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Removal treatments alter the recruitment dynamics of a global marine invader - Implications for management feasibility

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ABSTRACT

Frameworks designed to prioritise the management of invasive non-native species (INNS) must consider many factors, including their impacts on native biodiversity, ecosystem services, and human health. Management feasibility should also be foremost in any prioritisation process, but is often overlooked, particularly in the marine environment. The Asian kelp, *Undaria pinnatifida*, is one of the most cosmopolitan marine INNS worldwide and recognised as a priority species for monitoring in the UK and elsewhere. Here, experimental monthly removals of *Undaria* (from $0.2\,m^2$ patches of floating pontoon) were conducted at two marinas to investigate their influence on recruitment dynamics and the potential implications for management feasibility. Over the 18-month experiment there was no consistent reduction in *Undaria* recruitment following removals. Cleaning of pontoon surfaces (i.e. removal of all biota) led to significant short-term reductions in recruitment but caused a temporal shift in normal recruitment patterns. Non-selective removal (i.e. all macroalgae) generally promoted recruitment, while selective removal (i.e. *Undaria* only) had some limited success in reducing overall recruitment. The varied results indicate that the feasibility of limiting *Undaria* is likely to be very low at sites with established populations and high propagule pressure. However, where there are new incursions, a mixture of cleaning of invaded surfaces prior to normal periods of peak recruitment followed by selective removal may have some potential in limiting *Undaria* populations within these sites. Multi-factorial experimental manipulations such as this are useful tools for gathering quantitative evidence to support the prioritisation of management measures for marine INNS.

1. Introduction

Invasive non-native species (INNS) can cause significant environmental impacts to the native communities to which they are introduced (Simberloff et al., 2013; Early et al., 2016). There is also major economic cost associated with their management, control and remediation (Pimentel et al., 2005; Williams et al., 2010). Consequently, there is increasing pressure to control the introduction, spread and proliferation of INNS. New legislative tools, such as those adopted in the EU (EU, 2014) and USA (Federal Register, 2016), aim to improve prevention via greater biosecurity, containment and eradication of INNS. Rapid response eradication is generally accepted as the best management option once a new species is detected and biosecurity measures have clearly failed (Beric and MacIsaac, 2015; Early et al., 2016). But when an INNS becomes widespread, available management options are often limited, and can be highly costly, time-consuming and ineffective, especially in highly connected marine environments (Bax et al., 2003; Simberloff et al., 2013; Early et al., 2016; Courtois et al., 2018). As environmental managers have finite resources with which to tackle an ever-increasing number of INNS, management prioritisation procedures are clearly needed (Bonanno, 2016; McGeoch et al., 2016; Seebens et al., 2017; Courtois et al., 2018).

In order to design a prioritisation framework, many factors must be considered, including ecological and economic impacts, the provision of ecosystem services and effects on human health (McGeoch et al., 2016; Epstein, 2017). Many of these factors can be highly subjective and are hard to define and quantify. Therefore more attention has recently been given to the important and less subjective issue of management feasibility (Molnar et al., 2008; Panetta and Novak, 2015; Booy et al., 2017; Corbin et al., 2017). Understanding the likely effectiveness, practicality, risk, cost, impact and timeframe of management options should be fundamental to any prioritisation process.

Evaluating the feasibility of management actions for INNS in terrestrial ecosystems is aided by the historic nature of introductions, the quantity of research and the pre-existence of numerous management programmes (Kettenring and Adams, 2011; Veitch et al., 2011; Panetta

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and Novak, 2015; Corbin et al., 2017). In contrast, the management of INNS in marine ecosystems is comparatively new and understudied, although some control and eradication programmes have been implemented (Bax et al., 2003; Williams and Grosholz, 2008; Beric and MacIsaac, 2015). The inherent connectivity of marine environments can promote the spread of INNS and re-entry to cleared areas (Ruiz et al., 1997; Bax et al., 2003), while their relative inaccessibility renders monitoring efforts and management actions far more difficult (Ruiz et al., 1997; Bax et al., 2003; Thresher and Kuris, 2004; Booy et al., 2017). Large-scale management of marine INNS is, therefore, highly costly. Thus, small-scale eradication or control experiments, or trials, can be an important step in determining management feasibility and prioritisation (Lovell et al., 2006; Williams and Grosholz, 2008).

The kelp, *Undaria pinnatifid*a, is one of the most cosmopolitan marine INNS worldwide (Epstein and Smale, 2017b). Native to the north-west Pacific rocky coastlines of Japan, Korea, Russia and China (Saito, 1975), *Undaria pinnatifida* (hereafter referred to as *Undaria*) can now be found in many parts of the north-east and south-west Atlantic, south-west and east Pacific, and the Tasman Sea (Epstein and Smale, 2017b; South et al., 2017). As an INNS *Undaria* is generally more widespread and abundant on artificial rather than natural substrates (Floc'h et al., 1996; Fletcher and Farrell, 1999; Cremades et al., 2006; Russell et al., 2008; Veiga et al., 2014; Kaplanis et al., 2016). Both marinas and aquaculture sites are strongly linked to introduction vectors and would therefore be expected to have high propagule pressure. They also contain large expanses of artificial substrates on pontoons or buoys which are held at a constant shallow depth, providing ideal conditions for the establishment and proliferation of *Undaria* populations (Fletcher and Farrell, 1999; Cremades et al., 2006; Grulois et al., 2011; Minchin and Nunn, 2014; James and Shears, 2016a, 2016b). *Undaria* has also invaded natural habitats across its non-native range, predominantly on sheltered to moderately wave-exposed rocky reefs (Hewitt et al., 2005; Russell et al., 2008; Dellatorre et al., 2014; Minchin and Nunn, 2014; Epstein and Smale, 2017a). In many cases the introduction of *Undaria* into natural habitats has been linked to spill-over from source populations in nearby artificial habitats, however in some cases incursions may also occur directly into natural substrates (Floc'h et al., 1996; Fletcher and Farrell, 1999; Russell et al., 2008; Grulois et al., 2011; James and Shears, 2016b; Epstein and Smale, 2017a).

Undaria is one of the most cosmopolitan marine INNS, and is considered of major importance for conservation management; yet there has been little targeted control of this species in most of its non-native range (Epstein and Smale, 2017b). Where management has been implemented, there has been some success in limiting or excluding *Undaria* in isolated environments; however, most management attempts have led to reintroduction and wider-scale spread, with localised reductions in population density being rapidly reversed following cessation of management actions (Wotton et al., 2004; Hewitt et al., 2005; Thompson and Schiel, 2012; Forrest and Hopkins, 2013; Crockett et al., 2017).

Undaria sporophytes recruit from microscopic gametophytes that may grow vegetatively in the understory for up to 2 years (Pang and Wu, 1996; Thornber et al., 2004; Choi et al., 2005). In its native range, *Undaria* has a strictly annual life cycle with recruitment restricted to the winter months (Saito, 1975; Koh and Shin, 1990). In many parts of its non-native range the thermal cues for its strict annual life cycle are lost due to the temperate environmental conditions (James et al., 2015). In these locations recruitment may occur year-round or in multiple pulses per year, however a degree of annularity generally remains (Thornber et al., 2004; Cremades et al., 2006; Casas et al., 2008; Primo et al., 2010; James and Shears, 2016a, 2016b). Although temperature is considered the key factor influencing *Undaria* recruitment patterns (Saito, 1975; Floc'h et al., 1991; Gao et al., 2013; James and Shears, 2016a; Murphy et al., 2017), recruitment may be influenced by a variety of other factors including light, temperature, salinity, depth, exposure, nutrients and competition (Russell et al., 2008; Gao et al., 2013; Watanabe et al., 2014; Epstein and Smale, 2017b; South et al., 2017). More knowledge is needed on the recruitment dynamics of *Undaria* and the effect of removal treatments in order to better design management measures and understand the factors affecting the probability of management success.

Undaria was first recorded in the UK in 1994, attached to floating marina pontoons in Port Hamble (Fletcher and Manfredi, 1995). While the majority of records originate from southern England, it has also been recorded on the east and west coasts of England, north and south west Wales, on the east coast of Northern Ireland and the Republic of Ireland, and in Scotland at Queensferry (Epstein and Smale, 2017a). There is currently no known targeted management of *Undaria* occurring in the UK (Epstein and Smale, 2017b), although it does appear on a list of priority species for monitoring and surveillance of marine INNS as part of obligations to the Marine Strategy Framework Directive (Stebbing et al., 2015). It is highly likely that as *Undaria* continues its spread and proliferation around the UK (Minchin and Nunn, 2014; Epstein and Smale, 2017a), there will be further pressure to contain or restrict the species from proliferating in certain areas. Due to their association with introduction vectors, and their possible association with spread to natural habitats, marina and harbour environments are perhaps the best candidates for implementing management actions to limit proliferation and control the spread of *Undaria* populations in the UK (Epstein and Smale, 2017a).

Four different removal treatments were applied to patches of marina pontoon during an 18-month manipulative experiment, to investigate their effects on *Undaria* recruitment patterns and elucidate the potential for control or removal of *Undaria* from marinas. There are various potential methods to control marine INNS, including biocontrol, genetic modification, biocides, herbicides and environmental remediation, however as with most plant invasions, the most commonly employed and widely accepted methods are selective physical removal or full clearance of invaded substrates (Bax et al., 2001; Thresher and Kuris, 2004; Anderson, 2007; Kettenring and Adams, 2011). The treatments in this experiment were selected to incorporate different aspects of potential physical removal methods – those which target the macroscopic INNS only, those which incorporate a more substrate-wide exclusion method, and those which target both the macroscopic and microscopic sources of INNS (Critchley et al., 1986; Wotton et al., 2004; Glasby et al., 2005; Coutts and Forrest, 2007; Forrest and Hopkins, 2013).Treatments were maintained at two marinas in Plymouth, UK, to: 1) examine how different physical and temporal removal methods effect recruitment patterns; 2) identify dissimilarities in recruitment patterns and the influence of removal methods between marinas from the same locality; 3) discern which removal method may be most efficient at reducing or excluding *Undaria*; and 4) consider the feasibility of managing *Undaria* within marina environments.

2. Methods

2.1. Site selection

Plymouth Sound is an enclosed embayment fringed by intense coastal development and large port facilities (Knights et al., 2016, Fig. 1). *Undaria* was first recorded in Plymouth Sound in 2003 within one of the waterfront marinas (NBN, 2017), and can now be found at all marinas and on much of the natural rocky-reef within the Sound at varying density and standing biomass (Epstein and Smale, 2017a). The current study was conducted at two marinas (Fig. 1), which were selected based on: 1) permission to access the facilities all-year round; 2) similar pontoon constructions; 3) large areas of pontoon which would not be disturbed by vessels or maintenance staff; 4) well established *Undaria* populations (*Undaria* was first recorded at the two chosen marinas in 2004 and 2010) (NBN, 2017). All manipulations were carried out on the vertical side of concrete-based floating pontoons, with

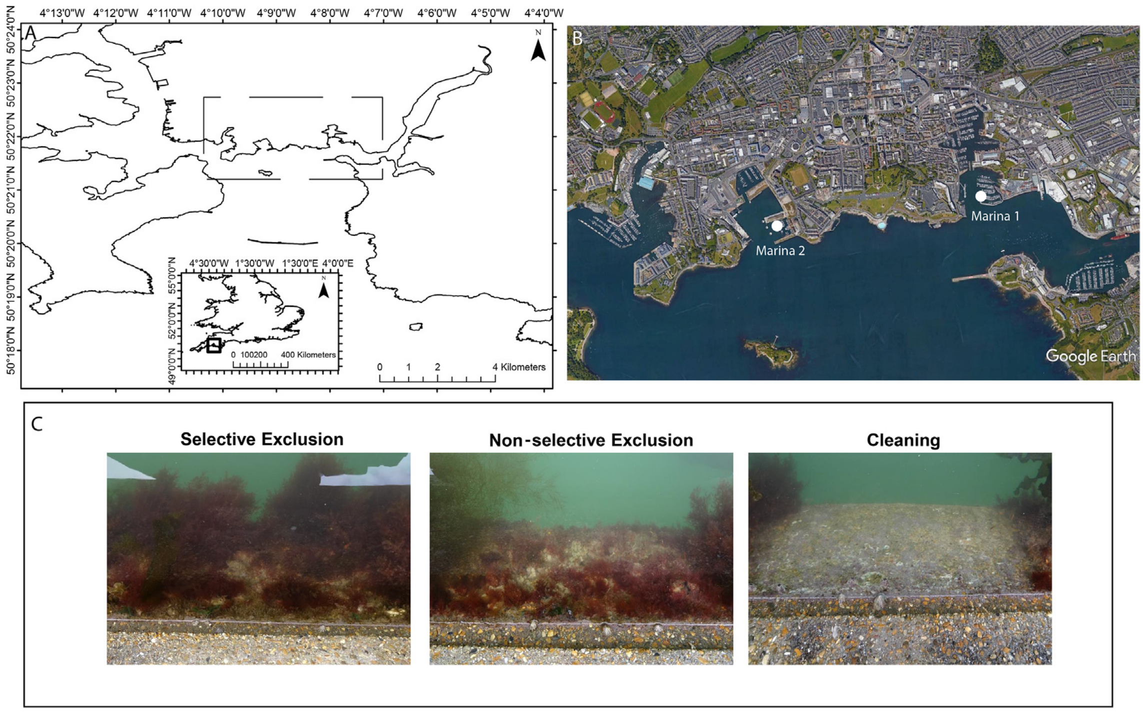

Fig. 1. (A) Plymouth Sound shown in context of southern UK (inset). Dashed line indicates the Plymouth waterfront area, box on inset map indicates position of Plymouth Sound. (B) Plymouth waterfront area with study sites indicated by white points (image from Google Earth™ 11/08/2016). (C) Representative examples of manipulations at the start of the experiment in March 2016.

the entire experimental area being fully immersed at all times. The depth of the manipulations was therefore 0–0.4 m from the surface. Only the sheltered side of pontoons (adjacent to the outer wave-wall) was used in order to minimise disturbance from vessels. As temperature is often considered the key driver of *Undaria* recruitment dynamics (Saito, 1975; James et al., 2015) *in situ* water temperature was recorded adjacent to the pontoons at both study sites (every 30 min, using a Hobo pendant data logger, Onset). Temperature exhibited typical annual fluctuation across the study period and was similar across the study sites (Fig. S1). Mean daily temperature was 13.87 °C (± 2.95 SD) at Marina 1 and 13.75 °C (± 2.88 SD) at Marina 2 and differences in mean daily temperature between sites did not exceed 0.35 °C (Fig. S1).

2.2. Removal treatments

At each marina 16 patches of pontoon, 0.2 m^2 in size, were assigned to one of four removal treatments in a pseudo-random manner to ensure relatively even spread of treatments across the study area. Each patch was marked using waterproof epoxy and coloured markers and were separated by 0.2 m^2 of unmanipulated pontoon (40–50 cm apart along the pontoon). The four treatments were: 1) monthly selective removal of *Undaria*; 2) monthly non-selective removal of all macroalgae; 3) cleaning of pontoon surfaces (removal of all biota) in spring followed by monthly non-selective removal of all macroalgae; 4) cleaning in autumn followed by monthly non-selective removal of macroalgae (Fig. 1). Unmanipulated controls were also established, which is outlined in section 2.4.

For all treatments *Undaria* recruits were extracted each month by cutting just above the holdfast (the average length of recruits was 8 cm meaning the remaining holdfast occupied inconsequential substrate space, and is likely to quickly degrade or dislodge as the meristematic zone occurs between the stipe and blade (Saito, 1975; Castric-Fey et al., 1999b; Choi et al., 2007)). To avoid any edge effects, only those recruits within the centre 0.16 m^2 of each manipulation were retained for further analysis (see below). For the non-selective removal treatments, all macroalgae were also trimmed back to a height of 1–2 cm from the substrate on each visit, to mimic management of *Undaria* by non-selective removal. The complete removal of all biota was conducted only once for each cleaning treatment (spring = March 2016; autumn = September 2016). In these treatments the pontoon was cleaned by scraping off all fouling with metal scrapers, then vigorously brushing the cleared pontoon surface with a wire brush. Although this may have left some microscopic fouling, the high level of abrasion removed all visible macroalgal and faunal fouling (Fig. 1). All cleaning treatments were then maintained as the non-selective removal treatments. The number of *Undaria* sporophytes removed from experimental patches during the initial cleaning/removal in March 2016 were counted, and there was no significant difference in abundance between removal treatments (Negative binomial GLM for each marina - Marina 1: $\chi^2 = 12.1$, p = 0.85; Marina 2: $\chi^2 = 11.9$, p = 0.87. Mean number of sporophytes (± SD) per treatment - Marina 1: 28.8 ± 15.5, 26.5 ± 10.3, 27.5 ± 14.8; Marina 2: 7.3 ± 1.7, 6.5 ± 4.5, 6.25 ± 2.8). All removals were maintained until September 2017.

2.3. Identification and categorisation

Identifying recruits of large brown macroalgae, or kelps, to species level can be challenging (Fig. 2). With experience once recruits attain at least ~7 cm in length *Undaria* can be visually identified in the field, as it is the only large brown macroalgal species found in Plymouth Sound that has a midrib and forms pinnate blade divisions (Fig. 2). For recruits of < 7 cm in length, identification to species required microscopic examination to detect the presence of Yendo cells which are absent from all other large brown macroalgal species in the study region (Drew, 1910; Kasahara, 1985; Castric-Fey et al., 1999b; Burrows, 2012) (Fig. 2). Once identified as *Undaria*, all recruits were categorised as either Type 0 or Type 1 recruits dependent on their developmental stage (Type 0 - absence of pinnate blade divisions and a defined midrib, Type 1 - same features present; adapted from Casas et al., 2008) (Fig. S2); lamina length of all recruits was also measured to the nearest 0.1 cm.

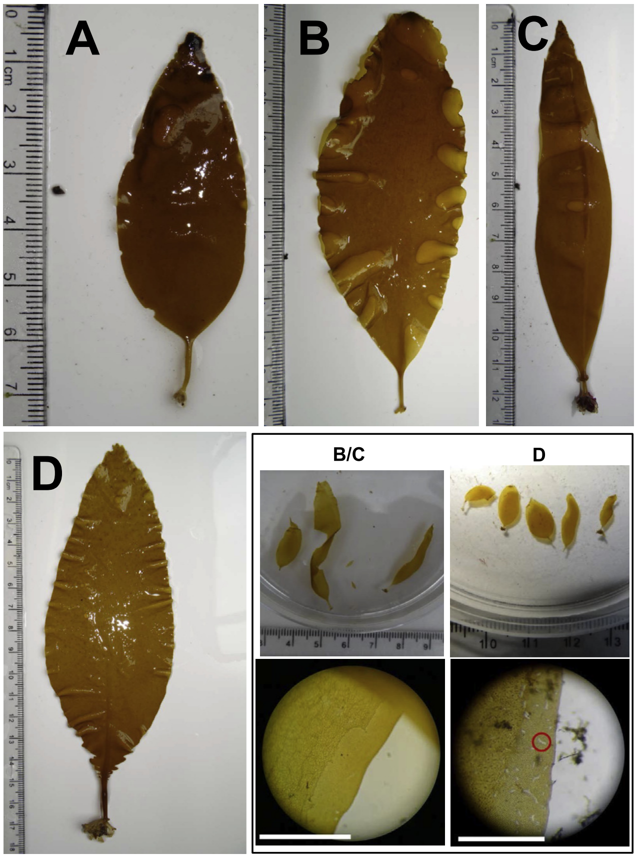

Fig. 2. Recruits of the four kelp species that can be found within marinas in Plymouth. *Laminaria digitata* (A), *Saccharina latissima* (B), *Saccorhiza polyschides* (C) and *Undaria pinnatifida* (D). Once recruits are ~ ≥7 cm in length (as shown in main figure) *Undaria* can be visually identified by the development of a midrib and a pinnate blade (D). Inset images show that confirmation of recruits < 7 cm in length as *Undaria* must be carried out using microscopic techniques by noting the presence of Yendo cells (example encircled) - illustrated by comparison to *S. latissima*/*S. polyschides* (identification uncertain). White bars indicate approximately 1 mm.

2.4. Recruitment patterns in unmanipulated areas

To monitor temporal variability in the recruitment of *Undaria* into unmanipulated areas, sampling of an adjacent untreated section of pontoon was carried out every 3 months at both marinas. During each sampling event, 10 haphazard 0.25 m^2 quadrats were placed randomly against the side of pontoons in each marina. Due to the relatively limited area available for sampling, a note of the position of each quadrat was taken to avoid overlapping quadrat samples during the study. All *Undaria* recruits (Type 0 and Type 1) were removed and enumerated (identification was confirmed as above). To allow for comparison with removal patches the density of *Undaria* recruits per 0.16 m^2 was calculated to the nearest whole plant.

2.5. Data analysis

Generalized Additive Mixed Models (GAMMs) were used to examine the effect of differing removal treatments on the temporal patterns and magnitude of *Undaria* recruitment at each marina separately. A GAMM is a non-linear regression technique whereby the response variable is modelled with non-parametric smooth functions, or “splines” (Wood 2004, 2006). GAMMs were applied using the *gam* command from the *mgcv* package in R 3.2.2 (Wood, 2004; Wood, 2011; R Core Team, 2015). The number of recruits was modelled as a function of “Treatment” (categorical; 4 levels: selective, non-selective, autumn clean, spring clean), “month” (continuous; 1–12) and “duration” (continuous; number of months the removal has been running: 1–18). The value of “duration” at each sampling event differed for the autumn cleaning treatment when compared to all other treatments, as the initial removal occurred in September 2016, whereas all other treatments were initiated in March 2016. Individual patch ID (16 levels) was also applied as a random factor to account for the repeated measure nature of this study. As the response variable is count data, all models were fitted using a Negative Binomial error distribution with a log link function, due to overdispersion from the Poisson distribution (Wood, 2011). The smoothing functions for the two continuous predictor variables were estimated by cubic regression splines (Wood 2004, 2006). The factor of month was defined with a cyclic cubic spline, taking into account its cyclical nature, allowing no discontinuity between January (1) and December (12). Appropriate smoothness for each applicable model term was estimated using Maximum Likelihood (ML) (Wood, 2011). Interactions between Treatment and the two continuous predictor variables were included within the initial models. Significance of the interaction terms was assessed using a Chi-Square test on the ML scores between models containing and excluding each interaction term; which was carried out using the *compareML* function from the *itsadug* package (van Rij et al., 2017). Where no significant difference was recorded between the two models, Akaike information criterion (AIC) and adjusted R^2 values were used to identify whether an interaction term should be retained in the optimal model. Model validation was carried out using the *gam.check* function from the *mgcv* package (Wood, 2017); diagnostic plots were evaluated and the basis dimensions used for smooth terms were checked to be adequate using k-index tests (Wood, 2017). Overall parametric differences between Treatments were assessed using Wald Tests, with the *wald_gam* function from the *itsadug* package (van Rij et al., 2017). Variation in the influence of duration and month on different treatments was assessed graphically using the *plot.gam* function from the *mgcv* package (Wood, 2017).

To assess differences in recruitment patterns between removal treatments and unmanipulated areas, negative binomial generalized linear models (nbGLMs) were constructed for unmanipulated data and each removal treatment separately. Only those timepoints when both removal and unmanipulated data were collected were used in this analysis. Each nbGLM modelled the number of recruits as a function of “Removal” (categorical; 2 levels: unmanipulated and one of the four removal treatments), “Date” (categorical; 6 levels for all treatments except autumn removal – 4 levels), and their interaction. Testing for significant pairwise differences between removal treatments at each sampling point was carried out by releveling the Date factor within nbGLMs. All nbGLMs were carried out using the *glm.nb* command from the *MASS* package (Venables and Ripley, 2002).

Mapping was carried out within ArcMap 10.3.1 (Fig. 1). All statistics were carried out in R 3.2.2 (R Core Team, 2015). The *dplyr* package (Wickham and Francois, 2015) was used for data manipulation and all graphs were created using *ggplot2* (Wickham, 2009) or base R (R Core Team, 2015).

3. Results

During the experiment, a total of 2138 and 368 *Undaria* recruits were removed from Marina 1 and Marina 2, respectively. The highest number of recruits from a single removal patch was 151 inds. 0.16 m^{-2}, recorded in April 2016 within a non-selective removal treatment in Marina 1. Most recruits were Type 0 plants, with 75% of sampled individuals being classed as this developmental stage (Fig. S3). The average lamina length of recruits was 8.0 cm (± 7.5 SD) and ranged from 0.4 to 49.7 cm (Fig. S4). Growth and development of recruits was fastest in late spring and summer, with larger recruits and the majority of Type 1 plants being found between April and August (Fig. S3, Fig. S4).

Across all treatments and both marinas there were only 28 out of

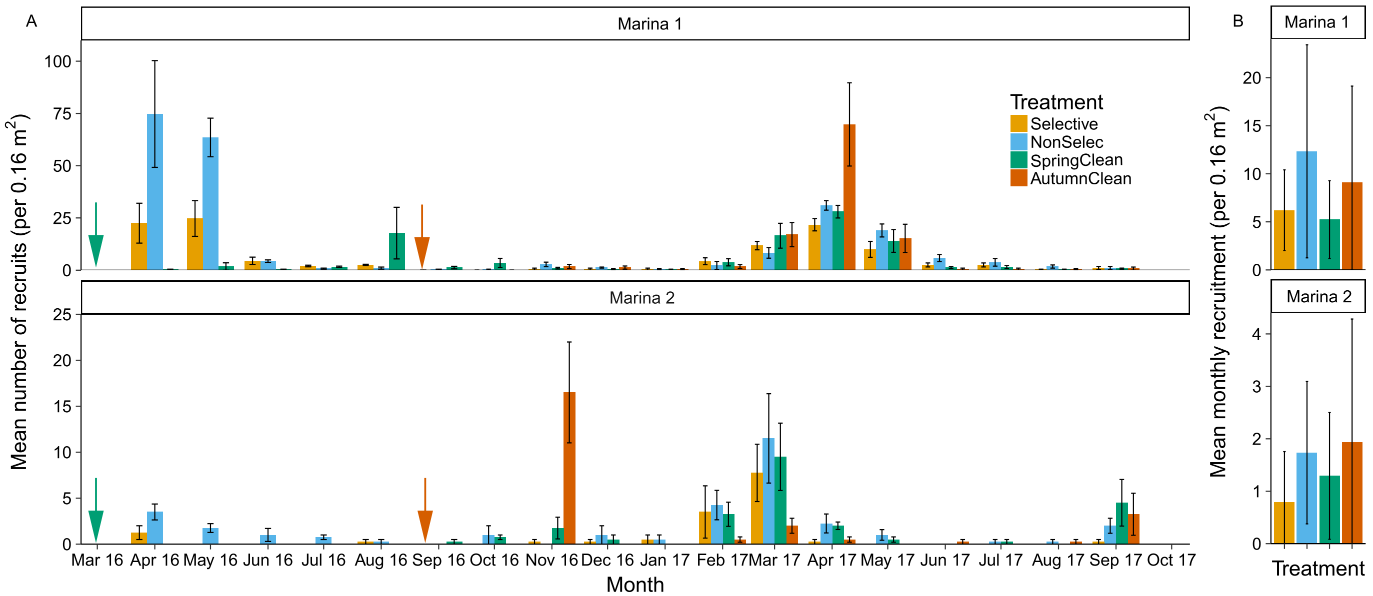

Fig. 3. (A) Mean number of *Undaria pinnatifida* recruits (± standard error) found at each monthly removal for the four treatments at each marina separately. Arrows indicate when each treatment was initiated: green = selective, non-selective and spring cleaning, orange = autumn cleaning. (B) Mean monthly recruitment (± standard error) across the study period within each removal treatment. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

132 occasions where no recruits were found in a monthly removal treatment, highlighting the limited success of the experimental removals. In general, most of the recruits were found in late winter and spring, with peak recruitment in Marina 1 from March–May, and a slightly earlier peak in recruitment at Marina 2 from Feb–April (Fig. 3). Mean monthly recruitment across the study period was highly variable among treatments, however the non-selective removal and autumn cleaning treatment generally had higher recruitment than the selective removal and spring cleaning treatments at both marinas (Fig. 3). At the start of the experiment (Apr–Jul 16) non-selective removal had the highest recruitment of all four treatments at both sites (Fig. 3). In contrast, cleaning in the spring led to the lowest recruitment. Towards the latter part of the experiment (Jan–Sept 17) recruitment patterns within non-selective, selective and spring removal treatments became more similar. There were, however, more distinct recruitment patterns in the autumn cleaning treatments. Cleaning treatments resulted in distinct peaks outside of the main recruitment periods, with high recruitment from the spring cleaning treatment in Marina 1 in Aug 2016, and from the autumn cleaning treatment in Marina 2 in Nov 2016 (Fig. 3).

GAMMs indicated a significant effect of Treatment, Duration and Month on recruitment at both marinas (Table 1). There was a significant interaction between Duration and Treatment shown by better model fit with inclusion of the interaction term at both marinas (Marina 1 – $\chi^2_{(6)} = 28.58$, $p < 0.001$; Marina 2 - $\chi^2_{(6)} = 10.40$, $p = 0.002$). The interaction term between Month and Treatment was also included in the optimal model for both marinas with significantly better model fit with its inclusion at Marina 2 ($\chi^2_{(3)} = 6.25$, $p = 0.006$); and although the Chi-sq test showed no significant difference at Marina 1, inclusion of the interaction term led to lower AIC score and higher adjusted R^2 (without interaction AIC = 1181, $R^2 = 0.60$, with interaction AIC = 1178, $R^2 = 0.68$).

Overall parametric differences between treatments were found at both marinas. Recruitment in the non-selective removal treatment was significantly higher than both the selective and spring clean removal treatments at both marinas; while at Marina 2 recruitment in the autumn clean treatment was significantly higher than both the selective and spring clean treatments (Table 2).

Duration of the monthly removal (i.e. the number of months for which the removal had been maintained) had a significant effect on recruitment within only a few treatments (Table 1). The spring cleaning treatment had a significant relationship with duration at both marinas, as recruitment was reduced after the initial cleaning treatment and generally increased over time, although recruitment did decline towards to end of experiment at Marina 1 (Fig. 4). Similarly, recruitment within the autumn cleaning treatment at Marina 2 was reduced due to the initial cleaning but then increased over time (Fig. 4). Duration was also significantly related to recruitment in the non-selective removal treatment at Marina 1, with recruitment decreasing slightly towards the middle of the experiment but then increasing towards the end.

At both marinas there were strong temporal patterns with month of the year significantly related to recruitment in all treatments, with each having a distinct monthly pattern (Table 1). At Marina 1, the selective removal treatment had a unimodal recruitment pattern, with peak recruitment in April and minimum recruitment in October–November (Fig. 4). The non-selective treatment had more consistent recruitment throughout the year with comparatively higher recruitment from September–December. The cleaning treatments both had distinct bimodal recruitment patterns, with a secondary peak in August and November for the spring and autumn treatments respectively (Fig. 4). Although different monthly patterns were found at Marina 2 (Fig. 4), there was a similar effect of treatment. The non-selective treatment led to more sustained recruitment than the selective removal, and both of the cleaning treatments induced distinct bimodal recruitment patterns (Fig. 4).

Variability in recruitment patterns between unmanipulated areas and the removal patches differed between treatments and time points (Fig. 5) as shown by significant Date-Treatment interactions within all pairwise comparisons (Table 3). The selective removal treatment had relatively lower recruitment compared to unmanipulated areas, with less recruits found at each sampling point except September 2017 at Marina 1 (Fig. 5). The patterns with all other treatments were less clear at both marinas; at some sampling points removal treatments had higher recruitment than in the unmanipulated areas but at other time points recruitment was comparably lower (Fig. 5). Recruitment into non-selective removals was higher than into unmanipulated areas in 6 out of the 12 contrasts, and lower in 5; spring cleaning was higher in 6 and lower in 6; and autumn was higher in 3 and lower in 5 (Fig. 5).

Table 1
Summary of results from generalized additive mixed models predicting number of *Undaira pinnatifida* recruits within each removal treatment at each marina separately. The results from Wald like tests for each coefficient are shown with relative degrees of freedom (df), effective degrees of freedom (edf), chi-square value (X^2) and p-values (*p*).

Model Terms	Marina 1			Marina 2		
Parametric terms	df	X^2	p	df	X^2	*p*
Treatment	3.00	8.03	0.046	3.00	16.53	< 0.001
Smooth terms	edf	X^2	*p*	edf	X^2	*p*
s (Month):TreatmentSelective	4.35	117.58	< 0.001	4.41	47.24	< 0.001
s (Month):TreatmentNonSelec	5.18	62.01	< 0.001	4.03	16.84	< 0.001
s (Month):TreatmentSpring	5.88	32.66	< 0.001	5.29	48.90	< 0.001
s (Month):TreatmentAutumn	5.34	135.78	< 0.001	6.66	60.02	< 0.001
s (Duration):TreatmentSelective	1.00	1.49	0.222	1.00	0.46	0.496
s (Duration):TreatmentNonSelec	2.21	7.21	0.039	3.13	3.52	0.539
s (Duration):TreatmentSpring	2.99	34.35	< 0.001	1.00	14.59	< 0.001
s (Duration):TreatmentAutumn	1.00	1.34	0.248	1.00	11.04	< 0.001
s (Plot)	< 0.01	0.00	0.544	7.41	23.78	< 0.001

4. Discussion

4.1. Efficacy of removal treatments

The current study highlights why the management of *Undaria* populations in invaded regions is logistically challenging and often unsuccessful. *Undaria* recruits may be present throughout the year, can be hard to identify and have temporally plastic recruitment patterns which can be altered by removal treatments. *Undaria* also recruits in extremely high densities onto artificial substrates following significant interventions such as monthly removals. This study should allow better decisions to be made on future management attempts, as our results suggest that the potential to limit *Undaria* recruitment is likely to be very low at sites with established populations and high propagule pressure. However, where there are new incursions, certain removal methods may have some potential to limit *Undaria* populations in artificial habitats.

Of the four removal treatments used in this study the non-selective removal was the least effective. Overall parametric differences indicated higher recruitment within this treatment when compared to spring clean and selective removal treatments at both marinas. Moreover, non-selective removal did not result in consistent reductions in recruitment in comparison to adjacent unmanipulated areas. It also induced more sustained and temporally consistent recruitment of *Undaria* throughout the year, and recruitment intensity did not decline during the duration of the experiment. This pattern was likely driven by the opportunistic life-history traits of *Undaria*, which enable it to take advantage of reduced competition resulting from the non-selective removal of all macroalgae (Valentine and Johnson, 2003; Edgar et al., 2004). This has been shown in previous studies, where a positive recruitment response of *Undaria* was recorded following diminished

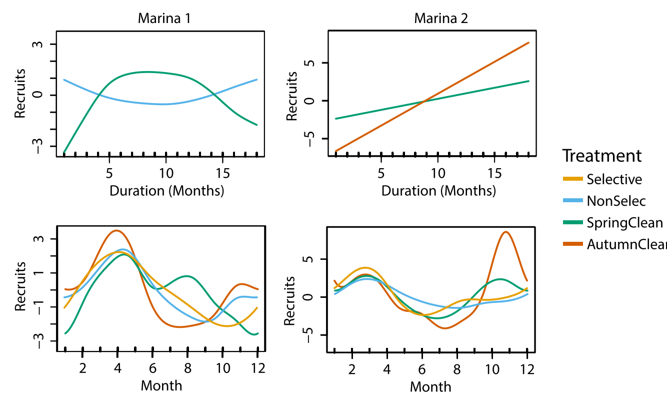

Fig. 4. Regression splines indicating the effect of duration of the removal treatments (cubic) and month of the year (cyclic) on recruitment of *Undaria pinnatifida* at each marina. Only those smoothing splines which were statistically significant are plotted.

interspecific competition from co-existing macroalgae. (Valentine and Johnson, 2003; Edgar et al., 2004; South and Thomsen, 2016; De Leij et al., 2017). A non-selective removal method would be easier to implement across wider spatial scales, due to the lack of need for identification skills, time and effort to search for *Undaria*, and the relatively simple logistics involved with mechanically trimming back fouling from pontoons. However, due to the limited success in reducing *Undaria* recruitment intensity in this study, it is unlikely to be a viable control option and may even promote recruitment and ultimately enhance population density.

Although full cleaning of the pontoon surface led to significant short-term reductions in recruitment, recruitment generally increased

Table 2
Post-hoc comparison of pairwise intercept differences between removal factors from GAMMs at each marina separately. Wald like tests compare parametric components only, without considering smooth terms. Parametric coefficient estimates are shown (with the Selective treatment as the intercept level), with pairwise chi-square value (χ^2) and p-values (*p*). Degrees of freedom are always equal to 1 due to pairwise testing. Significant pairwise differences shown in bold ($\alpha < 0.05$).

Treatment	Marina 1							Marina 2						
	Estimate	Selective		Non-selec		Spring		Estimate	Selective		Non-selec		Spring	
		χ^2	*p*	χ^2	*p*	χ^2	*p*		χ^2	*p*	χ^2	*p*	χ^2	*p*
Selective	0.830							−1.938						
Non-selec	0.405	**4.35**	**0.037**					1.770	**9.54**	**0.002**				
Spring	−0.088	0.20	0.657	**7.01**	**0.008**			0.295	0.18	0.670	**6.86**	**0.009**		
Autumn	0.173	0.23	0.629	0.44	0.509	0.55	0.460	2.195	**8.90**	**0.003**	0.48	0.490	**6.81**	**0.009**

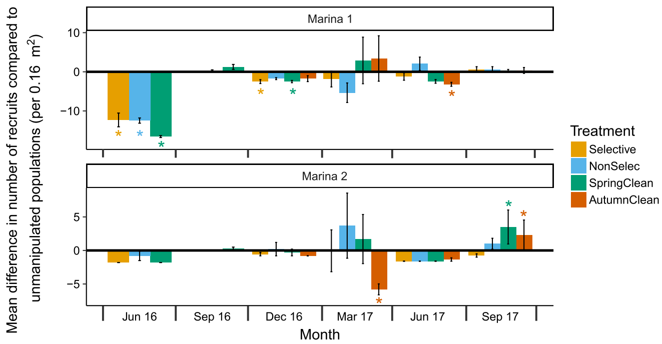

Fig. 5. Comparison of *Undaria pinnatifida* recruitment between unmanipulated areas and removal treatments. Mean difference in number of recruits between unmanipulated areas and removal treatments (± standard error) is shown for 6 time points where both unmanipulated and removal recruitment was measured (data for autumn treatment for 4 time points only – Dec 16 onwards). Asterisks indicate significant pairwise differences between a given treatment and unmanipulated areas at each sampling point.

over the time-course of the experiment. Both autumn and spring cleaning treatments led to short-term reductions in recruitment, with reductions particularly apparent for the spring cleaning treatment which was applied immediately prior to the peak recruitment period of *Undaria.* This short-term reduction was evident at both marinas when compared to recruitment in other removal treatments in April–July 2016, and to unmanipulated areas in June 2016. This reduction is probably due to removal of the microscopic 'seed-bank' of *Undaria* gametophytes during rigorous cleaning of the pontoon surface (Schiel and Thompson, 2012; Forrest and Hopkins, 2013; Morelissen et al., 2016). Similar short-term reductions in *Undaria* abundance have been seen in previous studies that used heavy abrasion to clear experimental patches of artificial or natural substrates (Curiel et al., 2001; Thompson and Schiel, 2012; Morelissen et al., 2016). Although cleaning of pontoons using highly abrasive methods before peak recruitment periods of *Undaria* may be viable in reducing abundance in the short term, cleaning treatments also induced a change in *Undaria* recruitment dynamics. As confirmed by this study, *Undaria* has the potential to recruit throughout the year in the UK and northeast Atlantic (Castric-Fey et al., 1999a; James et al., 2015; Murphy et al., 2016), however the majority of recruitment generally occurs in late winter through to early spring (Fletcher and Farrell, 1999; Minchin and Nunn, 2014; Murphy et al., 2017). The cleaning treatments altered this typical recruitment pattern by inducing bimodal rather than unimodal patterns, with notable recruitment pulses in late autumn as well as spring. While low levels of recruitment were observed for 1–2 months following cleaning in some cases, additional peaks in recruitment occurred 2–6 months after the treatments were initiated. If the cleaning methods used in this study effectively removed all gametophytes from the pontoon surface, the observable sporophyte recruits must have originated from recently settled spores. Accelerated development of *Undaria* spores to sporophytes may be viable in as little as 15–20 days (Pang and Wu, 1996; Thornber et al., 2004; Choi et al., 2005), and our study suggests that development of sporophytes may occur within this time frame in marina environments. Even so, our results suggest that maturation of spores to sporophytes in high densities is likely to occur over a greater time frame of 2–6 months.

The plastic recruitment dynamics recorded from the cleaning treatments in this study would render long-term control methods more challenging to design, perhaps requiring frequent pontoon cleaning to significantly limit the population in the long term. The complete cleaning of pontoon surfaces will also impact a wide range of other native and non-native fouling species, and would also require considerable expenditure and effort. Such disturbance may have unintended consequences in facilitating other INNS which can establish on marina pontoons (e.g. *Didemnum vexillum*, *Bugula neritina*, *Styela clava*) (Britton-Simmons and Abbott, 2008; Bishop et al., 2015); while disturbance to native species may reduce ecosystem services provided by the fouling assemblages on pontoons including nutrient uptake and biofiltration by sessile invertebrates (Russell et al., 1983; Allen et al., 1992). Whether such a treatment would be logistically achievable, have net benefit, and be successful in limiting *Undaria* populations on a wider scale, requires further investigation.

There was no consistent reduction in recruitment from selective removal of *Undaria,* however there was evidence that this treatment was relatively successful in limiting recruitment. Any significant pairwise parametric differences between other treatments indicated lower recruitment in the selective removal treatment. Recruit density was also generally lower in selective removal treatments when compared to unmanipulated areas and the treatment did not induce deviation from typical annual recruitment patterns. This removal method would require less physical effort than other methods used in this study; although more time would be needed to search pontoon surfaces for *Undaria* recruits and some taxonomic training and expertise would be necessary. Intuitively, this method would reduce overall *Undaria* population density in the long term, by removing individuals before they reach reproductive maturity and thereby reducing localised propagule pressure. However, it is unlikely to lead to local eradication as some individuals will inevitably be missed and the microscopic gametophyte stage is not targeted within the management action. Indeed, this has been demonstrated in Australasia, where long term removals led to declines in *Undaria* population density, but not eradication, with localised reductions in population density being rapidly reversed following cessation of management actions (Hewitt et al., 2005; Forrest and Hopkins, 2013).

Table 3
Sequential likelihood ratio tests for Negative Binomial generalized linear models comparing each removal treatment to unmanipulated recruitment data for each marina separately. Chi-square value (χ^2) and p-values (*p*) are given for each coefficient - "Removal" (difference between removal treatment and unmanipulated), "Date", and their interaction ("Removal*Date").

Coefficient	Selective			Non-selec			Spring			Autumn		
	df	X^2	p	df	X^2	p	df	X^2	p	df	X^2	p
Marina 1												
Removal	1	12.86	< 0.001	1	12.41	< 0.001	1	11.96	< 0.001	1	0.07	0.793
Date	5	247.08	< 0.001	5	230.50	< 0.001	5	219.19	< 0.001	3	105.94	< 0.001
Removal*Date	5	12.00	0.035	5	16.38	0.006	5	54.44	< 0.001	3	9.53	0.023
Marina 2												
Removal	1	4.64	0.031	1	0.81	0.367	1	0.42	0.518	1	7.51	0.006
Date	5	173.37	< 0.001	5	155.85	< 0.001	5	141.62	< 0.001	3	61.34	< 0.001
Removal*Date	5	17.06	0.004	5	13.17	0.021	5	33.06	< 0.001	3	20.67	< 0.001

4.2. Spatial and temporal context

Our study was carried out at two marinas only 1.5 km apart, yet considerable differences in *Undaria* recruitment dynamics were observed between sites. Although the overall effects of removal treatments were similar between both marinas, each had temporally distinct peak recruit periods, highly disparate recruit densities and different temporal recruitment patterns. Temperature is often considered as a key factor influencing *Undaria* recruitment patterns (Saito, 1975; Floc'h et al., 1991; Gao et al., 2013; James and Shears, 2016a; Murphy et al., 2017), but thermal regimes were similar across sites. Disparity in population dynamics between nearby sites has been observed in previous studies, including those conducted within marinas and on natural reef habitats (Schiel and Thompson, 2012; James and Shears, 2016a). The population dynamics of *Undaria* may be influenced by a variety of factors including light, temperature, salinity, depth, exposure, nutrients and competition (Russell et al., 2008; Gao et al., 2013; Watanabe et al., 2014; Epstein and Smale, 2017b; South et al., 2017). More research is needed to examine how population dynamics of INNS vary between sites and habitats, and how spatial variability may influence both ecological impacts and potential management approaches.

Although data was not collected on the composition of co-occurring macroalgae in different treatments or background populations, the community was dominated by a mixture of filamentous and foliose reds, filamentous browns, and seasonal pulses of foliose green algae, interspersed by low numbers of the native kelps *Saccharina latissima* and *Saccorhiza polyschides.* Variation in co-occurring species between plots may have influenced recruitment dynamics both within treatments, and between treatments and background populations. Even so, experimentation was conducted over a relatively small area of pontoon surface which did not vary greatly in its algal community (Epstein pers. obs.). As no significant difference in *Undaria* abundance was detected at either marina at the start of the experiment it would seem evident that any variation in co-occurring community did not exert a strong influence on *Undaria* populations before the manipulations commenced.

It should be noted that the treatments examined here were implemented over relatively small sections of pontoons and over a fixed period of time. Larger scale, or longer-term, management actions may have differing results, such as if *Undaria* was to be removed from an entire site or marina. Multi-factorial experimental manipulations are, however, useful tools for gathering quantitative evidence to support the prioritisation and design of management measures for marine INNS. Implementing a similar experiment at a marina-wide scale would be extremely challenging, requiring replicate marinas and treatments. The data gathered from this small-scale experimental manipulation should aid in the design and prioritisation of future management.

Within marinas *Undaria* is predominantly recorded attached to the sides of floating pontoons, where relatively high light availability and large areas of available substrate may favour recruitment, development and growth. However, fully implemented management measures would need to be carried out over a much wider scale in terms of depth range and habitat type in order to successfully exclude, or significantly limit the density and spatial extent of *Undaria* populations. This may include the entirety of pontoon surfaces, wave-walls, boat hulls, pontoon struts, nearby rocky reefs and even hard substrates on the sea floor below marina structures. Management actions would also need to be sustained over a longer time period than was carried out in this study, as shown by the limited temporal effect and results from previous management attempts in other regions (Hewitt et al., 2005; Forrest and Hopkins, 2013; Crockett et al., 2017). Direct targeted management would also have to be accompanied by stringent biosecurity to avoid further introductions from other invaded ports and marinas. Our experiment was also conducted within one region of the UK, in two marinas of similar design and construction. It is possible that in other regions, or habitat types, the population dynamics and effects of removal treatments may differ. Nonetheless, the results of this study are likely to be applicable to many other situations and will be of importance in informing future management actions.

4.3. Future perspectives for management

In the UK, *Undaria* has been present since at least 1994 and although it has been recorded across many regions, it is still largely constrained to artificial habitats, specifically ports and marinas (Epstein and Smale, 2017a). As a priority species designated under the Marine Strategy Framework Directive in the UK (Stebbing et al., 2015), it is necessary to consider the efficacy and feasibility of actions to control its spread. As marinas are considered hotspots of introductions and strongholds of population growth, there may be opportunities to reduce its spread to nearby natural habitats by managing source populations in artificial habitats (Epstein and Smale, 2017a). Marinas can also act as stepping-stones to the *Undaria* invasion, with fouling on hulls of commercial and recreational vessels leading to its spread to uninvaded ports and marinas (Fletcher and Farrell, 1999; Russell et al., 2008; Dellatorre et al., 2014; Zabin, 2014; Kaplanis et al., 2016). Reducing the size of *Undaria* populations in invaded marinas may therefore, also reduce the probability of its transport to new sites or regions. Where *Undaria* has been established for many years and can be found in high abundance on both artificial and natural substrates, such as within Plymouth Sound, it seems that there will be very low likelihood of successful management. However, this study should inform the design of future management measures for *Undaria,* particularly when it is first recorded in newly-invaded locations and where controlling population expansion in artificial habitats may reduce its spread to natural habitats or artificial habitats in uninvaded regions (Zabin, 2014; Epstein and Smale, 2017a). We must be cautious however, as where previous management has been implemented, there has been some success in limiting or excluding *Undaria* in isolated environments; however, most management attempts have led to reintroduction and wider-scale spread, with localised reductions in population density being quickly reversed (Wotton et al., 2004; Hewitt et al., 2005; Thompson and Schiel, 2012; Forrest and Hopkins, 2013; Crockett et al., 2017). Overall we suggest that cleaning of pontoons prior to main recruitment periods, and selective removal of *Undaria* before maturity, may have some potential to reduce recruit density in newly-invaded locations and therefore overall abundance and propagule pressure influencing adjacent habitats. As previously stated, any direct management measure will have to be accompanied by carefully designed and stringent biosecurity measures to avoid re-introductions and further spread.

It is highly probable that *Undaria* will continue to expand its range across temperate regions of the world, which will present opportunities to test the efficacy of management measures across wider spatial scales and varying ecological contexts. Experimental removal studies, such as this, may be a useful tool for management prioritisation of other INNS, particularly in the marine environment where large-scale species control experiments are generally lacking and difficult to undertake. Further research on the management of marine INNS is needed, including testing small and large-scale experimental removal or exclusion measures, to better quantify management feasibility and aid in designing management prioritisation frameworks. Difficult decisions will have to be made on what management is prioritised and implemented, and in which situations and circumstances the presence of an INNS is accepted (Bonanno, 2016; Epstein, 2017). There may be challenging trade-offs of impacts on biodiversity against ecosystem services that INNS provide (Davis et al., 2011; Epstein, 2017).

Conflict of interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2018.06.022.

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