

Ecological tipping points for an invasive kelp in rocky reef algal communities

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ABSTRACT: Invasive species are affecting coastal ecosystems worldwide and there are many potential mechanisms that allow their spread into native communities. To investigate this phenomenon, we used an experiment in which the canopy of the southern bull kelp *Durvillaea antarctica* was removed in 2 seasons and community development was followed over 3 yr. The invasive kelp *Undaria pinnatifida* recruited almost exclusively into plots from which the natural canopy had been removed. We examined, through a series of regression tree models and change point analyses, the gradients of community responses that allowed the successful recruitment of this invasive species. Analyses revealed a range of coinciding conditions, especially a decline in furoid cover below 20% and an increase in turf cover above 80%, that facilitated *Undaria* recruitment. The abundance of molluscan grazers and cover of subcanopy algae had lesser effects on *Undaria* recruitment. In an ecological sense, there was a clear tipping point in the interaction between canopy loss and the subsequent expansion of coralline turf that allowed communities to switch from dominance by native species to seasonal dominance of *Undaria*. This study illustrates the complex nature of disturbance thresholds and interactions within the native communities that can facilitate the spread and recruitment success of *Undaria*.

KEY WORDS: Tipping point · Threshold · Rocky reef · Native algae · Invasive algae · Regression tree

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INTRODUCTION

Invasive species are considered to be one of the greatest threats to native marine communities worldwide (Bax et al. 2003, Molnar et al. 2008). Eradication of such species is almost impossible and always expensive. Once introduced, there is often an initial slow spread before traction is gained in native communities (Crooks 2005, Molnar et al. 2008, Lyons & Scheibling 2009). Propagule pressure, cryptic habitats and disturbance to native communities can allow invaders to spread rapidly along coastlines and even become a dominant feature of coastal marine habitats. Because invasive species can affect a wide range of community and ecosystem functions, their dominance can represent a significant tipping point in native communities, species abundance and ecosystem processes and functions. For example, invasive

bivalves can greatly alter filtration rates and benthic characteristics of communities (e.g. the Asian clam *Potamocorbula amurensis* in San Francisco Harbour; Carlton et al. 1990, Ruiz et al. 1997) and invasive algae can change networks of interactions within rocky reef ecosystems (e.g. the invasion of *Sargassum muticum* in Europe and North America; Stæhr et al. 2000, Thompson et al. 2002, Britton-Simmons 2004, Salvaterra et al. 2013). Native communities may exhibit ecological resistance to invasion through the ability of native species to retain space, recruit effectively and out-shade or overgrow other species (Shea & Chesson 2002). Understanding how invasive species gain traction in communities is problematic, however, given the vast array of life histories that invasive species possess and the types of communities they arrive into. For any given invasive species, this process will involve an interaction of its life his-

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tory with multiple characteristics of invaded habitats and the species that already occur there, which can either slow or accelerate spread. Changes in abundances of native species within the community, possibly through a physical disturbance, could cross an 'ecological threshold' and result in a rapid or abrupt non-linear change in the abundance of invasive species (Groffman et al. 2006, Dodds et al. 2010, Daily et al. 2012). Ecological tipping points, or thresholds, often have been studied with regards to the effects of invaders on native species (Gooden et al. 2009, Panetta & Gooden 2017), but have rarely been examined as mechanisms for invasion establishment.

Much has been written about the invasiveness and spread of the Japanese kelp *Undaria pinnatifida* (hereafter *Undaria*), which now occurs in dozens of countries worldwide (Hay & Luckens 1987, Fletcher & Farrell 1998, Valentine & Johnson 2003, Casas et al. 2004, Miller & Engle 2009, Dellatorre et al. 2014). There is good experimental evidence that this species primarily invades open spaces in native canopies, which often occur through natural disturbances (Valentine & Johnson 2003, Thompson & Schiel 2012, Carnell & Keough 2014). Its competitive ability may be poor as there is relatively little evidence that it can actively displace native species (Forrest & Taylor 2002, Thompson & Schiel 2012, South et al. 2016). However, its great abundance in some areas and often-exclusive occupation of large patches suggest there may be slow and sequential impacts on the abundance and, potentially, distribution of native species (Russell et al. 2008, Carnell & Keough 2014). These may, therefore, represent transitions whereby native communities are effectively replaced by an invasive kelp.

Other invasive macroalgae such as *S. muticum* and *S. horneri* share many of the invasive characteristics of *Undaria* in that they can become enormously abundant, produce large biomass and spread in native communities over relatively short periods of time (Stæhr et al. 2000). The very large reproductive output of these species and their fast population turnover (generally annual) allow them to take quick advantage of disturbances or open spaces that may appear on reefs usually dominated by perennial species in temperate areas. In New Zealand, *Undaria* is one of the very few large, habitat-forming seaweeds that are annual (Schiel & Foster 2006) and can quickly invade newly disturbed areas or as space becomes available (Thompson 2004, Thompson & Schiel 2012). Furthermore, *Undaria* seems to be one of the few large canopy algae able to recruit into thick coralline turfing algae, which can extensively cover primary substratum and seem to afford some protection to the

microscopic phases of *Undaria* during its recruitment (Thompson 2004, Thompson & Schiel 2012).

Undaria has spread extensively along the coastline of New Zealand and has formed very dense populations outside of the initially invaded harbour areas (Hay & Luckens 1987). It has dispersed and spread to invade the low intertidal and shallow subtidal zones of the cooler waters of southern New Zealand (Forrest et al. 2000, Stuart 2004, Russell et al. 2008), and there is speculation it is displacing native species (Stuart 2004, Bollen et al. 2016). Here we use a multi-year data set, based on experimental disturbances, to estimate and analyse ecological thresholds in macroalgal communities and analyse the types of interactions and changes that allow *Undaria* to spread. In essence, the location of these thresholds can be considered a tipping point at which there is rapid change in the abundance or recruitment of *Undaria* following a small change in the abundance of native taxa. Typically, such tipping points involve different levels of stressors, usually physical, and various statistical models are used to analyse how small changes in those stressors might affect threshold responses of a species invasion or some other ecological process.

Instead of analysing across a gradient of physical stressors (cf. Schiel et al. 2016), we examined ecological communities through time and analysed how their changing composition permitted the seasonal invasion of dense populations of *Undaria*. In semi-exposed and exposed conditions in southern New Zealand, the intertidal-subtidal margin is typically dominated by the large furoid *Durvillaea antarctica* (Taylor & Schiel 2005) and a suite of other smaller furoid species (Schiel 2006). *D. antarctica* (hereafter *Durvillaea*) has recently been separated into *D. antarctica* and *D. poha* (Fraser et al. 2012). *Undaria* has extensively occupied these low shore zones since the late 1990s (Stuart 2004, Russell et al. 2008).

Here we test analytically the ecological drivers that enhance recruitment and abundance of the invasive kelp *Undaria* on a wave-exposed open coast system, and determine the thresholds (if any) within the native community composition that act as mechanisms for the recruitment and dominance of *Undaria*.

MATERIALS AND METHODS

Experimental design

Using a time series with a set of fixed areas in space allows us to examine and test the relationships between species as they come and go, subjected to the

same suite of physical circumstances and potential stressors, while minimising the potentially great spatial variability found when sampling larger areas in rocky reef systems. The data used in these analyses were derived from a long-term experiment that involved disturbance to the canopy of the habitat-forming alga *Durvillaea*. This is the world's largest fucoid alga, which dominates low intertidal-immediate subtidal areas along the outer coast of southern New Zealand. Canopies of this alga were experimentally removed in 2006 and the trajectories of communities in disturbed and control areas were followed for several years. *Undaria* has been in New Zealand since 1987 (Hay & Luckens 1987) and one of its original invasion sites was Moeraki (South Island) (Stuart 2004) where it occurred for around a decade, mostly in the small and somewhat protected harbour rather than on the wave exposed open coast. However, *Undaria* recruitment subsequently occurred in experimental plots in exposed coastal areas, as described in this study.

The study site was North Reef at Moeraki (45° 21' 23" S, 170° 51' 40" E) and the basic design consisted of nine 2 × 2 m plots within the *Durvillaea* zone. Three were left as controls, 3 had *Durvillaea* removed in March 2006 and 3 had *Durvillaea* removed in November 2006, in order to test the timing of impact on community development. Plots were monitored between 3 and 7 times annually over 3 yr. Within each plot, all algal and sessile invertebrate species were estimated for percent cover, and mobile invertebrates were counted. Additionally, densities of the large canopy-forming algae (e.g. *Durvillaea*, *Cystophora torulosa*, *Carpophyllum maschalocarpum*, *Undaria*) were recorded.

To investigate the role of native communities in facilitating *Undaria* invasion to the open coast we used 13 explanatory variables: cover of *Durvillaea* canopy algae, subcanopy algae (not including *Durvillaea* recruits), encrusting coralline algae, coralline turfing algae (predominately *Corallina officinalis*, *Arthrocardia corymbosa* and *Jania rosea*), bare space, grazer abundance (snails, chitons, limpets), sessile invertebrate cover (barnacles and mussels), predator abundance (stars, whelks), sediment cover, total taxa richness, season, time after experiment initiation, experimental treatment (control, March removal, November removal) and experiment plot number. 'Plot number' (treated as a categorical variable) represents within-treatment replicates (Plots 1 to 3 were controls, Plots 4 to 6 had canopy removal in March and Plots 7 to 9 had canopy removal in November), and allowed examination of within-treat-

ment variation. The subcanopy category combined the abundance of 99 subcanopy taxa, comprising mostly red algae but also including a suite of brown and green algae, most of which had low abundance (combined subcanopy total of generally <20% per plot).

Ecological drivers of the presence and abundance of *Undaria*

To determine which variables were most important in driving the presence and abundance of *Undaria* we used gradient boosted regression tree (BRT) models in the 'dismo' package in R (Hijmans et al. 2017). Regression trees use recursive partitioning of the response data and deviance reduction to determine the relative influences of explanatory variables (Friedman 2001, 2002, Elith et al. 2008). These models are extremely flexible and are not constrained by the assumptions of linearity; they cope well with some collinearity among predictors, and deal with complex higher order indirect interactions (Elith et al. 2008). BRT models are therefore appropriate for use with large, complex ecological data sets which are often non-linear, highly heteroscedastic, contain frequent zero values and involve direct and indirect interactions (Legendre & Legendre 1998). They often outperform more traditional regression-based models with ecological data, such as general additive models or general linear models (see Leathwick et al. 2006, Olden et al. 2008). The boosting process increases model accuracy by adding new models to the ensemble sequentially and the final result is averaged across hundreds to thousands of trees (Elith et al. 2008, Natekin & Knoll 2013).

Time lags are a feature of this type of ecological data, because of the variable life histories and reproductive and recruitment periodicity of component species. To enable identification of potential time lags between the explanatory variables and the abundance of *Undaria* across our data set we ran a cubic-spline interpolation of the data and extracted monthly values (our smallest sample interval) of taxa across the time series. Temporal autocorrelation in *Undaria* was assessed using the autocorrelation function (acf) in R (R Core Team 2016). Models were run on interpolated data.

Across the 13 explanatory variables, collinearity was identified using variance inflation factors (VIF) in combination with Spearman's rank correlations. Variables that showed a collinearity greater than Spearman's $\rho = 0.7$ were removed until all vari-

ables remaining had a VIF of <3 (Zuur et al. 2009). Time lags between the explanatory variables and *Undaria* abundance were identified using the cross-correlation function (ccf) across a 1 yr period, which is realistic for this species. This is because *Undaria* has an annual life history in New Zealand, with a visible sporophyte between March and December, but over the warmer months it is in its microscopic gametophyte and sporophyte stages (Hewitt et al. 2005, Schiel & Thompson 2012).

Models were fit on the interpolated data set using the 'gbm.step' function to determine the relative importance of each explanatory variable and the optimal number of trees to run, and then simplified to find the most parsimonious model (based on the cross-validation deviance reduction) using the 'gbm.simplify' function which removes explanatory variables one at a time. Models were run across a range of tree complexities (3 to 5), learning rates (0.01 to 0.05) and bagging fractions (0.5 to 0.75) (see Elith et al. 2008). Models used the Poisson distribution for *Undaria* count abundance data (density per plot). Model visualisation does not occur over individual trees (as the result is averaged across many trees) but rather is achieved through the use of partial dependence plots in which the relationship between each explanatory variable and the response is shown with all other model variables set at their conditional mean. Model validation was evaluated using 10-fold cross-validation of the model on a withheld portion of the data to estimate its performance (Natekin & Knoll 2013). Overfitting can be an issue with these models, but use of deviance reduction in model validation, along with subsampling of data (testing across an array of 'bag fractions') and using 'shrinkage' (via the learning rate) to control the relative contribution of each tree to the overall result can all decrease the probability of overfitting to improve the generalization of the model.

Variables that were identified from the BRT models as being the most important in driving the abundance of *Undaria* were then examined in detail to identify any thresholds, or tipping points that influenced the abundance of *Undaria*.

Identification of tipping points or thresholds in ecological drivers

A variety of techniques can be used to identify ecological change points in species that affect other species (e.g. piecewise regression, quantile piecewise regression, Bayesian change point analysis and non-

parametric change point analysis [NCPA]; Qian et al. 2003, Daily et al. 2012). These address slightly different questions and differ in their assumptions of the data and the type of data they use (Brenden et al. 2008). We used 2 techniques to capture both single and potentially multiple thresholds in the response of *Undaria* to a range of ecological variables. These techniques are often used separately to identify the main response thresholds, most often using physical data as predictors than ecological data (King & Richardson 2003, Brenden et al. 2008, Smith & Tran 2010, Wagenhoff et al. 2012). Using them together for complex ecological data can provide a more robust view of important thresholds in the response data. Both techniques are non-parametric in their approach, where no assumptions are made about the distributional structure of the data (Sharkey & Killick 2014). The first, NCPA via data partitioning, provides a broad assessment across the whole data set in identifying the most likely change point for each predictor. In this case, it was used to determine a single threshold in the cover of canopy algae, coralline turfing algae, subcanopy algae and bare space on the presence of *Undaria* (the combined effects of these were already examined by BRT above). NCPA is analogous to BRT (discussed above) but uses only 1 tree and a single predictor to split the response data into 2 homogenous groups based on deviance reduction (King & Richardson 2003, Qian et al. 2003, Scott et al. 2011, Daily et al. 2012). It is the first split in the model that identifies where most of the variance occurs. We used 'rpart' (Therneau et al. 2017) to run the NCPA analysis. NCPA will always find a split in the data, so we used the approximate χ^2 test to assess the significance of splits (Qian et al. 2003, Miltner 2010, Daily et al. 2012). Uncertainty around the change point was estimated through bootstrapping (1000 NCPA iterations), expressing the results as 95% confidence intervals (CIs) (Efron & Tibshirani 1994, Qian et al. 2003).

The second technique used was the 'process-Stream' function in the non-parametric changepoint analysis package 'cpm' in R (Ross 2015). Ideally, this should produce the same or similar change points as those identified using NCPA. This function tests for multiple change points, in contrast to NCPA, which identifies 1 split in as described above. It runs sequential 2 sample tests at every possible split point in the data set where the test statistic is based on ranks (Sharkey & Killick 2014, Ross 2015). Change points are identified where there is a significant change in the mean and/or variance of the response data. This technique makes no assumptions with regard to the distribution of the data other than inde-

pendence of data points. The temporal autocorrelation within *Undaria* abundance was therefore removed by running this model on the first order differences of $(\text{time}_k - \text{time}_{k-1})$ where k = a sampling period. This removed dependence between data points through time. Three parameters were defined in this test, as follows: (1) The average run length (ARL_0) represents the mean number of observations before the occurrence of a false positive (Ross 2015). This is computationally expensive and is set at discrete values (Ross 2015). We used the lowest set value of 370. (2) The 'startup' parameter defines the number of observations after which the algorithm will begin to look for change points. We used the default base value of 20. (3) We used the Mood test statistic to detect changes in scales in non-Gaussian distributed data. Like a Mann-Whitney test, the Mood test assesses the extent to which the ranks observed deviate from those expected. The Mood test has consistently been shown to outperform many other non-parametric tests (Sharkey & Killick 2014).

RESULTS

General patterns

Persistent elements of the system were: (1) the canopy of *Durvillaea* in control plots, which remained at around 100% for most of the experiment, until a storm in Year 3 (Fig. 1A); (2) the basal understory of coralline turfing algae, which varied over time and increased following the removal of the canopy (Fig. 1B,C); and (3) annual pulses of *Undaria*, which occurred almost exclusively in removal plots and were greater in March removal plots than in November removal plots (Fig. 1B,C). *Durvillaea* was just beginning to recover in the removal plots towards the end of the study period. A noteworthy feature of this time series is that only a few *Undaria* ever recruited into the control plots beneath the *Durvillaea* canopy, but numbers of *Undaria* reached a maximum of more than 200 plants in the removal plots (with a corresponding maximum cover of ~100%). In terms of the full community, 99 subcanopy species occurred in control and removal plots during the course of the experiment. These consisted of several furoid species and a suite of understory red, green and brown algae. Most of these occurred at very low abundance (typically <1% cover) and many of them were seasonal.

There was generally low collinearity among the 13 input explanatory variables. Encrusting coralline algae were excluded from the main analysis as their

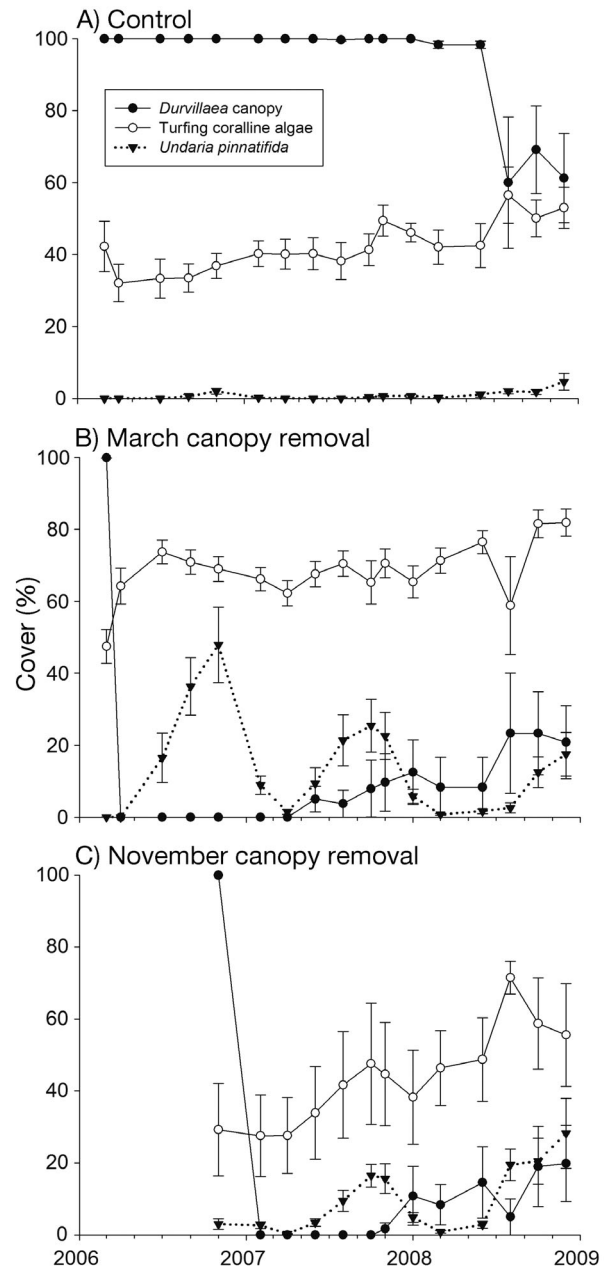


Fig. 1. Mean (\pm SE) percent cover of *Durvillaea antarctica* canopy algae, coralline turfing algae and the invasive kelp *Undaria pinnatifida* on rocky reefs in southern New Zealand, from March 2006 to December 2009, in (A) control plots and plots with canopy removed in (B) March and (C) November

cover was highly negatively correlated with cover of coralline turfing algae (Spearman's $\rho_{482} = -0.82$, $p < 0.001$). The factor 'treatment' was excluded due to its high correlation with the percent cover of *Durvillaea* ($\rho_{482} = -0.74$, $p < 0.001$). 'Plot number' encapsulates conditions in each individual plot, which incorporate not only the treatment (control, March

removal, November removal) but also the variation in dynamics of *Undaria* and other components of the community among plots and within treatments. Its inclusion in the final BRT models significantly reduced the overall deviance by including and accounting for the often large within-treatment variation. Naturally, 'Month' and 'Season' were correlated (0.54), but both were included in the analysis as collinearity was under the threshold of 0.7 and this allowed us to explore the effect of different temporal scales on the recruitment of *Undaria*.

Drivers in the abundance of *Undaria*

Of the 13 variables used, only 7 were included in the final model. The most parsimonious model with the greatest cross-validation correlation (0.92, SE = 0.02) and the lowest deviance (2.93, SE = 0.4) included cover of coralline turfing algae (lagged at 9 mo), cover of canopy algae (lagged at 1 mo), plot number, abundance of molluscan grazers, cover of subcanopy algae, cover of bare space and season (Table 1).

The most important variable in the model was cover of coralline turfing algae, lagged at 9 mo (36.1%, Table 1), with *Undaria* abundance greatest when coralline turfing algae had a cover of >75% (Fig. 2A). The next 2 most important variables were canopy cover lagged at 1 mo (25.7%) and plot number (13.2%). The fitted function of *Undaria* abundance against *Durvillaea* canopy showed a steep decline as canopy cover increased, with virtually no *Undaria* when canopy cover was >50% (Fig. 2B). All removal plots (Plots 4 to 9) had more *Undaria* than control plots (Plots 1 to 3), with March removal plots (Plots 4 to 6) having both a greater abundance and variability than November removal plots (Plots 7 to 9) (Fig. 2C). The relative importance values of grazers, primary bare space and subcanopy algae was ~7% in each case (Table 1, Fig. 2D–F). When all other variables were set at their marginal means, there were no clear trends in effects of grazers with respect to *Undaria* (Fig. 2D). *Undaria* abundance was generally greater in plots when the percentage of bare space was below ~10% (Fig. 2E) and subcanopy algal cover was low (<40%; Fig. 2F). Although *Undaria* is seasonal, with greatest abundance in late winter and spring, season as a variable in the model was outweighed in importance by the biotic variables (Table 1).

When testing for interactions across the suite of predictor variables in our model, the most important were between cover of coralline turfing algae and *Durvillaea* canopy cover (Fig. 3A) and between cover

Table 1. Relative importance of each explanatory variable (scaled to 100%) in the most parsimonious boosted regression tree (BRT) model of the abundance of *Undaria pinnatifida* on rocky reefs in southern New Zealand following experimental removal of the natural canopy. Tree complexity = 3, learning rate = 0.01, bagging fraction = 0.5, family = Poisson. CV: cross validation

| Variable | % relative importance |
|-------------------------------------|-----------------------|
| Coralline turfing algae | 36.1 |
| Canopy algae | 25.7 |
| Plot number | 13.2 |
| Molluscan grazers | 7.6 |
| Subcanopy algae | 7.0 |
| Bare space | 6.7 |
| Season | 3.7 |
| Number of trees | 4150 |
| Explained deviance in training data | 97% |
| Residual deviance in training data | 3% |
| CV deviance | 0.293 (SE = 0.44) |
| CV correlation | 0.92 (SE = 0.02) |

of coralline turfing algae and subcanopy algae (Fig. 3B). *Undaria* reached peak abundances when coralline turfing algae exceeded around 80% cover and the canopy was < ~20% cover (Fig. 3A). The pattern for turfing coralline algae by subcanopy algae interaction was less distinct (Fig. 3B), with *Undaria* abundance generally greatest when turfing coralline algal cover was >80% and subcanopy algal cover was <30%. These interaction plots show that there are relatively few situations (low canopy, high turf) where significant recruitment occurs for *Undaria*.

Detecting ecological thresholds in native species cover that determine the abundance of *Undaria*

NPCA on the fitted GBM values was used to determine ecological thresholds (or ranges of thresholds) in cover of the algal canopy, coralline turfs, subcanopy, bare space and on the abundance of molluscan grazers. NPCA will always find a split in the data, where the deviance between the 2 groups of *Undaria* abundance is maximised (Table 2, Fig. 4); here all splits were statistically significant (χ^2 test, $p < 0.05$). The marginal plots show that the greatest density of *Undaria* occurred where cover of coralline turfing algae was >82% (Fig. 4A), *Durvillaea* canopy cover was <56% (Fig. 4B), molluscan grazer abundance was <35 individuals per plot (Fig. 4C), subcanopy cover was <8% (Fig. 4D) and bare space was <4% (Fig. 4E). In ecological systems, thresholds are more often than not ranges rather than precise values and

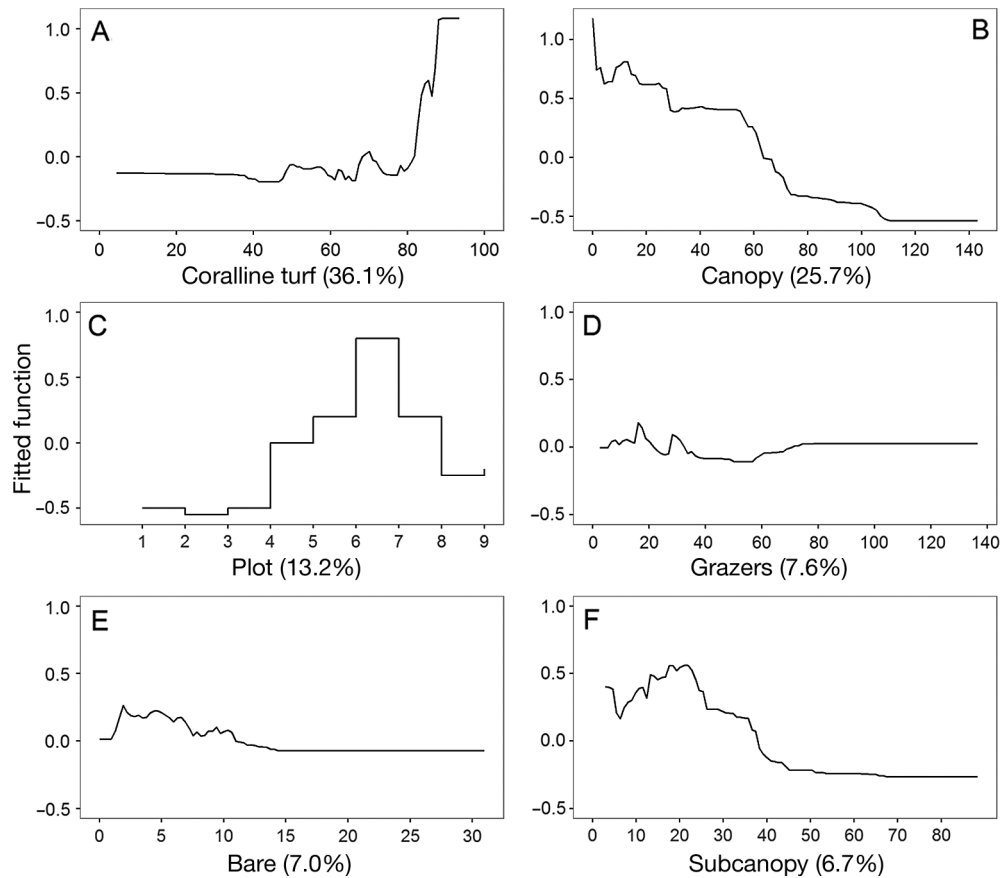


Fig. 2. Partial dependence plots of the conditional mean on the fitted *Undaria pinnatifida* densities from the most parsimonious boosted regression tree (BRT) model, presented in descending order of their relative importance (indicated by brackets in x-axis of each panel). (A) Cover of coralline turf (lagged at 9 mo), (B) cover of native canopy algae (lagged at 1 mo), (C) plot number (1–3 are controls, 4–6 are March removals, and 7–9 are November removals), (D) abundance of molluscan grazers, (E) cover of bare space, and (F) cover of subcanopy native algae

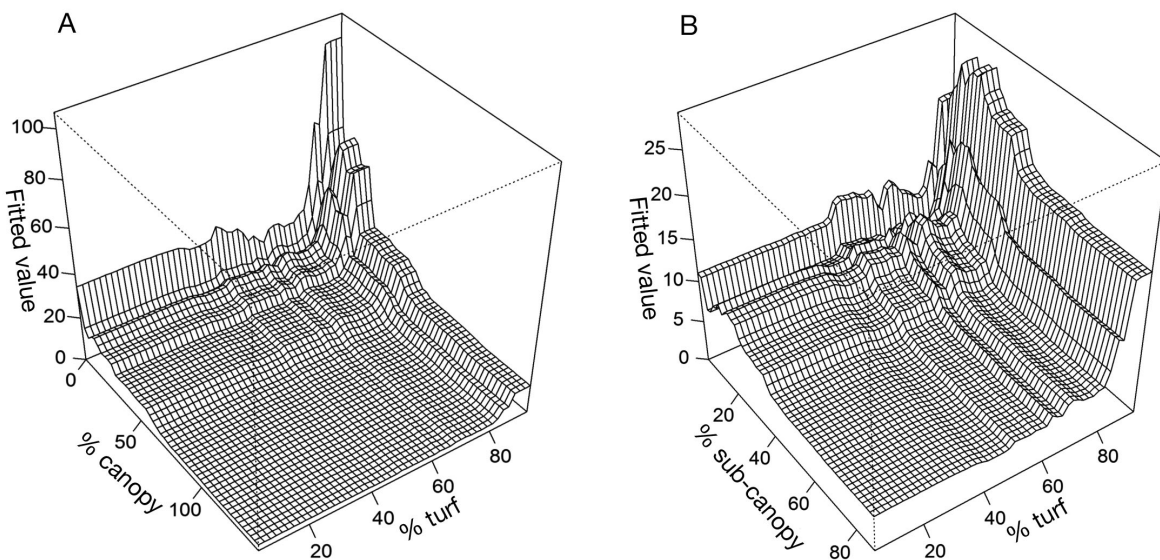


Fig. 3. Interaction plots between predictor variables affecting fitted *Undaria pinnatifida* density values on rocky reefs in New Zealand following removal of the natural canopy: (A) % canopy cover and % coralline turfing algae; (B) % subcanopy algae and % coralline turfing algae. Note differing y-axis scales

Table 2. Change point thresholds found in the top 5 predictor variables of the density of *Undaria pinnatifida* on rocky reefs in New Zealand following removal of the natural canopy (see Table 1). Non-parametric change point analysis (NPCA) finds the single change point in each data set that maximises deviance reduction (χ^2 test, $p < 0.05$), while the change point analysis (package 'cpm' in R) process stream function finds all significant change points in the data set ($p < 0.05$)

| Variable | NPCA (%) | CPM process stream (%) |
|-------------------------|----------|------------------------|
| Coralline turfing algae | 82 | 46, 57, 82 |
| Canopy algae | 56 | 15, 63, 95 |
| Molluscan grazers | 35 | 14, 35 |
| Subcanopy algae | 8 | 7, 15 |
| Bare space | 4 | 3, 9 |

the 95% CIs for each of these threshold values were calculated. In these results the CI ranges are large, ranging between 30 and 60% cover (Fig. 4A–E).

In addition to the single threshold determined by the NPCA above, the change point process stream function was used on the same data set to identify if there were multiple thresholds (Table 2). These thresholds closely aligned with the NPCA. Where they were not accurately aligned (i.e. in the case of canopy algae), the CI of the NPCA encompassed the multiple change points (Table 2). The multiple change points identified not only the most statistically significant threshold, as previously identified by NPCA, but also identified other, less significant threshold splits in the data.

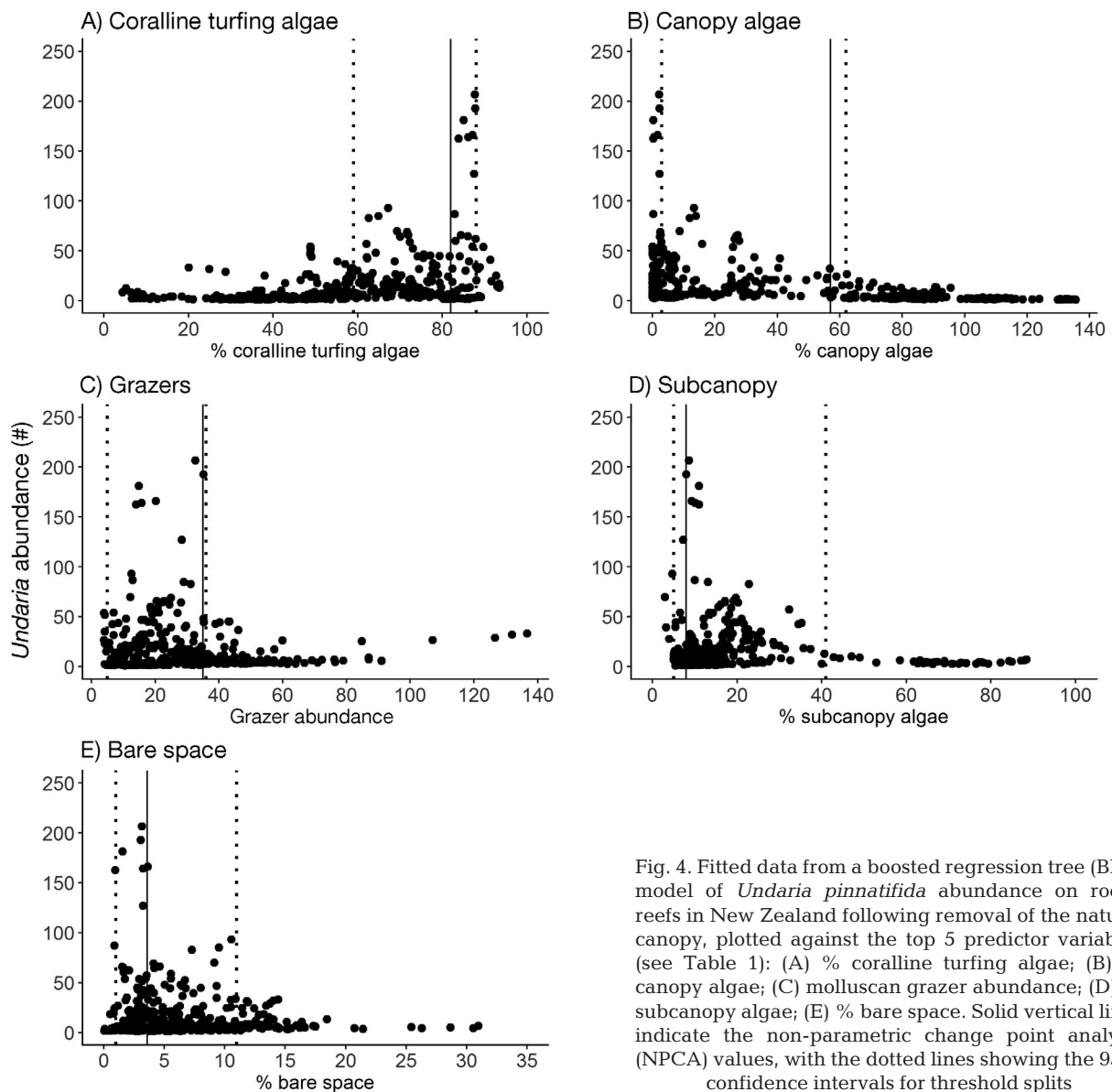


Fig. 4. Fitted data from a boosted regression tree (BRT) model of *Undaria pinnatifida* abundance on rocky reefs in New Zealand following removal of the natural canopy, plotted against the top 5 predictor variables (see Table 1): (A) % coralline turfing algae; (B) % canopy algae; (C) molluscan grazer abundance; (D) % subcanopy algae; (E) % bare space. Solid vertical lines indicate the non-parametric change point analysis (NPCA) values, with the dotted lines showing the 95% confidence intervals for threshold splits

DISCUSSION

The relationships between native communities and invasive species are critical elements in understanding changes to the structure and function of communities worldwide (Thomsen et al. 2014). Some of these changes may be dictated by disturbances and shifting trophic dynamics (Valentine & Johnson 2003, 2004, Thompson & Schiel 2012), but all have a large component that depends on ecological relationships and the resilience of native communities, as well as the life histories of key species. Here we have shown a cascading effect caused by the loss of canopy-forming macroalgae and the response of benthic algal turfs, and demonstrated the ability of an invasive kelp to take advantage of that changed structure by occupying space. There was a clear gradient of effect predicated on the abundance of the dominant native furoid alga and coralline turf, which demonstrates the interaction of ecological factors that can produce an altered community structure.

Partial and full canopy loss is a frequent feature of intertidal and shallow subtidal communities, particularly after large storms (Seymour et al. 1989, Underwood 1999, Speidel et al. 2001, Schiel & Lilley 2007). Over 25 yr, for example, furoid canopy loss along the South Island of New Zealand occurred after storm-generated waves of around 2.5 m (Schiel 2011). On each occasion, the losses occurred over a day or two, but recovery of the canopy ranged from 1 yr up to 8 yr (Schiel & Lilley 2011, Schiel et al. 2016). The loss of furoid canopies results in a changed community, especially when the understory is exposed to desiccation stress (Lilley & Schiel 2006). These assemblage-wide effects can last for nearly a decade (Schiel & Lilley 2011) and lead to long-term reductions in primary productivity (Tait & Schiel 2011a,b). There is considerable site-to-site variation in effects (Schiel 2006), but in all cases recovery begins with significant recruitment of canopy-forming algae. The slow recovery of furoid canopies has been noted worldwide and is not unique to New Zealand (Underwood 1998, Jenkins et al. 2004). The role of benthic turfs, however, is less well understood. 'Turfs' may include a wide range of species (Connell et al. 2014) but, in New Zealand, the primary substratum is almost invariably covered by encrusting and turfing coralline algae, which can form a dense matrix over the substratum. These typically 'burn off' after being exposed when canopies are removed (Lilley & Schiel 2006), but slowly expand again over time. They often accumulate sediments and therefore can act synergistically in preventing recruitment of furoids, which

simply cannot attach firmly or survive as germlings in the matrix (Alestra et al. 2014, Alestra & Schiel 2015). As shown in this study, however, after dense furoid canopies are removed and their whiplashing and shading effects diminished, corallines can expand rapidly over the substratum. This effectively prevents, or at least delays, furoids from re-establishing.

Many studies have shown that *Undaria* is adept at capturing space after disturbances to canopy species (Valentine & Johnson 2003, Edgar et al. 2004, Valentine & Johnson 2004, Schiel & Thompson 2012, South & Thomsen 2016). In New Zealand, this can occur in 2 ways. Even small gaps in native furoids can be filled by this kelp if they are produced by disturbances when conditions favour the recruitment of *Undaria* (i.e. during the cooler parts of the year). If gaps are small, native furoids can expand and recapture space within a year (Valentine & Johnson 2003, Thompson & Schiel 2012). The other important mechanism is that *Undaria* is the only large alga that seems capable of recruiting successfully into coralline turf (Thompson & Schiel 2012). It is reproductively active during the warmer months (Schiel & Thompson 2012) and seems to have little, if any, desiccation resistance in its early life stages (Thompson 2004). However, it is postulated that it is the protective habitat of turf that allows *Undaria* to expand along low intertidal and shallow subtidal areas, particularly over the summer months that experience harsh sunlight and high desiccation (Thompson 2004).

Taken together, the loss of canopies and the expansion of coralline turf highly favour this invasive kelp. These conditions effectively present a complex, interactive tipping point between dominant native and non-native canopies; there is a non-linear increase in *Undaria* that is largely dependent on the presence of coralline turfs and the absence of a perennial native canopy. It may be the case that in any given area these tipping points are themselves ephemeral, because there is little evidence that *Undaria* can actually outcompete native furoid species over the long term (Thompson & Schiel 2012, South et al. 2016). Because of its annual life history, visible *Undaria* sporophytes are scarce or absent from most shores over the warmer months (around November to April; Schiel & Thompson 2012, South et al. 2016) when many furoids are reproductively active (Schiel 1988), which provides an opportunity for furoids to recapture space if conditions are right (Gorman & Connell 2009, Thompson & Schiel 2012). It is in conditions of frequent disturbance or persistence of corallines that *Undaria* remains abundant. It is significant that the wave climate that leads to these

conditions may be occurring more frequently, with maximal wave forces and the number of extreme events producing waves up to 6 m both increasing in New Zealand's South Island (Schiel et al. 2016).

In our study, tipping points occurred across a range of values along 2 ecological axes. Based on the interactive graph (Fig. 3A), there was clearly a positive interactive effect when the furoid canopy cover was below ~20% and coralline turf cover was above ~80%. Along with a change in the abundance of *Undaria*, in many cases there was also a change in the variance of abundance (Fig. 4). For example, when turf was below ~50% in plots where the native canopy had been removed, there was an almost constant response of *Undaria* (<50 individuals), but the variance of *Undaria*'s abundance increased greatly after turf reached ~60% cover (Fig. 1). Conversely, when the canopy and subcanopy cover was <~40%, there was high variation in the density of *Undaria*, but there was a uniform response when the cover was >40% (Fig. 2). Similarly, there was a highly variable response of *Undaria* to grazers when they were present in smaller numbers, but few *Undaria* occurred beyond a density of >50 grazers per plot. The identified tipping points associated with thresholds in the cover and abundance of key native components of the community may occur over a range of values rather than at specific points, as indicated by wide confidence intervals (Fig. 4). These confidence intervals were based on the iterations of the empirical, univariate data, and reflect the variable nature of single factor spatial and temporal responses. Nevertheless, they show clear transitions in the response of *Undaria*. It appears to be relatively common to see increases in temporal variability of communities near transition points and regime shifts (Carpenter & Brock 2006, Hewitt & Thrush 2010).

While we identified one tipping point (or ecological range), there were potentially multiple points that facilitated the localised invasion of *Undaria* (cf. Table 2), indicating the complex and varied interactive processes that occur at local scales. These results suggest that native communities are resistant to change unless the canopy species is removed but are not very resilient in the presence of expanding turfs and invasion of *Undaria*. Interestingly, when a broad threshold is crossed, the new configuration itself can be resilient but only if corallines persist or if disturbance is frequent.

In this study we have delineated the gradients of ecological mechanisms that foster the recruitment and abundance of an invasive kelp. As with all such macroalgae that have invaded the temperate zone

worldwide, this kelp has now become a regular feature of algal beds and has occupied a niche that is disturbance-mediated in native communities. Its prolific reproductive output, with hundreds of millions of spores per plant (Thompson 2004, Schaffelke et al. 2005, Schiel & Thompson 2012), availability of gametophytes and sporelings during winter when most storms occur, and ability to settle both into bare gaps and coralline patches, give it a distinct advantage over less prolific, slower-growing fucoids. The gradients we have delineated are a culmination of a series of biophysical, ecological and life-history interactions that highlight how other tipping points may occur in complex systems. These types of complexities, interactions and disturbance thresholds will increasingly need to be identified and be taken into account by policy makers and managers in ecological risk assessments (Foley et al. 2015, Selkoe et al. 2015).

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LITERATURE CITED

- ✦ Alestra T, Schiel D (2015) Non-trophic responses of algal communities to nutrient enrichment: interactions among coralline turfs, ephemeral algae and perennial fucoids. *Mar Ecol Prog Ser* 538:145–156
- ✦ Alestra T, Tait LW, Schiel D (2014) Effects of algal turfs and sediment accumulation on replenishment and primary productivity of furoid assemblages. *Mar Ecol Prog Ser* 511:59–70
- ✦ Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. *Mar Policy* 27:313–323
- ✦ Bollen M, Pilditch CA, Battershill CN, Bischof K (2016) Salinity and temperature tolerance of the invasive alga *Undaria pinnatifida* and native New Zealand kelps: Implications for competition. *Mar Biol* 163:194
- ✦ Brenden TO, Wang L, Su Z (2008) Quantitative identification of disturbance thresholds in support of aquatic resource management. *Environ Manage* 42:821–832
- ✦ Britton-Simmons KH (2004) Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. *Mar Ecol Prog Ser* 277:61–78
- ✦ Carlton JT, Thompson JK, Schemel LE, Nichols FH (1990) Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. I. Introduction and dispersal. *Mar Ecol Prog Ser* 66:81–94
- ✦ Carnell PE, Keough MJ (2014) Spatially variable synergistic effects of disturbance and additional nutrients on kelp recruitment and recovery. *Oecologia* 175:409–416
- ✦ Carpenter SR, Brock WA (2006) Rising variance: a leading indicator of ecological transition. *Ecol Lett* 9:311–318

- ✦ Casas G, Scrosati R, Piriz ML (2004) The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). *Biol Invasions* 6:411–416
- ✦ Connell SD, Foster MS, Airoidi L (2014) What are algal turfs? Towards a better description of turfs. *Mar Ecol Prog Ser* 495:299–307
- ✦ Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Ecoscience* 12:316–329
- ✦ Daily JP, Hitt NP, Smith DR, Snyder CD (2012) Experimental and environmental factors affect spurious detection of ecological thresholds. *Ecology* 93:17–23
- ✦ Dellatorre FG, Amoroso R, Saravia J, Orensanz J (2014) Rapid expansion and potential range of the invasive kelp *Undaria pinnatifida* in the Southwest Atlantic. *Aquat Invasions* 9:467–478
- ✦ Dodds WK, Clements WH, Gido K, Hilderbrand RH, King RS (2010) Thresholds, breakpoints, and nonlinearity in freshwaters as related to management. *J N Am Benthol Soc* 29:988–997
- ✦ Edgar GJ, Barrett NS, Morton AJ, Samson CR (2004) Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. *J Exp Mar Biol Ecol* 312:67–87
- Efron B, Tibshirani RJ (1994) An introduction to the bootstrap. CRC press, Boca Raton, FL
- ✦ Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *J Anim Ecol* 77:802–813
- ✦ Fletcher R, Farrell P (1998) Introduced brown algae in the North East Atlantic, with particular respect to *Undaria pinnatifida* (Harvey) Suringar. *Helgol Meeresunters* 52: 259
- Foley MM, Martone RG, Fox MD, Kappel CV and others (2015) Using ecological thresholds to inform resource management: current options and future possibilities. *Front Mar Sci* 2:95
- ✦ Forrest BM, Taylor MD (2002) Assessing invasion impact: survey design considerations and implications for management of an invasive marine plant. *Biol Invasions* 4: 375–386
- ✦ Forrest BM, Brown SN, Taylor MD, Hurd CL, Hay CH (2000) The role of natural dispersal mechanisms in the spread of *Undaria pinnatifida* (Laminariales, Phaeophyceae). *Phycologia* 39:547–553
- ✦ Fraser CI, Spencer HG, Waters JM (2012) *Durvillaea poha* sp. nov. (Fucales, Phaeophyceae): a buoyant southern bull-kelp species endemic to New Zealand. *Phycologia* 51:151–156
- ✦ Friedman JH (2001) Greedy function approximation: a gradient boosting machine. *Ann Stat* 5:1189–1232
- ✦ Friedman JH (2002) Stochastic gradient boosting. *Comput Stat Data Anal* 38:367–378
- ✦ Gooden B, French K, Turner PJ, Downey PO (2009) Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities. *Biol Conserv* 142: 2631–2641
- ✦ Gorman D, Connell SD (2009) Recovering subtidal forests in human-dominated landscapes. *J Appl Ecol* 46:1258–1265
- ✦ Groffman PM, Baron JS, Blett T, Gold AJ and others (2006) Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* 9:1–13
- ✦ Hay CH, Luckens PA (1987) The Asian kelp *Undaria pinnatifida* (Phaeophyta: Laminariales) found in a New Zealand harbour. *N Z J Bot* 25:329–332
- ✦ Hewitt CL, Campbell ML, McEnnulty F, Moore KM, Murfet NB, Robertson B, Schaffelke B (2005) Efficacy of physical removal of a marine pest: the introduced kelp *Undaria pinnatifida* in a Tasmanian Marine Reserve. *Biol Invasions* 7:251–263
- ✦ Hewitt JE, Thrush SF (2010) Empirical evidence of an approaching alternate state produced by intrinsic community dynamics, climatic variability and management actions. *Mar Ecol Prog Ser* 413:267–276
- ✦ Hijmans RJ, Phillips S, Leathwick J, Elith J (2017) Package 'dismo'. r.adu.org.za/web/packages/dismo/dismo.pdf
- ✦ Jenkins S, Norton T, Hawkins S (2004) Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure. *J Mar Biol Assoc UK* 84:327–329
- ✦ King RS, Richardson CJ (2003) Integrating bioassessment and ecological risk assessment: an approach to developing numerical water-quality criteria. *Environ Manage* 31: 795–809
- ✦ Leathwick J, Elith J, Hastie T (2006) Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. *Ecol Modell* 199:188–196
- Legendre P, Legendre L (1998) Numerical ecology. 2nd English edn. Elsevier, Amsterdam
- ✦ Lilley SA, Schiel DR (2006) Community effects following the deletion of a habitat-forming alga from rocky marine shores. *Oecologia* 148:672–681
- ✦ Lyons DA, Scheibling RE (2009) Range expansion by invasive marine algae: rates and patterns of spread at a regional scale. *Divers Distrib* 15:762–775
- Miller KA, Engle JM (2009) The natural history of *Undaria pinnatifida* and *Sargassum filicinum* at the California Channel Islands: non-native seaweeds with different invasion styles. In: Damiani CC, Garcelon DK (eds) Proc 7th California Islands Symp. Institute for Wildlife Studies, Arcata, CA, p 131–140
- ✦ Miltner RJ (2010) A method and rationale for deriving nutrient criteria for small rivers and streams in Ohio. *Environ Manage* 45:842–855
- ✦ Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Front Ecol Environ* 6:485–492
- ✦ Natekin A, Knoll A (2013) Gradient boosting machines, a tutorial. *Front Neurobot* 7:21
- ✦ Olden JD, Lawler JJ, Poff NL (2008) Machine learning methods without tears: a primer for ecologists. *Q Rev Biol* 83: 171–193
- ✦ Panetta FD, Gooden B (2017) Managing for biodiversity: impact and action thresholds for invasive plants in natural ecosystems. *Neobiota* (Berlin) 34:53
- ✦ Qian SS, King RS, Richardson CJ (2003) Two statistical methods for the detection of environmental thresholds. *Ecol Modell* 166:87–97
- R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org
- Ross GJ (2015) Parametric and nonparametric sequential change detection in R: the cpm package. *J Stat Softw* 66: 1–20
- ✦ Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *Am Zool* 37:621–632
- ✦ Russell LK, Hepburn CD, Hurd CL, Stuart MD (2008) The expanding range of *Undaria pinnatifida* in southern New Zealand: distribution, dispersal mechanisms and the invasion of wave-exposed environments. *Biol Invasions* 10:103–115

- Salvaterra T, Green DS, Crowe TP, O’Gorman EJ (2013) Impacts of the invasive alga *Sargassum muticum* on ecosystem functioning and food web structure. *Biol Invasions* 15:2563–2576
- Schaffelke B, Campbell ML, Hewitt CL (2005) Reproductive phenology of the introduced kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) in Tasmania, Australia. *Phycologia* 44:84–94
- Schiel DR (1988) Algal interactions on shallow subtidal reefs in northern New Zealand: a review. *N Z J Mar Freshw Res* 22:481–489
- Schiel DR (2006) Rivets or bolts? When single species count in the function of temperate rocky reef communities. *J Exp Mar Biol Ecol* 338:233–252
- Schiel DR (2011) Biogeographic patterns and long-term changes on New Zealand coastal reefs: non-trophic cascades from diffuse and local impacts. *J Exp Mar Biol Ecol* 400:33–51
- Schiel DR, Foster MS (2006) The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. *Annu Rev Ecol Syst* 37:343–372
- Schiel DR, Lilley SA (2007) Gradients of disturbance to an algal canopy and the modification of an intertidal community. *Mar Ecol Prog Ser* 339:1–11
- Schiel DR, Lilley SA (2011) Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. *J Exp Mar Biol Ecol* 407:108–115
- Schiel DR, Thompson GA (2012) Demography and population biology of the invasive kelp *Undaria pinnatifida* on shallow reefs in southern New Zealand. *J Exp Mar Biol Ecol* 434-435:25–33
- Schiel DR, Lilley SA, South PM, Coggins JH (2016) Decadal changes in sea surface temperature, wave forces and intertidal structure in New Zealand. *Mar Ecol Prog Ser* 548:77–95
- Scott JT, Haggard BE, Sharpley AN, Romeis JJ (2011) Change point analysis of phosphorus trends in the Illinois River (Oklahoma) demonstrates the effects of watershed management. *J Environ Qual* 40:1249–1256
- Selkoe KA, Blenckner T, Caldwell MR, Crowder LB and others (2015) Principles for managing marine ecosystems prone to tipping points. *Ecosyst Health Sustain* 1:1–18
- Seymour R, Tegner M, Dayton P, Parnell P (1989) Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuar Coast Shelf Sci* 28:277–292
- Sharkey P, Killick R (2014) Nonparametric methods for online change-point detection. STOR601 Research Topic II. STOR-i Centre for Doctoral Training, Lancaster University, Lancaster
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176
- Smith AJ, Tran CP (2010) A weight-of-evidence approach to define nutrient criteria protective of aquatic life in large rivers. *J N Am Benthol Soc* 29:875–891
- South PM, Thomsen MS (2016) The ecological role of invading *Undaria pinnatifida*: an experimental test of the driver–passenger models. *Mar Biol* 163:175
- South PM, Lilley SA, Tait LW, Alestra T, Hickford MJ, Thomsen MS, Schiel DR (2016) Transient effects of an invasive kelp on the community structure and primary productivity of an intertidal assemblage. *Mar Freshw Res* 67:103–112
- Speidel M, Harley CD, Wonham MJ (2001) Recovery of the brown alga *Fucus gardneri* following a range of removal intensities. *Aquat Bot* 71:273–280
- Stæhr PA, Pedersen MF, Thomsen MS, Wernberg T, Krause-Jensen D (2000) Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. *Mar Ecol Prog Ser* 207:79–88
- Stuart MD (2004) Review of research on *Undaria pinnatifida* in New Zealand and its potential impacts on the eastern coast of the South Island. DOC Science Internal Series 166. Department of Conservation, Wellington
- Tait LW, Schiel DR (2011a) Dynamics of productivity in naturally structured macroalgal assemblages: importance of canopy structure on light-use efficiency. *Mar Ecol Prog Ser* 421:97–107
- Tait LW, Schiel DR (2011b) Legacy effects of canopy disturbance on ecosystem functioning in macroalgal assemblages. *PLOS ONE* 6:e26986
- Taylor DI, Schiel DR (2005) Self-replacement and community modification by the southern bull kelp *Durvillaea antarctica*. *Mar Ecol Prog Ser* 288:87–102
- Therneau T, Atkinson B, Ripley B, Ripley MB (2017) Package ‘rpart’. <https://cran.r-project.org/web/packages/rpart/rpart.pdf> (accessed on 20 Apr 2016)
- Thompson GA (2004) Mechanisms of invasion and persistence of the invasive kelp *Undaria pinnatifida* (Harvey) Suringar within intertidal areas of southern New Zealand. PhD thesis, University of Canterbury, Christchurch
- Thompson GA, Schiel DR (2012) Resistance and facilitation by native algal communities in the invasion success of *Undaria pinnatifida*. *Mar Ecol Prog Ser* 468:95–105
- Thompson R, Crowe T, Hawkins S (2002) Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environ Conserv* 29:168–191
- Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Mar Ecol Prog Ser* 495:39–47
- Underwood A (1998) Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. *J Exp Mar Biol Ecol* 231:291–306
- Underwood A (1999) Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. *J Exp Mar Biol Ecol* 232:125–140
- Valentine JP, Johnson CR (2003) Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. *J Exp Mar Biol Ecol* 295:63–90
- Valentine JP, Johnson CR (2004) Establishment of the introduced kelp *Undaria pinnatifida* following dieback of the native macroalga *Phyllospora comosa* in Tasmania, Australia. *Mar Freshw Res* 55:223–230
- Wagenhoff A, Clapcott JE, Goodwin E (2012) Review of river ecosystem threshold models. Prepared for the ‘Management of cumulative effects of stressors on aquatic ecosystems’ research project (C01X1005). Cawthron Report No. 2259, Cawthron Institute, Nelson
- Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York, NY