17 years of tropicalisation and kelp loss shift trophic composition and lead to more winners than losers in a fish community

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Abstract

Species redistributions are causing novel interactions and leading to profound regime shifts globally. In temperate reefs, the range expansion of tropical herbivorous fish has been linked to the disappearance of temperate kelps, but consequent effects on resident fish communities are not clear. Here, we show overall increases in species richness and abundance (measured as probability of occurrence) of both tropical and temperate fishes identified on video surveys over a 17-year period of kelp loss. Tropical herbivores increased most markedly as kelp declined, while temperate planktivores declined, a potential consequence of tropicalisation not previously identified that suggests important changes to energy pathways. We identified 22 tropical and temperate species from four trophic guilds that significantly increased in occurrence, and only four temperate species that declined. Morphological trait space models suggest increases in fish diversity and overall occurrence are unlikely to be driven by uniqueness of traits amongst tropical range expanders.

INTRODUCTION

One of the most widespread consequences of climate change is the global redistribution of life on Earth (Chen *et al.* 2011; Poloczanska*et al.* 2013; Pecl *et al.* 2017). The climate-mediated movement of species into novel environments alters species assemblages and this can have flow-on effects for ecosystem functioning and services (Pecl *et al.* 2017). Ecological impacts of species redistributions can be particularly severe when foundation species are affected, as this can have cascading impacts on associated species and lead to regime shifts, whereby one ecosystem state shifts to an alternative state (Hughes *et al.* 2013).

Climate-driven species redistribution models generally predict net biodiversity declines and biotic homogenisation at a global scale (Magurran *et al.* 2015; Savage & Vellend 2015). However, following changes in environmental conditions, species diversity can initially increase at the local scale (Hiddink & Ter Hofstede 2008; Walther *et al.* 2009). Emerging evidence shows that patterns of increased diversity are often masked by biological processes not easily observed, including lag times and transitional stages (Daskalova*et al.* 2020) and/or observations reflecting a turnover of species where numbers of "winners" and "losers" are similar and diversity appears to be maintained where lost species are offset by new ones (Dornelas *et al.* 2019; Finderup Nielsen *et al.* 2019). The need for long-term datasets to uncover assemblage changes is therefore paramount for accurately predicting ecosystem change.

There are large-scale coordinated efforts to document the arrival of range-expanders into new areas (Robinson *et al.* 2015), but we know relatively little about their interactions with and responses of recipient communities

(Bates *et al.* 2014; Svenning *et al.*2014). Additionally, we lack understanding of how climate-mediated losses of species, and the traits associated with those species, affect ecosystem processes (Wardle *et al.* 2011). Such understanding is critical to the development of management tools for mitigating impacts of range expanding organisms on ecosystem function and services.

Biogeographic transition zones where abiotic and biotic conditions allow for the interaction of organisms from different geographical origins are experiencing rapid changes in the marine realm (Horta e Costa *et al.* 2014; Troast *et al.* 2020). Transition zones provide a unique opportunity to understand the impact of range shifting organisms because populations of species from the surrounding environmental extremes already exist and interact. Transition zones allow us to examine the processes and mechanisms that facilitate successful species expansions, as well as those which make resident species resilient within their native range despite the establishment of range-expanders. The identification of mechanisms that facilitate changes in abundance for some species under these conditions may help identify range expanders and/or at-risk species from the surrounding systems and for similar systems elsewhere. For example, recent evidence from tropical/temperate transition zones has shown that, despite historical mixing of tropical and temperate species, the increasing abundance of range-expanding tropical herbivorous fishes can overgraze seaweeds and lead to regime shifts by maintaining reefs in canopy-free states (Vergés *et al.*2014; Bennett *et al.* 2015).

In recipient systems where range-expanding species are becoming more common, predicting coexistence with resident species is critical to understand the eventual structure and functioning of those systems. Mechanisms that underpin coexistence are complex and influenced by multiple ecological and evolutionary processes acting simultaneously (Pinsky 2019). However, the well-established field of invasion ecology can be used as a starting point to make predictions about climate-driven species redistributions (Wallingford *et al.* 2020) whereby the trait space of range expanders can then be empirically quantified (Sunday *et al.* 2015). For instance, trait-based analyses of invading species are often used to predict the likelihood of competitive interactions with resident/native species and effects on the recipient community (van Kleunen *et al.* 2010). Invasive species often show generalist traits that facilitate success in novel environments, often to the detriment of resident specialist species (Clavel *et al.*2011). Dynamic environments often favour generalist species that more readily adapt (Kassen 2002) and so we could expect that, in a range expansion context, resident specialist species may be the most vulnerable.

For transition zones affected by climate change, species coexistence may continue to be possible if incoming species show unique traits (Paciogllu*et al.* 2020), i.e. do not directly compete with residents or are able to show plasticity in resource use in a novel setting (Jackson & Britton 2014). However, there are cases where expression of unique traits may not be beneficial if the system is already disturbed/degraded (Bulleri *et al.* 2020). Alternatively, resident populations may be far below carrying capacity (for example due to fishing in marine systems), and thus even if incoming species substantially overlap in trait (niche) space, competitive exclusion will not occur and coexistence between migrants and residents can persist.

On the east coast of Australia, the Solitary Islands region is a sub-tropical transition zone within a climate change hotspot (Hobday & Pecl 2014). This region is strongly influenced by the East Australian Current, a western boundary current that is strengthening in response to climate change and which can facilitate the poleward range expansion of marine species (Ridgway & Hill 2012; Castro *et al.* 2020). An increasing abundance of tropical herbivorous fishes has been linked to the decline of temperate habitat-forming kelp in this region (Vergés et al. 2016). The kelp *Ecklonia radiata* is a critical component of Australia's temperate reefs that supports ecologically and economically important fish and invertebrate species (Wernberg *et al.* 2019). The loss of seaweeds in eastern Australia is part of a global "flattening of kelp forests" (Filbee-Dexter & Wernberg 2018) whereby canopy seaweeds are replaced by low biomass turfing algae or corals (Vergés *et al.* 2019). How this shift in benthic cover affects resident fish communities in a tropicalisation context is largely unknown, however declines in kelp-dependent species may be expected concurrent with the decline of this foundation species.

Here, we surveyed tropicalised reefs within the Solitary Islands region to quantify changes in fish assemblages during a period of kelp loss. In particular, the study period encompasses a shift in benthic cover where temperate kelp *Ecklonia radiata* was completely lost, did not recover, and was largely replaced by turfing algae and corals (Vergés et al. 2016). We analysed baited remote underwater video surveys (BRUVS) collected over 17 years from 2002-2018, with total kelp loss occurring from 2009 (Vergés *et al.* 2016). Abundance and morphological traits of individual fish species were assessed. We used the morphology of individual fish species within the community to investigate the potential for trait differentiation that may be indicative of meaningful competitive interactions *sensu* (Azzurro *et al.* 2014) between tropical and temperate associated species of similar feeding guild (herbivores, invertivores, piscivores and planktivores). With particular interest in the vulnerability of temperate species, we specifically asked: 1) How has the probability of occurrence of tropical and temperate fishes from different trophic guilds changed over 17 years, encompassing the transitional period from kelp to turf dominated reefs? 2) Are there any species, tropical or temperate, that have significantly increased and/or decreased in abundance over this period? Based on the analysis of fish morphological traits, 3) is the overall "trait space" of incoming tropical fishes different from that of resident temperate ones, and 4) are changes in fish abundance linked to unique morphological traits?

MATERIAL AND METHODS

Study site

We quantified changes in fish assemblages within the Solitary Islands region in New South Wales, eastern Australia (Supplementary Figure 1). Previously, Vergés et al. (2016) showed that kelp disappeared from multiple mid-shelf reefs (<6km offshore) reefs after 2009. These reefs support mixed communities of tropical, subtropical and temperate fish (Malcolm *et al.* 2010), and over the last decade have experienced gradual warming (Vergés *et al.* 2016). In particular, we analysed the fish community at 5 individual reefs spanning ~20km of coast; Jeffrey Shoal (-30.24913, 153.1993), Sawtell Reef (-30.36616, 153.13127), Split Bommie North (-30.24125, 153.20163), Split Bommie West (-30.24071, 153.19235) and Whitmore (-30.34795, 153.13901) (SI. Fig. 1). Three of these sites (Jeffrey Shoal, Split Bommie North and Split Bommie West) are located inside the Solitary Islands Marine Park, which was established in 1998 with existing management rules commencing in 2002. These three study sites are within Habitat Protection Zones, where recreational fishing and some types of commercial fishing (e.g. line fishing) are allowed. The other two sites (Sawtell and Whitmore) are outside the Solitary Islands Marine Park and managed under general fishing regulations (e.g. with bag and size limits).

Sampling of fish assemblages

The fish community within each site was surveyed using Baited Remote Underwater Video surveys (BRUVS). Three replicate BRUVS were deployed at each site at least 200m apart and within 5-10mins of each other, with each survey lasting 30mins. Sampling was done once a year, at a similar time of the year (Austral winter), over a 17-year period between 2002 and 2018, except for 2012, 2016 and 2017 when no sampling was done. BRUVS units consisted of video cameras attached to a metal frame and bait pole with a bait bag containing ~800g of pilchard (*Sardinops neopilchardus*) 1.5m in front of the cameras. The maximum number of individuals of a species in a single frame (MaxN) was recorded for each site and year using SeaGIS Event Measure software (seagis.com.au) as a conservative measure of relative abundance, as this method eliminates the chances of recounting the same fish. All fish within the field of view within 3m of the camera were identified to species level where possible.

Each fish species identified in the BRUVS was then classified into one of four trophic guilds: planktivore, herbivore, invertivore or piscivore, based on the predominant food source for adult individuals of the species as reported in the literature e.g. (Allen 1999; Malcolm*et al.* 2007) and/ or on Fishbase (Froese & Pauly 2000). Using these same sources, species were also classified into ecoregion (tropical or temperate) based on distribution data (see full list of species and assigned trophic guild and distribution in Supplementary Table 2). For species that show a strong distributional crossover, ecoregion was allocated based on whether the core range extends furthest towards either the tropics or in a poleward direction.

Temporal changes in the fish community

To determine how relative total fish abundance changed over time, MaxN values for all individual species were combined to get a single count of individuals per BRUV replicate over the 17-year study period. Similarly, the total number of species observed in individual BRUV drops across years was used to determine changes in species richness over time. These data were then fitted to separate linear mixed models (LMM) using the R package lme4 Version 1.1-23 (Bates *et al.* 2020) with Time (Year; 2002-2018) as a normalised continuous predictor variable and Site (n=5) as a random effect.

Probability of occurrence was determined for each individual species identified in BRUVS surveys over the 17-year study period. Generalised linear mixed models (GLMM) assuming binomial distributions were run for each individual species and trophic guild (planktivore, herbivore, invertivore, piscivore) for both tropical and temperate ecoregions using the R package lme4 with Time (year; 2002-2018) as a normalised continuous covariate and Site (n=5) as a random effect in the model. Statistical significance for LMM and GLMM was determined using likelihood ratios tests (alpha=0.05). Some species were rare (i.e. only captured on BRUVS surveys < 3 times within 2002-2018) and did not yield enough information to fit the model and were excluded from probability models (but included in niche models below). We then calculated the mean (± standard error) probability of occurrence for each trophic group for both ecoregions by fitting estimates derived from species' GLMM models to a linear model with time as the continuous predictor variable using the R package stats (version 3.6.0 (RCoreTeam 2020)). As an estimate of how similar trends for individual species were to trends of their respective region/trophic guild group, we examined the relationship between the slope estimate of each species and the slope estimates of the respective group using Pearson's correlation coefficient (stats package, version 3.6.0; (RCoreTeam 2020) values given in SI Table 2).

Geometric morphometric analysis

To compare the uniqueness or generality of functional traits of resident temperate and range-expanding tropical fish species, we modelled niche similarity based on body shape analysis of theoretically competing fishes within the same trophic guild. Body shape metrics can be used as a proxy for ecological niche in fishes given the significance of morphological traits in determining a species' relative ecological niche breadth (Azzurro *et al.* 2014; Smith *et al.* 2016). The morphospace (2D relative trait space encompassing all species within the community) of each fish was modelled using an image of the left side of an adult individual (images sourced from (Allen 1999; Froese & Pauly 2000)). For each image, 27 points of ecological significance were defined following (Farré *et al.* 2013) then scaled and quantified using TPS DIG2 v. 2.31 (Rohlf 2004) following (Azzurro *et al.*2014). Relative warp analysis of images was conducted using tspRELW v.1.70 (Rohlf 2015) and coordinates generated from the first 2 warps (accounting for 52% variability) were used to plot relative community trait structure in two-dimensional space. Voronoi polygons were generated using R package 'deldir' Version 0.1-25 (Turner 2020) to define the theoretical niche space occupied by a species (i.e. the maximum polygon size around the species centroid). Voronoi area was retained as a proxy for relative niche space and used as a way of determining the potential for competitive interactions between neighbouring species, with larger Voronoi areas representing high niche dissimilarity (Du *et al.* 2012).

As a metric of morphological similarity between each species and the overall community mean, we generated a variable termed 'distance', calculated as the Gower distance between each point and the community weighted mean centroid (CWM). CWM was determined using the package 'FD' Version 1.0-12 (Laliberté & Legendre 2010; Laliberté *et al.*2014) and a lingeos correction to correct for negative values generated by a non-Euclidean matrix. This metric is used as a similarity proxy, where species with body shapes similar to the mean body shape will have small distance values and are therefore not be considered unique amongst the group, or do not show potential to uptake a different set of resources amongst the group.

Rare species that were not abundant enough to estimate probability of occurrence through time using the GLMMs described above were still included in the morphometric model but were given an occurrence change value of 0 to represent a null probability of occurrence relative to the theoretical niche size. We then ran two linear models where area and distance metrics generated for each species were used as predictor variables for mean change in probability of occurrence, which was calculated by subtracting the 2002 estimated probability of occurrence from the 2018 estimated probability of occurrence (SI, Table S1). If unique traits are important for determining competitiveness within the community, we would expect that species that show large positive changes in probability of occurrence would have high uniqueness metrics.

RESULTS

The total MaxN over time increased from 56 (±9) in 2002 to 82 (±17) in 2018, an average increase of 46.4% (Chi = 0.003, df = 1, 209, p 0.003;R^2 = 0.038; Fig. 1*a*). Similarly, species richness also increased over time from a mean of 10 (±1) to 18 (±0.8) (an 80% increase) (Chi = < 0.001, df = 1, 209, p < 0.001,$R^2 = 0.338$; Fig. 1*b*).

The probability of occurrence of tropical fishes from all trophic guilds combined increased over time (Chi = < 0.001, df = 1, 1948, p < 0.001, $R^2 = 0.051$). When broken down into trophic guilds, three of the four guilds for tropical fishes showed a significant increase in probability of occurrence over time - herbivores, piscivores and invertivores - while planktivores showed no change (Fig 2a; SI T1). Temperate fish also increased overall (Chi = < 0.001, df = 1, 2598, p < 0.001, $R^2 = 0.006$) with a significant increase for piscivores and invertivores and no change for herbivores (Fig 2b, SI Table 1). There was, however, a significant decline in temperate planktivorous fishes (Fig. 2b; SI Table 1).

Out of 110 species, we identified 26 that individually showed significant changes in probability of occurrence over time (GLMM slope estimates and p-values in supplementary Table 2) (Fig.3). Most of these species (22 out of 26) increased in probability of occurrence through time, and this included both tropical and temperate affiliated species (Fig. 3). However, we also identified 4 temperate-associated species that significantly declined over time: the planktivore *Atypicthys strigatus* (Fig. 4; Chi < 0.001, slope estimate (Year) = -0.036; df = 1,48; $R^2 = 0.100$), the invertivores*Ophthalmolepis lineolata* (Fig. 3; Chi < 0.001, slope estimate (Year) = -0.025; df = 1,48; $R^2 = 0.886$) and*Pictilabrus laticlavius* (Fig. 3; Chi < 0.001, slope estimate (Year) = -0.006; df = 1,48; $R^2 = 0.522$) and the piscivore *Dinolestes leweni* (Fig. 3; Chi < 0.001, slope estimate (Year) = -0.004; df = 1,48; $R^2 = 0.794$).

As a proxy for ecological niche space, body shape of all fish species present in the community was modelled using geometric morphometrics analysis. The complete list of Voronoi area size and distance to community weighted mean for each species are given in supplementary Table 2. Figure 4 shows a visual representation of the relative body shape analysis for each trophic guild. Species that showed a significant probability change (species labelled by picture) were randomly placed within their respective groups, with no obvious group outliers (Species not labelled).

Each species' distance to the community weighted mean (CWM) and their Voronoi area derived from the morphometric model were tested as possible explanatory variables for change in probability of occurrence over time. Neither distance ($F_{1,75}$=0.102, p= 0.75) nor area (log(area):$F_{1,\ 75}$=0.50, p=0.482) in trait space were significant predictors of occurrence.

DISCUSSION

Climatic changes are leading to species redistributions and consequent impacts on ecosystem function and services are starting to emerge in some regions (Pecl et al. 2017). In our study system – shallow reefs within a warming tropical-temperate transition zone where a major habitat, kelp forests, is declining - we found clear shifts in the abundance and trophic composition of a fish community. Our results show overall increases in fish abundance for most trophic groups, including both tropical and temperate species. Tropical herbivores increased most dramatically, whereas temperate planktivores were the only trophic guild that declined, with no corresponding increase in tropical planktivores observed. Our results here suggest that changes in pathways of energy flow may be one of the main impacts of climate change for tropicalised systems, with planktonic inputs becoming less important, while a higher proportion of algal productivity gets consumed locally by increasingly abundant herbivores.

Our 17 year study period encompassed the loss of kelp as one of the dominant foundation species on these tropicalised reefs (Vergés *et al.* 2016). We therefore expected to observe declines of temperate fish species that use kelp as a resource (directly or indirectly) for food, cover and/ or shelter. However, 22 of the 26 species that changed in abundance showed an increase in probability of occurrence, and this included both tropical and temperate species. Overall, this suggests that tropicalised reefs that have lost kelp can sustain greater fish biomass than previous kelp-dominated states. These results are consistent with observed patterns along the latitudinal coast of Eastern Australia, which show that total fish biomass in shallow reefs is an order of magnitude higher in warmer subtropical reefs than in higher latitude reefs which are dominated by kelp (Holland *et al.* 2020).

What remains to be established is what is fuelling increases in fish abundance, as well as an increase in diversity in these tropicalised reefs? One potential explanation is that new ecological niches are becoming available as foundation species like kelp decline. However, we found no evidence that tropical fishes increasing in abundance fill underrepresented niche spaces. Despite a shift from kelp to turf, neither tropical nor temperate fishes showed a distinct set of traits that may facilitate success in a shifted environment. For example, within the herbivore group, tropical fishes that have dramatically increased over time do not fill a distinct trait space when compared with temperate herbivores based on their morphometric traits. Morphometric analysis also did not show any evidence for an increase in generalist species, a proposed mechanism for successful establishment of invaders in the more general field of invasion biology.

An alternative explanation for the observed increase in fish biomass is that the bottom-up resource base in the system has increased. In particular, as reefs become tropicalised, it is plausible that a higher proportion of the primary production is consumed and retained within the local reef system through the observed increases in the abundance of herbivorous fish. In temperate kelp forests about 80% of kelp production is exported as detritus (Krumhansl & Scheibling 2012), whereas in tropical systems, herbivorous fish consume 50-100% of turf primary production produced in situ (Hay 1991). As fast-growing turf algae replace canopy forming kelp, the turnover rates of primary production (time taken to replace biomass) accelerates and the proportion of primary productivity consumed locally may be increasing, leading to higher fish biomass (Vergés *et al.* 2019). Increasing abundance of herbivorous fish in tropicalised reefs may also lead to more localised recycling of nutrients, as more local consumption also means greater supply of nutrients via excretion (Allgeier *et al.*2017). In turn, this may lead to a higher production of nutritious detritus, an important food source for many nominal herbivorous fish (Wilson *et al.* 2003).

A third possibility for the observed increase in richness and abundance with no addition of unique niches, also related to the resource base of the system, is that the fish community studied here is currently well under the carrying capacity of the system. Thus, despite a phase shift, increased high fish biomass is still supported making competitive exclusion currently less important for predicting species change in occurrence. Perhaps the increasing abundance of range expanding fishes has a low net effect on the resident community because the loss of structurally complex kelps has not significantly reduced the carrying capacity of these reefs, which may have alternative types of microhabitats and resources. An increase in richness and abundance could be a combination of both an increase in retained primary productivity and a fish community at abundance levels not limited by competition. However, while this may explain an increase in tropical species over the study period, a cumulative increase in abundance of temperate plus tropical species is less clear.

It is important to note that many of the species observed increasing in abundance have cosmopolitan distributions throughout Australia. While they contribute in our samples to biodiversity enhancement at the local scale, they may in fact be contributing to broader scale homogenisation of biodiversity. Scaling up local losses of rare or endemic species results in a net decrease in regional scale diversity. While in these tropicalised reefs we found that net gains in species seem to outweigh net losses, Finderup Nielsen et al. (2019) show that localised increases in species richness can mask broader patterns of biotic homogenisation where rare, range-restricted species are almost always disproportionally the losers. We found evidence of that here with a mix of tropical and temperate fishes increasing and only temperate species showing a decline. Although BRUV surveys can underestimate richness and diversity metrics, roving underwater visual censuses undertaken by divers in the Solitary Islands during 2001-2017 also reported strong increasing patterns of species richness for tropicalised mid-shelf reefs (Malcolm & Ferrari 2019).

The positive correlation between kelp decline and overall fish abundance and species richness may be reflecting a transitional stage, with further responses lagging and yet to manifest. For instance, a recent global synthesis of assemblage changes associated with terrestrial forest loss has shown that despite evidence for short-term positive effects on species diversity, there can be lagged responses of up to decades post tree-loss disturbances, particularly when assemblages include species with long generation times (Daskalova *et al.*2020). Similarly, lag effects have been identified in response to reduced structural complexity following mass bleaching in coral reefs where, despite initial maintenance of biomass, evidence from size structure analysis revealed that adult fish lost through natural mortality are not replaced by juveniles in the long term (Graham*et al.* 2007). In a similar way, there may be a time-lag response to the loss of kelp for long-lived fish species that depend on this habitat for recruitment or during their juvenile life stages, but are less dependent on kelp during their adult stages. This fish community is likely still in transition and longer-term effects of a climate mediated phase shift may not yet be fully realised. Continued long-term monitoring of assemblages following disturbances will be key to fully understand the impacts of habitat change on biodiversity.

Temperate planktivores were the only group that declined over time. The decline in planktivores observed was largely driven by a decline in the Australian Mado (*Atypichthys strigatus*), an abundant species on subtropical and temperate rocky reefs in south-eastern Australia. Small schooling planktivores such as *A. strigatus* can be considered outliers in BRUV analyses because they form large groups with highly stochastic distribution; thus, these results need to be interpreted with caution. Our results suggest that declines of this broad trophic group were unlikely due to direct negative competitive interactions with tropical planktivores, which did not change throughout the study period. It is interesting to note that an expansion in the distribution of*A. strigatus* towards the cold edge of its thermal range and into Tasmania has been documented (Last *et al.* 2011). This may suggest that the decline of this species may be driven by physiological effects of warming driving a range contraction at the warm edge rather than shifts in ecological interactions, although complex indirect effects not quantified here could also explain such declines. Given the dominance and important role of planktivores in fuelling food webs in shallow coastal reefs across Australia and New Zealand (Truong *et al.*2017), a potential range contraction of this species may have important ecological implications.

In contrast, the decline of the two temperate wrasse species (*Ophthalmolepis lineolatus* and *Pictilabrus laticlavius*) observed in our study may be directly linked to the decline of kelp, as these species are known to display a behavioural preference for this macroalgal habitat (Barrett 1995; Edgar *et al.* 2004; Tuya*et al.* 2009; Fulton *et al.* 2016). Kelp canopies may be important for both wrasses through the provision of shelter and refuge from predation (Tupper & Boutilier 1997); and structurally complex kelp holdfasts harbour high invertebrate densities that provide a profitable food source for wrasses (Morton *et al.* 2008). In the case of the other species observed declining, the piscivore *Dinolestes leweni*(Long-fin Pike), we note that this species occupies a relatively unique niche by the standards of our model, i.e it occupies a large area within the convex hull and is not clustered towards the mean. This may indicate niche requirements that are not shared by others in the guild, and may now no longer be available, e.g. a specialist diet of a declining species. In their core range, long-fin pike are abundant and feed on small bodied planktivores including *A. strigatus* (Truong *et al.* 2017).

Shifts in predator-prey interactions due to climate change and species redistributions are largely unexplored. Here we briefly consider that the decline of the four temperate species identified in this study could be partly caused by an overall increase in piscivory, given that ten out of the 22 species observed increasing in abundance are piscivores with only one temperate associated piscivore showing a decline. While in-depth dietary analysis would be required to test this, loss of canopy cover of kelp may also make some species more vulnerable to predation. A factor that may have potentially contributed to increased predatory fish abundance is the establishment of the Solitary Islands Marine Park in 2002. Although none of the study sites are within sanctuary zones where fishing is totally prohibited, it is possible that increases in predator abundance are influenced by a spill over effect, i.e. the emigration of juveniles and/ or adults from protected sanctuary zones to nearby areas. Most studies find however, that spill over occurs at distances within 200m from no-take zones (Di Lorenzo *et al.* 2020), and our study sites were located further away. We therefore consider it unlikely that fishing regulations are influencing changes in fish abundance in our study sites, with the notable exception of the observed increases in the threatened black cod (*Epinephelus daemelli*) which are likely to be a response to targeted management recovery plans for this species (Harasti & Malcolm 2013).

To summarise, our results suggest that although tropicalisation and associated loss of kelp can lead to increases in fish diversity and overall fish abundance, it is also leading to the loss of some temperate species and is causing major changes in pathways of energy flow, as reflected by rapid shifts in trophic composition. We hypothesise that continued warming and tropicalisation will favour range expanding species and may lead to increases in fish abundance and biomass. Our data here also suggests that this may be to the detriment of some temperate associated species. In particular, we observed the decline for four temperate fishes (Australian mado, southern maori wrasse, senator wrasse and long fin pike), which may be the first species identified as vulnerable to changes associated with tropicalisation for this region. The continued growth of tropical fish populations on high latitude reefs means that losses of temperate associated fishes may go undetected particularly if these are not target fisheries species.

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FIGURE LEGENDS

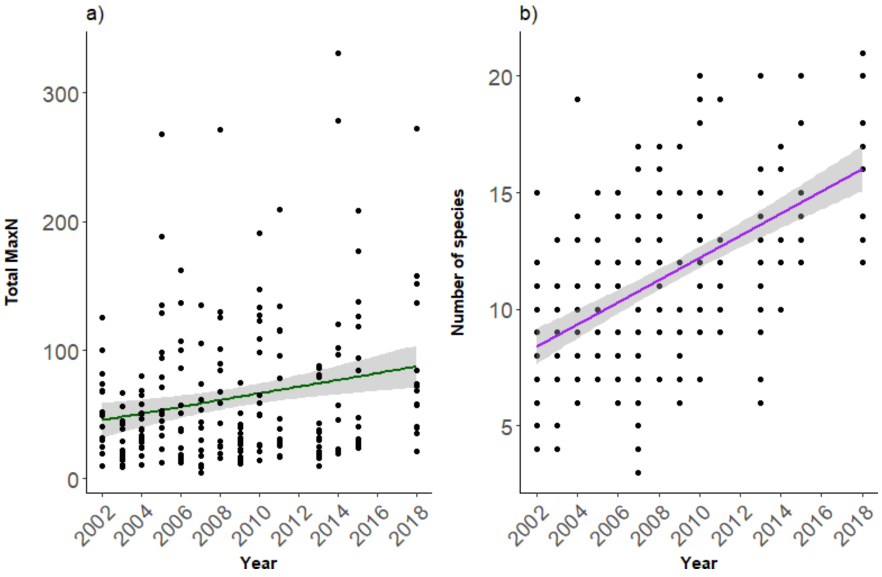
Figure 1. a) Total MaxN of all species identified in individual BRUVs videos and b) number of species identified from 2002-2018 (data not available from 2012; 2016; 2017). Green (a) and purple (b) lines are predicted values from the respective linear mixed models (N = 213).

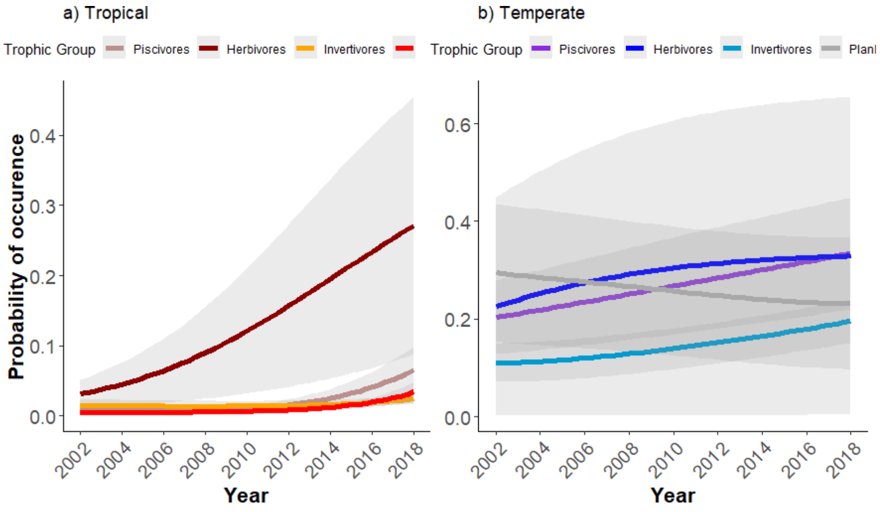
Figure 2: Estimated probability of occurrence (mean +/- S.E., n=50) for marine fishes associated with a) tropical and b) temperate systems categorised by tropic group (piscivores, herbivores, invertivores and planktivores) from 2002-2018 for mid-shelf reefs in SIMP where total kelp decline was observed.

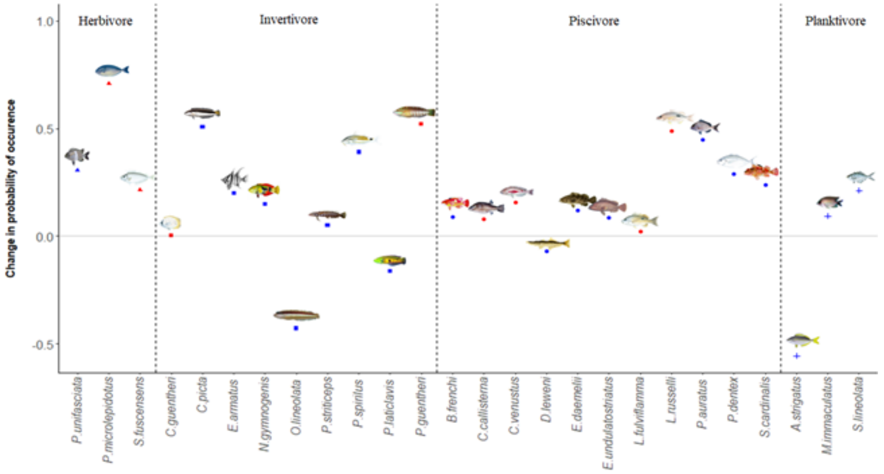
Figure 3: Change in probability of occurrence for species whose probability of occurrence changed significantly; either increasing (positive slope) or decreasing (negative slope) over the study period. Red symbols indicate tropical associated species and blue symbols indicate temperate associated species.

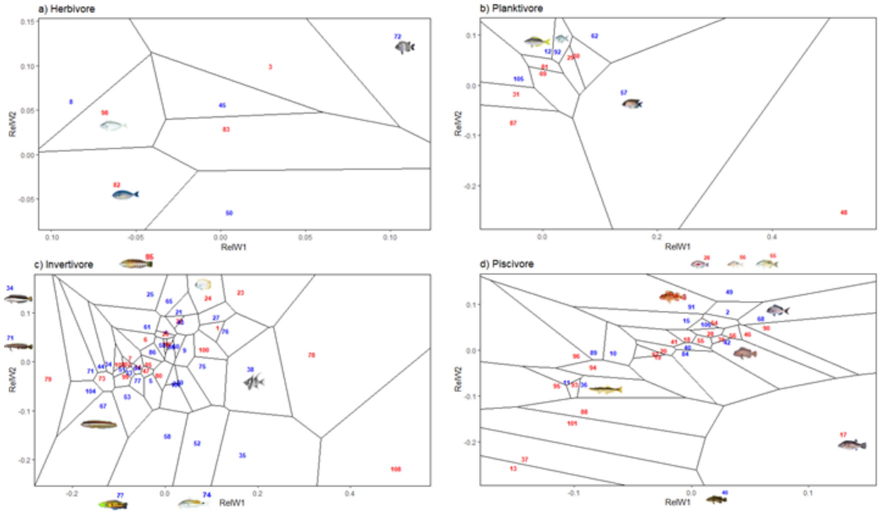
Figure 4 : Geometric morphometrics model for fin-fish species identified using BRUV surveys on tropicalised reefs. Numbers are species identity as outlined in Supplementary Table 2 and colours represent ecoregion, temperate (blue) or tropical (red). Position of number represents the position of each species relative to the group and surrounding segment represents the Voronoi polygon that species. RELW axes 1 and 2 represent 52% of body shape variability across the community.

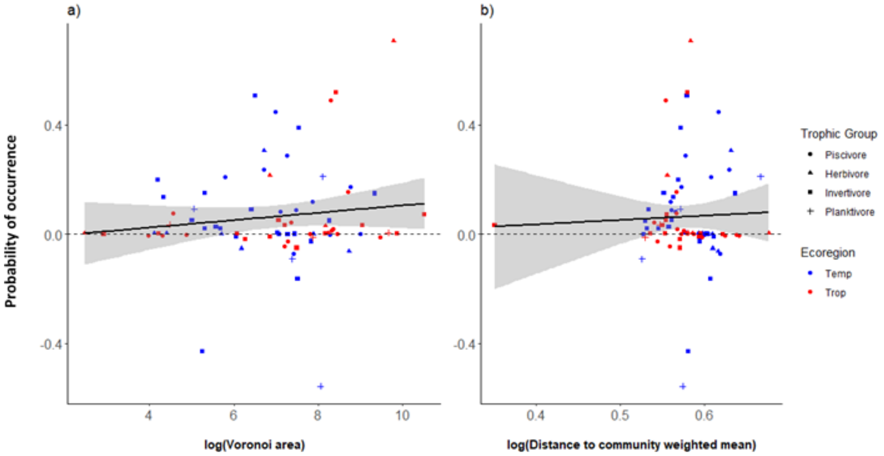
Figure 5 : Relationship between change in probability of occurrence and a) modelled Voronoi area and b) distance from the community weighted mean of fish species associated with temperate (blue symbols) or tropical ecoregion (red symbols) for each trophic guild (Piscivore, Herbivore, Invertivore, Planktivore).






Herbivore
Invertivore
Piscivore
Planktivore
Change in probability of occurence
1.0
0.5
0.0
-0.5
P.unifasciata
P.microlepidotus
S.fuscensens
C.guentheri
C.picta
E.armatus
N.gymnogenis
O.lineolata
P.striticeps
P.spinilus
P.laticlavis
P.guentheri
B.frenchi
C.callisterna
C.venustus
D.leweni
E.daemelii
E.undulatostriatus
L.fulviflamma
L.russelli
P.auratus
P.dentex
S.cardinalis
A.strigatus
M.immaculatus
S.lineolata


a) Herbivore
b) Planktivore
c) Invertivore
d) Piscivore
RelW1
RelW2


a)
b)
Probability of occurrence
0.4
0.0
-0.4
4
6
8
10
0.4
0.5
0.6
log(Voronoi area)
log(Distance to community weighted mean)
Trophic Group
Piscivore
Herbivore
Invertivore
Planktivore
Ecoregion
Temp
Trop