

Decadal changes in sea surface temperature, wave forces and intertidal structure in New Zealand

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ABSTRACT: Predictions of the effects of climate change in the coastal zone require an understanding of the relationships between environmental and biotic variables. These are often highly complex and uncertain because of the many ways marine biota interact with each other under different environmental conditions. We use data collected over the past several decades to determine changes in the key environmental variables and area-specific changes in the dominant habitat-forming macroalgae. Sea surface temperature (SST) data and wave heights from ERA-Interim reanalysis were analysed for 3 areas of the east coast of New Zealand's South Island to detect trends over the past 30 yr. We then used detailed benthic survey data acquired quarterly or half-yearly in 2 tidal zones at the same coastal areas from 1994 onwards. There were significant increases in the mean SST at 2 of the 3 areas, with average increases of 0.16°C per decade over 3 decades. Maximum SST did not increase, but the minimum seawater temperatures did, by up to 0.34°C per decade. Mean significant wave height also increased over this period by 0.06 m per decade, and maximum wave height by up to 0.3 m per decade at 2 of the 3 areas. Boosted regression tree analysis was used to determine any consistent patterns between physical variables and benthic algal cover. Generally, air temperature and the Southern Oscillation Index (SOI) were the most influential variables on cover of furoid macroalgae. SST and wave height were also important but less influential. Furoid cover increased with maximum air temperature beyond ca. 22 to 24°C, and cover decreased during La Niña periods at the most northern site, but increased during La Niña periods at the most southern site. The relative contributions of SST and wave height variables to the models were area- and tidal zone-specific. Overall, this study showed highly variable effects of a changing climate on an ecologically important habitat-former, highlighting the problems of dealing with ecological and climate variables that operate at differing spatial and temporal scales. We discuss this with respect to community structure and dynamics.

KEY WORDS: Climate change · SST · Wave forces · Canopy-algae · Community dynamics

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INTRODUCTION

The effects of climate change in the coastal zone involve a complex interplay of environmental variables and biotic interactions (Stenseth et al. 2002, Walther et al. 2002, Harley et al. 2006, 2012, Helmuth et al. 2006, Hoegh-Guldberg & Bruno 2010, Doney et al. 2012). Changes in ocean temperature, wave action, wind forces, chemistry and circulation can also act synergistically with other anthropogenic stres-

sors, such as invasive species (Carlton 2000, Occhipinti-Ambrogi 2007), disease vectors (Harvell et al. 2002), pollutants (Schiedek et al. 2007) and overfishing (Brander 2007, Cochrane et al. 2009, Rijnsdorp et al. 2009) to drive change in individual species and communities (Harley et al. 2006).

Just how environmental change will translate to changes in ecological communities is highly uncertain because of the numerous ways marine biota interact with each other under different environmental condi-

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tions. For example, physiological tolerances to stress, attachment strength for benthic species, and density-dependent processes involving competition and facilitation may all react differently to changing environmental conditions, and differentially affect species and, therefore, community structure and function.

Given the complexities of forecasting, one potentially useful precursor is 'hindcasting', that is, using historical data for analysing relationships between environmental variables and marine community structure at specific areas. What do we know about long-term changes in environmental variables and coincident community responses? For a hindcasting approach to be useful, there must be long-term records of key physical and biotic variables, so that correlations and changing patterns can be discerned. Even so, this approach is fraught with difficulties because of potential mismatches in the scale between environmental variables and biotic or community responses (Burrows 2012). For example, phytoplankton and mobile fishes can respond quickly to changing thermoclines, and their shifting distributions can often be readily matched with changes in temperature (Walther et al. 2002, Perry et al. 2005, Last et al. 2011, Poloczanska et al. 2014). Attached communities, however, can react both immediately through direct mortality or have lags in their responses involving impaired or delayed reproductive output, or compromised growth that may operate differentially over seasons or years, even with relatively constant elevated temperatures (Schiel et al. 2004, Mieszkowska et al. 2006, Johnson et al. 2011). Furthermore, projections of future changes often fall outside the range of those experienced to date, suggesting that biotic changes could exceed the range of historic change.

Nevertheless, the use of historical data over several decades should encompass a wide range of climate conditions and multiple El Niño/La Niña or other large-scale, multi-decadal climate events (e.g. Pacific Decadal Oscillation [PDO] or the North Atlantic Oscillation [NAO]) that span a wide array of temperature stresses, high wave events and nutrient stresses (Trenberth & Hoar 1997, Stenseth et al. 2002, Di Lorenzo et al. 2008), and their effects on benthic communities (Barry et al. 1995, Stenseth et al. 2002, Helmuth et al. 2006, Garrabou et al. 2009, Wernberg et al. 2012a).

On many temperate rocky reefs, stands of canopy-forming macroalgae provide the dominant cover (Schiel 2004, Schiel & Foster 2006, Wernberg et al. 2012b). In the intertidal zone, stands of algae can facilitate the presence of many other species because of the canopy cover they provide, which offers habitat

and protection from heat stress to understory organisms. On at least some reefs, particularly in the mid tidal zone, overall species richness can be positively correlated with the cover of canopy algae (Speidel et al. 2001, Schiel & Lilley 2007, Airoidi et al. 2008, Crowe et al. 2013). Therefore, the presence and abundance of canopy-forming fucoid algae has a direct bearing on the diversity of intertidal communities. Because of this, the factors that account for the structure of fucoid populations have a direct bearing on the diversity of patches and their temporal and spatial arrays.

It is known from a wide range of studies over many decades that community structure can be related to the wave climate, including frequency and intensity of wave forces (Stephenson & Stephenson 1949, Dakin 1960, Menge & Sutherland 1976, 1987), and to sea and air temperatures (Lewis 1964, Morton & Miller 1968, Southward et al. 1995). These can operate over highly localized scales (Helmuth 1998, Denny & Gaylord 2010) as well as broad biogeographic scales (Helmuth et al. 2002, Harley & Helmuth 2003, Blanchette et al. 2008), and affect reproductive output, dispersal, recruitment, attachment in species and interactions between species (e.g. through competition, predation or facilitation). Therefore it is anticipated that biological communities will respond to a changing climate over small and large scales.

This study has 2 objectives. The first is to examine changes in coastal climate variables and macroalgal cover over recent decades; the second is to test the hypothesis that changes in macroalgal cover are directly related to changes in climate variables. We use a 30 yr data set of offshore sea surface temperature (SST), air temperature, wave climate and the Southern Oscillation Index (SOI). This is the full data set available for these variables in southern New Zealand. We then test the relationships between climate variables and macroalgal populations on 3 of the largest rocky intertidal reefs along the east coast, for which we have a 20 yr data set. The utility of these relationships is examined in the context of both descriptions and predictions of change.

MATERIALS AND METHODS

The data in this paper relate to 3 areas spread along 500 km of the east coast of the South Island in New Zealand. These were focal areas for long-term surveys of assemblages (see 'Study areas'). For a map of study areas and further descriptions, refer to Schiel (2011).

Sea surface temperature

Historical SSTs were obtained from the National Oceanic and Atmospheric Administration's (NOAA) extended reconstruction of SST database version 3b (ERSST v.3b; Reynolds et al. 2007, Smith et al. 2008; <http://www.ncdc.noaa.gov/data-access/marineocean-data/extended-reconstructed-sea-surface-temperature-ersst-v3b>). These data are derived from the International Comprehensive Ocean Atmosphere Data Set (ICOADS) and use *in situ* measurements that are reconstructed statistically and applied to those areas (spatially or temporally) that have sparse data. The output is daily SST (°C) on a coarse $2 \times 2^\circ$ resolution grid. Data were taken from cells directly offshore of our 3 survey areas from 1982 to 2014. To assess changes in the minimum, maximum and mean temperatures, data were filtered to get the mean of the lowest 5% of temperatures per year, the overall annual mean and the mean of the highest 5% of temperatures per year. To gauge the relationship between these offshore-derived data and onshore water temperatures, we correlated the grid data with data derived from sensors in the low intertidal zone (using Onset HOBO temperature loggers Tidbit v2 and Pendant 8k). These onshore sensors were deployed in all sites for parts of the study period.

Air temperature

Daily maximum air temperatures were collated from the National Institute for Water and Atmosphere's (NIWA) CliFlo database (<http://cliflo.niwa.co.nz>). Data were downloaded from the coastal weather station in closest proximity to our survey areas that collected data continuously between 1994 and 2014. The Cape Campbell and Kaikoura weather stations were less than 1 km from their corresponding monitoring areas. The Moeraki weather station was ca. 60 km from our area. Daily data were filtered to get the maximum air temperature per quarter. As for SST, air temperatures were analysed because both can influence the abundance and distribution of intertidal organisms and communities. We are well aware that actual air temperatures in the intertidal zone can vary considerably from those recorded in weather stations (cf. Lilley & Schiel 2006). To this end, therefore, we analysed the relationship between maximum daily air temperatures, as recorded by the nearest weather station, and maximum daily air temperature data from the intertidal sensors (Onset HOBO, as above) deployed at each area during parts of the study period.

Wave climate

Significant wave height (H_s ; equal to $4m_0^{1/2}$, where m_0 is the zeroth moment of the wave spectrum; this is the average of the top one-third of waves) was sourced from the European Centre for Medium Range Forecasting (ECMWF) ERA-Interim reanalysis (Dee et al. 2011). This is a general circulation model that is guided by quality-controlled measures from *in situ* and remotely sensed observational data (Dee et al. 2011). Spatial resolution is at $0.75 \times 0.75^\circ$ cells, and the mid-point for cells used was between 38 and 43 km from our coastal survey areas. ERA-Interim output is currently available from 1979 to early 2015. The 6-hourly data were used to calculate the minimum, mean, 95th percentile and maximum H_s per analysed time period. Along with the overall area mean and the 95th percentile value, we also used the absolute minimum and maximum values. Also calculated were the number of days per time period that had H_s values less than or greater than 2 SD from the area mean, and the number of days that had H_s values greater than 3, 4 and 5 m, to attempt to identify those infrequent but severe weather events that potentially have large consequences on coastal biotic communities. The ERA-Interim wave model is not able to resolve complex coastal bathymetry, and as such we use its wave data to explore links between coastal communities and larger-scale wave variability. We use the reanalysis in lieu of *in situ* wave data, which are not available over this time period around New Zealand. The accuracy of ERA-Interim H_s was demonstrated to be high by Coggins et al. (2015) in the seas surrounding New Zealand.

For coastal New Zealand, there is a finer-resolution coastal wave model (NIWA Coastal Explorer), which is along the 50 m isobaths and therefore is better able to represent coastal waves than the coarser ERA-Interim data. However, these did not overlap our biological data collection. Given that our biological data spanned 1993 to 2015 and the NIWA Coastal Explorer data stopped in 2001, we chose to use the coarse ERA-Interim data so that analyses were based on a consistent data series corresponding to our biological time series (see 'Materials and methods: Intertidal community surveys'). For the time periods in which data from NIWA Coastal Explorer and ERA-Interim overlap (1979 to 2001), we correlated the 2 series to confirm that the ERA-Interim data, despite being offshore, were representative of coastal wave forces. The NIWA Coastal Explorer data and the ERA-Interim data were positively correlated at each of our 3 areas with R^2 values of 0.89 to 0.95 (see Fig. S1 and

text in the Supplement at www.int-res.com/articles/suppl/m548p077_supp.pdf.

Southern Oscillation Index

The SOI can be a proxy for a range of environmental influences and can be associated with production dynamics (e.g. Zeldis et al. 2008, 2013). Monthly SOI values were obtained from the National Center for Atmospheric Research (NCAR) Climate and Global Dynamics division (Trenberth 1984, Trenberth & Hoar 1996; <http://www.cgd.ucar.edu/cas/catalog/clinind/soi.html>). The SOI is computed using the difference in the monthly mean sea level pressure anomalies between Tahiti and Darwin. Values that are persistently negative are indicative of an El Niño phase, while persistently positive values are indicative of a La Niña phase. During El Niño in New Zealand, there are characteristically stronger winds from the west, often leading to more rain. In winter, the winds tend to come from a southerly direction, bringing colder temperatures (Gordon 1986, Mullan 1996, Kidson & Renwick 2002). During strong La Niña phases in New Zealand, there are more northeasterly winds bringing more rain to the northeastern parts of the North Island, and less rainfall to the southwest of the South Island (Gordon 1986, Mullan 1996, 1998, Kidson & Renwick 2002). During the time period for which we have biological data (1993 to 2015), El Niño events occurred in 1994–1995, 1997–1998, 2002–2003 and 2009–2010. La Niña events were in 1998–2000, 2007–2008 and 2010–2011. Moderate events are defined as those with at least 3 consecutive periods (months) with a SOI value between 1 and 1.4 SD above or below the mean. Strong events were defined as those with at least 3 consecutive periods with a SOI value greater than 1.5 SD above or below the mean (Null 2015).

Intertidal community surveys

Study areas

Long-term surveys were done at 3 of the largest rocky intertidal reefs on the east coast of the South Island of New Zealand. The reef at Cape Campbell (41°43'26" S, 174°16'41" E) is nearly 800 m long and is openly exposed to the east. It has a shallow slope, with the high shore dominated by bare rock with limpets (predominately *Cellana* spp.) and ephemeral algae (*Porphyra* spp., *Scytosiphon lomentaria*, *Ulva*

spp.). The mid shore and upper low shore is dominated by a sparse cover of furoid algae, primarily *Hormosira banksii*, with a primary substratum dominated by *Corallina officinalis*. The low shore and shallow subtidal zones are dominated by the southern bull kelp *Durvillaea antarctica* (a furoid). To the south, at Kaikoura, is Wairepo Reef (42°25'61" S, 173°42'42" E). This area is well described in the literature (see Schiel & Taylor 1999, Lilley & Schiel 2006, Schiel 2006). Wairepo is an extensive algal dominated platform, spanning 850 m along the coast. An array of offshore rocks and reefs provide some protection from the onshore waves, but this area still receives large waves from a northeasterly direction. The high shore is dominated by bare rock with limpets (*Cellana* spp.) and snails (*Diloma aethiops* and *Lunella smaragdus*), the mid shore by a dense canopy of *H. banksii*, and the low shore by a matrix of furoid algae (*H. banksii*, *Cystophora torulosa*, *Cystophora scalaris*, *Carpophyllum maschalocarpum*). Farther south is Moeraki (45°21'23" S, 170°51'40" E), a 400 m long, northeasterly facing, volcanic rock reef that is also well described in the literature (Schiel & Taylor 1999, Lilley & Schiel 2006, Schiel 2006). The high shore is mostly large boulders, with sand covering the flatter platforms. These boulders are dominated by ephemeral algae and grazing gastropods (similar species to Cape Campbell and Kaikoura). The mid shore is dominated by a dense canopy of *H. banksii*, with *C. officinalis* and *Jania* spp. dominating the understory. The low shore is dominated by *Cystophora* spp., the invasive *Undaria pinnatifida* and *D. antarctica*.

Data collection

The intertidal communities at these 3 coastal areas were monitored consistently between 1993 and 2015. At each area, permanent 30 m transects were marked in 2 tidal zones, and along each transect 10 haphazardly placed 1 m² quadrats were sampled. Percent cover of all species of algae (>~3 mm) was calculated and counts for all mobile invertebrate species were carried out. Monitoring was generally quarterly (seasonally) between 1994 and 2007, and twice yearly (summer and winter) from 2007 to 2014 (see Schiel 2011 for a full description of the survey protocol). Our intention was to process and analyse the physical data on the same time scales as these biological data. Analysis here will focus on the total summed percent cover of the ubiquitous, canopy-forming furoid macroalgal species, which included *H. banksii*, *C. torulosa*, *C. scalaris*, *Cystophora retro-*

flexa and *C. maschalocarpum*. Owing to layering of these species, total cover could sum to >100%. These canopy formers are known to be foundation species on New Zealand and Australian intertidal reefs (Schiel 2004, Lilley & Schiel 2006, Bishop et al. 2009). We focus on these species because they facilitate much of the diversity on these reefs and there is a strong positive relationship between their abundance (cover) and the diversity in the associated community (Lilley & Schiel 2006, Schiel & Lilley 2007, Bishop et al. 2009).

For analysis, we used the mean of the 10 quadrats at each survey in the low and mid tidal zones separately. To make the survey time series comparable to the environmental data sets for analysis of any time lags the physical variables might impose on the cover of macroalgae, we cubic spline interpolated the canopy data and extracted the quarterly (seasonal) percent covers.

Statistical analyses

Here, we sought to (1) describe and analyse the temporal and spatial trends in the physical and biological variables; and (2) use boosted regression tree analysis to identify any variables that are consistently important in driving macroalgal abundance.

Physical variables

Because we were looking for trends, linear regression was used to determine any changes in annual minimum, mean, 95th percentile and maximum SST ($^{\circ}\text{C}$) and H_s (m) through time at the 3 areas. Where significant trends were found, we calculated the increase in $^{\circ}\text{C}$ and metres per decade using the regression equations of the line of best fit for those where significant relationships were found.

Macroalgal cover

Time series of the cover of macroalgae were examined visually for spikes, steps and gradual increases or decreases. We focused on the time periods immediately following the largest wave events—those quarters that included the 95th percentile of maximum wave heights (>6.59 m at Cape Campbell, >7.09 m at Kaikoura and >5.76 m at Moeraki) and quarters during which there was a high number of days with waves >3 m.

Factors affecting the cover of macroalgae

Boosted regression tree (BRT) models were used to examine the relationship between the physical variables (i.e. over the time period for which we had corresponding macroalgal data) and cover of furoid algae in the low and mid zones at the 3 sites. BRTs are an ensemble method that uses boosting, or the combination of results from many individual regression trees into one model, thereby increasing the model's accuracy (Elith et al. 2008). BRTs are shown to be extremely useful tools when analysing large, complex ecological data sets with non-linear patterns as well as interactions between predictors with missing data points (Friedman 2001, 2002, De'ath 2007, Elith et al. 2008). They often outperform more traditional regression modelling techniques (e.g. generalised additive models [GAMs], generalised linear models [GLMs]; see Leathwick et al. 2006, Olden et al. 2008). For a complete description of BRT models and their derivation see Friedman (2001, 2002), De'ath (2007) and Elith et al. (2008). Variables that were highly collinear with each other ($r > 0.7$) were removed from the variable list and, through model simplification, 5 of the 19 variables were fitted into the BRT models (Table 1). Time lags of the physical variables against furoid cover were identified using the cross-correlation function (ccf) in the R 'stats' package, by correlating each physical variable with up to 8 quarter (2 yr) lags against furoid cover in each site by zone combination separately (Shumway & Stoffer 2011). This was considered to be a meaningful lag time, given the perennial nature of these species and long trajectory of recovery following disturbance (Schiel & Lilley 2011). There proved to be no seasonal patterns in the anomaly cover of furoid macroalgae at 5 of the 6 area–zone combinations, and only a weak seasonal effect in the Kaikoura low zone, with more furoid cover in summer and autumn compared to winter and spring (generalised least squares with autocorrelation moving average correlation structure, corARMA [1,0] $t_{2,81} = -2.73$, $p = 0.01$). Therefore, owing to seasonal patterns not being strong and consistent we chose not to deseasonalize the response data and, instead, analyses were run on the anomaly cover (to conform to a Gaussian error distribution).

All BRT models were fitted in R v.3.2.2 using the 'dismo' package (Hijmans et al. 2015) based on code developed by Elith et al. (2008) and Elith & Leathwick (2015). Models were fitted using a range of learning rates (0.01 to 0.0001), tree complexities (3 to 5) and bagging fractions (0.5 or 0.75) using a Gaussian error distribution, and the best fit models are

Table 1. The 19 variables characterising the onshore physical environment at Cape Campbell, Kaikoura and Moeraki. **Bold:** variables included in the final BRT models; SST: sea surface temperature; H_s : significant wave height; SOI: Southern Oscillation Index; temp.: temperature

Physical characteristic	Variable	Variable description
SST (°C)	Minimum	Minimum quarterly SST (filtered from daily data)
	Mean	Mean quarterly SST (filtered from daily data)
	95th percentile	95th percentile of quarterly SST (filtered from daily data)
	Maximum	Maximum quarterly SST (filtered from daily data)
	Days < 2 SD	No. of days per quarter with SSTs < 2 SD from site mean
	Days > 2 SD	No. of days per quarter with SSTs > 2 SD from site mean
H_s (m)	Minimum	Minimum quarterly H_s (filtered from 6-hourly data)
	Mean	Mean quarterly H_s (filtered from 6-hourly data)
	95th percentile	95th percentile of quarterly H_s (filtered from 6-hourly data)
	Maximum	Maximum quarterly H_s (filtered from 6-hourly data)
	Days > 3 m	No. of days per quarter with records of H_s > 3 m
	Days > 4 m	No. of days per quarter with records of H_s > 4 m
	Days > 5 m	No. of days per quarter with records of H_s > 5 m
	Days < 2 SD	No. of days per quarter with H_s records < 2 SD from site mean
	Days > 2 SD	No. of days per quarter with H_s records > 2 SD from site mean
SOI	Monthly index	Monthly SOI values filtered to a quarterly mean
	5 mo mean	5 mo running mean SOI value
Rain (mm)	Total rainfall	Total rainfall per quarter (summed from daily data)
Air temp. (°C)	Max air temp.	Maximum quarterly air temperature (filtered from daily data)

shown here. Models were fitted using the `gbm.step` function and then simplified using the `gbm.simplify` function using 10-fold cross-validation procedure. Independent models were fitted to each of the 6 area–zone combinations. The BRT output shows the relative contribution of each predictor to the response (scaled up to sum to 100%) and the model fit can be evaluated by the correlation of the model to the training data set, the cross-validation correlation of the model to the left-out data (test data set) and the overall deviance. The models are visualized using partial dependence plots showing the relationship between physical variables on the furoid cover (centred around the mean) after accounting for the mean effects of all other predictors (Elith et al. 2008). Results from the final simplified models are presented to allow comparison of the relative contribution of predictor variables across zones and sites; however, only the 2 most important predictors per model are shown in the partial dependence plots.

RESULTS

Physical data

There was a clear significant warming trend through time in the mean of the lowest 5% of annual SST data at all areas and an increase in the annual

means at Kaikoura and Moeraki (Fig. 1). The annual average of the lowest 5% of SST rose at a rate of 0.19°C per decade at Cape Campbell, 0.34°C at Kaikoura and 0.30°C at Moeraki, based on the slopes of significant trends. Mean annual SST increased by 0.18°C per decade at Kaikoura and 0.14°C per decade at Moeraki over the past 33 yr, whereas the trend at Cape Campbell was not significant. It is interesting to note that the mean of the highest 5% of seawater temperatures did not significantly increase through time at any of the 3 areas (Fig. 1). These changes are reflected in the decadal trends for SST. For example, the average lowest 5% of seawater temperatures at Kaikoura was 9°C during the 1980s and rose to >9.5°C in the 2000s (Fig. 2B). Similarly, the mean seawater temperature rose between the 1980s and 2000s at 2 of the 3 areas (Fig. 2D,E,F), whereas the maximum 5% of temperatures did not change at any of the areas (Fig. 2G,H,I).

The variability in seawater temperature decreased through time at Cape Campbell and Kaikoura as indicated by error bars (Fig. 2; Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m548p077_supp.pdf). This was substantiated through an analysis of the coefficient of variation of SST through time in all areas for the lowest 5%, average, and maximum 5% of temperatures. In all cases, the coefficient of variation declined through time from 1980 to 2010. These declines were not always linear, but were par-

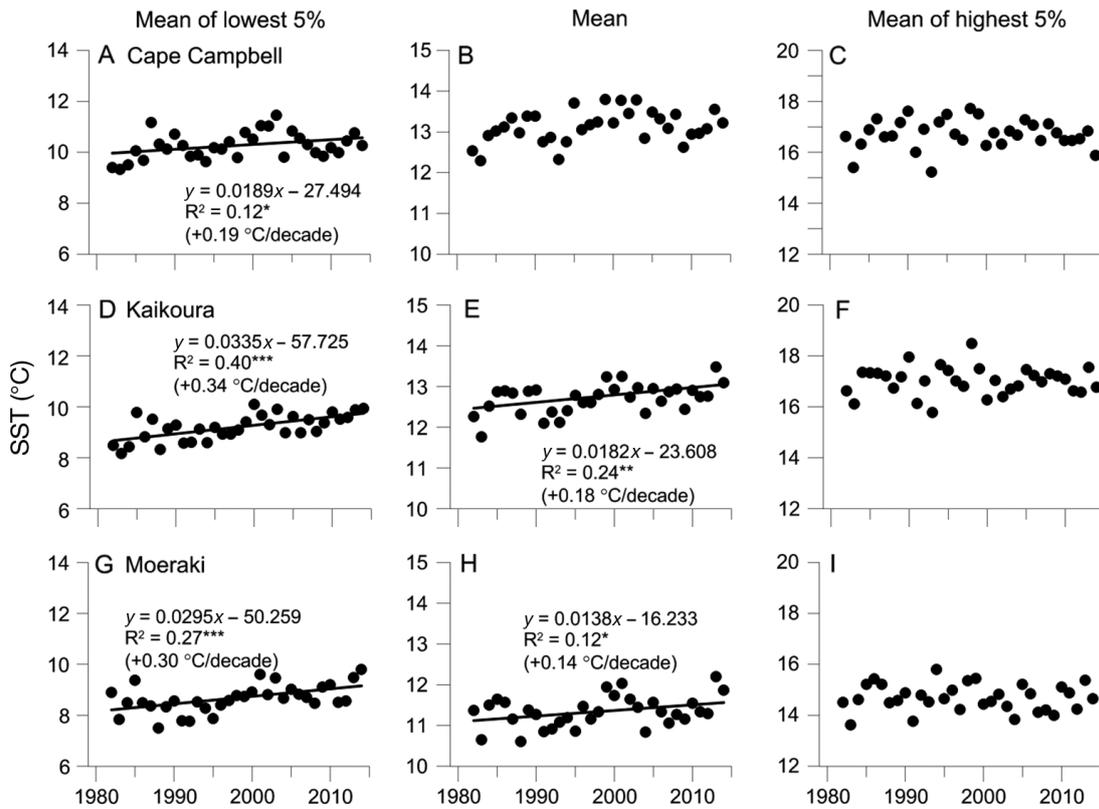


Fig. 1. Annual mean of the lowest 5% of sea surface temperature (SST), the whole data set and the highest 5% of SST for (A–C) Cape Campbell, (D–F) Kaikoura and (G–I) Moeraki. Plots with significant increases through time are shown with the trend lines, equations and the increase (°C per decade at each area). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

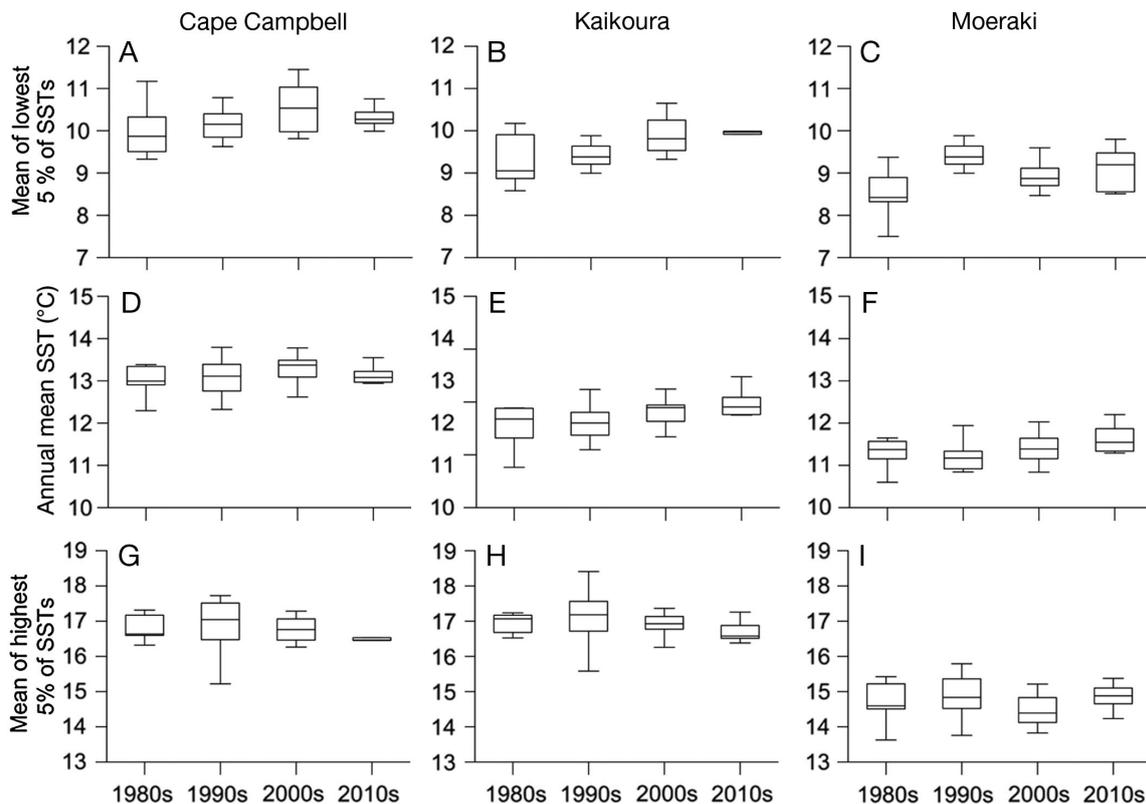


Fig. 2. Changes in (A–C) mean of the lowest 5% of annual SST, (D–F) overall annual means and (G–I) the mean of the highest 5% of annual SST per decade at (A,D,G) Cape Campbell, (B,E,H) Kaikoura and (C,F,I) Moeraki from 1982 to 2014. Mid-line: median; box limits: 75th and 25th percentiles; whiskers: uppermost and lowest observations

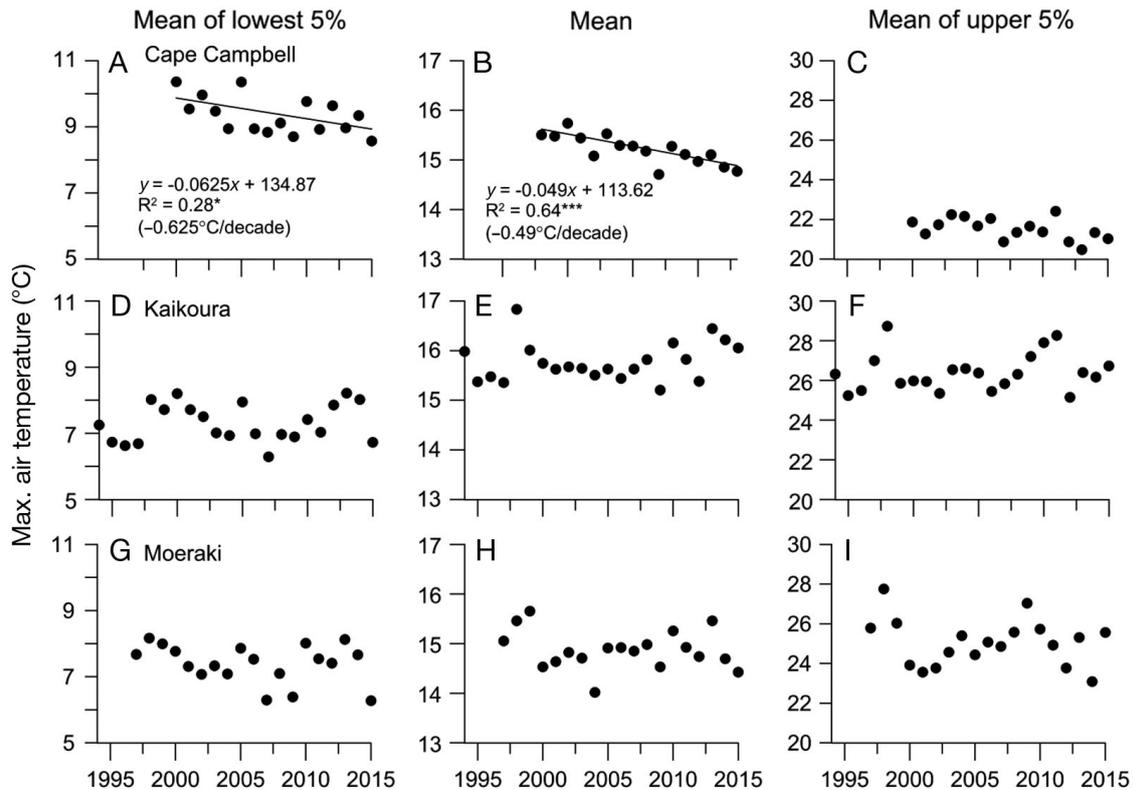


Fig. 3. Annual mean of the lowest 5% of air temperature, the whole data set and the highest 5% of maximum air temperature for (A–C) Cape Campbell, (D–F) Kaikoura and (G–I) Moeraki. Plots with significant increases through time are shown with the trend lines, equations and the decrease (°C per decade at each area). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

ticularly pronounced from the early 1990s onwards. The warming trends in the overall mean seawater temperature at Kaikoura and Moeraki appear to be driven by increases in temperatures during autumn and winter, but not during spring and summer (Figs. S3, S4 & S5 in the Supplement), a pattern that is consistent across all 3 areas. A north to south gradient in mean annual SST is clearly evident (most readily seen in Fig. 2), with warmer seawater temperatures at the most northern area (Cape Campbell), slightly lower temperatures at Kaikoura and up to 2°C cooler temperatures at Moeraki in the south.

An analysis of the relationship between offshore and available onshore seawater temperatures from low intertidal sensors showed strong correlations, ranging from $r_{>290} = 0.76$ to 0.83 (all p values < 0.001) across the 3 areas. Unfortunately, these onshore data were not available for long enough periods to be useful in our modelling.

Air temperatures recorded from the nearest weather stations to our study areas showed considerable variation among sites (Fig. 3). Average annual air temperatures varied between about 15 and 16°C at Cape Campbell and Kaikoura, but were around 1°C lower in Moeraki (Fig. 3B,E,H). The lowest 5% of an-

nual air temperatures were generally higher at Cape Campbell than the other 2 areas (Fig. 3A,D,G), but the upper 5% of temperatures were about 2 to 4°C lower at Cape Campbell and were much less variable (Fig. 3C,F,I). There were no significant trends through time except at Cape Campbell. In this area, both the average annual and lowest annual 5% of air temperatures decreased significantly (Fig. 3A,B). This region is heavily influenced by Cook Strait and is exceptionally windy, with winds generally from northerly or southerly quarters. Air temperature trends here over time may be influenced by the frequency of highs and lows in El Niño–Southern Oscillation (ENSO) events (Zeldis et al. 2008).

The air temperatures recorded from the land-based weather stations were significantly correlated with temperatures from intertidal loggers, ranging from $r_{>290} = 0.60$ to 0.83 (all p values < 0.001) across the 3 areas.

Wave height data showed significant increases at all areas (Fig. 4). The annual minimum, mean, 95th percentile and maximum H_s increased through time at Cape Campbell and Kaikoura, and the mean and 95th percentile increased significantly through time at Moeraki (Fig. 4). This shift in wave height, rather

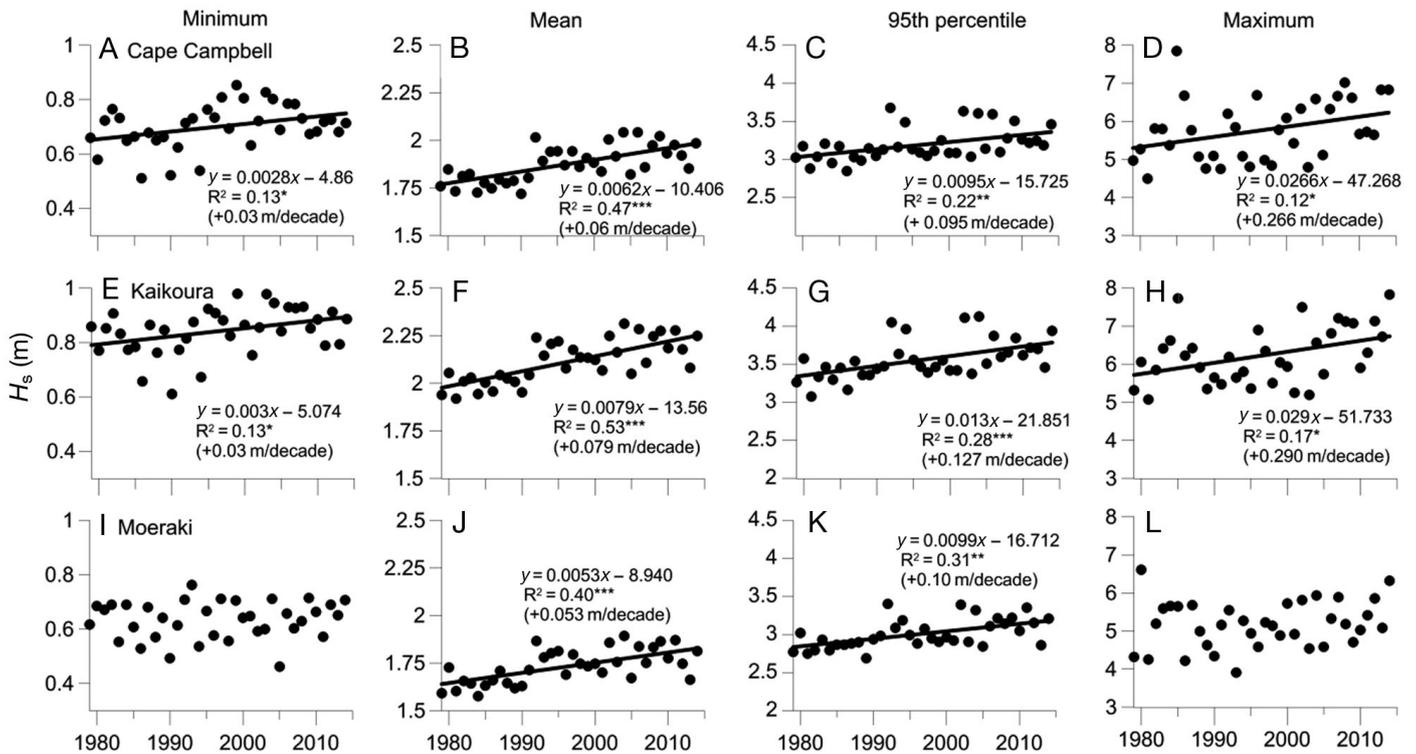


Fig. 4. Annual minimum, mean, 95th percentile and maximum significant wave height (H_s) for (A–D) Cape Campbell, (E–H) Kaikoura and (I–L) Moeraki. Six-hourly data were converted to annual values. Plots with significant increases through time are shown with the trend lines, equations and the increase or decrease (m per decade at each area). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

than being constant through time, appears to be driven largely by an upward step in H_s during the latter part of the data set (1996 to 2014; Fig. 4, Fig. S6 in the Supplement). The most obvious example of this is the mean wave height at Cape Campbell and Kaikoura, which increased in height and variability between 1996 and 2014 compared to the first half of the data set (1979 to 1996; Fig. 4).

The mean annual minimum H_s increased by ca. 0.03 m per decade and the annual maximum H_s increased by ca. 0.3 m per decade at the 2 northern, more wave-exposed areas of Cape Campbell and Kaikoura (Fig. 4). Decadal maximum H_s , however, increased by nearly 1 m at Cape Campbell and Kaikoura. The greatest increases in mean annual H_s were during autumn and winter, but there were clear decadal increases in H_s for all seasons across all areas (Figs. S7, S8 & S9 in the Supplement).

When we examined the raw 6-hourly H_s time series in 2 parts, arbitrarily splitting the data set in 2 (1979 to 1996 and 1997 to 2014), there was a clear increasing shift between time periods in the modes and tails of the H_s distribution at the 3 areas (Fig. 5). There was a shift towards larger waves and also an increase in the frequency of large wave events (>3 m). Fur-

thermore, the mean H_s increased by 11, 13 and 9 cm between the first and second half of the data sets at Cape Campbell, Kaikoura and Moeraki, respectively.

An examination of the physical variables in multivariate space showed that the overall climate envelope at each of the 3 areas is different (Fig. 6). A total of 78% of the variation was explained by principal coordinate analysis (PCO) axis 1, which incorporated the seasonal components of the data set. Cape Campbell, the northern-most area, had warmer seawater temperatures than Kaikoura and Moeraki, and higher air temperatures than Moeraki (Fig. 6, shown by PCO axis 2). The 95th percentile of H_s did not appear to drive differences between the areas in multivariate space, with all areas experiencing a wide range of wave height conditions. Kaikoura and Moeraki were significantly more variable than Cape Campbell in the 3 environmental variables (Permutation of dispersion, PERMDISP $F_{2,211} = 2.56$, $p < 0.05$).

Biological data

The total cover of habitat-forming fucoids was greatest at Kaikoura, and was generally greater in

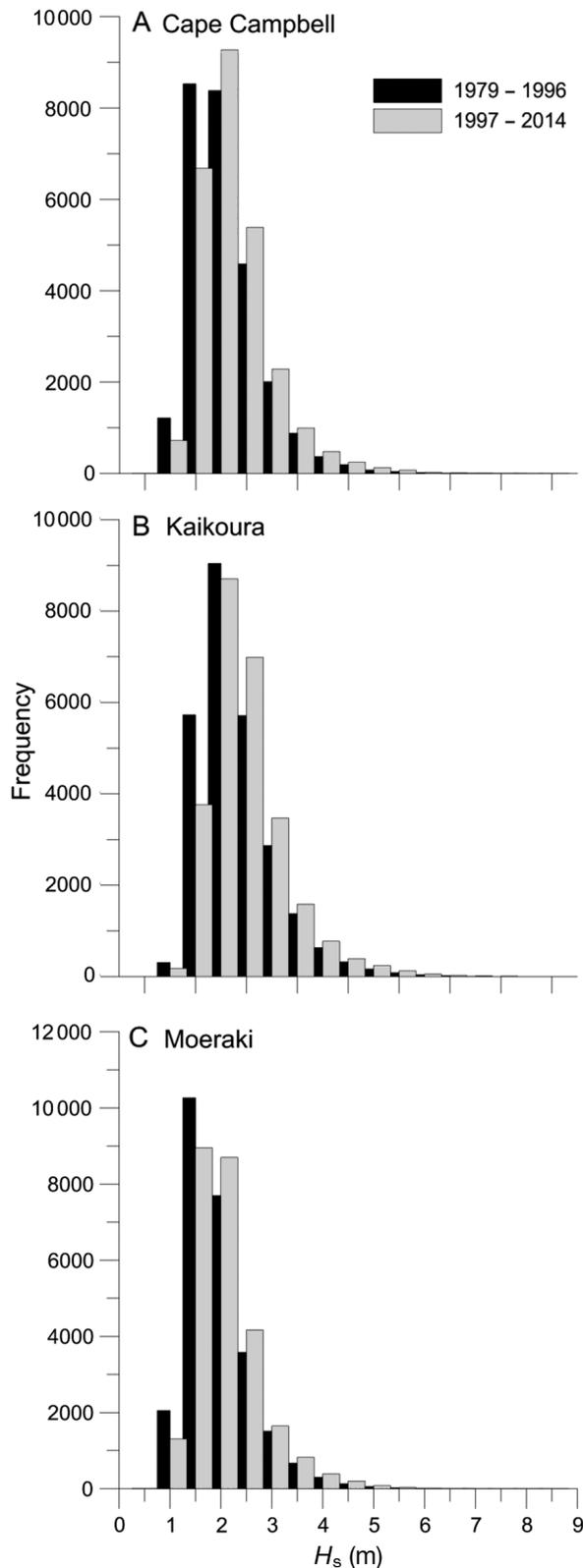


Fig. 5. The frequency distribution of 6-hourly H_s (m) between 1979 to 1996 (black bars) and 1997 to 2014 (grey bars) at (A) Cape Campbell, (B) Kaikoura and (C) Moeraki

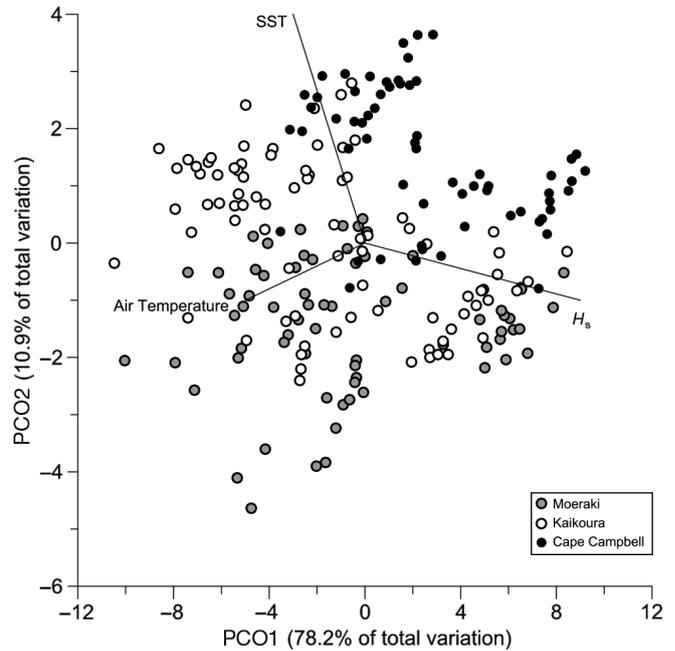


Fig. 6. PCO plot of the 3 main physical variables (H_s = 95th percentile of H_s , SST = 95th percentile of SST and the maximum air temperature) at each of the 3 areas (Cape Campbell, Kaikoura and Moeraki) quarterly between 1997 and 2013. Data were normalised and Euclidean distance was used

the low zone compared to the mid zone at all 3 areas (Fig. 7, Fig. S10 in the Supplement). The variability in cover was generally characterized by acute changes over relatively short time spans of a few years. The decreases in cover were especially evident in *Hormosira banksii*, the dominant furoid. This species occasionally underwent declines during moderate to strong El Niño events, such as in 1993–1994, 1997–1998, 2002–2003 and 2006. Strong La Niña events, such as in 2010, can also produce large waves and can be associated with furoid declines, but on the whole across the 20 yr data set not all declines were associated with obvious basin-wide ENSO events.

Following a major loss, recovery of canopy algae always occurred, although it could be slow (2 to 3 yr). In some cases, particularly on the low shore, there was high recruitment of other furoids, such as *Cystophora* spp., during the periods of *Hormosira* decline at Kaikoura and Moeraki (Fig. 7).

There appeared to be some broad changes in the cover of canopy algae during the latter half of the data set, at least in some places. For example, in the 10 yr after 2004 at Cape Campbell, there was an 88% increase in furoid cover in the low zone compared to cover between 1994 and 2004, with most of this occurring from 2010 onwards. At Kaikoura, following a

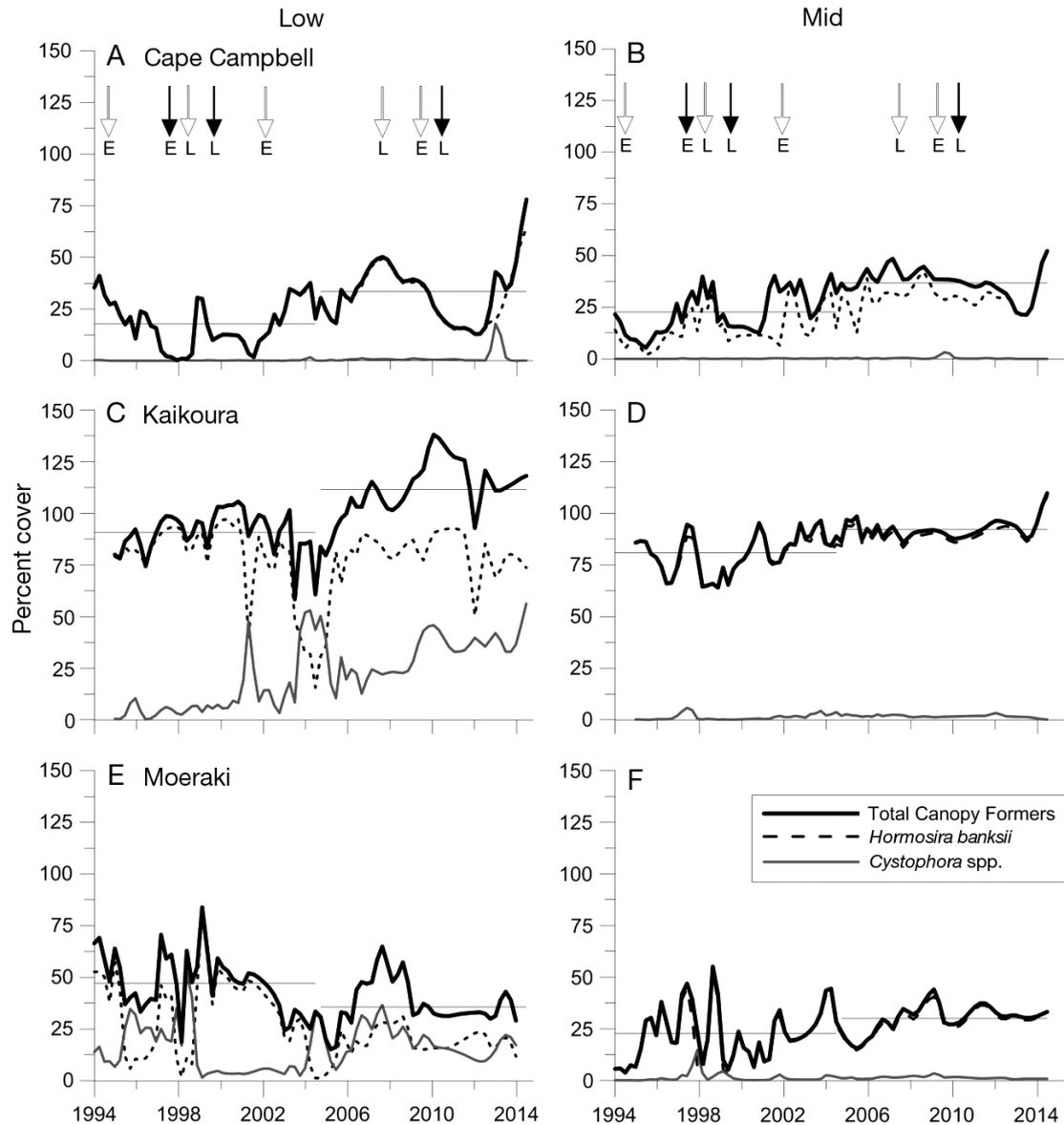


Fig. 7. Quarterly percent cover of total fucoid canopy-forming algae (thick solid black line), *Hormosira banksii* (black dotted line) and *Cystophora* spp. (grey solid line) in the lower (low) and upper (mid) low zone at (A,B) Cape Campbell, (C,D) Kaikoura and (E,F) Moeraki. Cover of total canopy-forming macroalgae could be >100% due to layering of multiple species. The *H. banksii* line appears absent in (A) Cape Campbell low, (D) Kaikoura mid and (F) Moeraki mid, but it mirrors the total canopy line. Moderate and strong El Niño-Southern Oscillation (ENSO) events are indicated by arrows in the 2 top panels: white arrow 'E': moderate El Niño; black arrow 'E': strong El Niño; white arrow 'L': moderate La Niña; black arrow 'L': strong La Niña. The overall means of the surveys between 1994 to 2004 and 2005 to 2014 are shown by the 2 thin black horizontal lines in each panel

decline in fucoid cover from 2002, a combination of *Hormosira* and *Cystophora* recruitment resulted in a 23% increase in fucoid cover in the low zone in the 10 yr from 2004 compared to the previous 10 yr. These changes were mirrored in the mid zone at all 3 areas, but not in the low zone at Moeraki. Fig. 7 shows that 5 of the 6 area-zone combinations, therefore, showed an increase in fucoid abundance between the early and late decades.

The cover of *Cystophora* was generally <10% at all areas except in the Kaikoura low zone, where it steadily increased through time, and at Moeraki low zone, where there were intermittent increases and decreases, with cover ranging between 3 and 30%. Drops in the cover of *H. banksii* coincided with increases in the cover of *Cystophora* spp., with the 2 competing for space at this border of the low intertidal zone. The percent cover of these 2 species was

negatively correlated in the low zone at Kaikoura ($r_{81} = -0.42$, $p = 0.01$) and Moeraki ($r_{81} = -0.51$, $p < 0.01$).

Low and mid zone abundances of fucoid canopy-forming algae were positively correlated at Cape Campbell ($r_{81} = 0.55$, $p < 0.01$), but not significantly correlated at either Kaikoura or Moeraki. Across all 3 areas, there was no significant correlation in cover of fucoid algae, indicating that influences were not coast-wide, but more area-specific (Figs. 7 & S10).

Factors affecting the cover of macroalgae

BRT models were run using all combinations of variables (Table 1) and then simplified to determine which variables were important across all area-zones. Through iterations of these, and using the `gbm.simplify` function to eliminate those variables that were collinear or those with little or no explanatory power, we identified 5 variables that were consistently important: the 95th percentile of SST, the maximum air temperature, the 95th percentile of H_s , the number of days per quarter with more than 5 m waves and the SOI. Here we present the results of BRT analyses relating these 5 variables to fucoid cover (expressed as an anomaly across years at each tidal height at each site; Table 2). In presenting our BRT results, it needs to be noted that much of the model variation is unaccounted for. For the relatively low sample size used here ($n = 85$ quarters, compared to the thousands used, for example, in Elith et al. 2008), the training correlation (ranging from 0.44 to 0.70) and the deviance explained (ranging from 3 to 46%) in the training data sets was reasonable in most cases for ecological data. However, the models were high in residual deviance and low in the cross-validation correlation. They therefore can be used to compare the relative contributions of explanatory variables across sites, but they would not be particularly useful for predictions.

Of the explained variation in the final models, 20 of the 30 physical-biological relationships had greater than 10% contribution to the models in at least one of the 6 area-zone models run (Table 2). Maximum air temperature had a high contribution to all area-zone combinations, as did SOI, whereas SST and waves tended to

have lesser explanatory power. Maximum air temperature had a similar pattern at 5 of the 6 area-zone combinations. Generally, as the maximum air temperature went up, so did the cover of fucoids (Fig. 8). For example, Fig. 8 shows that a transition point in cover occurred when the maximum air temperature was ca. 22°C at Cape Campbell and ca. 25°C at Kaikoura and Moeraki, but the upper limits of the increase were ca. 24°C at Cape Campbell and ca. 29°C at Kaikoura and Moeraki. It should be noted that these temperatures are from land stations and do not reflect the extreme temperatures that can be experienced at some sites in the intertidal zone (e.g. Lilley & Schiel 2006).

SOI had a variable influence on algal cover among areas. At Cape Campbell in both tidal zones and the Kaikoura mid zone, algal cover decreased as SOI decreased (i.e. towards La Niña conditions; Fig. 8B,D,G). At Moeraki, the opposite pattern held (Fig. 8J,L).

SST had a relative contribution of more than 10% at Kaikoura and Moeraki mid zone and Kaikoura low zone (cf. Table 2). Here, fucoid cover increased beyond about 15°C. The 95th percentile of H_s was inconsistent in its effects and produced no discernible pattern across area-zone models. The number of days per quarter with waves greater than 5 m in height was found to be an important variable only at Kaikoura, a reflection of more frequent high wave events at this site (cf. Fig. 5).

There were a few significant time-lagged cross-correlations between the physical variables and

Table 2. The relative contribution (scaled up to sum to 100%) of the 5 physical variables to macroalgal abundance expressed as an anomaly in the boosted regression tree (BRT) models. Each zone (low and mid) within each site (Cape Campbell, Kaikoura and Moeraki) had independent models fitted. For explanations of predictor codes see Table 1. Tree complexity, learning rate and bagging fraction for all models were 3, 0.001 and 0.5, respectively. **Bold:** predictors with a relative contribution of more than 10% within each area-zone model. Expl. var.: explained variation; corr.: correlation; CV: cross-validation

	Cape Campbell		Kaikoura		Moeraki	
	Low	Mid	Low	Mid	Low	Mid
SST 95	7.9	6.5	16.8	12.3	8.0	10.7
Air temp.	58.7	68.8	17.4	10.4	67.1	47.2
Wave 95	9.8	10.8	15.7	16.3	8.0	9.5
Wave days 5 m	6.1	2.0	11.9	12.2	0.01	0.07
SOI	17.4	11.9	38.1	48.6	16.8	32.4
No. of trees	1050	3200	1300	450	250	900
Expl. var. in trained data (%)	14.6	46.3	18.7	7.3	3.2	10.1
Residual deviance	194.3	127.4	208.2	81.6	183.6	108.0
Training data corr.	0.49	0.70	0.55	0.45	0.44	0.47
CV correlation (SE)	0.23	0.47	0.19	0.09	0.05	0.12
	(0.12)	(0.09)	(0.07)	(0.08)	(0.14)	(0.08)
CV deviance (SE)	223.5	96.2	257.3	89.4	193.9	125.7
	(35.6)	(7.5)	(38.8)	(17.9)	(39.4)	(14.1)

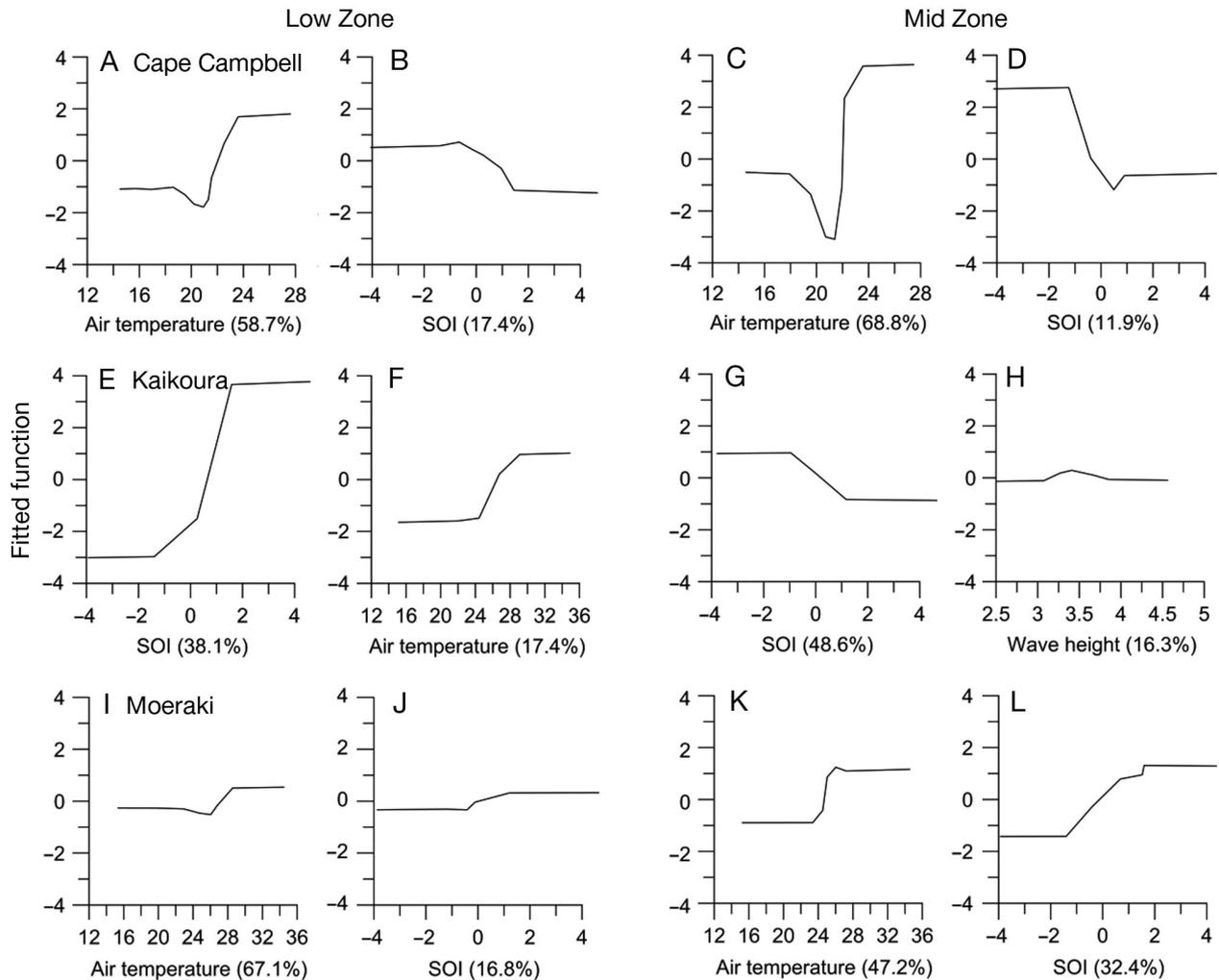


Fig. 8. Partial plots showing the influence of the 2 variables with the highest relative contribution on the cover of fucoid macroalgae in each area–zone BRT model at (A–D) Cape Campbell, (E–H) Kaikoura and (I–L) Moeraki. The 2 left panels are the low zones and the 2 right panels are the mid zones. The percent relative contribution is listed after the variable name on the x-axis

macroalgal cover. SOI was positively correlated with macroalgae cover at Kaikoura mid zone (time lagged by 1 yr; $r = 0.28$, $p < 0.05$) and at Moeraki mid zone (time lagged by 1 season; $r = 0.27$, $p < 0.05$). The relatively few significant relationships between lagged physical variables and macroalgal cover are a reflection of the high residual deviance and the relatively low explanatory power of the BRT models.

DISCUSSION

The research presented here was both a description of climate-related and ecological patterns and a test of their relationships. Contrary to our expectations, there were relatively few strong and consistent relationships between the physical and ecological

variables. Nevertheless, there were trends in both data sets and sufficient significant relationships that could lead to more predictive patterns. It is noteworthy that many of the trends and relationships were area-specific. Our physical data over the past 30 yr showed clear trends of increases in mean annual SST at 2 of the 3 southern New Zealand areas and increases in H_s at all 3 areas. Minimum and average annual SST increased at 2 of our 3 areas, by up to 0.36°C per decade. It was interesting to note that these rises occurred mostly during the winter months, indicating that extreme summer seawater temperatures do not appear to be on the rise in these southern areas. All areas had an increase in H_s , a pattern that spanned across all seasons and appears to be reflective of a stepwise increase during the mid-1990s, rather than a gentle linear increase through

time. These long-term trends have not, however, translated directly into a pervasive effect on intertidal communities. There were some intriguing long-term trends, for example in the decadal increases in fucoid cover at 2 areas. The often poor correspondence between many of the physical and biological variables was undoubtedly influenced by the differences in spatial and temporal scales over which they operate and were measured.

Where coastlines are contiguous from temperate to subtropical waters, changes in distributional patterns of key species or habitat-formers are often evident during periods of ocean warming. For example, southern populations of giant kelp *Macrocystis pyrifera* in Baja California, Mexico, died off in El Niño years (Dayton & Tegner 1984, Tegner & Dayton 1987, Edwards & Estes 2006), as did fucoid algae in southern California (Gunnill 1985). The stipitate kelp *Ecklonia radiata* suffered mass mortality and receding populations in Western Australia during warm water events (Smale & Wernberg 2013, Wernberg et al. 2013), and coral, algal and herbivorous fish distributions changed in temperate–tropical transition areas along eastern Australia (Hughes et al. 2003, Last et al. 2011, Vergés et al. 2014). It seems to be generally the case that seawater temperature is the primary driver of such changes, especially as species approach the geographic limits of their distribution and their physiological tolerances (Harley et al. 2006, Helmuth et al. 2006). It was interesting to note that over the decades of our study we observed no changes in the lower or upper zone limits of the dominant fucoids, which were mostly cosmopolitan or ‘southern’ species, and there were no ‘northern’ species detected in these southern areas, of the 242 species of algae and invertebrates recorded. Any climate change effects so far seem to involve a re-arrangement of the resident players, potentially operating through demographic responses to slightly warmer and more wave-driven waters, perhaps expected for these attached or semi-sessile benthic species that can be long-lived and have considerable time lags in their recovery processes after damage (cf. Schiel et al. 2004).

Increases in global surface air temperature have been well documented (Jones et al. 1999, Hughes 2000, Hansen et al. 2006), with the ecological effects ranging from genetic and physiological through to large-scale distributional changes. Our study, however, was carried out in areas centred within the temperate zone and not in transition areas with tropical waters. It is not clear whether the changes in air temperature, SST and wave height experienced over

decades at our sites were of sufficient magnitude to affect persistent decadal changes. Lilley & Schiel (2006) and Schiel & Lilley (2007) showed, for example, that intertidal temperatures can exceed 35°C in these areas, that burn-off of algae is common during such extreme periods and that recovery of algal communities can take at least 2 yr. Schiel & Lilley (2011) showed that fucoid recovery from a single disturbance can take 2 to 3 yr at Kaikoura and up to 8 yr at Moeraki. Temperature increases of 3°C over ambient levels can significantly reduce fucoid germling survival and this effect is exacerbated when combined with sediments and nutrients (Alestra et al. 2014, Alestra & Schiel 2015). Furthermore, it is known that fucoids fertilise and settle most successfully in calm conditions (Taylor et al. 2010), and that even single waves can detach recent settlers (Taylor & Schiel 2003). As wave forces and temperatures increase, therefore, critical thresholds may be exceeded, especially for early life stages of dominant algae.

Nevertheless, climate change is far more complex than just temperature change. The windfield patterns of the oceans are changing (Young et al. 2011, Swart & Fyfe 2012), leading to changes in wave forces. Young et al. (2011) found, for example, that there has been a significant increase in wind strength across the southern ocean since the 1980s. This has led to a general increase in wave heights, although the consistency of this pattern, on the coarse spatial scale of $2 \times 2^\circ$, is less defined than wind speed. The ramifications of these changes on temperate reef communities are far from clear. Following a large storm event with persistently high wave action over multiple days, the damage to intertidal and subtidal macroalgal stands is immediately apparent by the quantities of fresh algae in the beach wrack. In our data sets, however, it appeared that more subtle effects occurred over long time periods, perhaps with a thinning effect or weakened holdfasts following periods of high wave action, rather than absolute removal.

The degree to which the offshore wave conditions act as a proxy for onshore wave forces is not known, but is highly likely to be variable among areas. These onshore forces will be a product not only of the general wind and wave processes offshore, but of the area-specific angle of waves as they approach shore, the nearshore topography, morphology of reefs and refracted swells (Denny et al. 2003, Gorman et al. 2003, Helmuth & Denny 2003, O'Donnell & Denny 2008). O'Donnell & Denny (2008) showed, for example, that with respect to onshore organisms within confined areas of reefs, these forces can vary by orders of magnitude. All of these influences

affect the intensity of offshore wave action on on-shore communities, but the relationship between wave action and algal canopies could have been stronger if we had had direct measures of onshore waves. The ERA-Interim data, from which the wave data in our study were derived, do not necessarily have the ability to resolve coastal effects. Interpolation to the locations of coastal areas do not account for many processes. However, these data are the most resolved that were available and they are useful for investigating relationships between coastal areas and larger-scale wave variability. Similarly, Smale & Wernberg (2009) showed that while there is strong correlation between the offshore satellite-derived SSTs and temperatures on subtidal reefs, the overestimate of onshore benthic temperatures by 1 to 2°C meant that the ability to detect ecologically relevant small-scale variation in temperatures is lost using offshore estimates.

There may have been a dichotomy of effects; increases in SST over time may have favoured the slow expansion of cover of the dominant furoid *Hormosira banksii*, whereas decreases in canopy cover can result abruptly from high wave forces. This has similarities to a study by Cavanaugh et al. (2011), who found that losses of giant kelp in winter were correlated with wave height and later recovery was correlated with SSTs. It may be the case, therefore, that increases in both SST and wave forces could have great effects on benthic algae and associated species as they approach their physiological limits (Harley et al. 2006, Helmuth et al. 2006), change morphology to accommodate new conditions (e.g. Blanchette 1997), or simply die off in particular areas (e.g. Smale & Wernberg 2013). Only time will tell if an increasing frequency of large storms will change what are essentially pulse disturbances from strong occasional events into long-term press disturbances from repeated events affecting canopy cover (cf. Bender et al. 1984, Schiel 2006).

The SOI, which can be a proxy for SST and wave height among other climatic factors, was a useful factor in determining macroalgal cover. In New Zealand, extreme wave events can occur during both El Niño and La Niña conditions. At Cape Campbell, which is very exposed to the north and often tumultuous conditions of Cook Strait, algal cover tended to decrease during La Niña events when there are prominent northeasterly winds (Mullan 1996, 1998), and increase in El Niño and neutral periods (cf. Fig. 7). From 1994 to the mid-2000s, there were several strong El Niño and neutral periods that may have contributed to the cover of fucoids in 5 of the 6

area-zone combinations. Over all areas and shore heights combined there was an average increase of 32% in furoid cover between 1994 to 2004 and 2005 to 2014. In the low zone this increase was due mostly to the increased abundance of the furoid *Cystophora* spp., whereas in the mid zone this was almost entirely due to an increase in *H. banksii*. Our conclusion from this is that slightly warmer temperatures favoured furoid recruitment and growth. This is supported to some degree by our long-term experiments, which showed that furoid canopies tended to recover within 3 yr at Kaikoura, where SST is warmer, compared to 7 to 8 yr at Moeraki, which is several degrees cooler in temperature (Schiel & Lilley 2011). It also appears that wave forces tend to exert more ephemeral effects on these algae and that large storms are not frequent enough to remove fucoids and prevent their recovery over long periods. This may well change in the future if episodic events of large waves continue to increase in frequency (cf. Figs. 4 & 5), thereby acting as a long-term press disturbance. For the past decades, however, it appears that slight increases in temperature have favoured furoid-dominated communities. *Hormosira* has a small holdfast and is not particularly resistant to removal by waves (McKenzie & Bellgrove 2009), but it is one of the most resilient species to desiccation and can withstand long periods of emersion and light (Brown 1987). In very warm conditions such as those experienced on intertidal reefs in northern New Zealand, however, *Hormosira* individuals tend to be small and populations sparse. *Cystophora torulosa* is not desiccation resistant and its increase in abundance in our study areas is most likely due to facilitation by the canopy of *Hormosira*.

Our long-term experiments also showed there are considerable area-specific time lags in recovery processes after canopy species are removed or damaged (Schiel & Lilley 2011). Where canopies are removed, recovery of the furoid canopy itself can take between 3 and 8 yr (Schiel & Lilley 2011). Overall diversity of the communities can be highly correlated with percent cover of canopies (Schiel & Lilley 2007, Bishop et al. 2009), and recovery of understory communities following canopy removal can take many years (Schiel & Lilley 2011). Furthermore, the delays in the recovery of full communities can affect functions such as primary productivity, which also may not recover for several years (Tait & Schiel 2011). The mechanisms involve direct damage to canopies, weakened holdfasts, partial loss of individuals, subsequent burn-off of understory species that occurs for many months (Schiel & Lilley 2007, 2011), and

density-dependent processes involving recruitment, slow growth and recovery of canopy species that facilitate the understory community (Schiel 2006).

New Zealand presents an interesting test case for the effects of change in temperature and wave climate on temperate coastal communities. The country sits firmly within the temperate zone between 34° and 47°S. The northeastern coastline is influenced by subtropical waters from the north and, for many species, this region coincides with a warm water biogeographic province (Shears et al. 2008). For most kelps and furoids, coastal New Zealand has not yet seen a geographic recession or expansion of these key components of biogenic habitats, although large mid-intertidal furoid beds are more dominant in the south of the country. Our study was done along 500 km of the eastern South Island, covering a range from cold southern to slightly warmer northern waters (Schiel 2004). The northern area, Cape Campbell, is at the southern end of Cook Strait (separating the North and South Islands) and is influenced by warm northern waters and occasionally a warm core eddy from the southeastern coast of the North Island (Heath 1985, Vincent & Howard-Williams 1991, Schiel 2004, Chiswell et al. 2015). Kaikoura is inshore of the subtropical convergence and experiences occasional upwelling from deep trenches just offshore (Chiswell & Schiel 2001), and Moeraki in the south is bathed by the cold waters of the Southland Current (Heath 1985, Vincent & Howard-Williams 1991, Chiswell et al. 2015). It was anticipated in the early 1990s, when the coastal survey programme was initiated, that the rocky reefs at these areas would provide contrasting conditions and biotic trajectories through time.

As a final note, the practicalities involved in marrying environmental and ecological data sets presented great analytical challenges. In some New Zealand studies, highly resolved long-term environmental data have proved to be useful in delineating effects of production dynamics. For example, Zeldis et al. (2008) found that mussel yield could be predicted by environmental variables, and Zeldis et al. (2013) found that chemical and biological predictors collected locally were better than the physical predictors collected away from the farming regions. The environmental variables in our study had coarse spatial resolution but high temporal resolution (e.g. every 6 h for wave height data). The ecological data, although of high resolution spatially within areas, were collected 2 to 4 times annually. Damage from storm waves tends to occur rapidly, but the exact timing of storms relative to ecological sampling periods can manifest itself as a lagged effect on furoid cover.

Furthermore, each of the data sets has its own spatial and temporal scales, inherent noise and variability. Other analytical techniques than those presented here are known to deal reasonably well with these problems for particular types of data. We used GAMs to deal with the non-linearity of the data, and autoregressive integrated moving average models (ARIMA) and distributed lag models to deal with the temporal autocorrelation of the time series and potential time lags of the environmental predictors on macroalgal canopy cover. These showed similar results to the regression trees shown here in terms of the variables of most importance but, again, the explained variation was usually low and the residual variation was high. Finally, we attempted to display the environmental variables in multivariate space and extract the primary principal component axis as a predictor for canopy cover. All of these analyses were tried for our data and none produced more meaningful or interpretable results than what is presented here. We therefore opted for the simplest presentation of analyses that provided the clearest patterns and interpretations of the data, dealing well with the temporal autocorrelation and non-linearity of patterns.

Despite the inherent challenges in detecting climate effects in complex ecological communities, and the lack of obvious distributional changes, loss or incursions of new species, there are climate-related signals in these analyses. We initially chose these 3 locations because they are topographically similar, but they are clearly subject to different environmental conditions. One instructive feature of this study is that the major trends could not have been detected without multi-decadal data sets. As in a few other instructive long-term studies of ecological communities (e.g. Hawkins et al. 2003, 2008, Schiel et al. 2004, Southward et al. 2005, Cavanaugh et al. 2011, Hofmann et al. 2013), long-term series of highly resolved data can provide insights on community persistence and change that are not achievable otherwise. We must be prepared to note, however, as did Buston & Elith (2011 p. 6), that “partial responses may be real patterns in a noisy data set”.

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