefs quantified using underwater video
- Novel method using GoPro cameras to observe direct potting impacts
- Areas fished with pots characterised by species indicative of a healthy reef system
- Damage to long lived, slow growing taxa of potential concern
- Managers must decide what level of impact is 'acceptable'

KEYWORDS

Potting; *fishery management*; static gear; temperate rocky reef; *benthic ecology;* marine protected areas; *conservation;* underwater video; impact assessment; monitoring

1. INTRODUCTION

Temperate rocky reefs are characterised by sensitive, emergent epifauna, which are often long lived, slow growing and sensitive to human impacts. They provide important topographic complexity, and support commercially important species through, for example, provision of nursery areas, refuges from predators and habitat for the settlement of invertebrate spat (Beaumont, 2009; Beck et al., 2001; Beukers-Stewart and Beukers-Stewart, 2009; Dayton et al., 1995; Grecian et al., 2010; Hiddink et al., 2011; Jennings and Kaiser, 1998; Jennings et al., 2001; Monteiro et al., 2002; Parsons et al., 2016; Ryer et al., 2004). These systems are vulnerable to habitat destruction caused by fishing gear impacting the benthos (Gray, 1997; Gray et al., 2006; Kaiser et al., 2006; Sangil et al., 2013; Sheehan et al., 2017). The consequences of this are varied, but may result in broad scale, assemblage level change such as change in species composition, reduction in biomass, diversity and productivity and the removal of key species, all of which compromise the resilience of the ecosystem and its role in providing habitat to support species of commercial importance (Auster et al., 1996; Bradshaw et al., 2002; Collie et al., 1997; Jennings and Kaiser, 1998; Roberts and Polunin, 1991). Complexity and biodiversity within an ecosystem are key to its resilience, and are consequently of key relevance to marine conservation and human wellbeing (Cardinale et al., 2012; Howarth et al., 2014). Thus, in order to maintain the ecosystem services provided by rocky reefs it may be necessary for management measures to be implemented to reduce the impact of damaging fishing activities on sensitive habitats and species (Worm et al., 2006).

The coastal location of temperate rocky reefs makes them easily accessible for vessels of any size and they are targeted by commercial fisheries across the globe (Figure 1). In particular, these areas are favoured by fisheries for crustaceans, such as crab and lobster, which inhabit rocky reefs, or softer sediment occurring in areas between and within rocky reef patches (Howard and Bennett, 1979; Martel et al., 1986; Sheehan et al., 2013a). Crustacean fisheries associated with rocky reefs occur as a global industry throughout the northern and southern temperate zones, present in 48 countries, which also have multi-use MPAs within their waters (data derived through literature review; Figure 1). They are commonly located in inshore, shallow reef areas and target species include, for example, edible crab (*Cancer pagurus*) in north west Europe (e.g. Bannister, 2009; FAO, 2017), Juan Fernández rock lobster (*Jasus* *frontalis*) in Chile (e.g. Arana et al., 2011), mud crab (*Scylla* spp.) in Africa (e.g. Le Vay, 2001) and spiny red rock lobster (*Jasus edwardsii*) in Southern Australia (e.g. Treble et al., 1998).

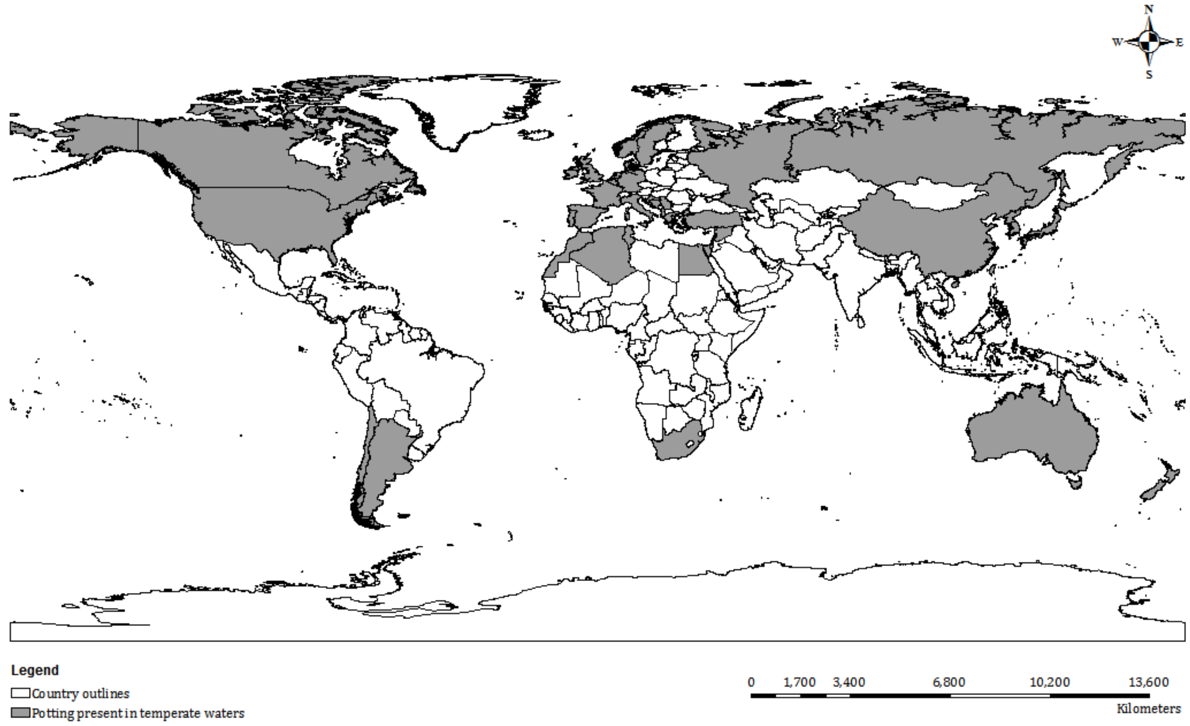

Figure 1: Global map showing countries where potting is conducted in temperate waters and where multi-use MPAs exist. Data sourced from literature searches. Map created using ArcGIS 2017.

Crustacean fisheries are a very valuable component of the UK fishing industry, with 1,342 vessels fishing with pots and traps in 2016; the majority of which were under 10m vessels fishing in inshore waters (Seafish, 2017). In 2017, total shellfish landings accounted for 38 % of all landings by UK vessels into the UK and abroad, and during the year of 2017, 34,100 tonnes of crab and lobster were landed into the UK by UK vessels, worth £98.1 million (MMO, 2018).

The most common method of capture for crustacean species are pots and traps (termed ‘pots’ from here on in). All pots are referred as “static gear” as they are deployed and left to soak in situ, before being hauled after a period of time. The design and material of the pots varies between locations, with pots made of wood, metal or plastic, but all share this common mode of operation, meaning that the impacts may be assumed to be broadly similar (Slack-Smith, 2001).

Where MPAs are designated to protect temperate rocky reefs it is possible that they will overlap with areas where pot fishing occurs, and, as potting has commonly been an activity assumed to have little or no impact (Jennings & Kaiser, 1998), it is often permitted where MPAs are multi-use. There is, however, increasing attention placed on this, with researchers and policy makers wishing to understand more about potential impacts from potting to ensure such activities are compatible with the conservation goals of MPAs (e.g. Casement and Svane, 1999; Coleman et al., 2013; Eno et al., 2001; Lewis et al., 2009; Rees, 2018; Shester & Micheli, 2011; Stephenson et al., 2017; Troffe et al. 2005; Walmsley et al., 2015). Impacts from pots may occur during deployment, soak time or hauling of the pot, impacting the benthos and associated taxa through contact with the pot and/or end weight, or from scour caused by the associated ropes.

Rocky reef habitats are thought to have a medium-high sensitivity to potting impacts and a medium level of resilience (defined as the time required for a habitat (and its constituent species and physical features) to recover to its characteristic state after disturbance), (Eno et al., 2013). Impacts pose a threat in particular to long lived, slow growing sessile epifauna that characterise rocky reef habitats (Coleman et al., 2013; Jennings and Kaiser, 1998; Sheehan et al., 2013b), including species of gorgonian, soft coral, bryozoan and erect branching sponges which are known to be particularly vulnerable due to their erect body-forms, and life histories

(Coleman et al., 2013; Langmead et al., 2010). Despite these risks, the impact of pots on benthic marine ecosystems is often regarded as minor in comparison with the impact of mobile benthic gear (Jennings and Kaiser, 1998), and consequently, research efforts have been focussed on the assessment of mobile gear.

The limited research that has taken place has suggested that whilst some damage does occur it is unlikely to be significant (see Casement and Svane, 1999; Coleman et al., 2013; Eno et al., 2001; Lewis et al., 2009; Shester & Micheli, 2011; Stephenson et al., 2017; Troffe et al. 2005) unless potting intensity is high (defined as ~ 30 pots per 500m^2) where some decline in abundance of indicator species was identified by Rees (2018). The true footprint of potting (contact that the pot makes with the benthos) has not yet been fully quantified, however, and there is a need for more evidence relating to the underwater behaviour and habitat interaction of pots to support these conclusions (Eno et al., 2013; Stephenson et al., 2017).

Studies suggest that recovery of emergent slow-growing fauna from the impacts of bottom towed fishing gear occurs on decadal timescales (Babcock et al., 1999; Watling and Norse, 1998), but that potting activity is unlikely to impede recovery of benthic systems (Blyth et al., 2004; Sheehan et al., 2015; Sheehan et al., 2013b). What is not clear, however, is whether potting activity compromises their ability to reach a fully functional state (Tett et al., 2013) or whether it allows them to meet their ecological goals and achieve favourable conservation status (Jones, 2002). Furthermore, in areas where more destructive fishing practises are restricted, use of static gear may increase (Mangi et al., 2011) and the consequences of this need to be understood.

The global presence of potting on rocky reefs makes these questions of key importance and more research is required to answer them, particularly in light of the drive for evidence-based policy development and decision making (e.g. Defra, 2011; European Commission, 2015; House of Commons, 2017;), and the requirement to meet international targets for marine conservation. One such target is the Convention on Biological Diversity (CBD) Aichi Biodiversity Target 11 which has resulted in an increasing number of marine protected areas (MPAs) globally (Thomas et al., 2014) and calls to increase protection of each marine habitat from 10-30 % (WCC-2016-Res-050-EN; IUCN WCPA, 2018; IUCN, 2014, 2016; O'Leary et al., 2016) by 2030 (Johnson et al., 2019).

The requirement to meet these targets increases the likelihood of new MPAs being designated multi-use, and consequently the chance of sites being located on areas of rocky reef where potting occurs. Designation decisions require an ecosystem approach to management to be taken where humans are considered integral to the ecosystem and socio-economic factors are considered alongside ecological (Pikitch et al., 2004; Gaines et al. 2010). As part of these decisions there is also an increasing emphasis on assessing management effectiveness of multi-use sites, with those newly designated designed to include representation targets requiring spatially accurate mapping of habitat types (Day & Dobbs, 2013; Johnson et al., 2019; Pomeroy et al., 2005; Garces et al., 2013) in order to avoid the push for meeting targets coming at the expense of the quality and effectiveness of regulation and management (De Santo, 2013). Increasing our knowledge of impacts and their consequences is therefore vital for effective assessment of these sites and ensuring we implement appropriate management measures.

The aim of this research was therefore to provide robust evidence, which quantified whether the extractive activity of potting is compatible with designation of multi-use MPAs. This was achieved using the Inshore Potting Agreement (IPA) area in South Devon, UK as a test case study site. Unfortunately the nature of human use of the ocean and the relatively recent addition of marine protected areas around the UK coast means that there were no pristine control areas available for this study, hence the following research questions were addressed: (a) is benthic condition and provision of ecosystem services greater in areas within an MPA where trawling has been excluded but potting is permitted than in areas where trawling occurs; (b) what are the mechanisms of physical potting interaction with the benthos and (c) what is the true footprint of potting. For ease of understanding, these are termed (a) benthic condition (b) mechanisms of potting interaction, and (c) true footprint of potting.

1.1 Case study site: The Inshore Potting Agreement, South Devon, UK

Although not initially designated this way, the IPA falls under the commonly recognised definition of an MPA (Kelleher 1999) as bottom towed fishing gear was excluded in 1978 from large areas to reduce conflict between mobile and static gear types. This led to the establishment of a zoned fisheries management scheme which was incorporated into statutory legislation in 2002 (Hart et al., 2003) and has provided ecological benefits to areas where bottom towed fishing gear was excluded (Blyth et al., 2004). Furthermore its use aligns with that of IUCN Category VI MPA, which allows the protection of natural ecosystems and sustainable use of natural resources, when conservation and sustainable use can be mutually beneficial (Day et al., 2019). The area is overlain by the Start Point to Plymouth Sound and Eddystone Site of Community Importance (SCI), designated for the protection of reef habitat under the Habitats Directive (Council Directive 92/43/EEC) and from which bottom towed fishing gear was excluded in 2014 (Figure 2), (Natural England, 2013), and overlaps the Skerries Bank and Surrounds Marine Conservation Zone. The presence of the MCZ was not considered during the study as management plans were not yet established.

The IPA covers an area approximately 500 km^2 and includes zones where static gear (pots and static nets) is exclusively allowed, areas where towed gear is exclusively allowed and areas where gear types are managed seasonally (Figure 2). The area is managed by the Devon & Severn Inshore Fisheries & Conservation Authority whose remit cover 0-6 nm and who seek to ensure that their management secures the right balance between social, environmental and economic benefits.

The IPA area is very important both locally and nationally for its brown crab (*C. pagurus*) fishery, with landings from boats into the ports of Dartmouth and Salcombe the largest in England, totalling almost £3.4 million in 2014 (Marine Management Organisation, 2015). Fishers in the area use two different types of pot, inkwell and parlour (see Figure 3). The difference in potential impact of these pot types is unknown, with fishers choosing which to use based on the type of boat they work from and personal preference due to differences in size and shape between the pots (South Devon & Channel Shellfishermen, pers comm.).

Due to the long history of management within the IPA it is possible to test whether, following approximately 35 years of exclusion of bottom towed fishing gear, the relative health of the ecosystem is greater within the exclusion area than outside where bottom towed fishing gear use continues. In the absence of pristine control sites, this method can help determine whether the presence of potting activity has allowed the ecosystem to recover and deliver more ecosystem services than unprotected areas, or whether potting interactions are compromising benthic rocky reef habitats and the ability of a site to achieve or maintain favourable conservation status (Jones, 2002).

In the context of this study the term 'relative health' is used due to the absence of data to allow an *a priori* definition of health to be determined. The work of Tett et al. (2013) can be used to develop indicators for the relative health of the ecosystem. The indicators selected included univariate metrics such as number of individuals (individuals m^{-2}), number of taxa (taxa m^{-2}), diversity (Simpson's 1-λ), number of individuals of selected indicator taxa including *Eunicella verrucosa* and *Pentapora foliacea* which are known to be sensitive to fisheries impacts (individuals m^{-2}), and assemblage composition.

Using the metrics outlined above, the study examined the hypotheses that:

(1) Benthic condition:

H1 = number of taxa, number of individuals, diversity and assemblage composition differ between potted areas where bottom towed fishing is not permitted and areas open to bottom towed fishing

(2) Mechanisms of potting interaction*

H2 = during pot hauls the seabed contact area is smaller than the total possible contact area for inkwell and parlour pots

(3) True footprint of potting*

H3 = during pot hauls fewer benthic fauna are damaged or removed than not damaged within the seabed contact area for inkwell and parlour pots

*Observation of fishing methods and discussion with members of the fishing community in the study area influenced survey design for the mechanisms of potting interaction and true footprint of potting. It may be assumed that a pot will drag constantly across the benthos during the haul, but the uneven topography of a rocky reef area dictates that whilst pots are likely to make some contact the entire base of the pot would not be likely to drag along the benthos; and as such the area of impact (seabed contact area) may be smaller than might initially be assumed (total possible contact area).

H1 was tested using video footage taken from a towed flying array across ten areas and over three years, and H2 and H3 were tested using video footage taken from cameras mounted on pots for two gear types (parlour and inkwell) across three areas and two years.

2. METHODS

2.1 Case study site & survey design

The survey was conducted in South Devon UK, in the IPA area, with the majority of sites also within the SCI (Figure 2). Surveys took place on an annual basis over the summer months from 2013-2015 for benthic condition and 2014 & 2015 for mechanisms of potting interaction and true footprint of potting.

The target habitat type was rocky reef as defined by the Habitats Directive as ‘habitats where animal and plant communities develop on rock or stable boulders and cobbles’ (Jackson & McLeod, 2000). Suitable habitat was identified within the areas overlapping the SCI using sidescan data provided to Devon & Severn IFCA (D&SIFCA) by Cefas, and from a video survey report completed for Natural England (Ross, 2011). In addition, and particularly for the areas outside the SCI where no habit mapping was available, the working knowledge of the fishers and D&SIFCA was used (Figure 2). No data on frequency of fishing activity was available, but potters fish specific areas and there is known to be little space available for additional boats to join the fishery (Blyth et al., 2002; Devon & Severn IFCA, pers. comm.), giving confidence that sites known to be potted would have been regularly fished.

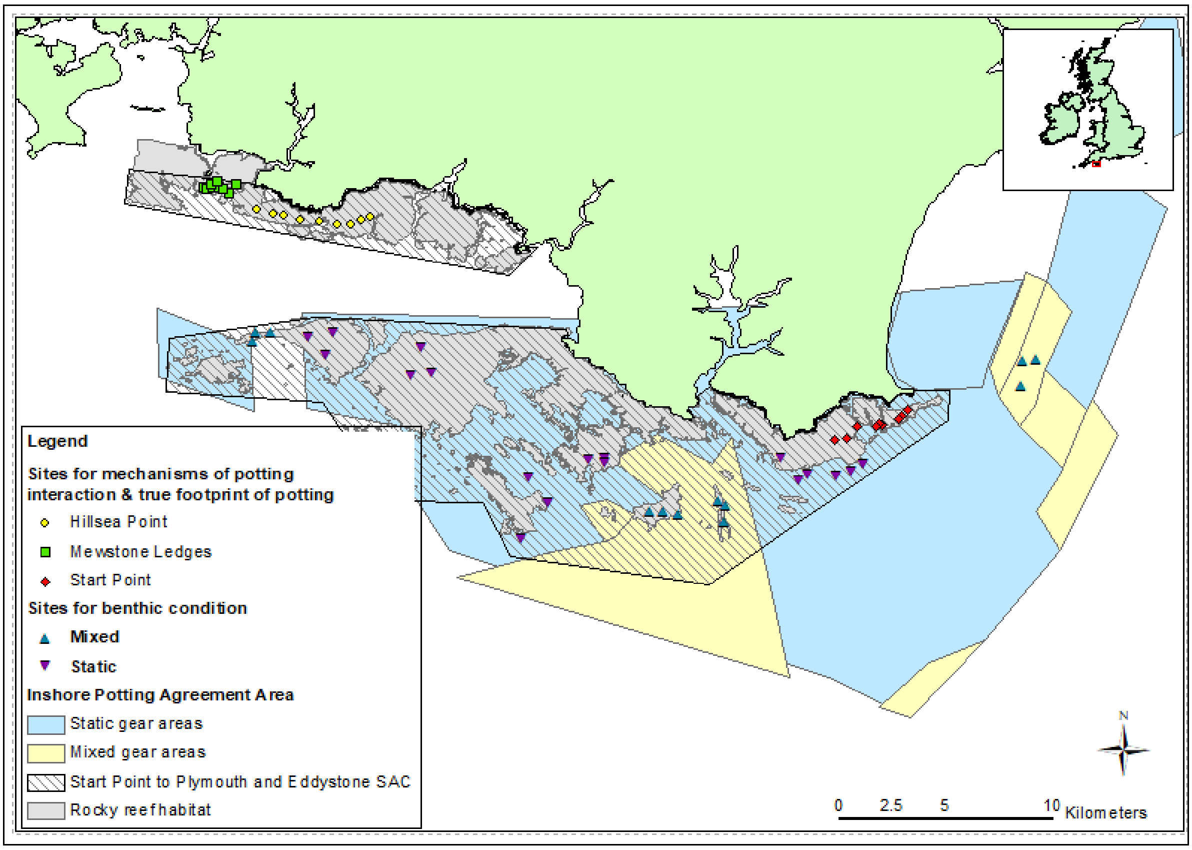

Figure 2: Survey sites for: benthic condition (Mixed – blue triangles, Static – purple triangles) mechanisms of potting interaction & true footprint of potting (Start Point – red circles, Hillsea Point – yellow circles, Mewstone Ledges – green squares). Map created using ArcGIS 2017

2.2 Benthic condition

Two treatments were selected, "Static" where only static gear (mainly pots) had been fished since the IPA was established in 1978, and "Mixed", where areas are open to both mobile and static gear (only one area was open to mobile gear alone and did not provide enough suitable habitat type). A total of 30 sites were sampled at a target depth of 50 m, and were distributed across the survey area in groups of three "Locations" (A-J see Figure 2) to account for any effects resulting from the known differences in topography and exposure to tidal streams. Eighteen sites were sampled in the Static treatment, and 12 in the Mixed (Figure 2). At each site a 20-minute video transect was recorded to sample sessile and sedentary taxa using a High Definition camera mounted on a flying array towed behind the boat at a speed of approximately 0.4 knots, equating to approximately 200 m per tow (Figure 3). The method followed that developed by Sheehan et al. (2010) to ensure that sampling was cost-effective, relatively non-destructive and to minimise the risk of snagging on uneven rocky reef or boulders (Sheehan et al., 2016).

Sampling aimed to quantify differences in the univariate metrics: number of individuals (m^{-2}), number of taxa (m^{-2}), diversity (Simpson's 1-λ) and a number of selected indicator taxa (m^{-2}), namely *Alcyonidium diaphanum, Alcyonium digitatum*, branching sponges, *Cliona celata, Eunicella verrucosa, Metridium senile, Pentapora foliacea* and *Urticina felina,* plus the multivariate metric assemblage composition. Indicator taxa were those expected to be susceptible to damage from fishing impacts (Coleman et al., 2013; Langmead et al., 2010) and were selected based on life history, tolerance to disturbance and recoverability, following Jackson et al. (2008) and Langmead et al. (2010).

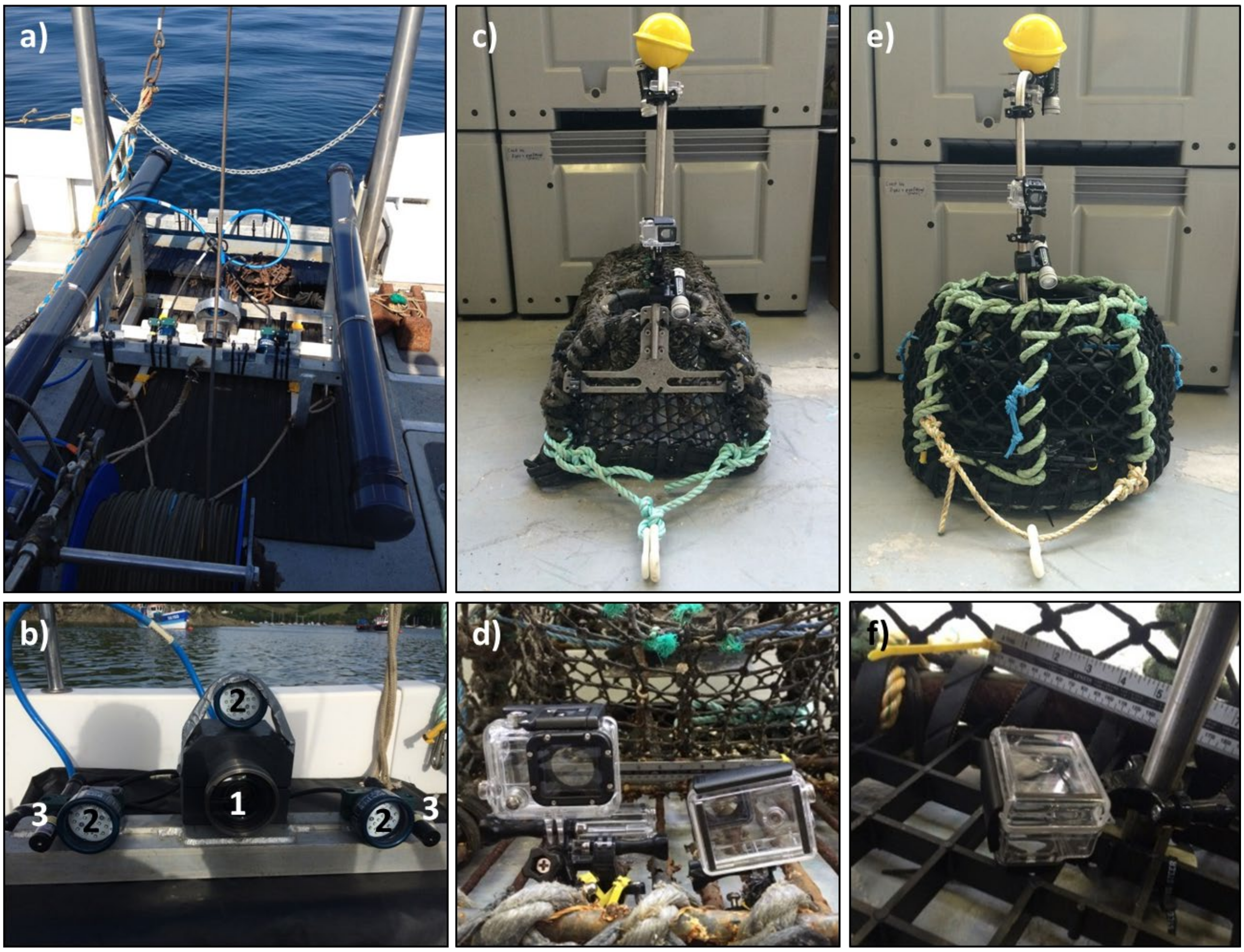

Figure 3: a) flying array on deck, b) flying array HD camera (1), LED lights (2) and lasers (3), c) set up of GoPro cameras mounted on a parlour pot d) back view camera (left hand side) and the inside view camera (right hand side), e) set up of GoPro cameras mounted on an inkwell pot, and f) the down view camera

2.2.1 Field methods

The video system included a HD camera (Bowtech Products Limited, Surveyor-HD High Definition Underwater Colour Zoom Video Camera, 720p), LED lights (Bowtech Products Limited, LED-K-Series Underwater LED Light), and two laser pointers to allow the field of view to be calibrated (Apinex Inc. BALP-LG05-B105). The camera was positioned at an oblique angle to the seabed with the LED lights mounted on either side and above the camera, and the lasers fixed outside of the lights 30 cm apart (Figure 3). The camera was connected via an umbilical to a Bowtech System power and control unit, which gave topside control of the focus, zoom and aperture of the camera and the intensity of the lights.

2.2.2 Video analysis

Data were extracted by examination of individual HD video frames taken at two second intervals to avoid overlap using 3Dive Frame Extraction software (Cybertronix). Images were overlain with a 0.25 m^2 counting grid calibrated using the position of the lasers which allowed extraction of density and percentage cover information for each taxon. Strict criteria were adhered to during the selection of frame grabs suitable for analysis following methods developed by Sheehan et al., (2013b) and Stevens et al. (2014), and only those where the habitat fitted the definition of a rocky reef (Jackson & McLeod, 2000) were included. Once those suitable for analysis were finalised, 30 frame grabs were randomly selected for analysis (Stevens et al., 2014). Data were averaged by transect prior to analysis to avoid pseudo-replication.

All taxa present in each frame were identified to the lowest taxonomic level possible. Number of individuals was enumerated using count (ind. m^{-2}) or cover (% m^{-2}) as appropriate. Taxonomically similar species that could not be distinguished with confidence, such as branching sponges or hydroids, were grouped to ensure confidence in the data recorded.

2.2.3 Data analysis

Multivariate and univariate analyses were conducted using Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson (2001); Clarke and Warwick (2001)) based on similarity matrices using PERMANOVA+ for Primer in PRIMER 6 (Clarke and Warwick, 2001).

Multivariate data were dispersion weighted and fourth root transformed to down weight species with large or erratic abundances and allow rarer species to contribute to the outcome (Clarke et al., 2006). Bray-Curtis similarity indices were used to construct similarity matrices. Univariate data were also fourth root transformed and Euclidean dissimilarity indices were used to construct similarity matrices (Clarke and Warwick, 2001). Each term in the analyses used 9999 permutations of the appropriate units (Anderson and Braak, 2003).

Four factors were used in the analyses, Year (random: 2013, 2014, 2015), Treatment (fixed: Static, Mixed), Location (random and nested in Treatment: 6 Static, 4 Mixed) and Site (random, nested in Location: 3 per Location). The lowest significant effect was interpreted for each test ($P < 0.05$) and significant interactions involving fixed factors were interpreted using pairwise tests. Data were visualised using Non-metric Multi-Dimensional Scaling (nMDS) with vectors overlain showing key SIMPER results.

2.3 Mechanisms of potting interaction and true footprint of potting

A total of 27 sites were selected, in three areas, Start Point (SP), Mewstone Ledges (ML) and Hillsea Point (HP), (Figure 2). At each site, one string of inkwell pots and one string of parlour pots were deployed approximately 200 m apart, with four pots per string, and GoPro Hero 2, 3 and 4 Silver and Black edition (GoPro Inc) cameras fitted to alternate pots. Each camera pot had 5 cameras mounted to give: (a) a bird's eye view over the pot; (b) an inside view from within the pot; (c) a downwards view through the base of the pot (d) a rope view of where the rope connecting the pot attached (e) a backwards view at the opposite end to where the rope attaches to the pot to show the ground the pot was being hauled over (Figure 3). Surveys were conducted from commercial fishing vessels to ensure that pot deployment and hauling was representative of true fishing conditions (for detailed descriptions of how this was conducted, please see Supplementary Material).

As discussed, the uneven topography of a rocky reef area dictates that pots are likely to make some contact but that the entire base of the pot would not be likely to drag along the benthos during hauling; and as such the area of impact (seabed contact area) may be smaller than might initially be assumed (total possible contact area). Estimation of impact based on length of total possible contact area would therefore result in an overestimation.

Sampling aimed to quantify the mechanisms of potting interaction and the true footprint of a pot through quantification of: settle duration (seconds from point of first contact to becoming stationary) pot stability during the soak, haul duration (seconds from first movement to clearing the reef), total possible contact area (defined as total distance travelled x area of base of pot (m^2)) and seabed contact area (defined as distance where pot contacted seabed x area of base of pot (m^{-2})), (see Figure 4). The start and end GPS position of the haul were unknown. To estimate the length of each tow the known pot dimensions were used as a reference to visually assess how much distance was covered by each pot. Videos were played x2 slower than real-time to aid this assessment.

In addition, biotic metrics were also used: number of individuals ((not damaged, damaged, removed), (number of individuals m^{-2})), and for selected indicator taxa known to be sensitive to fishing impact (Coleman et al., 2013; Jackson et al., 2008; Langmead et al., 2010), *Alcyonium digitatum*, branching sponges, *Cliona celata, Eunicella verrucosa and Pentapora foliacea*, number of individuals ((not damaged, damaged, removed), (m^{-2})) was also calculated.

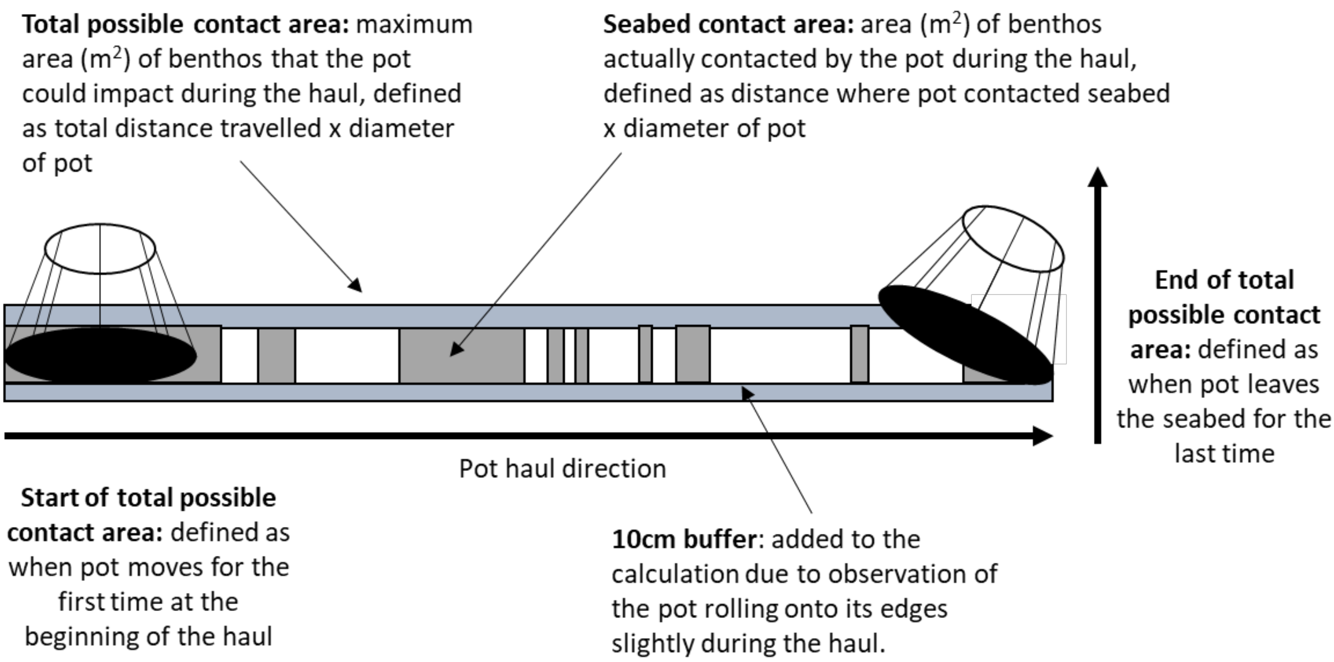

Figure 4: Diagrammatic example of how the total possible contact area and seabed contact area were calculated during the pot haul

The strings of pots were set as they would be under normal fishing conditions, in approximately 30 m of water. End weights were used to anchor each end of the string, and a leaded line joined the string to the buoy on the surface. Leaded line was also used between the pots, which were deployed for 25 minutes, allowing sufficient time to settle, and were then hauled and redeployed at the next site.

All cameras were set to record in the 1080p, 30 frames per second mode, giving high quality footage while conserving battery life. Two Underwater Kinetics Aqualite torches were also mounted on each pot, one under the rope view camera and the other by the bird's eye camera to counteract poor light conditions (Figure 3).

2.3.1 Video analysis

Despite having five cameras mounted on the pots, it became apparent that all metrics except for the rope movement were best quantified using the video from the bird's eye camera. The rope view camera was used for assessing rope movement. Whilst the other three cameras provided useful observational information and contributed to the understanding of the pot movements and impacts, they were not used for data analysis. The greatest constraint on the survey was the battery life of the GoPro cameras and on the few occasions where they did not last for the full haul the data were excluded from the analysis.

2.3.1.1 Mechanisms of potting interaction

HD video was watched from each camera view for each haul, and data were extracted for each metric (for details see section 2.3). A 10 cm buffer was added to the pot area to calculate the total possible contact area and seabed contact areas as video analysis revealed that pots were often unstable as they moved across the ground during the haul, resulting in some slight rolling onto their sides (Figure 4). The seabed contact area is therefore expected to be a calculation of maximum impact.

2.3.1.2 True footprint of potting

Taxa were identified to the highest taxonomic level possible, although taxonomically similar species were grouped to avoid misidentification, with groupings as stated in benthic condition. Hauls were conducted at a relatively constant speed so video quality was consistent and only those species for which a positive ID could be made with confidence were included in the analysis. Description of taxon damage is given in Table 4, where 'abrasion' is visible rubbing commonly resulting in clouding of the water suggesting tissue removal, and 'sections removed' where injury occurred resulting in clouding of the water and the presence of small sections of tissue in the water column. The implications of these were considered comparable and the definitions apply to interactions from both the pots and the ropes.

2.3.2 Statistical analysis

Data were pooled per string (two pots) and multivariate and univariate analyses were conducted for data on seabed contact area and number of individuals using Permutational Multivariate Analysis of Variance (PERMANOVA+, (Anderson, 2001; Clarke and Warwick, 2001)) based on similarity matrices using PERMANOVA+ for Primer in PRIMER 6 (Clarke and Warwick, 2001). Multivariate data were square root transformed and Bray Curtis similarity indices were used to construct similarity matrices. Univariate data were untransformed and Euclidean dissimilarity indices were used to conduct similarity matrices (Clarke and Warwick, 2001). Each term in the analyses used 9999 permutations of the appropriate units (Anderson and Braak, 2003).

Three random factors, Year (2014, 2015), Location (Start Point (SP), Mewstone Ledges (ML), Hillsea Point (HP)), and Site (1-9 nested in Location) and one fixed factor Pot Type (Parlour (P), Inkwell (I)) were used in the analysis. To test whether the number of individuals not damaged was significantly greater than the number of individuals damaged or removed, a repeated measures approach to ANOVA was used with the additional random factor Pot haul path (1-102), nested in Year, Pot type and Site (added as the measures of individuals not damaged, damaged and removed were taken from the same pot haul path for each haul (Bob Clarke, pers. comm.)), and the fixed factor Response (No Damage (ND), Damaged (D) and Removed

(R). The lowest significant effect was interpreted for each test ($P < 0.05$) and significant interactions involving fixed factors were interpreted using pairwise tests.

2.3.3 Effect size analysis

In addition to the statistical testing, effect size was also calculated on un-pooled data to allow further examination of the impacts of potting and the differences between the two pot types.

2.3.3.1 Mechanisms of potting interaction

For each pot haul, the strip length (total distance moved during the haul) was estimated from the video using visual reference points on the seabed. Seabed contact area was estimated as the number of pot lengths where the pot was in contact with the seabed, multiplied by the footprint of the pot.

Seabed contact area and strip length (total distance (m) moved during the haul; note this differs from total possible contact area (m^2)) were calculated for each pot. The effect of strip length, pot type (fixed factors), location and year of sampling (random factors), and their interactions on seabed contact area was tested using linear models in the software package R (R Core Team 2019) with the lme4 package (Bates et al., 2015). Overall effects of the two pot types were calculated as mean contact areas and (95 %) confidence intervals using the package emmeans (Lenth 2019).

2.3.3.2 True footprint of potting

The effect of pot hauling on benthic fauna was explored for the identified assemblage, and for species grouped according to body type (erect-emergent and low-encrusting) based on the BIOTIC database (MarLIN, 2006) for each species or its closest available relative. Species were quantified in terms of abundance not damaged, damaged or removed. For pot-level observations, the mean value of species responses was calculated for each pot, before estimating effect sizes and confidence intervals. For body type statistics, abundances were calculated for each species, then a mean for each body type within each pot was calculated, before calculation of mean effects and confidence intervals. Mobile benthic species were omitted from this analysis owing to only one record of damage.

Effects were calculated as fractions of fauna removed, damaged or undamaged by the two different pot types, with overall mean fractions and 95 % confidence intervals calculated using a nonparametric bootstrap method from the Hmisc package (Harrell, 2019). Responses were compared between pot types using Wilcoxon-Mann-Whitney tests in the R package coin (Hothorn et al., 2008), and effect sizes calculated as Wilcoxon r values using the R package rstatix (Kassambara 2020).

3. RESULTS

When interpreting the results, the phrasing 'significantly greater' has been used where there is statistical significance ($p < 0.05$). Where the phrase 'consistently greater' is used there has not been a statistical significance identified, but highlighting the trends seen was felt to be of importance. All significant interactions are reported below. Full PERMANOVA tables and results from linear modelling and effect size analyses can be found in the supplementary material (Tables S1-S10).

3.1 Benthic condition

A total of 91 taxa were recorded from eight phyla. A significant Treatment effect was identified for the abundance of "cover" individuals ($p < 0.05$), with abundance significantly greater in the Static than Mixed treatment (Static = 16.88 m^{-2} % ± 1.75, Mixed = 8.73 m^{-2} % ± 2.16; Figure 5). Abundance of "count individuals", number of taxa and diversity was also consistently greater in the Static than the Mixed treatment (Count: Static = 549.41 ind. m^{-2} ± 54.86, Mixed = 260.45 ind. m^{-2} ± 16.24; Number of taxa: Static = 20.37 m^{-2} ± 0.35, Mixed = 17.00 m^{-2} ± 0.49; Diversity: Static = 0.54 ± 0.01, Mixed = 0.49 ± 0.02; Figure 5), although no Treatment effect was identified.

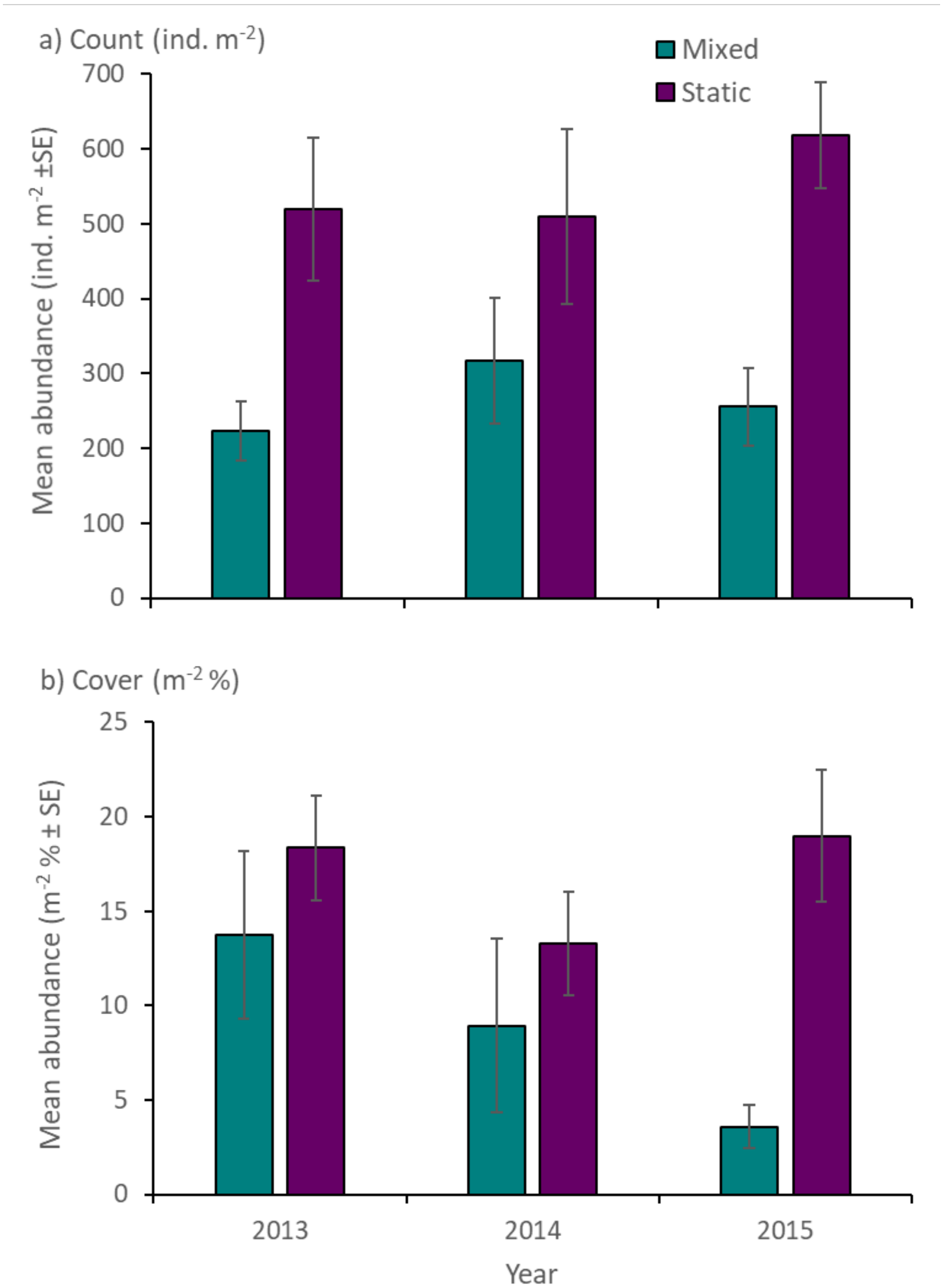

Figure 5: Mean abundance of all a) Count (individuals m^{-2} ± SE) and b) Cover (m^{-2} % ± SE) individuals in the Static and Mixed treatments per year (2013, 2014, 2015)

Despite significant temporal and spatial variation, a significant treatment effect was identified for assemblage composition, with two distinct groupings apparent ($P < 0.05$, Table 1, Figure

6): despite some overlap, sites in the static treatment were more similar to each other than to the sites in the mixed treatment.

Source	df	MS	Pseudo-F	P(perm)
Year	2	3812.80	3.16	**0.0002**
Treatment	1	13717.00	1.82	**0.04**
Location(Treatment)	8	6373.50	2.80	**0.0001**
Year x Treatment	2	1833.80	1.55	0.07
Site(Location(Treatment))	20	1326.90	1.68	**0.0001**
Year x Location(Treatment)	16	1178.60	1.50	**0.0004**
Res	37	787.55		
Total	86			

Table 1: PERMANOVA to test the differences in assemblage composition between Years (2013, 2014, 2015), Locations (A-J, nested in Treatment), Sites (1-30, nested in Location) and Treatments (Static, Mixed). Data were dispersion weighted and fourth root transformed prior to the construction of a Bray Curtis resemblance matrix. Bold values indicate significant differences.

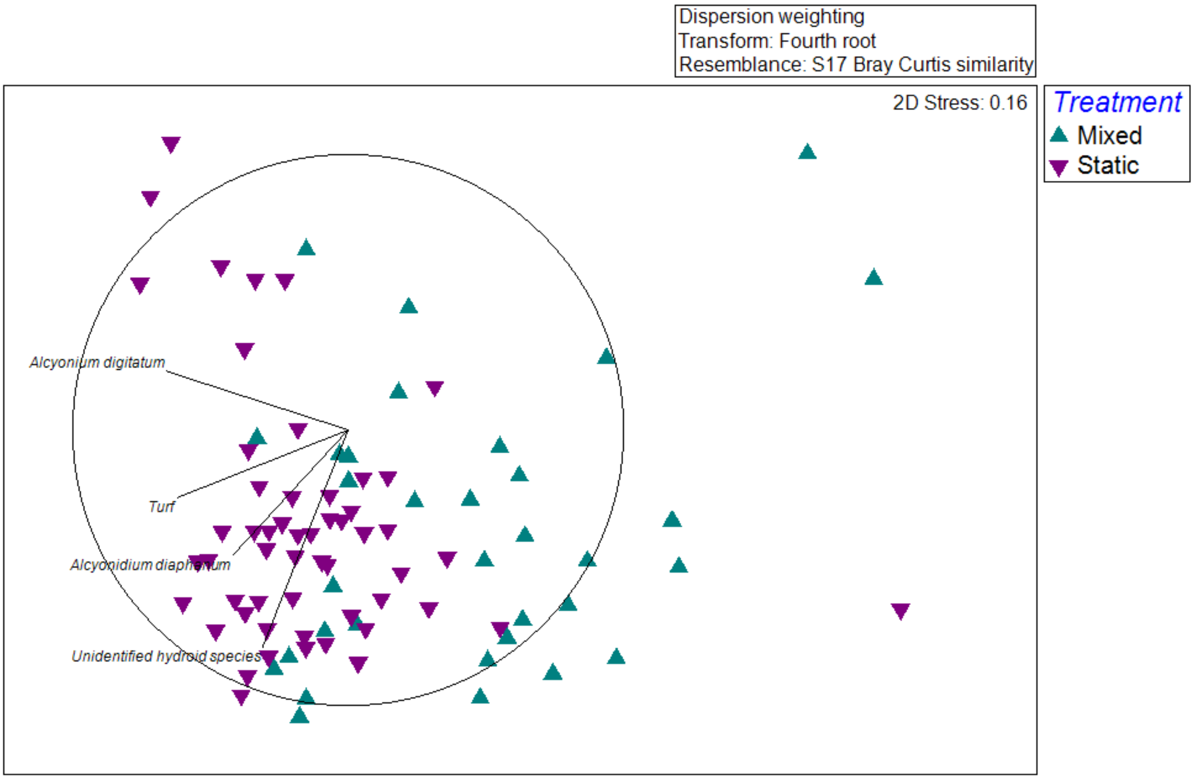

Figure 6: nMDS ordination illustrating similarities in assemblage composition between Treatments. Vectors show key species driving differences as identified through SIMPER

Results of SIMPER (Table S4; Supplementary material) showed the distinction between Treatments was driven primarily by differences in the abundance of hydroid and bryozoan turf, *A. digitum*, hydroids, and *Alcyonidium diaphanum* (Figure 6; cumulative contribution = 34.10 %). Abundance was greatest in the Static treatment for all but one indicator, *M. senile* (Table S4; Supplementary material). Treatment effects were identified for *A. digitatum*, *C. celata* and *M. senile* and as with assemblage composition some variation was observed between random factors for most indicators.

3.2 Mechanisms of potting interaction

Pots took an average of 3.46 seconds (± 0.27) to settle (from first touch to stationary), with Inkwell pots taking 3.29 seconds (± 0.35) and Parlour pots taking 3.63 seconds (± 0.42). The majority of pots (82.5 %) landed upright, with more parlour than inkwell pots landing on end (Parlour = 17.82 %, Inkwell = 4.04 %), as would be expected due to their design. Pots were relatively stable (no movement = 86.36 % of soaks), although movement did occur in some instances (some occasional movements = 8.08 % of soaks; small movements throughout soak = 4.04 %; large movements throughout the soak = 1.52 % of soaks).

The pots took 41 seconds (± 3.24) to haul (from first movement to clearing the seabed for good). The total time that the pots moved across the seabed (rather than being stationary or off the seabed), however, was 20.71 seconds (±1.36), meaning that they were in contact with the seabed for approximately half the time it took for them to be lifted clear. Rope movement during the soak was observed for 51.02 % of soaks, although 45.91 % of the time this movement was described as minimal, where the rope moved slightly with the tide but no scour or species impacts were observed.

3.2.1 Seabed contact area

The total possible contact area (total distance travelled x area of base of pot) was 6.20 m^2 ± 0.61, and the length of the seabed contact area (distance where pot contacted seabed x area of base of pot) was 3.04 m^2 ± 0.24 (49.07 % of the total possible contact area).

Differences between pot types were apparent with a significant Pot x Site(Location) interaction identified; total possible contact areas were significantly larger than seabed contact areas for both pot types, and were larger for inkwell pots than for parlour pots (inkwell, total possible contact area = 7.16 m^2 ± 1.00, seabed contact area = 3.51 m^2 ± 0.40, parlour, total possible contact area = 5.24 m^2 ± 0.67, seabed contact area = 2.57 m^2 ± 0.24, $P < 0.05$; Table 2). These trends were consistent between Areas.

Table 2: Mean, N, standard error (SE), minimum (Min) and maximum (Max) values for seabed and total possible contact area by pot type (Inkwell and Parlour)

	Mean	N	SE	Min	Max
Seabed contact area					
Inkwell	3.51	54.00	0.40	0.00	15.56
Parlour	2.57	54.00	0.24	0.00	7.16
Total possible contact area					
Inkwell	7.16	54.00	1.00	0.00	27.45
Parlour	5.24	54.00	0.67	0.00	24.26

Linear modelling indicated mean seabed contact areas varied by pot type and strip length ($F_{2,91}$ = 74.9, $p < 0.0001$) (Supplementary Material, Table S6), increasing linearly with strip length (Figure 7). This pattern was consistent between pot types, with no significant interaction between strip length and pot type. For completeness, pot-specific relationships between strip length and contact area are presented in the Supplementary Material (Table S7).

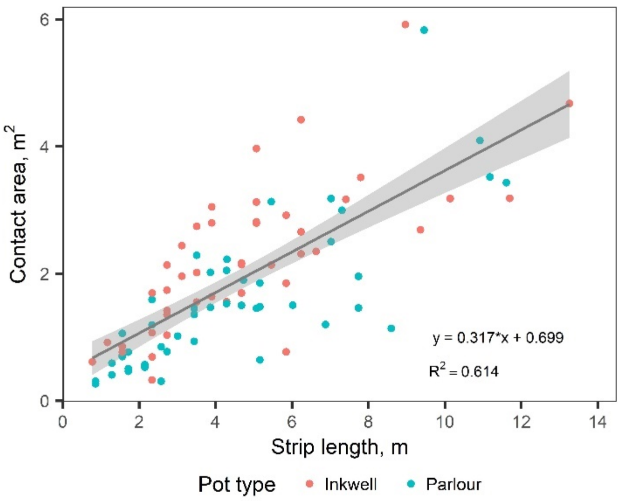

Figure 7: Contact area of pots during hauling as a function of distance travelled during the haul (strip length), for the two pot types, Inkwell (red) and Parlour (blue). Linear model fit and 95 % confidence interval overlaid.

3.3 True footprint of potting

A total of 18 taxa were identified from the videos (Table 4), from six phyla. Abundance across all sites was greatest for the solitary baked bean ascidian *Dendrodoa grossulaira* (8.46 ind. m^{-2} ± 2.95), macroalgae (2.20 ind. m^{-2} ± 0.40) and the soft coral *A. digitatum* (1.75 ind. m^{-2} ± 0.28), (Table 4).

Species name	Common name	Phylum	Damage description	Total	Inkwell			Parlour		
					ND	D	R	ND	D	R
Alcyonidium diaphanum	Sea chervil	Bryozoa	Abrasion	0.33 ± 0.11	68.72	31.28	0.00	71.66	27.77	0.57
**Alcyonium digitatum*	Dead Man's Fingers	Cnidaria	Abrasion and/or sections removed	1.75 ± 0.28	63.76	26.63	9.60	66.87	21.05	12.09
Asterias rubens	Common starfish	Echinodermata	None	0.11 ± 0.03	100.00	0.00	0.00	100.00	0.00	0.00
	*Branching sponges	Porifera	Abrasion and/or sections removed	0.18 ± 0.06	50.59	49.41	0.00	83.52	16.48	0.00
**Cliona celata*	Boring sponges	Porifera	Abrasion and/or sections removed	0.10 ± 0.02	44.58	54.26	1.16	76.48	22.23	1.29
Dendrodoa grossularia	Baked bean ascidian	Chordata	Abrasion	8.46 ± 2.95	61.97	37.90	0.13	66.38	31.42	2.20
Diazona violacea	Football ascidian	Chordata	None	0.003 ± 0.002	0.00	0.00	0.00	100.00	0.00	0.00
Echinus esculentus	Edible sea urchin	Echinodermata	None	0.03 ± 0.01	100.00	0.00	0.00	100.00	0.00	0.00
**Eunicella verrucosa*	Pink sea fan	Cnidaria	Abrasion	0.12 ± 0.03	44.96	55.04	0.00	64.62	35.38	0.00
Flustra foliacea	Bryozoans	Bryozoa	Abrasion and/or sections removed	0.22 ± 0.10	57.85	42.15	0.00	68.49	31.51	0.00
Gymnangium montagui	Yellow feathers	Cnidaria	Abrasion and/or sections removed	0.005 ± 0.005	0.00	0.00	0.00	0.00	100.00	0.00
Holothuria forskali	Cotton spinner	Echinodermata	None	0.09 ± 0.02	100.00	0.00	0.00	100.00	0.00	0.00
Laminaria digitata	Kelp		Abrasion and/or sections removed	0.003 ± 0.003	80.00	20.00	0.00	0.00	0.00	0.00
	Macroalgae		Abrasion and/or sections removed	2.20 ± 0.10	71.69	27.26	1.05	90.34	9.66	0.00
Marthasterias glacialis	Spiny starfish	Echinodermata	Abrasion and/or damage to a leg	0.26 ± 0.04	100.00	0.00	0.00	97.70	2.30	0.00
	Massive sponges	Porifera	Abrasion and/or sections removed	0.13 ± 0.04	65.50	34.50	0.00	74.80	25.20	0.00
Nemertesia antennina	Sea beard	Cnidaria	Abrasion and/or sections removed	0.23 ± 0.09	86.59	13.41	0.00	83.54	16.46	0.00
**Pentapora fascialis*	Ross coral	Bryozoa	Abrasion and/or sections removed	0.07 ± 0.02	13.39	82.13	4.49	60.83	36.95	2.23

Table 4: Description of the damage caused to the taxa present in the pot haul path, mean number of individuals (individuals m^{-2}) and percentage of individuals (individuals m^{-2}) Not Damaged (ND), Damaged (D) and Removed (R) during the haul. An asterix (*) denotes indicator taxa.

Of the 18 taxa identified, 14 suffered damage from pot impacts, including all five indicator taxa, and individuals of six taxa were removed from the reef, including three indicator taxa (Table 4). Pot hauling damaged or removed between 25 and 30 % of observed epibenthic species recorded by the pot-mounted cameras (Table 5), with broadly consistent patterns between pot types for all responses ($p > 0.05$), and small effect sizes (Wilcoxon r) of 0.124 and 0.127, and 0.006 for the responses Not Damaged, Damaged, and Removed, respectively.

Table 5: Pot-level effects. Mean fraction of all species abundance responses to pot hauls for Inkwell (n = 45) and Parlour (n = 46), 95 % confidence intervals (CI) and standard error (SE)

Pot type	Response	Mean fraction	Lower CI	Upper CI	SE
Inkwell	Not Damaged	0.697	0.629	0.769	0.035
	Damaged	0.282	0.214	0.350	0.037
	Removed	0.021	0.011	0.035	0.006
Parlour	Not Damaged	0.754	0.696	0.803	0.029
	Damaged	0.217	0.168	0.275	0.027
	Removed	0.029	0.014	0.049	0.009

3.3.1 Species specific responses

Only four species suffered no damage or removal from potting activity; individuals of *Echinus esculentus*, *Holothuria forskali* and *Asterias rubens* were observed to roll (*E. esculentus*) or be moved out of the way by the pressure wave from a pot. No damage was observed suggesting they may be able to withstand the gentle movement caused. During the survey no instances of direct impact were observed, however.

In four of the five instances where rope movement occurred, the rope was in full contact with the substratum; impact was, however, limited to abrasion of *A. digitatum* and *E. verrucosa*. Five instances occurred where damage was evident from rope contact during the haul, including four occasions (3.70 % of hauls) where rope caught on *A. digitatum* causing abrasion and the removal of two individuals from the reef.

The mean number of individuals (all taxa) was 0.79 ind. m^{-2} ± 0.17. A significant Year x Location x Response interaction was identified, and despite some spatial variation there were significantly more individuals not damaged (0.54 ind. m^{-2} ± 0.05 (68.35 %)) than damaged (0.23 ind. m^{-2} ± 0.03 (29.11 %)), not damaged than removed (removed = 0.02 ind. m^{-2} ± 0.00 (2.53 %)) and damaged than removed.

There were four taxa for which more individuals were more damaged than not damaged, three of which were indicator species; (Inkwell pots: *C. celata* (D = 54.26 %, ND = 44.58 %), *E. verrucosa* (D = 54.04 %, ND = 44.96 %) and *P. foliacea* (D = 82.13 %, ND = 13.39 %); Parlour pots *Gymnangium montagui* (D = 100 %, although only one colony was observed during the study and this was damaged by a parlour pot haul)).

The taxa removed from the reef included two upright, branching taxa, *Alcyonidium diaphanum* and *A. digitatum*, two taxa with massive forms projecting from the reef, *C. celata* and *P. foliacea*, *D. grossularia* which attaches to the reef at its base and has a lifespan of 1-2 years (MarLIN, 2006) and macroalgae which was observed in dense clumps at some sites and whose growth is annual.

3.3.2 Indicator taxa responses

The most abundant indicator taxon was *A. digitatum* (1.15 ind. m^{-2} ± 0.18) and the least abundant was *P. foliacea* (0.03 ± 0.01 m^{-2}) but abundance varied between sites and years for all species (Figure 8). All indicator taxa were damaged during the haul, but only individuals of *A. digitatum*, *C. celata* and *P. foliacea* were removed (Table 4, Figure 8). A significant Pot Type x Site(Location) interaction was identified for the response of *A. digitatum* to potting impact (Pot Type x Site(Location), $P < 0.05$, Table S8; Supplementary material), and while no significant pairings were identified there were significantly more individuals not damaged than damaged. The distribution of all indicator taxa was patchy, but it is important to note that pots were not damaging all individuals that fell within the total possible contact area, and instances of removal were uncommon.

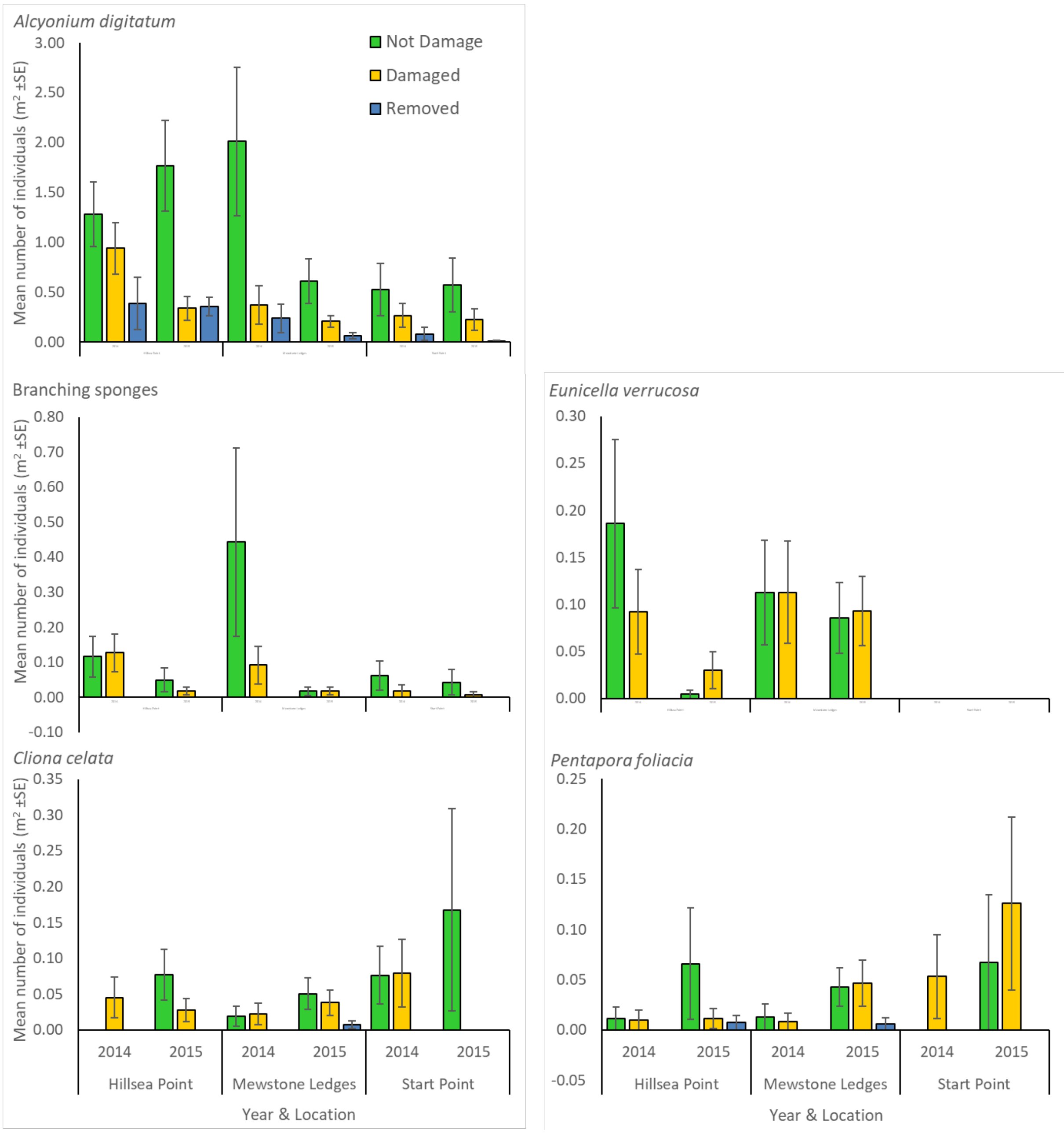

Figure 8: Number of individuals (individuals m^{-2} ± SE) of the 5 indicator species, *Alcyonium digitatum*, Branching sponges, *Cliona celata*, *Eunicella verrucosa*, and *Pentapora foliacea* at the different Locations (SP = Start Point, ML = Mewstone Ledges, HP = Hillsea Point) and different Year (1 = 2014, 2 = 2015). Note the scales on the Y axis vary.

3.3.3 Response by body type

Both groups of species (erect emergent, low encrusting) were impacted by pot hauling, and this was consistent across pot types ($p > 0.05$) for both groups. Small effect sizes for comparisons between pot types within each response type were observed, with Wilcoxon r values up to 0.142 for erect emergent species, and 0.099 for low encrusting species (Supplementary Material, Table S10).

For erect emergent species, the proportion of species not damaged was greater than that of those damaged or removed, but for low encrusting species the fraction of species in the damaged and no damage categories were similar (Table 6). The response of low encrusting species is more variable, but this may be due to the lower number of samples in which low encrusting species were recorded (Table 6).

Table 6: Responses of benthic fauna to pot hauling by body type and pot type. Fractional abundance responses of each body type were calculated for each pot prior to calculation of mean values, 95 % confidence intervals (CI) and Standard Error (SE).

		Erect emergent					Low encrusting				
Pot type	Response	n	Mean fraction	Lower CI	Upper CI	SE	n	Mean fraction	Lower CI	Upper CI	SE
Inkwell	No damage	43	0.664	0.589	0.736	0.036	19	0.504	0.311	0.714	0.109
	Damaged	43	0.311	0.238	0.385	0.039	19	0.486	0.275	0.684	0.109
	Removed	43	0.025	0.013	0.042	0.007	19	0.011	0.000	0.032	0.011
Parlour	No damage	46	0.706	0.628	0.775	0.038	12	0.597	0.333	0.833	0.135
	Damaged	46	0.261	0.192	0.342	0.038	12	0.389	0.153	0.667	0.137
	Removed	46	0.033	0.015	0.056	0.01	12	0.014	0.000	0.042	0.014

4. DISCUSSION

This study aimed to determine whether, with the removal of trawling, potting allows for greater relative health of the ecosystem, and to quantify the mechanisms and true footprint of potting. The results have shown that whilst areas fished with static gear (predominantly pots) had consistently greater abundance, species richness and diversity than those open to bottom towed fishing, significant differences were only identifiable for assemblage composition and abundance of cover taxa, where there was significantly greater abundance in static treatments (partial acceptance of hypothesis 1). They have also shown that the seabed contact area is smaller than the total possible contact area for both pot types, with contact areas smaller for parlour pots, and seabed contact area increasing linearly with strip length (distance travelled during the haul), (acceptance of hypothesis 2). Finally, despite significant spatial and temporal variation, significantly more species were not damaged within the total possible contact area than were damaged or removed, but, 25-30% of taxa were damaged or removed, and erect emergents were found to be particularly vulnerable to pot impact (acceptance of hypothesis 3).

4.1 Benthic condition

For a system to be considered fully functional it would be expected that in addition to significant differences in assemblage composition, abundance, diversity and species richness would be significantly greater in static gear areas (Tett et al., 2013) and this was not the case. The finding of a significant difference in assemblage composition was, however, important. Species characterising areas fished with static gear were more representative of fully functional benthic rocky reef areas than areas open to bottom towed fishing gear. This was demonstrated by a greater abundance of all but one taxa and differences between treatments being driven by biogenic habitat forming species of hydroid, bryozoan and soft coral (Beck et al., 2001; Beukers-Stewart and Beukers-Stewart, 2009; Dayton et al., 1995; Jennings and Kaiser, 1998; Jennings et al., 2001; Monteiro et al., 2002; Ryer et al., 2004). Biogenic habitat is particularly important for slowing water movement and stabilising sediment, increasing structural complexity and promoting greater biodiversity and productivity through increasing the range of habitats and surface area for settlement (Bradshaw et al., 2003).

The results are in partial agreement with those of others studies considering potting impacts, most of which identified no significant negative impacts. It has confirmed, however, that there are potential concerns with potting identified here, which most other studies have not identified, and consequently that potting is more destructive than originally thought. Eno et al. (2001) concluded that pot fishing had no immediate detrimental effect on the benthos, finding no significant difference in abundance of taxa before and after potting impacts. Coleman et al. (2013) found no detectable effect of potting on benthic assemblages over a four year period at Lundy Island (UK) with differences over time apparent in both potted and control sites. Stephenson et al. (2017) found no decline in abundance of benthic species even following periods of intensive potting in NE England (equivalent to 30,000 pot hauls $month^{-1}.km^{-2}$), as they also identified any changes in their control areas. They concluded that even where potting activity causes damage to erect species, the frequency with which a pot would be expected to impact the same area twice means that species would be able to recover (recovery time given as 6-36 months) sufficiently between fishing events (Stephenson et al., 2017).

In contrast, and similarly to this study, the findings of Rees (2018) raised some concerns. They concluded that that only cessation of potting activity would truly permit recovery of species following the removal of bottom towed fishing gear within an MPA (Rees, 2018). The study, which experimentally potted at different intensities, found significant treatment impacts for the indicator species *P. folicacea* and *Phallusia mammillata* with abundance especially impacted in high intensity potting areas (Rees, 2018).

In addition, the results of this study can be compared to those of Blyth et al. (2004) who surveyed the IPA area in 2002 and concluded that areas fished using static gear had significantly greater species richness and biomass than sites open to bottom towed fishing gear, and also partially of Sheehan et al. (2015) who identified recovery of benthic assemblages in the Lyme Bay MPA despite the continuation of potting activity. The differences between these findings and the results of the current study may suggest a decline in species richness over time in the survey area, may be a result of differences in survey methodology and metrics (Sheehan et al., 2016) or may be down to external factors such as natural variation or fishing pressure at a local or regional scale (Babcock et al., 1999).

When considering the potential for external factors to confound the results of this study, the winter storms of 2013/2014 must be acknowledged. These were substantial in the south-west of the UK and would have had an impact on benthic communities. Wave height in the study area reached 5.25 m during the peak of the storms in February 2014 compared to an average annual wave height for the period 2007 – 2013 of 3.69 m (Channel Coastal Observatory, 2014). The storm season prevented fishers from going to sea to retrieve their gear, so pots were left on the ground (in water depth of approximately 60 m) with many losses suffered (South Devon & Channel Shellfishermen Ltd, Pers comm.). A study carried out in Lyme Bay on comparable habitat into the impacts of the 2013/2014 storms found significant reductions in abundance, diversity and richness after the storms, and significant impacts on selected indicator taxa within the MPA. Sites closed to bottom towed fishing gear became more similar to those open to bottom towed fishing gear outside the MPA (Sheehan et al, unpublished data), and due to the proximity of Lyme Bay to the IPA, it may be that similar trends would have been identified here if temporal comparisons were possible with sufficient 'before' data.

In a study of Caribbean lobster traps, Lewis et al. (2009) found that movement during storms and hurricanes caused abrasion, fragmentation and removal of corals and sponges with a reduction in benthic species cover. The true impacts of potting may therefore have been confounded by impacts from the storms and this must be acknowledged in interpretation of the results.

4.2 Mechanisms of potting interaction

This study is the first of its kind to quantify the seabed contact area during pot hauls. It has shown that the haul is the period during which damage may be caused by potting activity, but the finding that seabed contact area is roughly half that of the total possible contact area is of importance for furthering understanding of potting impact. Furthermore, the existence of significant differences in impact between parlour and inkwell pots may be of relevance to future decisions on sustainable potting gear and management of potting activity, particularly where habitats may be considered to be at risk.

4.3 True footprint of potting

Significant spatial and temporal variation was apparent in the data, but despite this, significantly more species were not damaged than were damaged or removed. With the exception of *D. violacea* which was not directly contacted by the pots, the species not damaged were sedentary but mobile. Similarly to the observations made by Eno et al. (2001) about sea pens in soft sediment, it was noted that mobile taxa were moved out of the way of the pot by the pressure wave caused as it neared the seabed, suggesting that they are less susceptible to damage than sessile species.

Damage included abrasion, and removal of sections of the individual. 25-30 % of taxa were damaged or removed and all five indicator species were damaged in some way, with more instances of damage than no damage occurring for *C. celata*, *E. verrucosa* and *P. foliacea*. These taxa are long-lived and slow growing species that were thought to be most susceptible to potting impacts and would take the longest to recover (Langmead et al., 2010). Impacts of abrasion are not well studied, but evidence suggests that species such as sponges and soft corals may be left vulnerable to disease (Bavestrello et al., 1997; Hiscock, 2007; Shester and Micheli, 2011; Wassenberg et al., 2002). Abrasion was observed for *E. verrucosa*, and although colonies are thought to be able to re-grow over a period of about 1 week if damaged (Hiscock, 2007), if areas of the coenenchyme are scraped off and recovery fails to occur promptly they may be vulnerable to colonisation by epibiota (Bavestrello et al., 1997). This could cause mechanical stress through increased resistance to water movement, and susceptibility to weakening from the burrowing activities of epibiota.

Two indicator species known to be important for ecosystem function were *E. verrucosa* which creates complex elevated surfaces available for the settlement of spat and acts as habitat for other organisms (Howarth et al., 2011; Jones et al., 1994) and *P. foliacea* a functionally important bio-constructor forming biogenic reefs (Cocito and Ferdeghini, 2001; McKinney and Jackson, 1989) and structurally complex habitat important as a nursery habitat for juvenile fish (Bradshaw et al., 2003). Impacts on these two species would be of particular concern due to their long projected recovery time of 17-20 years (Kaiser et al., 2018). In the case of *E. verrucosa*, although few instances occurred where a pot landed directly on top of an individual, where this did occur the results were similar to those of other studies. Eno et al. (2001) observed that it tended to ‘bounce back’ once the pot had passed, while Shester and

Micheli (2011) reported no incidence of removal of gorgonians as a result of lobster trap impact in the Gulf of Mexico and Rees (2018) found that whilst abundance decreased over time in areas fished at the highest potting density (~30 pots per 500m^2), this was not significant.

Pots contacting *P. foliacea* commonly caused pieces to break off. Of the 16 colonies observed, only one was removed from the reef, but their fragile and brittle structure meant that more individuals were damaged than not damaged. The longer-term implications of damage are unknown, and due to the low abundance of *P. foliacea* across the study site, conclusions were not possible. The findings of Rees (2018) of a significant difference in abundance between control/low potting density sites and medium/high density sites may be cause for concern, however. This study did not calculate potting density across the site so direct comparisons cannot be made, but the results of Rees (2018) suggest that impacts may be more substantial in areas where abundance is greater. What can be concluded here is that as abundance was greater in the static treatment, the impact of potting has a lesser effect than the impact of trawling on this species; a conclusion also drawn by Sheehan et al. (2015).

When considering body type, the finding that despite their greater vulnerability, a smaller proportion of erect emergents were damaged or removed compared to those not damaged is of note. For low encrusting organisms, similar numbers were damaged and not damaged. The greater variability seen for these taxa may be due to the low number of encrusting species recorded, or it may be a result of pots making contact with a larger area of the species in question owing to differences in morphology between body types. The work of Stephenson et al. (2017) which found no significant impact of potting on benthic organisms also commented that encrusting species are unlikely to be damaged as their size and shape enable them to withstand impacts from physical disturbance and abrasion; a result which does not seem to hold true here.

4.4 Implications for management

This study has contributed to the evidence base for assessing the impact of potting on temperate rocky reefs. It is the first study to quantify the true footprint of potting, the first to use GoPro cameras for such work, and one of the first to consider the impact of a string of pots throughout their deployment, soak and haul. The findings suggest that current levels of potting within the IPA are allowing benthic condition to be maintained and the relative health of the ecosystem to be greater than in adjacent areas where bottom towed fishing gear operates, but they have raised concerns over impacts, in particular those to some long lived and slow growing taxa, which are particularly sensitive to potting. The haul has been identified as the time during which most impacts may occur, and despite the fact that the area of damage is not the entire pot haul path, potting has been found to be more destructive than previously thought.

In particular, the damage caused to sensitive taxa may be of concern; and with the longer-term impacts unknown it is difficult to predict the consequences. The behaviour of pot fishing makes it very unlikely that pots would be deployed such that they would land, soak and haul in the same location on successive trips, however (Eno et al., 2001), and a recovery time of between 6-36 months for the majority of species (Jackson, 2004; Tyler-Walters, 2006; Tyler-Walters & Ballerstedt, 2007; Budd, 2008) also gives some confidence that species may recover without further disturbance occurring (Stephenson et al., 2017). Consideration must however, be given to recovery trajectories of the most sensitive species which may be as long as 17-20 years (Kaiser et al., 2018). The presence of these species throughout the potted areas of the IPA, and the time over which the IPA management has been in place suggests that the reefs may be resilient to current potting levels, but the lack of comparable historical data prevents temporal comparisons and it is unknown whether abundance would be greater if potting levels were reduced or potting was no longer permitted in the area.

The call for ecosystem based fisheries management means that regulators must decide what level of impact is 'acceptable' and will not compromise the ability of an MPA to meet defined conservation objectives and targets. The D&SIFCA have responsibility for this in the study area. Alongside consideration of ecological impact, they must consider the value of the fishing activity occurring within a protected area and determine the social and economic impacts of management decisions. This study has contributed to a decision to allow potting activity to continue at current levels in the Start Point to Plymouth Sound & Eddystone SCI highlighting its value in supporting decision-making (D&SIFCA, pers. comm.). Continued monitoring of the IPA is required, however, to ensure continued confidence in this decision, and the adaptive management approach of the D&SIFCA should mean that if any decline was identified the continuation of potting in the area would be reviewed.

The results will be applicable globally where similar habitats and species are found and similar potting methods used. As such, they are particularly important in light of the global drive to increase the coverage of MPAs in order to meet Aichi Biodiversity Target 11 by 2020, and the need to take an ecosystem approach to management, which incorporates social and economic elements (CBD, 2010; Pikitch et al., 2004; Gaines et al., 2010). The increasing designation of multi-use MPAs necessitates identification of extractive activities, which are compatible with meeting conservation goals whilst supporting a viable fishing industry. Potting may be such an activity, but the results suggest careful monitoring of impact is needed, as it cannot be described as a benign fishing method. Furthermore, the issue of shifting baselines must be recognised, especially with regard to what constitutes a fully functional rocky reef ecosystem as continued anthropogenic pressure may result in gradual change and loss of ecosystem services if management measures are not effective (Tett et al., 2013).

4.5 Further work

The body of literature surrounding the impact of potting has grown, but the differences between the findings of this and other studies suggest that, as expected, more research is required to further knowledge and understanding of potting impacts. Any future work should build on that already completed. In particular, this work has highlighted the need for consideration of impacts on key species, the effect of depth, string length and position of pot on the string, and development of long-term studies, which can assess change over time and have the power to overcome confounding factors.

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Supplementary material

Description of pot setting and hauling process

When setting pots, the fishers used cast iron end weights at either end of the sting. The skipper set the boat on course and steamed slowly whilst the gear deployed. The end weight was deployed first and then each pot followed in turn and was taken through an open door in the side of the vessel once the slack rope had become taught. Pots and ropes were arranged on deck such that they deployed automatically as the boat steamed. Once the final end weight was deployed, the surface bouy followed, and the pots were left on the sea bed.

The haul process involved picking up the surface bouy, then winching the line in so that the end weight and then each pot re-entered the vessel over the side to be stacked on deck in turn and the rope coiled ready for the next deployment.

Results for benthic condition

Table S1: PERMANOVA to test the differences in number of count and cover individuals between Years (2013, 2014, 2015), Locations (A-J, nested in Treatment), Sites (1-30, nested in Location) and Treatments (Static, Mixed). Data were fourth root transformed prior to the construction of a Euclidean distance resemblance matrix. Bold values indicate significant differences

Source	**df**	**MS**	**Pseudo-F**	**P(perm)**
Count taxa				
Ye	2	3820.50	3.08	**0.001**
Tr	1	12338.00	1.57	0.08
Lo(Tr)	8	6756.80	2.89	**0.000**
YexTr	2	1925.50	1.58	0.07
Si(Lo(Tr))	20	1345.30	1.67	**0.0001**
YexLo(Tr)	16	1212.80	1.51	**0.0004**
Res	37	804.24		
Total	86			

Source	**df**	**MS**	**Pseudo-F**	**P(perm)**
Cover taxa				
Ye	2	3338.60	1.97	**0.07**
Tr	1	19842.00	3.41	**0.01**
Lo(Tr)	8	4890.30	1.79	**0.002**
YexTr	2	1429.70	0.86	0.51
Si(Lo(Tr))	20	1591.50	1.52	**0.02**
YexLo(Tr)	16	1656.80	1.59	**0.02**
Res	37	1045.20		
Total	86			

Table S2: PERMANOVA to test the differences in number of taxa and diversity (Simpsons 1-λ) between Years (2013, 2014, 2015), Locations (A-J, nested in Treatment), Sites (1-30, nested in Location) and Treatments (Static, Mixed). Data were fourth root transformed prior to the construction of a Euclidean distance similarity matrix. Bold values indicate significant differences

Source	**df**	**MS**	**Pseudo-F**	**P(perm)**
Number of taxa				
Ye	2	0.10	7.55	**0.01**
Tr	1	0.26	3.44	0.07
Lo(Tr)	8	0.07	1.25	0.26
YexTr	2	0.01	0.91	0.43
Si(Lo(Tr))	20	0.05	4.97	**0.0001**
YexLo(Tr)	16	0.01	1.37	0.21
Res	37	0.01		
Total	86			

Source	**df**	**MS**	**Pseudo-F**	**P(perm)**
Diversity				
Ye	2	0.00	0.17	0.85
Tr	1	0.01	0.27	0.95
Lo(Tr)	8	0.04	1.72	0.06
YexTr	2	0.01	2.00	0.16
Si(Lo(Tr))	20	0.02	3.38	**0.0004**
YexLo(Tr)	16	0.01	1.28	0.27
Res	37	0.01		
Total	86			

Table S3: ANOVA to test the differences in number of individuals of the indicator taxa *Alcyonidium diaphanum, Alcyonium digitatum,* Branching sponges, *Cliona celata, Eunicella verrucosa*, *Metridium senile, Pentapora foliacea* and *Urticina felina* between Years (2013, 2014, 2015), Locations (A-J, nested in Treatment), Sites (1-30, nested in Location) and Treatments (Static, Mixed). Pairwise tests were used to examine significant interactions between fixed factors. Data were fourth root transformed prior to the construction of a Euclidean distance resemblance matrix. Bold values indicate significant differences.

Source	df	MS	Pseudo-F	P(perm)
Alcyonidium diaphanum				
Ye	2	3.91	8.53	**0.003**
Tr	1	0.75	0.70	0.64
Lo(Tr)	8	1.56	2.31	**0.01**
YexTr	2	0.18	0.40	0.66
Si(Lo(Tr))	20	0.31	1.33	0.22
YexLo(Tr)	16	0.45	1.88	0.06
Res	37	0.24		
Total	86			
Branching sponges				
Ye	2	0.04	1.95	0.18
Tr	1	0.43	2.39	0.14
Lo(Tr)	8	0.18	3.55	**0.001**
YexTr	2	0.01	0.69	0.52
Si(Lo(Tr))	20	0.03	1.48	0.13
YexLo(Tr)	16	0.02	0.92	0.56
Res	37	0.02		
Total	86			
Eunicella verrucosa				
Ye	2	0.07	0.70	0.53
Tr	1	0.06	0.11	1.00
Lo(Tr)	8	1.30	8.54	**0.0001**
YexTr	2	0.11	1.12	0.36
Si(Lo(Tr))	20	0.05	2.79	**0.004**
YexLo(Tr)	16	0.10	5.17	**0.0001**
Res	37	0.02		
Total	86			
Pentapora foliacea				
Ye	2	0.03	5.17	**0.02**
Tr	1	0.01	1.25	0.36
Lo(Tr)	8	0.01	1.43	0.15
YexTr	2	0.00	0.23	0.79
Si(Lo(Tr))	20	0.00	1.34	0.20
YexLo(Tr)	16	0.01	2.08	**0.03**
Res	37	0.00		
Total	86			

Source	df	MS	Pseudo-F	P(perm)
Alcyonium digitatum				
Ye	2	0.35	2.57	0.11
Tr	1	19.09	6.56	**0.01**
Lo(Tr)	8	2.41	5.01	**0.0001**
YexTr	2	0.54	4.01	**0.04**
Si(Lo(Tr))	20	0.39	1.43	0.17
YexLo(Tr)	16	0.13	0.49	0.94
Res	37	0.27		
Total	86			
Cliona celata				
Ye	2	0.01	1.69	0.21
Tr	1	0.11	5.02	**0.02**
Lo(Tr)	8	0.02	1.48	0.13
YexTr	2	0.01	0.85	0.45
Si(Lo(Tr))	20	0.01	1.09	0.39
YexLo(Tr)	16	0.01	1.09	0.39
Res	37	0.01		
Total	86			
Metridium senile				
Ye	2	0.01	0.44	0.67
Tr	1	0.22	3.76	**0.05**
Lo(Tr)	8	0.05	1.54	0.11
YexTr	2	0.01	0.75	0.51
Si(Lo(Tr))	20	0.03	1.13	0.34
YexLo(Tr)	16	0.02	0.77	0.76
Res	37	0.03		
Total	86			
Urticina felina				
Ye	2	0.18	3.55	**0.04**
Tr	1	0.10	0.38	0.88
Lo(Tr)	8	0.39	4.75	**0.0001**
YexTr	2	0.03	0.52	0.62
Si(Lo(Tr))	20	0.04	1.16	0.33
YexLo(Tr)	16	0.05	1.65	0.10
Res	37	0.03		
Total	86			

	M&S
2013	0.073
2014	**0.017**
2015	**0.024**

Table S4: Results of SIMPER showing the contribution of different species to the differences seen between Mixed and Static treatments. * denotes indicator species. Bold text denotes the higher abundance.

	Mean abundance		**Diss/SD**	**Contrib%**
	Mixed	**Static**		
Turf	0.26	**0.48**	1.47	9.44
**Alcyonium digitatum*	0.13	**0.47**	1.41	9.43
Unidentified hydroid species	0.72	**0.81**	1.01	8.45
**Alcyonidium diaphanum*	0.23	**0.29**	1.22	6.78
Nemertesia antennina	0.17	**0.30**	1.28	6.10
Ophiothrix fragilis	0.06	**0.14**	0.49	4.83
Ophiocomina nigra	0.06	**0.16**	0.77	4.55
Unidentified bryozoan species	**0.12**	0.11	0.91	3.75
**Eunicella verrucosa*	0.07	**0.10**	0.62	3.20
**Urticina felina*	0.05	**0.09**	0.69	2.79
Pecten maximus	**0.10**	0.05	0.66	2.68
Halecium halecinum	0.06	**0.10**	0.99	2.62
Lanice conchilega	0.04	**0.05**	0.43	2.41
Cellepora pumicosa	**0.08**	0.06	0.75	2.34
Nemertesia ramosa	0.04	**0.08**	0.95	1.97
Flustridae spp.	0.01	**0.06**	0.49	1.58
Unidentified anemone	**0.05**	0.02	0.47	1.52
Unidentified macroaglae	**0.04**	0.02	0.56	1.47
Aequipecten opercularis	**0.04**	0.01	0.67	1.38
Unidentified cup coral	0.02	**0.05**	0.59	1.35
Dendrodoa grossularia	0.00	**0.05**	0.43	1.20
Echinus esculentus	0.01	**0.05**	1.02	1.20
Branching sponge 1	0.01	**0.04**	0.72	1.16
Marthasterias glacialis	0.02	**0.04**	0.84	1.08
Cliona celata	0.00	**0.04**	0.72	1.01
Metridium senile	**0.04**	0.00	0.41	0.99
Cerianthid spp.	**0.04**	0.00	0.38	0.92
Branching sponge 2	0.00	**0.04**	0.50	0.87
Sycon ciliatum	0.02	**0.03**	0.87	0.83
Pagurus bernhardus	**0.03**	0.00	0.58	0.78
Pentapora foliacea	0.02	**0.03**	0.80	0.75
Aglaophenia tubulifera	**0.03**	0.01	0.45	0.74

Average dissimilarity M : S = 60.64

Mechanisms of potting interaction

Table S5: PERMANOVA to test the differences in mechanisms of potting interaction between Years (Yr, 2014, 2015), Locations (Lo, Start Point, Mewstone Ledges, Hillsea Point), Sites (Si, 1-9, nested in Location) and Pot Types (Po, Inkwell, Parlour). Pairwise tests are used to examine significant interations between fixed factors. Data were untransformed prior to the construction of a Euclidean Distance resemblance matrix. Bold values indicate significant differences.

a)

Source	**df**	**MS**	**Pseudo-F**	**P(perm)**
Ye	1	3994.7	2.1721	0.276
Lo	2	867.56	0.69558	0.7059
Po	1	962.86	1.391	0.3825
Si(Lo)	24	641.58	0.77098	0.7364
YexLo	2	1778.1	2.1448	0.1355
YexPo	1	616.41	3.43	0.2075
LoxPo	2	143.23	0.57233	0.8087
YexSi(Lo)**	23	816.47	2.632	**0.0174**
PoxSi(Lo)	24	697.27	2.2584	**0.0381**
YexLoxPo	2	140.14	0.45176	0.6454
Res	19	310.21		
Total	101			

** Term has one or more empty cells

b)

Pairing	**SP**	**ML**	**HP**
Site 1			
P & I	0.4763	0.2478	0.2484
Site 2			
P & I	0.2489	0.2413	0.2412
Site 3			
P & I	-	0.4896	-
Site 4			
P & I	0.2384	-	0.4948
Site 5			
P & I	0.2342	0.504	0.2387
Site 6			
P & I	0.2467	0.2478	0.2363
Site 7			
P & I	0.522	0.5015	0.2641
Site 8			
P & I	-	0.2662	0.2239
Site 9			
P & I	-	0.5249	0.2344

Table S6: Contact area (m2) by pot type and linear relationship of contact area against strip length. Confidence level = 0.95. NB. Differences in mean occur between these figures and the statistical analysis as no pooling was required for this analysis.

Pot type	**Mean effect**	**Lower CI**	**Upper CI**	**SE**	**Intercept ± CI**	**Slope ± CI**	**Adjusted R^2**
Inkwell	2.12	1.91	2.34	0.108	0.699 ± 0.328	0.317 ± 0.054	0.614
Parlour	1.60	1.38	1.81	0.108			

Table S7: Pot-specific regression coefficients for the effect of strip length on pot contact area.

Pot type	Mean effect	Lower CI	Upper CI	SE	Intercept ± CI	Slope ± CI	Adjusted R2
Inkwell	2.12	1.91	2.34	0.109	0.688 ± 0.415	0.319 ± 0.077	0.610
Parlour	1.60	1.38	1.81	0.109	0.185 ± 0.400	0.314 ± 0.077	

Pot-specific responses derived from the model Contact area ~ Strip length * Pot type. This model did not perform as well (based on AIC) as the model Contact area ~ Strip length + Pot type, suggesting that there is no interaction between pot type and strip length. Pot types both respond similarly to movement along the seabed in terms of their contact areas.

True footprint of potting

Table S8: PERMANOVA to test the differences in true footprint between Years (Yr, 2014, 2015), Locations (Lo, Start Point, Mewstone Ledges, Hillsea Point), Sites (Si, 1-9, nested in Location) and Pot Types (Po, Inkwell, Parlour). Pairwise tests are used to examine significant interations between fixed factors. Data were untransformed prior to the construction of a Euclidean Distance resemblance matrix. Bold values indicate significant differences.

a)

Source	**df**	**MS**	**Pseudo-F**	**P(perm)**
Ye	1	16052	2.4495	0.1171
Lo	2	19696	1.9914	**0.0248**
Po	1	4754.3	1.4815	0.2381
Re	2	84028	7.3349	**0.0002**
Si(Lo)	25	4963.7	1.4588	**0.0363**
YexLo	2	6235	1.8007	0.0873
YexPo	1	3826.9	1.0687	0.4323
YexRe	2	5651.7	1.6358	0.1593
LoxPo	2	1546.7	0.64817	0.9011
LoxRe	4	6123.2	1.5427	**0.0259**
PoxRe	2	606.5	1.0605	0.449
YexSi(Lo)**	23	3397.6	No test	
PoxSi(Lo)**	24	3930.3	1.2702	0.1211
Si(Lo)xRe**	48	1574.4	0.96096	0.625
YexLoxPo	2	3402.9	1.1025	0.359
YexLoxRe	4	3324.9	2.0645	**0.0088**
YexPoxRe	2	964.37	0.59191	0.8437
LoxPoxRe	4	1315.8	0.88001	0.6917
YexPoxSi(Lo)**	19	3079.6	No test	
YexSi(Lo)xRe**	46	1576.3	No test	
PoxSi(Lo)xRe**	48	1286.2	0.93635	0.6863
YexLoxPoxRe	4	1721.9	1.2566	0.2115
Co(YexPoxSi(Lo))	0		No test	
YexPoxSi(Lo)xRe**	37	1370.2	No test	
Total	305			

** Term has one or more empty cells

b)

	SP	**ML**	**HP**
2014			
ND & D	0.6804	**0.0015**	**0.0026**
ND & R	**0.0154**	**0.0003**	**0.0003**
D & R	**0.0071**	**0.0008**	**0.0049**
2015			
ND & D	0.1719	**0.0011**	**0.0021**
ND & R	**0.0016**	**0.0002**	**0.0003**
D & R	**0.0021**	**0.0047**	0.0597

Table S9: ANOVA to test the differences in number of individuals for the indicator taxa *Alcyonium digitatum,* Branching sponges, *Cliona celata, Eunicella verrucosa* and *Pentapora foliacea* between Years (Yr, 2014, 2015), Locations (Lo, Start Point, Mewstone Ledges, Hillsea Point), Sites (Si, 1-9, nested in Location) and Pot Types (Po, Inkwell, Parlour). Pairwise tests are used to examine significant interations between fixed factors. Data were untransformed prior to the construction of a Euclidean Distance resemblance matrix. Bold values indicate significant differences.

Source	df	MS	Pseudo-F	P(perm)
Alcyonium digitatum				
Ye	1	3.75	0.50	0.63
Lo	2	11.72	0.97	0.53
Po	1	15.08	4.83	**0.04**
Si(Lo)	25	7.30	2.43	**0.02**
YexLo	2	7.39	2.47	0.08
YexPo	1	1.37	0.85	0.46
LoxPo	2	1.66	0.59	0.84
YexSi(Lo)**	23	2.94	2.21	**0.03**
PoxSi(Lo)**	24	3.58	2.69	**0.01**
YexLoxPo	2	1.51	1.13	0.33
Res	18	1.33		
Total	101			
Branching sponges				
Ye	1	0.84	1.58	0.35
Lo	2	0.38	0.97	0.55
Po	1	0.42	2.81	0.14
Si(Lo)	55	0.24	0.73	0.71
YexLo	2	0.47	1.45	0.26
YexPo	1	0.42	1.31	0.31
LoxPo	2	0.06	0.20	0.71
YexSi(Lo)**	37	0.32	No test	
PoxSi(Lo)**	0		No test	
YexLoxPo	0		No test	
Total	101			

	SP	ML	HP
1			
I & P	0.49		0.50
2			
I & P	0.25	0.25	0.24
3			
I & P		0.25	
4			
I & P	0.51		0.25
5			
I & P	0.51	0.24	0.49
6			
I & P	0.50	0.25	0.25
7			
I & P	0.50	0.50	0.50
8			
I & P		0.25	0.50
9			
I & P		0.24	0.50

Source	df	MS	Pseudo-F	P(perm)
Cliona celata				
Ye	1	0.12	4.07	0.12
Lo	2	0.08	1.73	0.16
Po	1	0.07	1.25	0.39
Si(Lo)	25	0.06	0.84	0.69
YexLo	2	0.03	0.39	0.78
YexPo	1	0.09	0.86	0.45
LoxPo	2	0.05	0.60	0.84
YexSi(Lo)**	23	0.07	1.41	0.18
PoxSi(Lo)**	24	0.06	1.15	0.34
YexLoxPo	2	0.10	2.00	0.13
Res	18	0.05		
Total	101			
Eunicella verrucosa				
Ye	1	0.13	1.49	0.32
Lo	2	0.21	1.91	0.10
Po	1	0.03	1.16	0.43
Si(Lo)	25	0.05	0.82	0.74
YexLo	2	0.09	1.35	0.26
YexPo	1	0.07	0.60	0.60
LoxPo	2	0.07	0.75	0.72
YexSi(Lo)**	23	0.06	0.93	0.59
PoxSi(Lo)**	24	0.06	0.82	0.71
YexLoxPo	2	0.12	1.83	0.15
Res	18	0.07		
Total	101			
Pentapora foliacea				
Ye	1	0.09	2.24	0.20
Lo	2	0.05	1.28	0.32
Po	1	0.06	2.11	0.18
Si(Lo)	55	0.04	0.91	0.52
YexLo	2	0.04	0.83	0.53
YexPo	1	0.07	1.56	0.22
LoxPo	2	0.01	0.31	0.75
YexSi(Lo)**	37	0.04	No test	
PoxSi(Lo)**	0		No test	
YexLoxPo	0		No test	
Total	101			

Table S10: Effect size (Wilcoxon r) and 95 % confidence intervals of pot type (inkwell and parlour) on fractions of individuals damaged, removed, or exhibiting no damage as a response to pot hauling. Effect sizes calculated using the package coin (Hothorn et al., 2008) in the R programme (R core team 2019).

	Erect emergent			**Low encrusting**		
Response	Effect size	Lower CI	Upper CI	Effect size	Lower CI	Upper CI
No damage	0.139	0.0096	0.34	0.099	0.0078	0.44
Damaged	0.142	0.0079	0.35	0.091	0.0041	0.44
Removed	0.010	0.0022	0.23	0.051	0.0074	0.40