Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas

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Abstract

Primary productivity of marine ecosystems is largely driven by broad gradients in environmental and ecological properties. In contrast, secondary productivity tends to be more variable, influenced by bottom-up (resource driven) and top-down (predatory) processes, other environmental drivers, and mediation by the physical structure of habitats. Here, we use a continental-scale dataset on small mobile invertebrates (‘epifauna’), common on surfaces in all marine ecosystems, to test influences of potential drivers of temperature-standardised secondary production across a large biogeographic range. We found epifaunal production to be remarkably consistent along a temperate to tropical Australian latitudinal gradient of 28.6°, spanning kelp forests to coral reefs (~3500 km). Using a model selection procedure, epifaunal production was primarily related to biogenic habitat group, which explained up to 45% of total variability. Production was otherwise invariant to predictors capturing primary productivity, the local biomass of fishes (proxy for predation pressure), and environmental, geographic, and human impacts. Highly predictable levels of epifaunal productivity associated with distinct habitat groups across continental scales should allow accurate modelling of the contributions of these ubiquitous invertebrates to coastal food webs, thus improving understanding of likely changes to food web structure with ocean warming and other anthropogenic impacts on marine ecosystems.

Keywords

Macrofauna, epifauna, benthic ecosystems, trophic ecology, community ecology

Introduction

The production and transfer of biomass among constituents of an ecosystem is affected by a diversity of processes that differ among scales. At local scales, biotic interactions such as competition [1], predation [2] and facilitation or ecological complementarity (as related to local species richness [3, 4]) influence productivity. In contrast, regional patterns in productivity tend to relate to larger-scale variation in primary producer characteristics, temperature, and nutrient availability (i.e. 'bottom up' processes; [5]). Reconciling these varied drivers of community productivity has long been a goal of ecologists, particularly in marine systems [6].

In this era of 'big data,' our capacity to simultaneously evaluate a suite of potential influences has yielded novel insights regarding productivity – a fundamental ecosystem property [7]. Phytoplankton productivity, for example, can now be readily assessed across large biogeographic scales using remote sensing tools [8-10]. However, secondary productivity—particularly biomass production at the basal consumer level, including many small heterotrophs that funnel energy through the food web—is less easily quantified, with laborious field assessments generally required [11, 12]. For this reason, comparisons of secondary productivity across broad biogeographic scales are relatively rare, and generalized ecological and environmental drivers are yet to be identified (but see [13, 14]).

Reef ecosystems are among the most productive and diverse on earth. The productivity of reefs is often quantified in terms of fish production [15], fisheries yield [16, 17], or the primary productivity generated by phytoplankton or benthic algae [18]. A substantial proportion of reef secondary production, though, is generated by small mobile invertebrates ('epifauna') that inhabit the surfaces of macroalgae, coral, and other benthic structures [11, 19]. Epifauna are highly abundant, diverse and ubiquitous on shallow reefs worldwide, and represent the main trophic link between benthic primary producers and small carnivores [20, 21]. Despite their fundamental role in coastal food webs, the drivers of epifaunal productivity—and thus, 'fuel' for most coastal food webs—have rarely been examined outside highly-controlled experiments [22, 23] and a few local- to regional-scale investigations [5, 13, 24].

Potential drivers of epifaunal productivity can be hypothesized based on documented patterns in other trophic groups and ecosystems, and on relationships described in previous studies of epifauna. Many biological processes are heavily influenced by temperature, and therefore strong latitudinal patterns in productivity are often reported. For example, in forests [25], open oceans [26], freshwater streams [14], and seagrass beds [27], productivity is generally highest at equatorial latitudes and lowest towards the poles, largely as a product of metabolic and growth rates scaling with temperature and light [28]. Concurrent spatial variation may also suggest unmeasured environmental factors, perhaps including evolutionary processes playing out over longer timeframes that favour more productive traits at low latitudes [29, 30]. Moreover, epifaunal secondary productivity may not respond as consistently as primary productivity to latitudinal temperature gradients. Although tropical/temperate differences have been observed [31], previous research indicates there may be no clear pattern in epifaunal productivity across smaller gradients or distinct locations [13, 32].

Both biotic (ecological) interactions and environmental drivers are fundamental determinants of food web structure and function [33], and their relative importance has been debated for several decades [6, 34]. Local-scale biotic interactions such as predation are clearly important in marine food webs [2, 22, 35, 36], and as such, variation in epifaunal productivity has often been discussed in terms of predation pressure [37-39]. Relationships between epifauna and various metrics of predation pressure, however, are inconsistent [22, 40]. Predation effects are further complicated by mesopredator release [41] and the fact that functional groups in addition to obligate invertivores, such as scraping and browsing herbivores, may ingest and assimilate epifauna [42, 43], leading to greater trophic transfer along unexpected pathways. The relationship between secondary productivity and biomass of potential predators may therefore vary along large-scale gradients due to both the functional composition of predator communities and the feeding behaviour within functional groups [44].

In concert with local-scale ecological interactions, broad-scale environmental drivers such as changes in resource supply can equally influence secondary productivity. This phenomenon may play out through changes in the abundance and composition of primary producers , which often correlate with changes in environmental conditions, for example light (moderated by factors such as depth and turbidity in marine ecosystems; [13, 45]) and nutrient availability [46]. Previous studies have indicated that food resources appear to set the ceiling on total production of epifaunal communities after accounting for metabolic contributions, with individuals redistributing along a size gradient to maximize community productivity depending on whether they are exposed to predators [22].

Local-scale environmental drivers may also affect secondary productivity, albeit often via interactions with local ecological processes or broad-scale environmental drivers. More complex, stable and/or diverse habitats may support higher faunal productivity through provision of greater abundance and diversity of food resources [11, 14, 47, 48], thus reducing competition among secondary producers, or through increased protection from predation [49]. Herbivorous amphipods often select more finely complex algal habitat based on the quality of predation refugia, rather than the nutritional quality of the algae [50]. In addition, while some algal species use chemical defences against fish herbivory, epifauna may be less sensitive to these defences, selecting better-defended algal habitats as a refuge against consumption by omnivores or herbivores [51]. Local-scale physical conditions – such as wave energy and current flow in marine systems [52, 53] – and nutrients [54] or pollutants [55], can all have substantial effects on faunal community structure and function. These factors, and others such as removal of top predators [7, 56, 57], are often related to proximity and density of human populations [58], and nearby industrial or agricultural activities [59, 60].

Here, we assembled a continental-scale dataset of shallow reef epifauna consistently surveyed along the east coast of Australia, with the overarching aim of identifying major drivers of variation in epifaunal secondary productivity across biogeographic provinces. Using multi-model inference, we tested six hypotheses relating to expectations from ecological theory and prior evidence (Table 1). We hypothesized that, like primary production, the major constraints on local secondary production across large scales would be set by the amount of resources and the abiotic environment, with smaller roles for biotic and other factors.

Methods

Study area and field sampling

Epifauna were sampled on shallow reefs at 11 eastern Australian locations, from southern Tasmania (43.3°S) to Lizard Island in the northern Great Barrier Reef (14.7°S) (Fig. 1). These locations represent a range of biogeographic regions, described in Appendix 1. A total of 132 samples of diverse benthic microhabitats (comprising the most common biogenic microhabitats available on rocky and coral reefs) and associated epifaunal invertebrates were collected via SCUBA. Site selection, and sample collection and preservation follow protocols described by Fraser, Stuart-Smith [61] and are presented in detail in Appendix 1.

Laboratory processing and description of variables

Productivity estimates

Preserved invertebrates from each sample were passed through a nested series of 12 sieves stacked in descending order of mesh size, following a $\log_{\sqrt{2}}$ series (8, 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71, 0.5, 0.355, 0.25, 0.18, 0.125 mm, after Edgar [62]). Invertebrates retained on each sieve were washed into petri dishes and counted under a dissecting microscope, with data binned by sieve mesh size.

Epifaunal abundance data by size bin were standardized to 1 m^2 planar seabed area (density) prior to analysis following Fraser, Stuart-Smith [61]. Standardization by seabed area was considered most appropriate for comparing epifaunal productivity to other trophic groups such as fishes in food web models.

To calculate productivity, epifaunal biomass as ash-free dry weight (AFDW) of individuals within each size bin was first derived from published estimates of mean biomass across macrofaunal taxonomic groups [62]. Productivity estimates were calculated using the general allometric equation given by Edgar [62]:

$$P = (10\text{\^{}}\big((-2.31 + 0.8 * \log 10(\mathrm{B} * 1000) + 0.89 * \log 10\mathrm{T})\big))/1000$$

where P is productivity of an individual (mg AFDW d^{-1}), B is the biomass of an individual (mg AFDW), and T is water temperature (°C) at the time of sampling. Productivity estimates of individual animals were then multiplied by density within each size bin, and size bin productivity estimates summed to provide total productivity estimates (mg AFDW m^{-2} d^{-1}) for each sample. Productivity was calculated for a standardized temperature of 20°C following Edgar [13], and hereafter referred to as P_{20}. The use of P_{20} is recommended to eliminate the effects of temperature when investigating food webs, assuming that metabolic and growth rates respond similarly to temperature change across trophic levels [13]. We note that this method for estimating biomass and productivity was originally established for individuals ≥0.5 mm; here we assume the equations used by Edgar [62] also apply to smaller individuals (≥0.125 mm) based on linear extrapolation of well-supported trends (i.e. R^2 ranging from 0.87 to 0.98 [67]). In Appendix 1 we elaborate on methods used for productivity estimates for samples collected using the venturi air-lift (i.e. from massive corals and turfing algae) and on methods used to visualize variation in epifaunal productivity among sampling locations.

Predictor variables

Predictor variables and the models in which they are applied are summarized in Table 1, while details of predictor variables are provided in Appendix 2. Appendix 1 presents detail on how and from where data were collected for each predictor variable.

Data analyses

Estimated epifaunal P_{20} per m^2 of seabed (estimated by multiplying the fraction of benthic cover provided by each microhabitat within each site by the estimated P_{20} associated with that microhabitat) was averaged within each of the 11 sampling locations to give mean P_{20} (mg AFDW m^{-2} d^{-1}) for each location. These data were plotted against latitude using a linear model in R (R Development Team 2017).

Six hypotheses were tested using multiple regression models parameterized with the appropriate predictors (Table 1) in a multi-model inference framework [63] (see [64] for the dataset and R code used for analysis). We fit a separate linear model to $\log_{10}$ transformed P_{20} (per m^2 of individual microhabitat sampled) to test each hypothesis with the set of associated predictor variables using the full (not summarized per location) dataset (n = 115) (Table 1). Assumptions of each model were tested using variance inflation factors (VIF) for independence of predictors and residuals were examined to ensure normality. We then used Akaike information criterion with small sample correction (AICc) to evaluate the likelihood of each model. We selected the best-supported model based on the Akaike weight, which describes the relative likelihood of each model given the candidate set of models. The Akaike weight (AICwt) ranges from 0-1, with 0 being no support and 1 being total support [63]. The best supported models were further evaluated by Type-III ANOVA using the *car* package

[65] and Tukey post-hoc comparison of means. We fit the models using R version 3.6.3 [66] and used the *AICcmodavg* package to compute Akaike weights [67].

Analyses described above were also conducted using temperature-dependent productivity (results presented in Table S1). However, since modelling temperature-dependent productivity as a function of temperature could lead to mathematical dependence between the response and the predictor, P_{20} was chosen as the preferred response variable.

Results

Across 28.6 degrees of latitude, we found little variation in total epifaunal community productivity (P_{20}; mg AFDW m^{-2} d^{-1}), at both the individual sample level and the location level based on the contribution of different microhabitats to total benthic cover (Fig. 2a). The lack of variation in productivity standardized by temperature (P_{20}) with latitude indicates that epifaunal productivity should maintain similar productivity relativities with other food web elements (e.g. fishes, primary producers), all equally varying with temperature as predicted by metabolic theory.

The habitat group model was overwhelmingly the best supported model to explain variation in epifaunal P_{20} (AICwt = 0.96; Table 1), suggesting that epifaunal secondary productivity is predominantly driven by characteristics of the immediate habitat group occupied by an assemblage (i.e. macroalgae, live coral, sessile invertebrate, or turfing algae). The microhabitat model, which includes finer but more numerous microhabitat categories than the habitat group model, was supported to a much lesser degree (AICwt = 0.04), suggesting that the explanatory power gained by this increased resolution was not worth the loss of additional degrees of freedom, while all other hypotheses had no support according to their Akaike weights (Table 1).

Within the habitat group model, epifaunal P_{20} differed significantly among habitat groups (*F*-value = 19.4, *P* <0.001; Fig. 2b; Table S2). Tukey pair-wise comparison of mean P_{20} among habitat groups indicated significant differences between macroalgae and live coral (*P* = 0.0033), and between turfing algae and live coral (*P* = 0.010). Epifaunal P_{20} also showed a significant positive correlation with branching (*F*-value = 6.3, *P* = 0.011; Fig. 3a; Table S2). However, the effect of branching varied significantly among habitat groups (*F*-value = 3.3, *P* = 0.024; Table S2), with the overall positive correlation between branching and P_{20} largely driven by macroalgae and turfing algae habitat groups (Fig. 3a).

Our model selection analysis suggests that the near constant epifaunal productivity observed on reefs along the east coast of Australia is a product of trade-offs in the dominant habitat groups across the latitudinal gradient (Fig. 4). Moving from tropical to temperate latitudes, the loss of live coral and associated secondary productivity is compensated by increased contributions by communities of epifauna inhabiting turfing algae and sessile invertebrate habitat groups, while macroalgal communities remain reasonably constant across the entire latitudinal range.

Discussion

Ecosystem productivity has historically been considered to be predominantly a function of environmental drivers that regulate the availability of resources [6, 7, 68]. Here, we find that habitat group primarily determines the degree of secondary productivity provided by small marine invertebrates to shallow reef food webs. Trade-offs in the local productivity afforded by each of four broad habitat groups (corals, macro- and turfing algae, and sessile invertebrates) led to a remarkably consistent trend in epifaunal secondary productivity from temperate to tropical zones.

While community structure and function have long been viewed through the lens of resource control, the controlling resource has often been framed in terms of biomass and energy transfer among trophic groups (i.e. carbon acquisition) [7, 13, 69, 70]. However, niche theory also acknowledges space as an important resource (i.e. the ‘Hutchinsonian’ niche), harkening back to seminal contributions on the organization of sessile organisms in rocky intertidal ecology [71, 72]. Habitat resources, additional to food resources, appear responsible for large-scale patterns in epifaunal community structure [61, 73]. This seems also to be the case in the current study with regards to their production, echoing a recent finding in communities of freshwater stream invertebrates in North America [14].

Why is habitat so important?

Several potential mechanisms may explain our finding. First, while epifaunal assemblages comprise a diversity of functional groups, herbivores (the ‘mesograzers’) typically dominate [13, 74]. Mesograzers tend to rely on microphytobenthic films and filaments, with some larger animals consuming macroalgae [75]. Macroalgal habitats present abundant food resources in the form of microphytobenthos and host algal tissue, potentially facilitating greater productivity of epifauna than habitats without these resources [35]. Filamentous turfing algae, in addition to offering a direct food source for mesograzers, tends to host microalgal films and capture high volumes of detritus [76], presenting an abundance and diversity of trophic resources for different epifaunal functional groups [75]. By contrast, live hard coral offers minimal food for herbivorous mesograzers [77, 78], making it largely food resource-poor except for particles trapped by coral polyps and the coral mucus consumed by some larger decapod taxa [79]. Epifauna selecting soft coral and sponge habitats, comprising the sessile invertebrate habitat group, are likely to encounter fewer food resources. Soft corals use allelopathic defences to resist colonisation by microphytobenthos and epiphytes, and consumption by epifauna [80]. Sponge tissue is consumed by some epifauna, however most sponge-dwellers consume external food sources [81, 82].

Variation in epifaunal productivity may also be influenced by differential predation susceptibility among benthic habitats. Habitat structural complexity and its role in shaping predator-prey relationships has long been discussed [49, 78, 83, 84], and may be a factor determining the relationship between epifaunal productivity and habitat groups. Epifaunal productivity increased with our metric of habitat complexity (degree of branching) (Fig. 3a), presumably due to the added protection from predators offered by more complex habitat [84, 85]. However, the degree to which this benefit is realized depends greatly on the habitat type (Fig. 3a, 3b). For example, macroalgal habitat was the most highly branched and supported among the highest estimates of epifaunal productivity, however live coral was also highly branched but supported the least productive epifaunal assemblages.

This apparent inconsistency raises the question of whether physical complexity provides actual or perceived refuges for epifaunal prey [78] and may be partly resolved by considering the scale at which complexity is quantified. While live branching coral is complex at scales ranging from millimetres to centimetres, the complexity of turfing algae is at a sub-millimetre to millimetre scale, and macroalgae complexity ranges from sub-millimetre through to centimetres [31]. In studies comparing macroalgae species [86] or artificial algal habitats of differing complexity [87], small invertebrates generally select more finely complex habitat that offers predation refugia appropriate for the invertebrate body sizes. Macroalgae complexity can also be finely partitioned by much larger herbivorous fishes [88]. If microhabitat complexity were quantified to higher resolution, for example by using fractal dimensions [89], stronger relationships between epifaunal productivity and habitat complexity would perhaps be evident, as would consistency between the complexity of habitat groups and the productivity they support.

In addition to complexity, predation pressure may vary as a result of particular characteristics of the different habitat groups. For example, while the heterotrophy of hard corals largely involves the consumption of zooplankton [90, 91], small epifaunal invertebrates could fall prey to coral polyps. Hard corals also often use physical defence strategies, such as ‘sweeper tentacles’, to resist colonization by small epiphytes and epifauna [92]. In addition, the rigid structure of branching hard coral limits the ability of mobile invertivores (e.g. fish) to penetrate the habitat in order to extract epifaunal prey [93]. Hence, branching coral can provide refugia for larger epifaunal invertebrates that may be less susceptible to consumption by coral polyps [39, 73, 94].

Fish communities on tropical reefs have been shown to comprise proportionally more herbivores compared with temperate reefs, which support more omnivorous fishes, while invertivores are consistently common across all latitudes [95]. While total fish biomass is used here as a proxy for predation pressure, understanding the differences in predation exposure for epifauna among different microhabitats would require more detailed study of the functional composition and feeding behaviour of local fish communities. For example, predation by omnivores or consumption of epifauna by herbivores may vary among algal microhabitats depending on chemical defences against fish herbivory or the palatability of algae, as epifaunal invertebrates may be insensitive to chemical defences [51] or choose less palatable algal microhabitats based on refuge quality [50].

Interestingly, neither site-scale estimates of predator biomass, nor temperature or primary productivity (assessed using water column chlorophyll content as a proxy) appeared to be explicitly related to variation in epifaunal productivity. Our use of P_{20} controls for a major environmental factor, temperature, although theory and recent studies suggest that temperature effects are most likely to manifest through enhancing the (consumable) resource base, rather than acting directly on community production [14, 96, 97]. Metabolic rate scales with temperature at approximately similar rates across trophic levels, resulting in proportionally similar production/temperature changes [13]. Given that habitat group affects potential food resources available for epifauna, whereas temperature had little apparent influence on secondary productivity, our results are consistent with the hypothesis that epifaunal productivity is limited predominantly by food resource ceilings [13, 22].

Ecological implications

Epifaunal invertebrates are extremely prolific in coastal and shallow reef ecosystems, with a very high proportion of their biomass consumed by larger invertebrate predators and fishes [11]. Consequently, epifaunal communities comprise a critical basal component in shallow marine food webs [85]. Understanding the factors that promote productive epifaunal communities is crucial for the goal of ensuring high trophic transfer and food web stability for coastal and shallow reef ecosystems. Given that the biotic habitat group occupied by the epifaunal assemblage was here found to explain >45% of the variance in secondary productivity along an extensive biogeographic gradient, understanding changes to benthic habitat group availability is the critical first step to achieving this goal.

In selecting microhabitats to sample, we attempted to include all common types of biogenic cover found on shallow coral and rocky reefs in eastern Australia. However, direct anthropogenic stressors, combined with climate change, are shifting the distribution and abundance of biogenic habitat groups common to rocky and coral reefs [98-100]. Our results reveal an important indirect pathway for the effects of global, regional, and local scale environmental changes to alter reef ecosystems. Ocean temperature has been identified as the most important driver of the benthic composition of biogenic habitat groups on both rocky and coral reefs [101]. Other important drivers include human population density, nutrient availability, wave exposure, and the density of habitat-transforming fauna such as herbivorous sea urchins or corallivorous crown-of-thorns sea stars [101-103]. Turf and sometimes macroalgae are succeeding corals lost to bleaching and other local stressors [98, 104, 105]. Macroalgae beds on rocky reefs are declining in many regions [106], often to be replaced by turf as oceans warm and voracious herbivores undergo range extensions and population outbreaks [100, 107, 108].

Mediated by shifts in available reef habitat groups, these drivers can potentially affect epifaunal invertebrate communities and food web processes. Our results imply changes to epifaunal secondary productivity should be predictable if habitat group transformation is well documented or accurately predicted. Replacement of live coral by turfing algae or macroalgae will likely increase epifaunal secondary productivity on tropical and subtropical reefs (Fig. 4) [94]. If turf replaces macroalgae on temperate reefs, a significant increase in epifaunal productivity may be expected, whereas the succession of subtropical macroalgae by turf is likely to result in minimal change (Fig. 4). Rather, relatively high epifaunal productivity may be maintained on subtropical reefs, as turfing and macroalgae both support similarly highly productive assemblages of epifaunal invertebrates.

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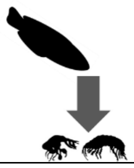
Tables

Table 1 The hypotheses (epifaunal community P_{20} is predominantly driven by: H1 – H6) and linear models tested to explain variation in epifaunal P_{20}, with predictions (P) included within models. Partial R^2 indicates the proportion of variance explained by each predictor within models; multiple R^2 indicates the raw unadjusted R^2 for each model. Model selection was based on the Akaike weight, which describes the relative likelihood of each model given the set of candidate models.

Hypothesis (H)	Model and Predictions (P)	Partial R^2	Multiple R^2	Akaike weight
H1 –Predation pressure 	**PREDATION MODEL**		0.032	<0.01
	P1 – P_{20} declines with increased total fish biomass	0.004		
	P2 – P_{20} declines with increased cryptic fish abundance	0.029		
H2 – Resource availability 	**RESOURCE MODEL**		0.122	<0.01
	P3 – P_{20} declines as depth increases (reducing light)	0.031		
	P4 – P_{20} increases with epiphyte load	0.048		
	P5 – P_{20} increases with chlorophyll-a	0.005		
	P6 – P_{20} increases with mean SST	0.038		
H3a – Characteristics of immediate habitat, fine microhabitat scale 	**MICROHABITAT MODEL**		0.594	0.04
	P7 – P_{20} varies significantly among microhabitats	0.548		
	P8 – P_{20} increases with habitat branching/complexity	0.025		
	P9 – P_{20} increases with the maximum length of habitat	0.021		
H3b – Characteristics of immediate habitat, coarse habitat group scale	**HABITAT GROUP MODEL**		0.450	0.96
	P10 – P_{20} varies significantly among habitat groups	0.344		
	P11 – P_{20} increases with habitat branching/complexity	0.030		
	P12 – the effect of branching on P_{20} varies among habitat groups	0.069		

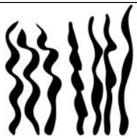
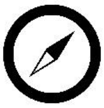
	P13 – P_{20} increases with the maximum length of habitat	0.007		
H4 – Local environmental factors 	**ENVIRONMENT MODEL**		0.114	<0.01
	P6 – P_{20} increases with mean SST	0.049		
	P14 – P_{20} declines with increased wave exposure	0.036		
	P15 – P_{20} declines with increased relief	0.009		
	P16 – P_{20} declines with increased slope	0.014		
	P17 – P_{20} declines with increased current strength	0.006		
H5 – Geographic location 	**SPATIAL MODEL**		0.091	<0.01
	P18 – P_{20} declines towards higher latitudes	0.054		
	P19 – P_{20} varies significantly with longitude	0.037		
H6 – Human population impacts 	**HUMAN IMPACTS MODEL**		0.077	<0.01
	P20 – P_{20} increases with human population density	0.077		

Figure legends

Fig. 1 Map of eastern Australia showing sampling locations, sampling dates and number of sites.

Fig. 2 Linear regression **(a)** of mean $\log_{10}$ total epifaunal community daily productivity (P_{20}) against latitude. The large black points represent mean P_{20} within each of the 11 sampling locations, estimated by multiplying the fraction of benthic cover provided by each microhabitat within each site by the estimated P_{20} associated with that microhabitat; the black line represents the regression of those data against latitude. The small grey points represent epifaunal P_{20} for individual samples; the grey line represents the regression of those data against latitude. Grey shading represents 95% confidence intervals.
Box plots **(b)** of variation in $\log_{10}$ epifaunal assemblage P_{20} among habitat groups. Horizontal lines in each box plot represent third quartile, median and first quartile. The whiskers extend to 1.5 x interquartile range. Dots represent outliers. Asterisks indicate significant differences between habitat group pairs (*$P<0.05$; **$P<0.01$).

Fig. 3 Linear regression **(a)** of mean $\log_{10}$ epifaunal P_{20} against microhabitat degree of branching, with colors indicating habitat groups, and black line the overall mean. Higher branching equates to higher complexity and translates to higher productivity on average. Points represent individual samples; grey shading represents 95% confidence interval of overall mean. Horizontal boxplots **(b)** show variation in the degree of branching within each habitat group. Vertical lines in each box plot represent third quartile, median and first quartile. The whiskers extend to 1.5 x interquartile range.

Fig. 4 Mean $\log_{10}$ epifaunal P_{20} associated with each habitat group across four climatic zones within the latitudinal gradient sampled. Mean P_{20} among habitat groups is represented for each climatic zone by the bar titled ‘All’. Climatic zones represent the following latitudinal ranges: cool temperate (-43.3 to -37.7°S), warm temperate (-37.6 to -31.9°S), subtropical (-31.8 to -26.1°S), tropical (-20.4 to -14.6°S).