Habitat heterogeneity drives scale-dependent biodiversity loss in a temperate marine ecosystem

Author Information

Samuel Starko[1,2*]†, Lauren Bailey[2,3], Elandra Creviston[2,3], Katelyn James[2,3], Alison Warren[2,4] & Christopher J. Neufeld[2*].

1. Department of Botany and Biodiversity Research Centre,
   University of British Columbia
   Vancouver, British Columbia, Canada, V6T 1Z4
2. Bamfield Marine Sciences Centre
   100 Pachena Rd.
   Bamfield, British Columbia, Canada, V0R 1B0
3. University of Victoria
   Victoria British Columbia, Canada, V8P 5C2
4. University of British Columbia Okanagan
   Kelowna British Columbia, Canada, V1V 1V7

* Equal contribution

† **Corresponding author**: samuel.starko@botany.ubc.ca

Key Words: biodiversity, biogenic habitat, bright spots, climate change, ecosystem functioning, ecosystem services, environmental stress, Laminariales

Running Head: Scale-dependent biodiversity loss

Abstract

Biodiversity loss is driven by interacting factors operating at different spatial scales. Yet, there remains uncertainty as to how fine-scale environmental conditions mediate biological responses to broad-scale stressors. We surveyed mid-latitude kelp bed habitats to determine whether local habitat heterogeneity has mediated changes in community diversity after more than two decades of climate warming and extreme temperature events. Local wave exposure conditions were instrumental in determining responses, with some habitats remaining stable and others experiencing near complete diversity loss, leading to local declines without regional extinctions. Wave-sheltered shores, which saw the largest declines, are the most common habitat type in the Northeast Pacific and may be especially sensitive to climate-related losses in kelp diversity and abundance. Our findings highlight how local gradients can interact with global drivers to facilitate diversity loss and demonstrate how incorporating differences between habitat patches can be essential to capturing scale-dependent biodiversity loss across the landscape.

Introduction

Ongoing biodiversity loss is expected to reduce ecosystem functioning and services (1) but uncertainty remains about the spatial scale at which to investigate the environmental drivers of such loss (2–4). Global stressors can interact with local factors to exacerbate or ameliorate community responses to ongoing global change (5–7). Yet, fine-scale microclimatic differences between sites are often ignored by both global climate models–which predict systematic shifts in the latitudinal ranges of species (8)–, and in meta-analyses of local diversity change–which group plots only by habitat-type (e.g. forest, marsh, grassland) or by region (e.g. (9–11)). These common approaches, although insightful, may miss functionally important trends in community diversity change if the stresses associated with a habitat patch depend more on local conditions than on regional patterns (12), or if declines in diversity are occurring at only a subset of sites within each habitat type. Understanding functionally-relevant biodiversity changes will therefore depend on determining the relative importance of both broad-scale and fine-scale stressors in driving long-term community shifts. While much work has focussed on how broad-scale stressors are driving the biological responses of communities (6, 8, 10, 13, 14), few studies have examined the role that local, fine-scale conditions play in facilitating them (6).

The rocky intertidal zone is an excellent model system for assessing the impacts of climate change on biodiversity loss (15). Intertidal organisms live near their physiological limits (5) and are sensitive to air temperatures, which tend to be more variable and extreme than seawater temperatures (5, 16). Local environmental gradients also have profound effects on intertidal systems. In particular, wave action plays a fundamental role in structuring intertidal communities (17, 18). Water movement from waves can increase productivity by eliminating nutrient-depleted or oxygen-rich boundary layers that are associated with low-flow environments (19). Furthermore, wave splash can ameliorate the stressors associated with aerial exposure, such as desiccation and thermal stress (5, 16). Given the importance of wave action on the physiology and ecology of organisms that live along rocky shorelines, exposure to waves is likely to affect how these organisms respond to global change. While thermal profiles of intertidal sites support the prediction that local conditions, such as wave exposure, will mediate community responses to climate change (16, 20), the scarcity of appropriate baseline community data have made this difficult to test in the field.

Here we explicitly test this hypothesis by investigating the role of a local wave exposure gradient on temporal changes in intertidal kelp bed habitats in Barkley Sound, British Columbia, Canada following 22 years of broad-scale climate warming and extreme temperature events (14, 15, 21). Kelp communities provide many important ecosystem services to humans through rapid growth and formation of habitat for commercially harvested animals (22), but as cold water species, kelps are expected to be sensitive to climate change. Tropicalization has already caused negative impacts on kelp forests near their range edges (14). However, interactions between global, regional and local processes have led to complex responses of kelp communities with large variability in the magnitude and direction of change (11, 23, 24) . Studies of local-scale temporal change in the abundance of kelp and other large brown algae are increasingly common (e.g. (11, 21, 25, 26)) and collectively demonstrate that local conditions can interact with global stressors to drive ecosystem responses to change. However, these studies have focused on a small number of species and have not examined temporal changes in kelp assemblage diversity. Moreover, it still remains unclear how natural variation in site-level environmental conditions will influence the responses of kelp-dominated ecosystems to global-scale climate change or at what scale to expect variation in biological responses.

To assess temporal changes in kelp diversity, we resurveyed intertidal sites (n=49) in 2017 that had previously been surveyed by Druehl & Elliot between 1993 and 1995(27). We identified all kelp species present at each site and quantified abundance at a majority of sites (n = 45). Surveys (performed between June 20 and Sept 9, 2017) were conducted on 20-50 m stretches of coastline and included the entire intertidal region, from Lower Low Water Large Tide (LLWLT) to the upper limit of marine organisms. A subset of these sites (N = 17) were surveyed in both June and September and no differences in kelp diversity were detected during this time. Sites occurred broadly throughout the region, and were situated across a range of wave exposures, slopes, aspects, and types of rocky substrates. Public data from nearby lighthouses show that both sea surface (SST) and air temperatures in Barkley Sound have reached abnormal highs between 1995 and 2017 with especially high temperatures occurring during the 2014 -2016 heatwave (Figs S1-S3, Supplemental Discussion).

Results & Discussion

Across the study system, we found widespread declines in kelp species richness and abundance mediated by local variation in wave action. Kelp species richness has not changed significantly at wave-exposed sites (Paired t-test: $t = 0.63511$, $df = 9$, $p = 0.5412$), while kelp communities at wave sheltered sites have been reduced to between zero and three species, regardless of their historical diversity (Fig. 1, Fig. 2). This is exemplified by a significant effect of wave exposure on proportional change in richness (ANOVA: $F_{47,1} = 17.27$, $P=0.00014$, Fig 2A, Fig S4). This habitat-dependent decline in diversity is further supported by the shallow slope of the rarefaction curve for wave-sheltered and moderate sites in 2017 (Fig 3D). At all wave exposures, average abundance also declined, highlighting how changes in abundance can be decoupled from changes in species richness, and this decline was greatest at wave sheltered sites (Fig 2B; ANOVA: $F_{43,1} = 4.396$, $P=0.042$).

Changes of between-site diversity (i.e. beta and gamma) also depended largely on wave exposure. While rarefaction curves of the entire region are similar between years across all sites, sheltered sites saw marked declines in both slope and asymptote (Fig 3), indicating spatial homogenization of these communities (28). Moreover, while at exposed sites the total number of species detected was slightly larger than in 1995, the total species pool at sheltered sites declined

from 11 species to 3 (Fig 2) with one of those species only present at one site. Despite these widespread declines in the number of species found at sheltered sites, species richness across the region did not change (Fig 3A inset, Fig S5; Supplementary Discussion). Taken together, our results show a strong disconnect in how kelp diversity has changed across scales and habitats: richness of the regional kelp assemblage has not changed, while local richness and average abundance has declined markedly, with diversity loss concentrated on wave-sheltered shores.

A few key implications arise from these findings. First, given the important ecological role of kelp (22, 29, 30), the declines that we document are likely to have cascading effects on the diversity of other organisms and on ecosystem functioning of intertidal communities (30, 31). While the affected kelp communities may yet recover following the 2014-2016 heatwave, our results suggest that wave-sheltered sites are particularly sensitive to increasing global temperatures. It could be hypothesized that declines on wave-sheltered shores may not affect regional productivity or habitat availability as much as would declines on wave-exposed shorelines, which are more diverse and more productive (18). Yet, positive interactions generated by kelp canopies may be especially important on wave-sheltered shores because these shores are more physiologically stressful (32). Furthermore, the lower diversity and productivity of sheltered shorelines is far outweighed by their sheer abundance in the Northeast Pacific (Fig. 4). We show that 57,000 km of wave-sheltered rocky shoreline exists from Oregon to central Alaska, virtually all of which (99.8%) occurs north (and east) of Washington's outer coast (Fig. 4A). Therefore, even small changes in kelp diversity on more sensitive wave-sheltered shores could have large effects on intertidal productivity if magnified across the landscape.

The apparent resilience of wave exposed kelp beds also has important implications for conservation and management. Recent efforts to understand biodiversity change in ecologically important biogenic habitats have identified areas where ecosystems are performing substantially better ("bright spots") or worse ("dark spots") than average (33). Our results demonstrate that a fine-scale environmental gradient, that can vary over tens of metres (34), has mediated the responses of kelp. Thus, kelp bright spots and dark spots may be located close together in space and should be examined at this fine scale. Wave exposed sites are highly productive and often represent hotspots of diversity in our system (27). Our results demonstrate that these sites may also be especially resilient against ongoing global change. Wave exposed sites may act as refugia

during times of extreme climate stress, potentially buffering kelp ecosystems against regional extinctions. Yet, given the distribution of wave exposure in the Northeast Pacific (Fig 4), dark spots are likely to be far more common. Although wave exposed sites might maintain regional diversity, abundant dark spots could have profound effects on ecosystem functioning and services (35).

In addition to reductions in diversity, we document widespread declines in the abundance of intertidal kelps in Barkley Sound. While the magnitude of decline was dependent on wave exposure (Fig 2B) and varied between species (Fig S9-S10), sites from all wave exposure categories declined significantly in average kelp abundance. Losses of kelp cover are common and a recent global meta-analysis found that more than one third of published subtidal kelp bed surveys show declines over the past 50 years (11). While many negatively affected kelp forest ecosystems are found near the warm-edge of kelps' latitudinal range(14, 23, 24, 36), our data suggest that similar declines are occurring in the intertidal zones of British Columbia, reasonably far from the warmer latitudinal limit of northeast Pacific kelp ecosystems (37). This supports previous work suggesting that central-and not just edge- populations of brown algae may be susceptible to large-scale increases in temperature (25). While declines may be attributable to recent heatwave events occurring over short timescales (38) (Fig S2-S3), rather than a response to gradual warming, recovery from ecosystem-wide declines is unlikely to occur rapidly in either case. Four of our sites lost all kelp species and thirteen others were reduced to a single, sometimes rare (< 5 % cover) species. Thus, many of our sites have experienced complete or near-complete collapses of kelp-dominated communities. Climate-related phase shifts from communities dominated by kelps to those dominated by other, less productive seaweed species, such as turfs, have unfavourable consequences for coastal productivity and ecosystem services (23). Phase shifts between kelp and turf or fucoid dominated ecosystems have been occurring worldwide for decades and many have yet to recover following initial kelp bed collapse (23, 39). This process, driven by feedbacks between biotic factors and the physical environment, is responsible for the resilience of degraded ecosystems worldwide (40, 41).

Another key implication of our results is that important biodiversity loss could easily remain hidden from studies not specifically designed with habitat heterogeneity in mind. Declines could be concentrated in only some habitats that may be stressful and low diversity to begin with. If

these marginal habitats lack novel diversity, studies that focus on regional patterns without considering habitat heterogeneity could miss losses caused by local gradients. Thus, habitat heterogeneity may directly contribute to the disconnect between diversity measurements taken at different scales (9, 10). Importantly, this means that without considering differences in site-level conditions, we would have missed the widespread biotic homogenization that has occurred only at wave-sheltered sites in our system. Capturing these losses in beta diversity is important to monitoring and conservation efforts because ecosystem functionality depends on having many species combinations across the landscape (1, 42). Yet, while our results support growing evidence that local habitat heterogeneity explains important variation in diversity loss (7, 15), few studies that examine responses to climate change incorporate these gradients into their analyses. Our results point to the need for a framework that better incorporates the interacting effects of stressors at different scales. Such an approach would hold much promise for identifying and predicting diversity loss not only at species' range edges but also along local gradients throughout the range of each species.

Habitat heterogeneity is ubiquitous in the natural world, but its importance in determining the responses of communities to climate change is often underappreciated (6). As the climate warms and average conditions change, heterogeneity of habitats will lead to variation in microclimates (5, 20) and thus will affect the biological responses of organisms. Therefore, rather than assess average responses across all communities in a region or across the globe (9, 10), we should work to identify the habitats that are most vulnerable to declines and determine whether they are abundant enough to influence ecosystem functioning across the landscape. Consistent declines across all habitat patches or at the most diverse, high quality habitats are likely not reasonable predictions for how communities will respond to climate change (43). Instead, diversity may be lost from marginal habitats and, if these habitats are common, the consequences to ecosystem functioning could be profound.

Methods

Study system

Barkley Sound, on the southwest coast of Vancouver Island, Canada, is a nearly 30 km wide inlet containing hundreds of islands. As such, it provides a wide range of local microhabitats.

Both wave-sheltered and wave-exposed sites are located throughout the area both near and far from the opening to the sound. Sites were accessed by boat. Historical survey data spans 1993-1995 with most (n = 46) sites sampled twice in 1993 (n = 19) or 1994 (n = 27) and 1995. However, three sites were only sampled in either 1993 (n = 2) or 1994 (n = 1) and not in 1995 (Supplementary Table 1).

Locating historically surveyed sites

Sites were located using GPS coordinates, photographs, and descriptions recorded in the original surveys. In particular, most sites were located using a photo that was often annotated with the exact location of the transect. A thorough description of the site was also given by the authors and allowed for location of some sites that did not have photographs. Sites were only resurveyed if they could be definitively located in at least one of these two ways using distinct geographic landmarks.

Survey techniques

Surveys were conducted following the methods of the original surveyors. Survey sites were uniform lengths of shoreline and included the area between the high tide line and LLWLT (approximately 3 m vertical distance). Presence and absence of all kelp species were determined for the entire survey area by carefully identifying all kelp species present in an area by morphology. Kelps are large, seasonally persistent and are easy to distinguish based on conspicuous morphological features(27). Thus, both our surveys and those done by the original surveyors were likely to result in unbiased, reproducible data. In order to quantify abundance, the intertidal was blocked into four zones: high intertidal (approx. > 2.5 m), mid intertidal (approx. 1.2 – 2.5 m), low intertidal (approx. 0.2 – 1.2 m) and shallow subtidal (0 – 0.2 m). Abundance of each species, in each zone, was then quantified based on visual estimation of percentage cover categories: absent (0 %), rare (< 5 %), common (6 – 20 %) and abundant (21 – 100 %). A species' assigned abundance was then taken from the zone of its greatest abundance.

Shoreline classification

The extent of rocky habitats of different wave exposures was determined using a comprehensive georeferenced linear shoreline dataset for the North American Pacific coast called

ShoreZone(44). ShoreZone data spans from Oregon to Alaska and is based on expert classification of shoreline units using low-elevation aerial imagery obtained from fixed-wing aircraft or helicopter and relevant geographic features. During segment classification, each shoreline unit is assigned a substrate class from high-resolution imagery, and assigned a wave-exposure class using a combination of fetch calculations and geographic and biotic features. For the current study, predominantly rocky shoreline was identified by selecting all shoreline units from this dataset which contained at least 25% rocky substrate (Shorezone coastal classes 1-20). Regional totals of the extent of shoreline containing only bedrock (ShoreZone coastal classes 1-5) were 44-78% shorter than regional totals reported in Fig. 4 but produced the same patterns of relative habitat types between regions.

Wave exposure quantification

Quantifying wave exposure is a known challenge to intertidal biologists, as local topography can influence water velocities in ways that many geographical indices fail to capture(34). Because the average shoreline unit in the ShoreZone dataset is between 300m and 500m long (much longer than our 20-50 m surveys), the ShoreZone wave exposure classification is not able to resolve small scale differences in exposure that fall within a single shoreline unit. Thus, for characterization of Barkley Sound sites, we used the site-specific wave-exposure categories provided by the original Barkley Sound surveyors (Druehl & Elliot (27)). This method categorized sites based on direct, qualitative observations of water motion (45) and the presence of indicator species. Importantly, site classifications using these two methods produced similar results: 96% of sites were within one wave exposure category of one another (and classifications at 67% of sites agreed completely). Sites that differed between methods included a tidepool that was set back from the shore and protected from incoming waves, three exposed headland sites in areas that were otherwise largely sheltered from waves, and two sites that were located on the wave-sheltered side of islands that were near the mouth of the sound where overall wave exposure is greater. Barring these few exceptions that arose largely due to differences in the scale at which wave exposure was assessed, the overall concordance of the two independent approaches suggests that scaling up to the broader region using the ShoreZone dataset is appropriate. We used a cartographical method previously developed (46) and tested (47) in Barkley Sound to further test the validity of these categories. In brief, this method is a continuous

index derived from the angle of unimpeded exposure to the predominant direction of offshore swell (southwest). It is therefore only effective for SW facing sites (47). We used all of our SW (180-270°) facing sites (N = 26) to ground-truth these wave exposure categories (ANOVA on ranks: $F = 17.24$, $P < 0.001$; Fig S6) and showed that sites categorized as "Protected" had significantly lower wave exposure index measures than "Moderate" and "Exposed" (Tukey HSD: $P < 0.001$ for both). There was also a strong, insignificant trend suggesting a difference between "Moderate" and "Exposed" sites (Tukey HSD: $P = 0.0637$). Together, this suggests that our wave exposure categories were appropriate.

Statistical analyses

All analyses were performed in R 3.4.1 (R Development Core Team, 2008). To assess whether wave exposure and survey year significantly influenced the richness and abundance of kelps at each site, we used ANOVAs on site-level proportional responses (ratio of historic to modern values) with wave exposure (fixed factor, three levels) as an explanatory variable. Comparisons were made to averages of historical survey data when more than one year was sampled during the 1993-1995 surveys (n = 46). Rarefaction and regional species pool extrapolation were performed using the "vegan" package in R. Modern (2017) trends were compared to 1995 data when available (n = 46) or else 1993 (n = 2) or 1994 (n = 1) data were used. However, separate comparisons to 1993-1994 (n = 49) and 1995 (n = 46) are provided in the supplementary (Fig S7, S8). While diversity of annual species was generally lowest in 1995, comparing separately to the different initial survey years did not influence our overall results. To rule out spatial effects, we tested for spatial correlation of proportional richness responses using Moran's I in the R package "ape".

Acknowledgements

This work would not have been possible without the initial surveys which were conducted by Druehl and Elliot and funded by Parks Canada. We thank the Huu-ay-aht First Nations, S. Rogers, B. Anholt, S. Gray, B. Rogers, T. Eastham, N. Wiewel and other Bamfield Marine Sciences Centre (BMSC) staff for making this work logistically feasible. Students in the 2017 Coastal Community Ecology class at BMSC contributed to field logistics and planning. We thank C. Harley, P. Thompson and M. Whalen for their many insightful comments on an earlier

version of this paper, and thank J. Sunday for helpful feedback on data interpretation. SS and CJN designed the study, collected and analyzed the data, and wrote the paper. LB, EC, KJ, and AW assisted with designing the study and collecting the data, and contributed to writing and editing the paper. The authors declare no competing interests.

Literature Cited

1. Isbell F, et al. (2017) Linking the influence and dependence of people on biodiversity across scales. *Nature* 546(7656):65–72.

2. Thomas CD (2013) Local diversity stays about the same, regional diversity increases, and global diversity declines. *Proc Natl Acad Sci* 110(48):19187–19188.

3. Gonzalez A, et al. (2016) Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. *Ecology* 97(8):1949–1960.

4. Cardinale BJ, Gonzalez A, Allington GRH, Loreau M (2018) Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. *Biol Conserv* 219:175–183.

5. Helmuth B, et al. (2002) Climate change and latitudinal patterns of intertidal thermal stress. *Science* 298(5595):1015–1017.

6. Helmuth B, et al. (2014) Beyond long-term averages: making biological sense of a rapidly changing world. *Clim Change Responses* 1(6). doi:10.1186/s40665-014-0006-0.

7. Russell BD, Connell SD (2012) Origins and consequences of global and local stressors: incorporating climatic and non-climatic phenomena that buffer or accelerate ecological change. *Mar Biol* 159(11):2633–2639.

8. Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421(6918):37–42.

9. Dornelas M, et al. (2014) Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science* 344(6181):296.

10. Vellend M, et al. (2013) Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc Natl Acad Sci* 110(48):19456–19459.

11. Krumhansl KA, et al. (2016) Global patterns of kelp forest change over the past half-century. *Proc Natl Acad Sci* 113(48):13785–13790.

12. Tewksbury JJ, Huey RB, Deutsch CA (2008) Putting the Heat on Tropical Animals. *Science* 320(5881):1296–1297.

13. Hughes RN, Hughes D, Smith IP (2013) Oceans and marine resources in a changing climate. *Oceanogr Mar Biol Annu Rev* 51:71–192.

14. Wernberg T, et al. (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* 353(6295):169–172.

15. Harley CDG (2011) Climate Change, Keystone Predation, and Biodiversity Loss. *Science* 334(6059):1124–1127.

16. Helmuth B, et al. (2016) Long-term, high frequency *in situ* measurements of intertidal mussel bed temperatures using biomimetic sensors. *Sci Data* 3:160087.

17. Denny MW (2006) Ocean waves, nearshore ecology, and natural selection. *Aquat Ecol* 40(4):439–461.

18. Leigh EG, Paine RT, Quinn JF, Suchanek TH (1987) Wave energy and intertidal productivity. *Proc Natl Acad Sci* 84(5):1314–1318.

19. Hurd CL (2017) Shaken and stirred: the fundamental role of water motion in resource acquisition and seaweed productivity. *Perspect Phycol*:73–81.

20. Fitzhenry T, Halpin PM, Helmuth B (2004) Testing the effects of wave exposure, site, and behavior on intertidal mussel body temperatures: applications and limits of temperature logger design. *Mar Biol* 145(2):339–349.

21. Reed D, et al. (2016) Extreme warming challenges sentinel status of kelp forests as indicators of climate change. *Nat Commun* 7:13757.

22. Steneck RS, et al. (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29(4):436–459.

23. Filbee-Dexter K, Wernberg T (2018) Rise of Turfs: A New Battlefront for Globally Declining Kelp Forests. *BioScience* 68(2):64–76.

24. Wernberg T, et al. (2011) Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *J Exp Mar Biol Ecol* 400(1):7–16.

25. Bennett S, Wernberg T, Joy BA, Bettignies T de, Campbell AH (2015) Central and rear-edge populations can be equally vulnerable to warming. *Nat Commun* 6:10280.

26. Pfister CA, Berry HD, Mumford T The dynamics of Kelp Forests in the Northeast Pacific Ocean and the relationship with environmental drivers. *J Ecol* 0(0). doi:10.1111/1365-2745.12908.

27. Druehl, L.D., Elliot, C.T.J. (1996) Parks Canada Barkley Sound Kelp Distribution.

28. Tyler CL, Kowalewski M (2017) Surrogate taxa and fossils as reliable proxies of spatial biodiversity patterns in marine benthic communities. *Proc R Soc B* 284(1850):20162839.

29. Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science(Washington)* 245(4914):170–173.

30. Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7(4):341–357.

31. Hautier Y, et al. (2018) Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. *Nat Ecol Evol* 2(1):50–56.

32. Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18(3):119–125.

33. Cinner JE, et al. (2016) Bright spots among the world's coral reefs. *Nature* 535(7612):416–419.

34. Helmuth B, Denny MW (2003) Predicting wave exposure in the rocky intertidal zone: Do bigger waves always lead to larger forces? *Limnol Oceanogr* 48(3):1338–1345.

35. Loreau M, et al. (2001) Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science* 294(5543):804–808.

36. Assis J, et al. (2017) Major shifts at the range edge of marine forests: the combined effects of climate changes and limited dispersal. *Sci Rep* 7:44348.

37. Bolton JJ (2010) The biogeography of kelps (Laminariales, Phaeophyceae): a global analysis with new insights from recent advances in molecular phylogenetics. *Helgol Mar Res* 64(4):263–279.

38. Lorenzo ED, Mantua N (2016) Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nat Clim Change* 6(11):1042–1047.

39. Filbee-Dexter K, Feehan CJ, Scheibling RE (2016) Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Mar Ecol Prog Ser* 543:141–152.

40. Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* 19(1):46–53.

41. O'Brien JM, Scheibling RE (2018) Turf wars: competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. *Mar Ecol Prog Ser* 590:1–17.

42. Fanin N, et al. (2017) Consistent effects of biodiversity loss on multifunctionality across contrasting ecosystems. *Nat Ecol Evol* 2:269–278.

43. Elahi R, et al. (2015) Recent Trends in Local-Scale Marine Biodiversity Reflect Community Structure and Human Impacts. *Curr Biol CB* 25(14):1938–1943.

44. Howes D (2001) BC biophysical shore-zone mapping system—A systematic approach to characterize coastal habitats in the Pacific Northwest. *Proceedings of the 2001 Puget Sound Research Conference, Seattle, Washington: 11p*.

45. Topinka J, Tucker L, Korjeff W (2009) The Distribution of Fucoid Macroalgal Biomass Along Central Coastal Maine. *Bot Mar* 24(6):311–320.

46. Burns KC, Neufeld CJ Plant extinction dynamics in an insular metacommunity. *Oikos* 118(2):191–198.

47. Neufeld CJ, Starko S, Burns K (2017) Disturbance and diversity in a continental archipelago: A mechanistic framework linking area, height, and exposure. 8(10):e01957.

Figures

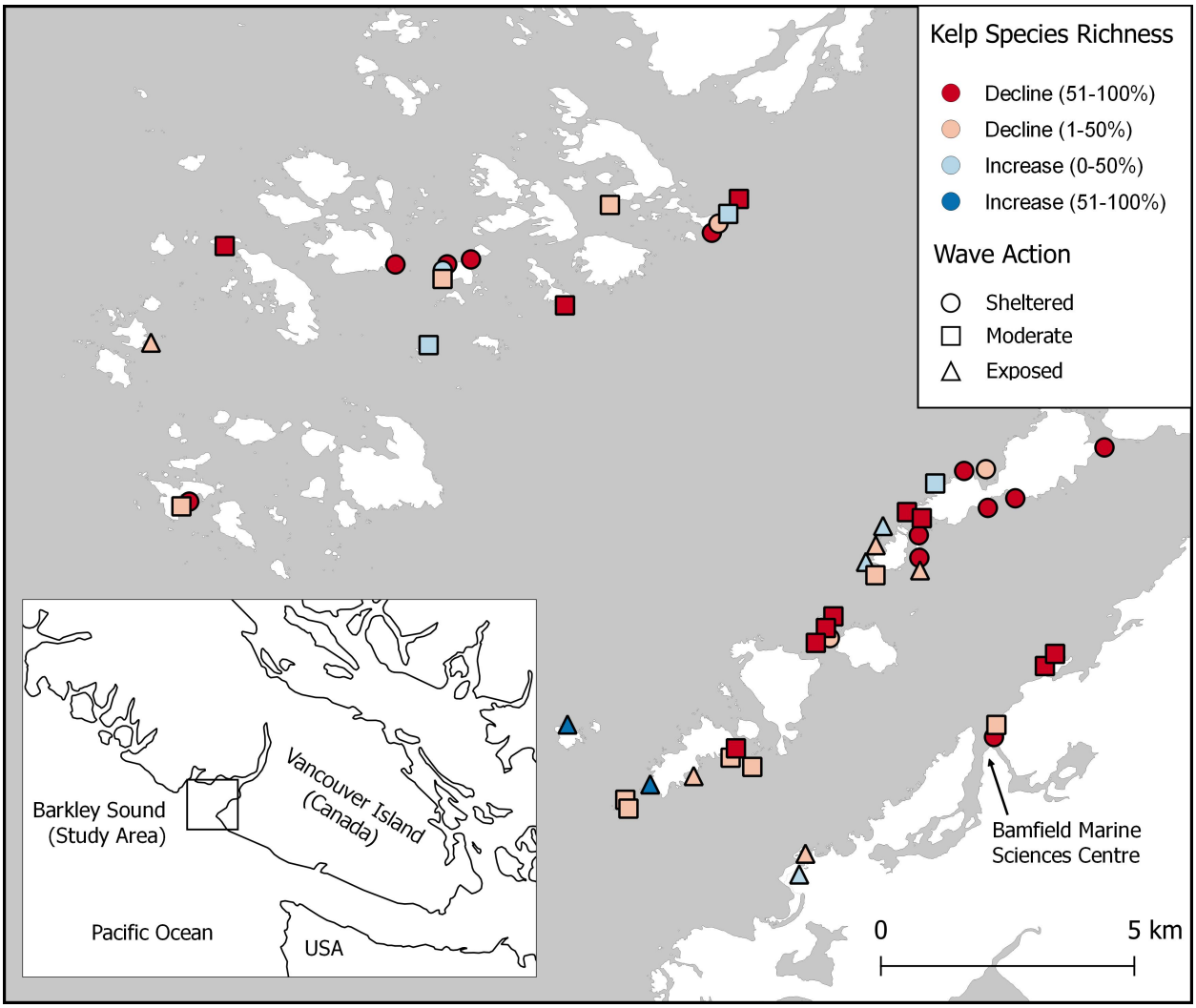

Figure 1. Study region. Study sites (n = 49) are coded for magnitude of change in kelp species richness (colour) and relative exposure to waves (shape). Due to the close proximity of some sites, some symbols have been moved slightly to avoid obscuring overlapping symbols. There was no effect of the spatial distribution of sites on proportional kelp richness change (Moran's I: I = 0.0303, p = 0.49676).

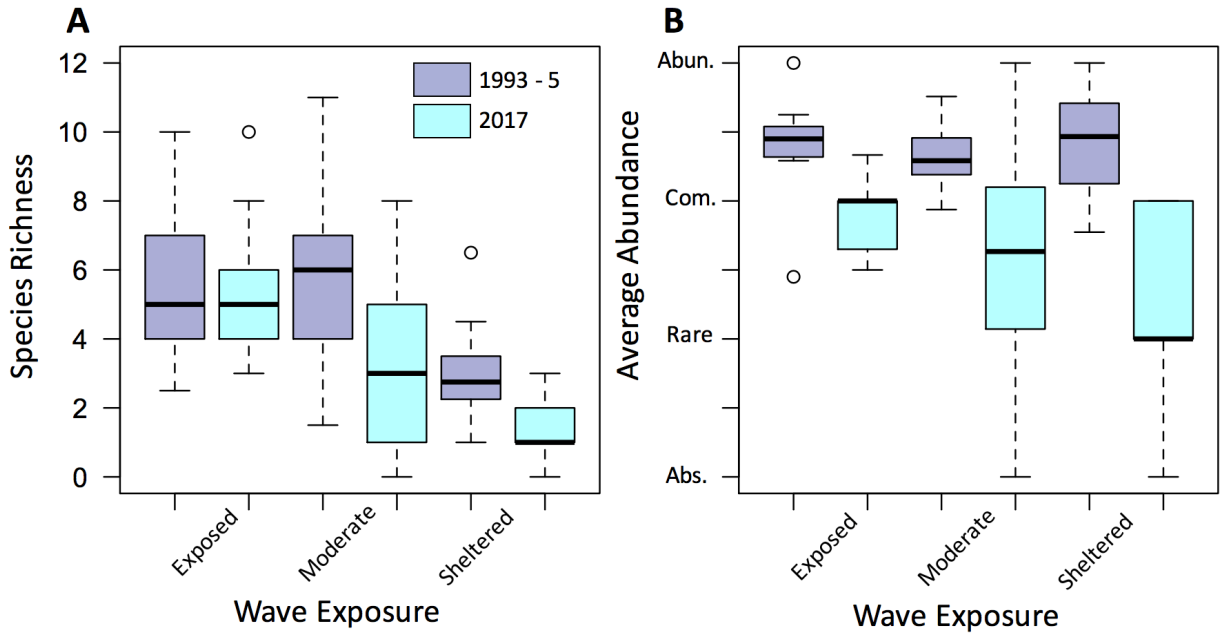

Figure 2. (A) Richness and (B) average abundance of species at each site (absent = 0, rare = 1, common = 2, abundant = 3) for historical (average of 1993 – 1995) and modern (2017) observations. There is a significant effect of wave exposure on site-wise proportional changes in richness (ANOVA: $F_{47,1}$ =17.27, P=0.000136) and abundance (ANOVA: $F_{43,1}$ = 4.396, P=0.0420).

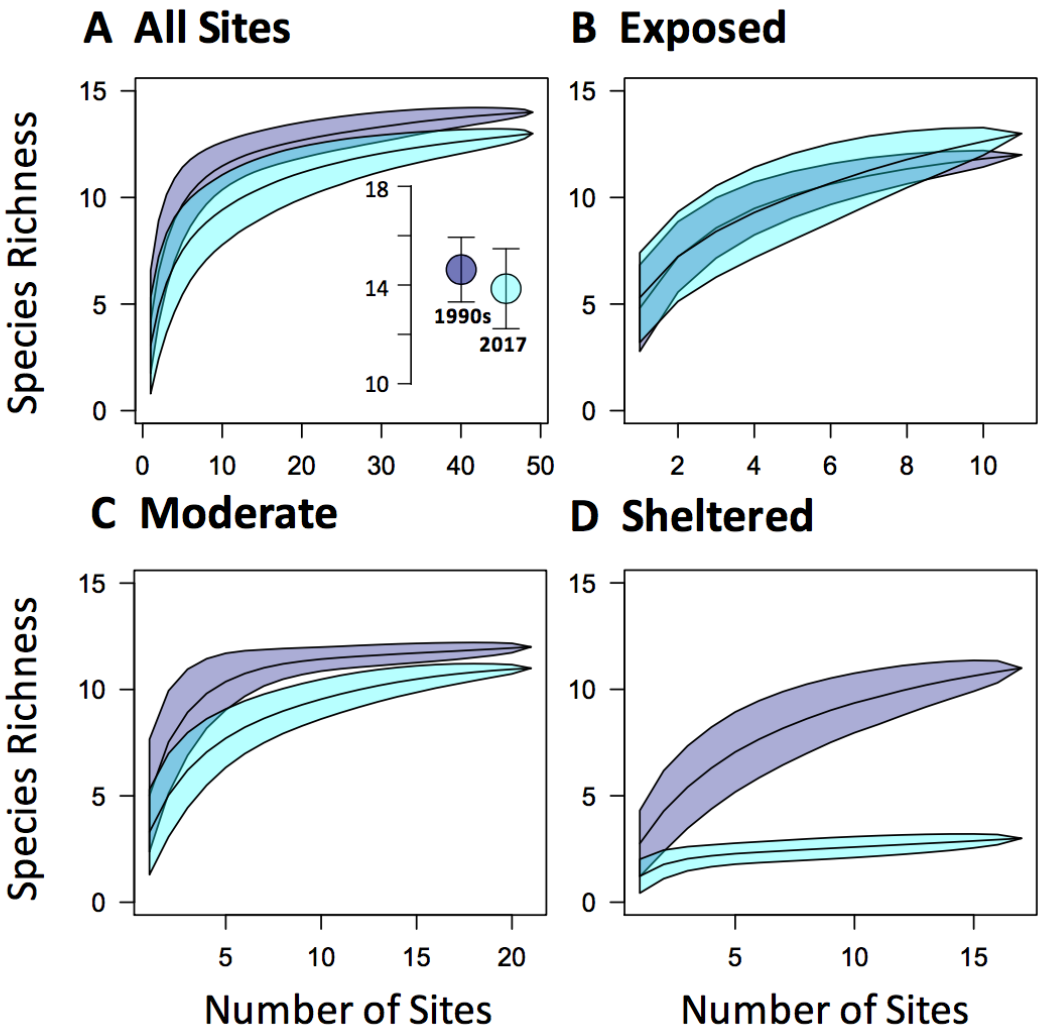

Figure 3. Rarefaction curves (10,000 iterations) for modern (2017) and historic (1995 for 46 sites, 1993 for 2 sites and 1994 for 1 site) surveys of sites in Barkley Sound. Analyses are broken down by (A) all sites, and then for (B) wave exposed, (C) moderately exposed sites and (D) sheltered sites plotted separately. The inset in (A) shows the results of a bootstrap extrapolation of total regional species richness of the Sound.

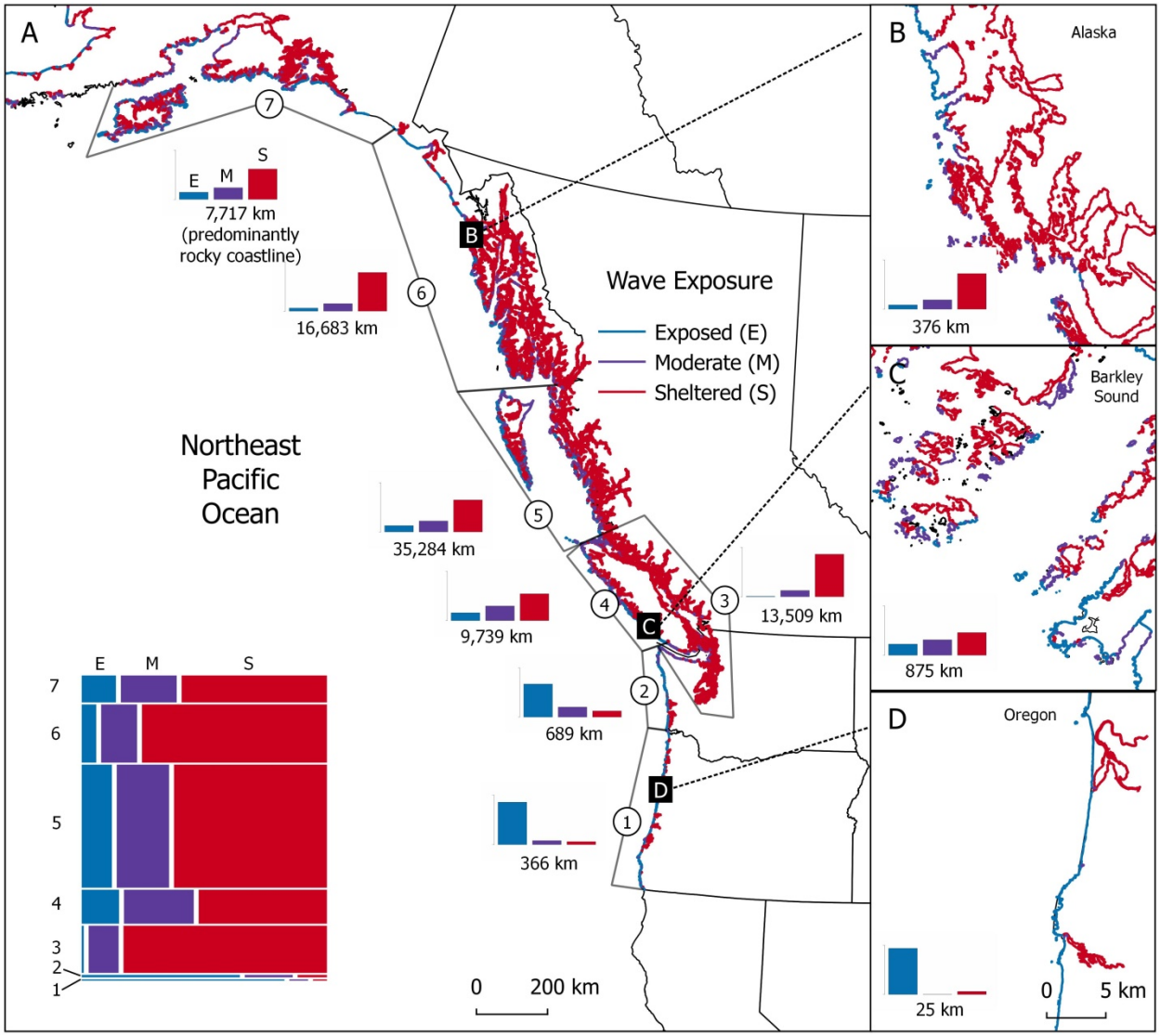

Figure 4. Northeast Pacific intertidal habitat classified by wave exposure. Wave-sheltered habitat makes up the majority of Northeast Pacific shorelines (A) and is abundant in British Columbia (C) and Alaska (B) but rare along the outer coast of Washington and Oregon (D). Bar plots show the proportions of rocky shoreline of different wave-exposures and are accompanied by the length of predominantly rocky shoreline in each region (A) or in each inset (B-D). Mosaic plot inset in A shows the relative proportions of rocky shoreline of different wave-exposures scaled by the length of coastline for each region. Regions from South to North: (1) Oregon coast, (2) Washington outer coast, (3) Salish Sea, Puget Sound, and Strait of Georgia, (4) western Vancouver Island, (5) northern British Columbia, (6) southern Alaska, (7) central Alaska.

Supplementary Information

Table S1. Information on resurveyed intertidal sites (N = 49)

Site	Location	Latitude	Longitude	Historic Survey Years	Survey 1 Date	Survey 2 Date	Historic Richness	Modern Richness
2	Taylor	48.82743	-125.198038	1993, 1995	05-Sep-17	NA	11	8
3	Execution	48.812146	-125.180139	1993, 1995	06-Sep-17	NA	9	8
4	Execution	48.812041	-125.179913	1993, 1995	06-Sep-17	NA	10	10
5	Grappler	48.838243	-125.13494	1993, 1995	24-Jun-17	06-Sep-17	3.5	3
6	Grappler	48.838181	-125.134626	1993, 1995	07-Sep-17	NA	2.5	1
7	Dixon	48.851866	-125.123474	1993, 1995	24-Jun-17	07-Sep-17	6.5	1
8	Dixon	48.852223	-125.122775	1993, 1995	24-Jun-17	07-Sep-17	5	1
9	EdwardKing	48.82448	-125.213356	1993, 1995	06-Sep-17	NA	7	5
11	Bordelais	48.818086	-125.230454	1993, 1995	05-Sep-17	NA	9.5	5
12	Bordelais	48.817634	-125.229917	1993, 1995	05-Sep-17	NA	8	6
13	EdwardKing	48.828558	-125.204139	1993	28-Jun-17	06-Sep-17	7	4
14	EdwardKing	48.828717	-125.204389	1993	06-Sep-17	NA	10	5
30	Wouwer	48.860772	-125.357202	1993, 1995	07-Sep-17	NA	4.5	3
32	Wouwer	48.861302	-125.357366	1993, 1995	07-Sep-17	NA	6.5	2
34	Clarke	48.888457	-125.373135	1993, 1995	27-Jun-17	09-Sep-17	5	4
36	Faber	48.894443	-125.298961	1993, 1995	27-Jun-17	NA	4	5
41	Dempster	48.904582	-125.263939	1993, 1995	27-Jun-17	09-Sep-17	4	1
43	Swale	48.925732	-125.221832	1993, 1995	09-Sep-17	NA	3	1
44	Swale	48.925484	-125.222428	1993, 1995	09-Sep-17	NA	3.5	4
45	Reeks	48.922616	-125.225964	1993, 1995	09-Sep-17	NA	4.5	2
46	Reeks	48.922907	-125.225972	1993, 1995	09-Sep-17	NA	3.5	3
76	Turtle	48.907905	-125.310621	1994, 1995	27-Jun-17	NA	1.5	0
77	Mullins	48.908379	-125.297087	1994, 1995	27-Jun-17	NA	2.5	1
78	Mullins	48.907967	-125.297332	1994, 1995	27-Jun-17	NA	1.5	1
79	Keith	48.910532	-125.290631	1994, 1995	27-Jun-17	NA	2	1

	Island by Parks Canada Float							
81	Cabin	48.923335	-125.255429	1994, 1995	09-Sep-17	NA	1.5	1
87	Ohiat	48.853069	-125.182697	1994, 1995	25-Jun-17	10-Sep-17	7	3
88	Ohiat	48.853069	-125.182697	1994, 1995	25-Jun-17	10-Sep-17	7	3
89	Ohiat	48.851451	-125.184224	1994, 1995	25-Jun-17	10-Sep-17	6	3
90	Ohiat	48.851917	-125.181785	1994, 1995	25-Jun-17	10-Sep-17	2.5	2
91	Mullins	48.907974	-125.297047	1994, 1995	27-Jun-17	NA	1	1
92	Ross	48.868131	-125.160674	1994, 1995	25-Jun-17	10-Sep-17	3	0
93	Ross	48.86774	-125.16022	1994, 1995	25-Jun-17	10-Sep-17	4	3
94	Ross	48.872095	-125.161593	1994, 1995	26-Jun-17	10-Sep-17	4	2
95	Ross	48.875072	-125.164307	1994, 1995	25-Jun-17	10-Sep-17	6.5	3
96	Ross	48.874192	-125.162649	1994, 1995	25-Jun-17	10-Sep-17	6	2
100	Sanford	48.865213	-125.171261	1994, 1995	04-Sep-17	NA	6.5	5
101	Sanford	48.86601	-125.173179	1994, 1995	04-Sep-17	NA	5	6
102	Sanford	48.87099	-125.171427	1994, 1995	06-Sep-17	NA	5	5
103	Sandford	48.870678	-125.17178	1994, 1995	06-Sep-17	NA	4.5	3
105	Flemming	48.884797	-125.150315	1994, 1995	26-Jun-17	NA	3.5	0
107	Flemming	48.884945	-125.14714	1994, 1995	26-Jun-17	NA	3	2
112	Flemming	48.878488	-125.144102	1994, 1995	26-Jun-17	08-Sep-17	3.5	1
113	Flemming	48.880801	-125.137096	1994, 1995	07-Sep-17	NA	2.5	1
114	Flemming	48.891793	-125.115041	1994, 1995	28-Jun-17	08-Sep-17	2	1
119	Folger	48.830687	-125.248756	1994, 1995	05-Sep-17	NA	2.5	5
121	Flemming	48.881603	-125.158976	1994, 1995	04-Sep-17	NA	4.5	5
123	EdwardKing	48.822012	-125.224653	1994, 1995	05-Sep-17	NA	3	5
155	Trickett	48.90721	-125.35684	1994	26-Jun-17	NA	4	0

Supplementary Results & Discussion

Causes of decline

It is unclear whether we have documented a permanent loss of kelp habitat or a temporary response to recent oceanographic events (Lorenzo & Mantua 2016[1],). Yet, the magnitude of the species loss and the multiannual life cycle of many affected kelp species, greatly suggest that that our results represent more than year-to-year variation that was missed during the initial three years of surveys. Extreme temperature events are predicted to increase in strength and frequency as a response of climate change (Jentsch et al 2007[2]). So, regardless of whether the responses we document are permanent, they suggest that wave-sheltered habitats are more sensitive to climate and oceanographic change. Long-term air temperature data from Cape Beale Lighthouse (Fig S2) and SST data from Amphitrite Lighthouse (Fig S3) in Barkley Sound suggest that numerous high temperature events have occurred between the 1993-1995 Parks Canada Survey and our 2017 surveys. Moreover, both air temperatures and water temperatures were higher between the 5-year period of 2013 – 2017 than between 1991 – 1995 (Fig S1).

There are multiple factors that could be contributing to the declines in kelp abundance we show. The only two species found reliably at sheltered sites were *Macrocystis pyrifera*, and *Egregia menziesii*, which are low intertidal species that are only exposed during the most extreme low tides. This suggests that warm air temperature anomalies over the past two and a half decades are a likely driver of the decline. Splashing of cool water during low tides could alleviate this increased stress at wave exposed sites, leading to the patterns that we show here (Harley and Helmuth 2003[3]). However, other factors are likely to be at play. During the recent 2014 – 2015 "Blob" and the 2016 El Nino, water temperatures were also abnormally high (Fig S3) and nitrogen levels were abnormally low (Lorenzo & Mantua 2016[1], Reed et al 2016[4]). Local mixing at sites with more water motion could mediate these stresses by improving nutrient uptake and by preventing pockets of warm water from forming at small scales. Nutrient availability may also influence thermal tolerance and so multiple stressors could be at play[5]. Regardless of the predominant driving mechanism behind the systematic degradation of wave-sheltered habitats, it

is perhaps not surprising that these were the habitats to see the largest declines; global stressors may be likely to have the largest impacts on habitats that are already stressful.

Regional species pool

Three species were detected by Druehl & Elliot but not by us: *Neoagarum fimbriatum, Saccharina latissima, & Laminaria ephemera.* These species have not gone regionally extinct, however, as they have been observed around Barkley Sound recently. *Neoagarum fimbriatum* and *Saccharina latissima* are subtidal species that sometimes have upper limits in the low intertidal. Thus, although they were detected by Druehl & Elliot, they were rare and not faithful to the sites at which they were found. *Neoagarum fimbriatum* was observed subtidally in Bamfield Inlet this year (2017). Although its upper limit was below LLWLT, it was still abundant there. *Saccharina latissima* was found in a tidepool at one site in 1993 (but not 1995). Although this species was not present at that site in 2017, we observed it subtidally at San Jose Islets at the northeast end of Barkley Sound (N 48.900675, W -125.054415). Thus, these two species may have moved deeper into the subtidal (and out of our survey range) but they have remained present within the Sound as of 2017. *Laminaria ephemera* was collected from Edward King Island in 2015 (Starko and Martone 2016[6]), near some of our sites, and was found in the wrack at nearby Pachena Bay (N 48.790481, W -125.120173) in 2016 (Starko per. obs.). Further support for no change in the regional species pool comes from strong overlap in the confidence intervals of the bootstrapped estimates of historic and current regional species richness produced using the R package 'vegan' (Fig S5).

Species-specific responses

There was substantial variation in the site-level responses of species. Even for species that declined on average, there were new colonisations and increases in abundance at some sites. While some species (e.g. *Egregia menziesii*) were found at more sites in 2017 than in the 1990s, other species have declined considerably and this was dependent on wave exposure (Fig S9). In order to assess whether species identity and wave exposure influenced changes in local abundance, we performed a Two-Way ANOVA on rank-transformed data. Abundance change was calculated by determining the difference between modern abundance and average historical abundance ranks (3 = abundant, 2 = common, 1 = rare) and wave sheltered and moderate sites

were pooled to increase the sample size for each species. There were significant, possibly interacting effects of species identity and exposure on abundance change (1995: Rank-Transformed Two-way ANOVA; Species: df = 7, F = 3.752, p = 0.00089, Exposure: df = 1, F = 14.947, P = 0.00033, Species*Exposure: df = 7, F = 1.932, p = 0.0682; 1993-1994: Rank-Transformed Two-way ANOVA: Species: df = 11, F = 4.557, p < 0.0001, Exposure: df = 1, F = 14.947, P < 0.001, Species*Exposure: df = 11, F = 1.755, P = 0.0631; Fig S9, S10) and modern species abundances differed significantly at all sites when compared to either 1993-4 (ANOVAs: Exposed: F = 4.4550, df = 9, P = 0.0001; Moderate: F = 3.4911, df = 9, P = 0.0011 ; Sheltered: F = 1.2690, df = 4, P = 0.2959) or 1995 data (ANOVAs: Exposed: F = 1.8357, df = 7, P = 0.0947; Moderate: F = 2.6131, df = 6, P = 0.0300 ; Sheltered: F = 4.4179, df = 3, P = 0.0098). For example, *Alaria marginata* increased in abundance or stayed the same at a majority of exposed sites, while it decreased substantially at sheltered and moderate sites (Fig S10, S11). This further highlights the need to consider local gradients when assessing the responses of individual species, as well as when studying community-level changes.

Supplementary References

1. Lorenzo, E. D. & Mantua, N. Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nat. Clim. Change* **6,** 1042 (2016).
2. Jentsch, A., Kreyling, J. & Beierkuhnlein, C. A new generation of climate-change experiments: events, not trends. *Front. Ecol. Environ.* **5,** 365–374 (2007).
3. Harley, C. D. G. & Helmuth, B. S. T. Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnol. Oceanogr.* **48,** 1498–1508 (2003).
4. Reed, D. *et al.* Extreme warming challenges sentinel status of kelp forests as indicators of climate change. *Nat. Commun.* **7,** 13757 (2016).
5. Thomas, M. K. *et al.* Temperature-nutrient interactions exacerbate sensitivity to warming in phytoplankton. *Glob. Change Biol.* **23,** 3269–3280 (2017).
6. Starko, S. & Martone, P. An empirical test of 'universal' biomass scaling relationships in kelps: Evidence of convergence with seed plants. (2016). doi:10.1111/nph.14120
7. Burns, K. C. & Neufeld, C. J. Plant extinction dynamics in an insular metacommunity. *Oikos* **118,** 191–198

Supplementary Figures

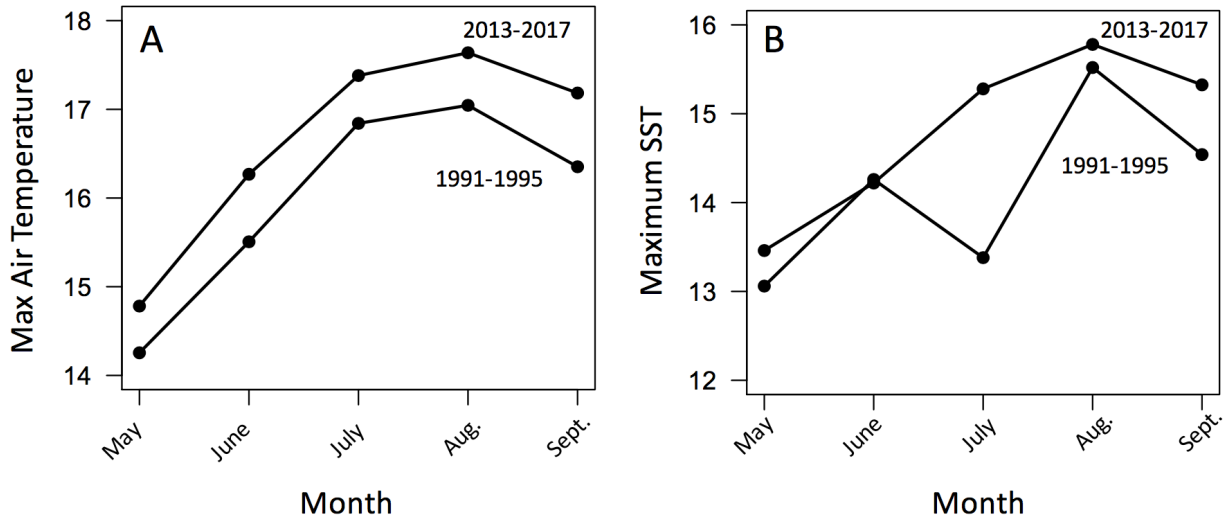

Figure S1. Maximum air and water temperatures between the periods of 1991 – 1995 and 2013 – 2017. Panel (A) shows the maximum daily temperature averaged by month and by time-period; data is from Cape Beale Lighthouse. Panel (B) shows the maximum monthly sea surface temperature averaged by time-period; data is from Amphitrite Lighthouse. Both lighthouses are located on the outer edge of Barkley Sound, British Columbia.

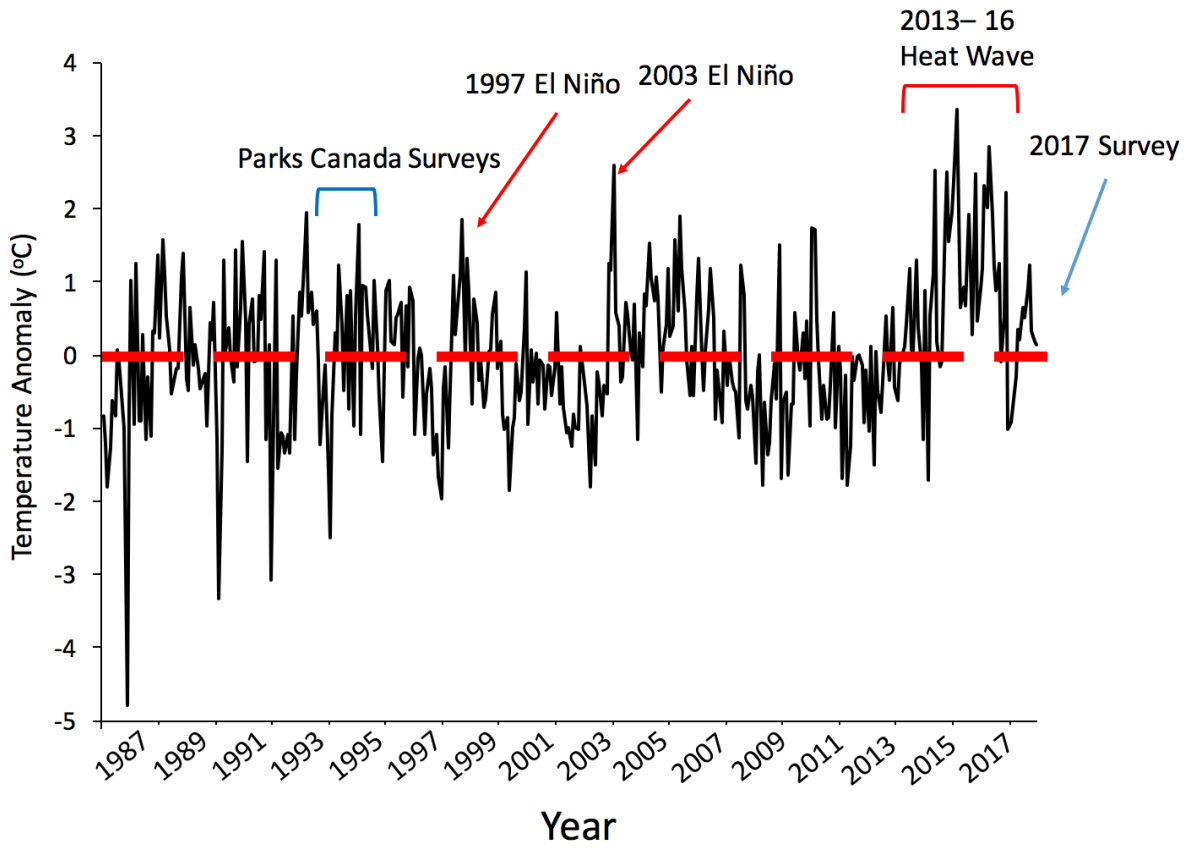

Figure S2. Anomalies in average monthly air temperature calculated as difference from a 32-year average (1985 – 2017). Data is from Cape Beale Lighthouse at the entrance to Barkley Sound. Survey dates and extreme climate events are indicated on the figure.

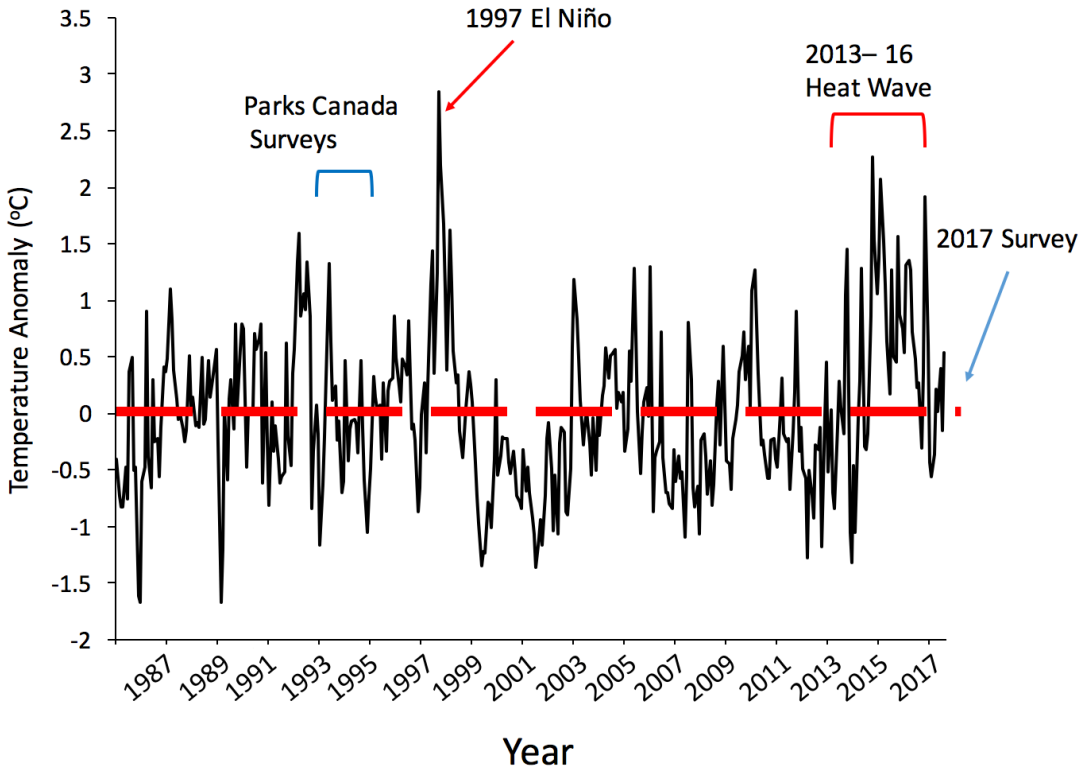

Figure S3. Anomalies in average monthly sea surface temperature (SST) calculated as difference from a 32-year average (1985 – 2017). Data is from Amphitrite Lighthouse at the entrance to Barkley Sound. Survey dates and extreme climate events are indicated on the figure.

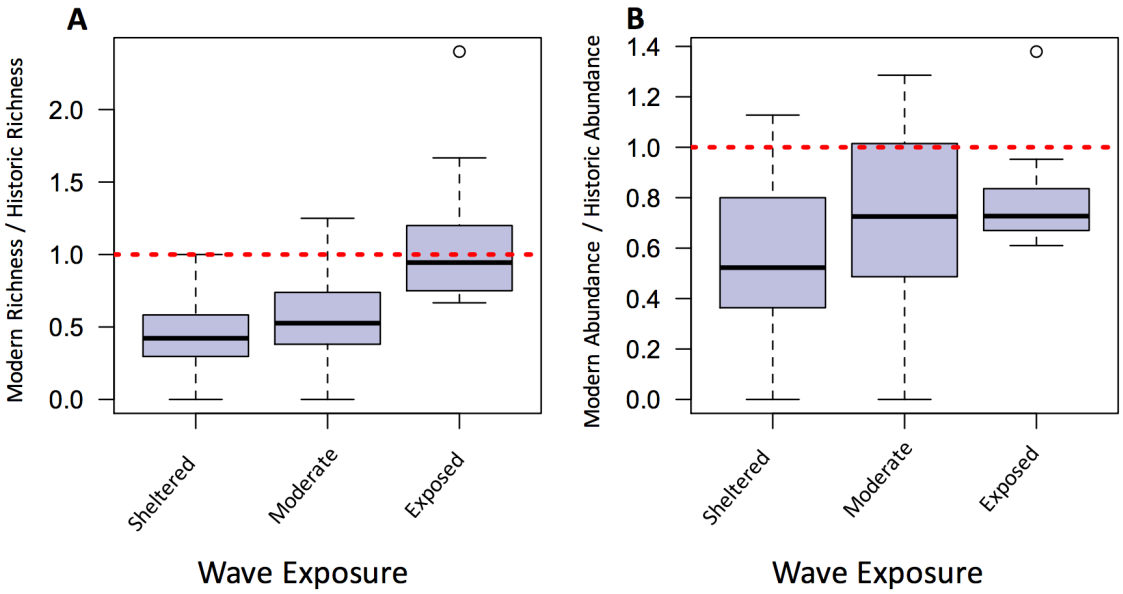

Figure S4. Proportional, site-level changes in (A) richness and (B) average abundance, broken down by wave exposure. Both panels display ratios of modern and average historic observations and red lines indicate zero change.

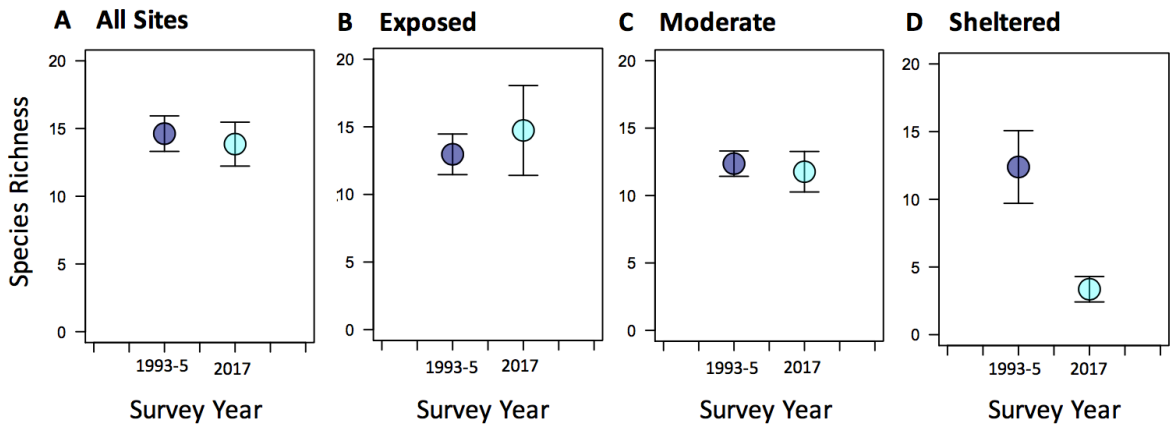

Figure S5. Results of a bootstrap extrapolation for (A) exposed, (B) moderate and (C) sheltered species pools, as calculated using the specpool function in the R package 'vegan'. Historical data include surveys from 1995 (n = 46), 1993 (n = 2) and 1994 (n = 1). Points represent bootstrapped estimates of species richness and error bars represent 95% confidence intervals.

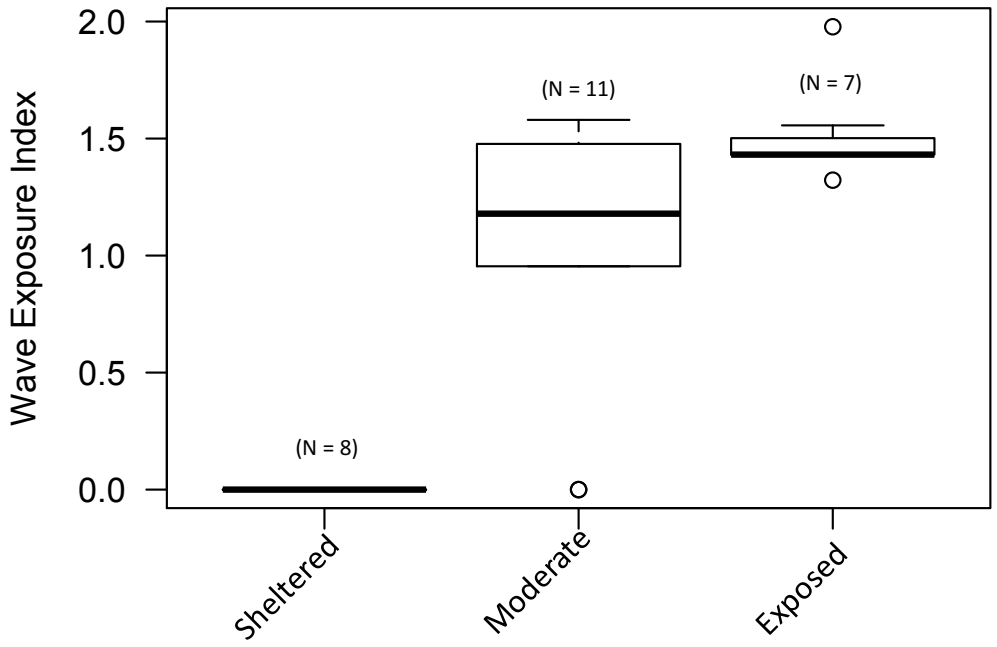

Fig S6. Boxplot of cartographical Wave Exposure Index measure (from Burns & Neufeld[7]) versus the wave exposure categories used in this study, for SW facing sites (N = 26).

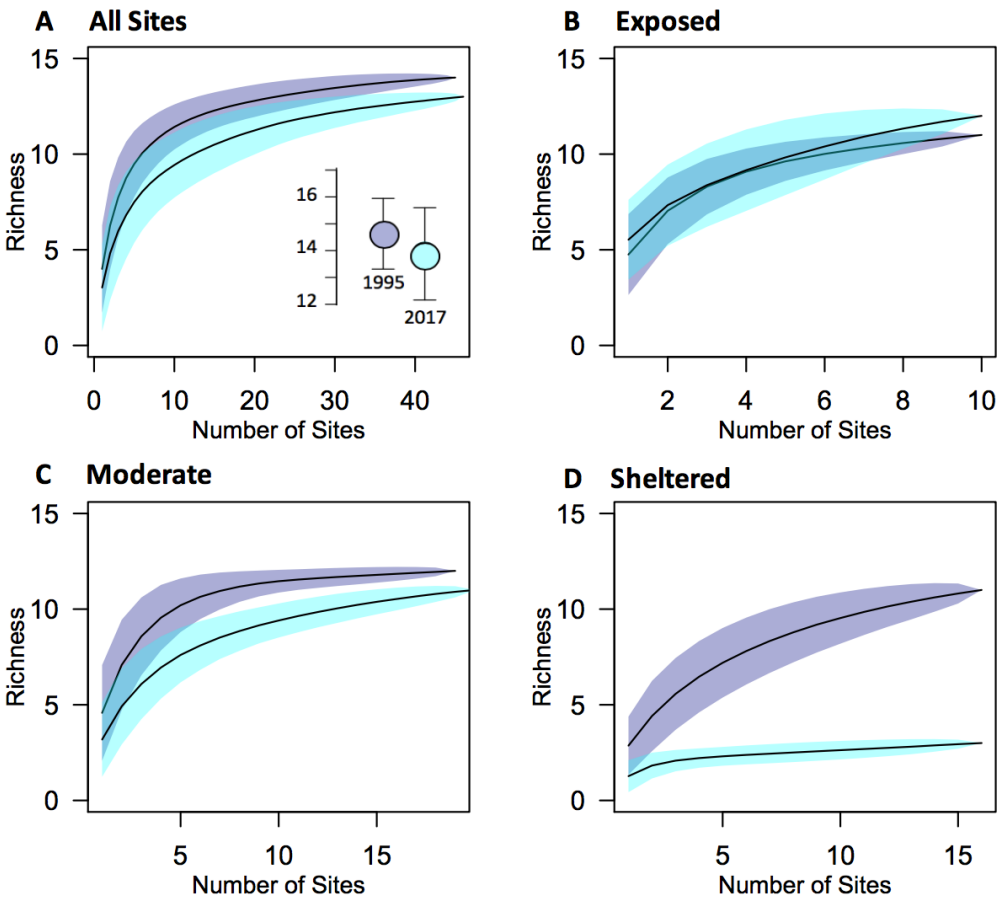

Figure S7. Rarefaction curves (10,000 iterations) for modern (2017) and 1995 surveys of sites in Barkley Sound (N = 46). Analyses are broken down by (A) all sites, and then for (B) wave exposed, (C) moderately exposed and (D) sheltered sites plotted separately. The inset in (A) shows a bootstrapped estimate of total regional species richness of the Sound.

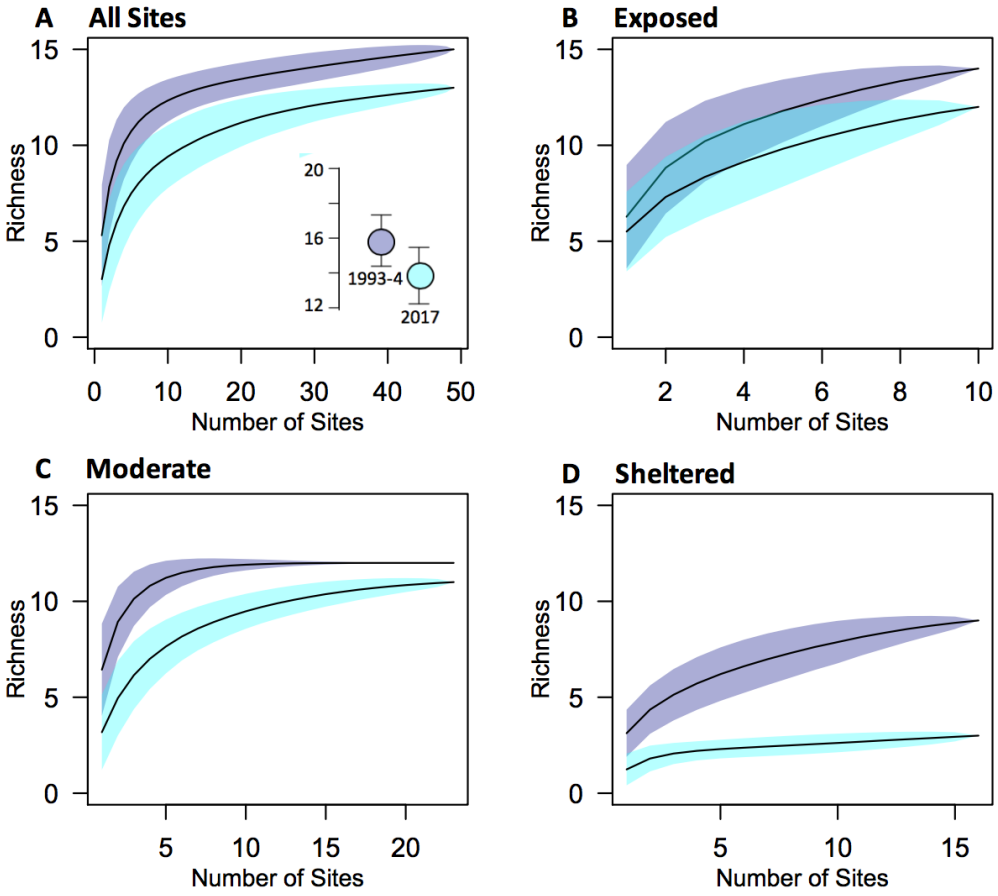

Figure S8. Rarefaction curves (10,000 iterations) for modern (2017) and 1993-4 surveys of sites in Barkley Sound (N = 49). Analyses are broken down by (A) all sites, and then for (B) wave exposed, (C) moderately exposed sites and (D) sheltered sites plotted separately. The inset in (A) shows a bootstrapped estimate of total regional species richness of the Sound.

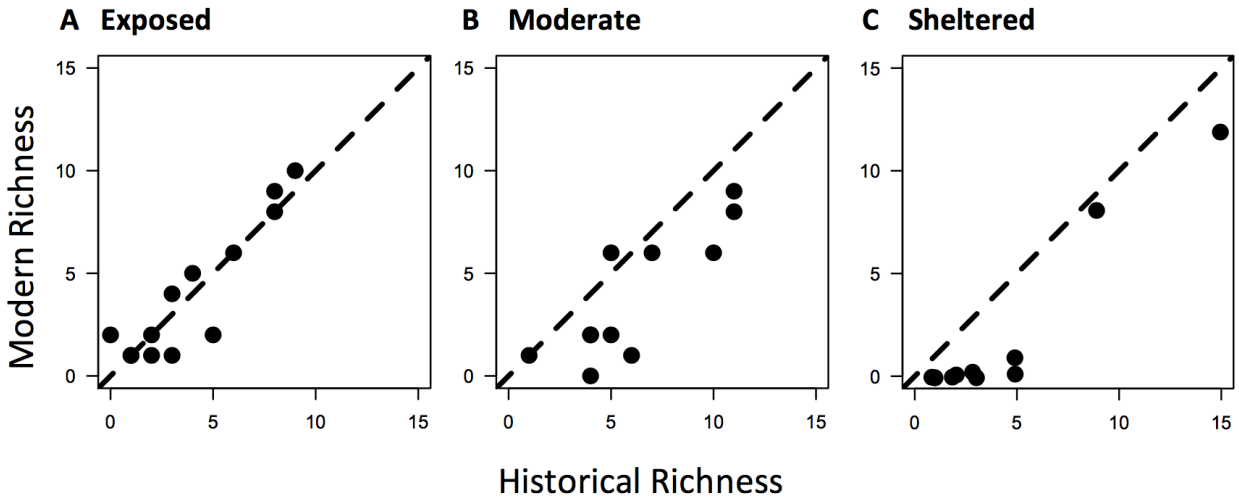

Figure S9. The number of sites occupied by each species in 2017 versus in 1995 (n = 46), 1993 (n = 2) and 1994 (n = 1) for (A) exposed, (B) moderate, (B) sheltered sites. Lines are 1:1 and represent no change, while the data-points are species. There was no significant effect of year on the number of sites occupied by species at exposed sites (Paired t-test: N = 14, t = 0, P = 1.0) but there was a significant effect of year on the number of sites occupied by species at moderate (Paired t-test: N = 12 , t = 3.14851, P = 0.0046) and sheltered sites (Paired t-test: N = 13 , t = 5.7565, P = 0.0002). Due to overlap, data-points in (C) are jittered.

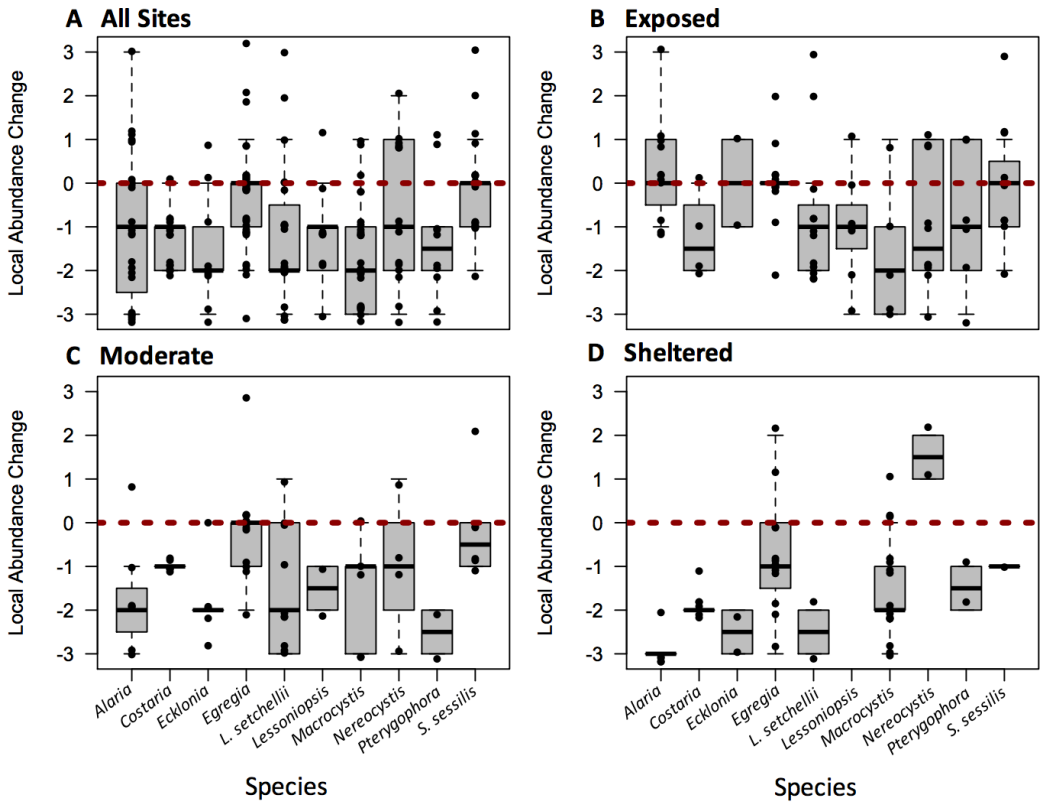

Figure S10. Change in local abundance rank (between 1995 and 2017) of each species at (A) all sites, (B) wave exposed, (C) moderate and (D) sheltered sites, measured as the difference in abundance rank (3 = abundant, 2 = common and 1 = rare) at sites where a species was present in either year.

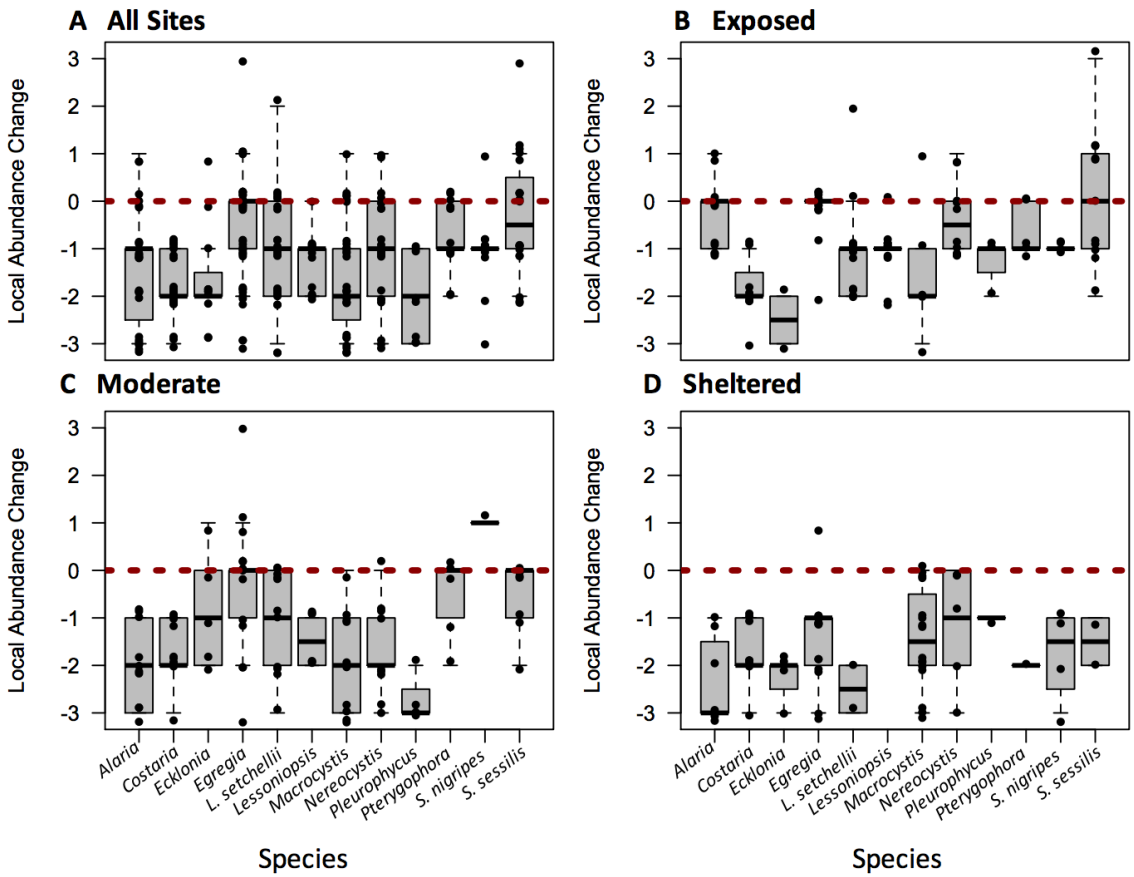

Figure S11. Change in local abundance rank (between 1993 or 1994 and 2017) of each species at (A) all sites, (B) wave exposed, (C) moderate and (D) sheltered sites, measured as the difference in abundance rank (3 = abundant, 2 = common and 1 = rare) at sites where a species was present either year.