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Cite this article: Zarco-Perello S, Langlois TJ, Holmes T, Vanderklift MA, Wernberg T. 2019 Overwintering tropical herbivores accelerate detritus production on temperate reefs. *Proc. R. Soc. B* **286**: 20192046.
http://dx.doi.org/10.1098/rspb.2019.2046

Received: 3 September 2019
Accepted: 22 October 2019

Subject Category:
Ecology

Subject Areas:
ecology, environmental science

Keywords:
climate change, tropicalization, seasonality, herbivory, kelp, detritus

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.4721495.

THE ROYAL SOCIETY
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Overwintering tropical herbivores accelerate detritus production on temperate reefs

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The tropicalization of temperate marine ecosystems can lead to increased herbivory rates, reducing the standing stock of seaweeds and potentially causing increases in detritus production. However, long-term studies analysing these processes associated with the persistence of tropical herbivores in temperate reefs are lacking. We assessed the seasonal variation in abundances, macrophyte consumption, feeding modes and defecation rates of the range-extending tropical rabbitfish *Siganus fuscescens* and the temperate silver drummer *Kyphosus sydneyanus* and herring cale *Olisthops cyanomelas* on tropicalized reefs of Western Australia. Rabbitfish overwintered in temperate reefs, consumed more kelp and other macrophytes in all feeding modes, and defecated more during both summer and winter than the temperate herbivores. Herbivory and defecation increased with rabbitfish abundance, but this was dependent on temperature, with higher rates attained by big schools during summer and lower rates in winter. Still, rabbitfish surpassed temperate herbivores, leading to a fivefold acceleration in the transformation of macrophyte standing stock to detritus, a function usually attributed to sea urchins in kelp forests. Our results suggest that further warming and tropicalization will not only increase primary consumption and affect the habitat structure of temperate reefs but also increase detritus production, with the potential to modify energy pathways.

1. Introduction

Primary consumption is fundamental for the transfer of energy across trophic levels and can exert a strong top-down control on the habitat structure and resilience of marine ecosystems, particularly in tropical regions [1]. Herbivores act as intermediate links between autotrophs, detritivores and secondary consumers, sustaining longer and more complex trophic chains in natural ecosystems [2]. At the same time, herbivores act as ecological engineers by regulating the cover of benthic macrophytes [3]. The intensity of herbivory follows a strong latitudinal pattern worldwide [4,5], in which tropical reefs dominated by corals have high rates of primary consumption mostly due to herbivorous fish [4,6–8], while temperate reefs dominated by large brown seaweeds experience lower rates of consumption, mostly caused by sea urchins and other mobile invertebrates [9]. Herbivorous fish are more abundant, more diverse and have more feeding strategies (e.g. browsers, grazers or scrapers) in the tropics than in temperate ecosystems [8,10–12], resulting in thousands of bites more on macrophytes per day [5,13–16]. However, as global climate change drives tropical species to shift their distribution towards higher latitudes, the guild of herbivorous fish in many temperate regions is experiencing a process of tropicalization, where the proportion of warm-water species increases and past latitudinal patterns become blurred [17].

Global warming is changing biodiversity configurations worldwide, causing poleward expansions of tropical species and creating new trophic interactions [18]. Among marine vertebrates, herbivorous fish have been some of the most successful in expanding their distribution ranges [17]. Tropical herbivorous fish of the families Scaridae (parrotfish), Kyphosidae (sea chubs) and Siganidae (rabbitfish) have established populations in temperate ecosystems, increasing herbivory rates and having a direct effect on the structural complexity of these habitats, reducing seaweed and increasing turf and bare rock cover in the eastern Mediterranean Sea [19,20], southern Japan [21] and temperate Australia [22,23], with rabbitfish being the most successful taxon in all these regions [23–25]. In addition, it has been proposed recently that the process of tropicalization can also affect temperate ecosystems indirectly by modifying the energy transfer between trophic levels [26]. Kelp forests generate great amounts of detritus, an important source of energy [27]. Currently, detritus is mainly generated by erosion or detachment of kelp sporophytes [28,29], with herbivory-derived detritus representing a small proportion and being mostly produced by sea urchins [27,30]. Herbivores shred macrophyte biomass and transform it into particulate detrital matter of higher nutritional value for multiple consumers [31,32]. This process can be accelerated with the arrival of tropical herbivorous fish to temperate ecosystems by increasing the rates of defecation, with the potential of altering fluxes of biomass and the composition of the benthic community [30,33,34].

Despite the socio-ecological importance that the transformation of kelp forests to turf ecosystems can have [35,36], there is a lack of studies that integrally evaluate the persistence of tropical herbivores over multiple seasons, their direct and indirect effects, and the interaction between these elements in tropicalized temperate ecosystems. Research to date has been restricted to assessments of seaweed consumption during warm (summer) conditions with no evaluations of its implication in detrital inputs on the temperate ecosystems or overwintering performance [16,19]. Assessments of these aspects across multiple seasons are of paramount importance since temperate winters can pose severe eco-physiological challenges to tropical fish adapted to more stable warmer environments [37,38]. Temperature modulates the metabolic rates of fish [39] and consumption of macrophytes [40,41], and in extreme cases can lead to high mortality rates associated with physiological stress and starvation [42,43]. Still, some tropical herbivores seem to be extending their distribution polewards successfully, but currently it is unknown how they are performing throughout the year in temperate reefs and how it compares with their temperate competitors and pre-tropicalization stages, information necessary to understand the magnitudes of change in current and future times. In this study, we sought to answer (i) whether rabbitfish overwintered in temperate reefs and suffered changes in abundances, (ii) which was their relative importance on transforming the standing stock of kelp and other macrophytes into detritus over the seasons of the year, and (iii) how this depended on the interaction between the number of herbivorous individuals and the environmental temperature, two factors that are predicted to increase in the future on temperate reefs. To test this, we assessed over multiple years (2016–2018) the seasonal variation in the abundances of the range-shifting tropical rabbitfish *Siganus fuscescens*, their herbivory rates in different feeding modes and their defecation rates, and compared these with the most important kelp consumers native of temperate reefs of Western Australia: *Kyphosus sydneyanus* and *Olisthops cyanomelas*.

2. Methods

(a) Location

The study was carried out at four temperate rocky reefs within Marmion Marine Park (Perth) in southwestern Australia (31°49.4 S, 115°44.0 E), where the rabbitfish *S. fuscescens* has established populations following a marine heatwave in 2011 [23]: Cow Rocks, Wreck Rock, Whitfords Rock and The Lumps. These reefs are separated from each other by 1 ± 0.1 km and are characteristic of the inshore limestone reefs along the coast of southwestern Australia, having similar environmental conditions associated with depth (approx. 5 m), wave exposure (1 km from land and subject to wind and oceanic swell of up to 4 m high) and substrate (limestone rock with reef flats, reef walls, crevices and overhangs). The reefs are dominated by the kelp *Ecklonia radiata* and the fucoids *Sargassum* spp., and are surrounded by meadows of the seagrasses *Posidonia sinuosa* and *Amphibolis* spp. [44].

(b) Herbivorous fish abundance and rates of herbivory

Fish abundance and herbivory rates were assessed during three consecutive years (2016, 2017 and 2018) in both the summer (November–April) and winter (July–September) seasons (summer: $n = 19$; winter: $n = 16$ days). During each sampling day at each reef, fish abundance was surveyed using stereo diver-operated video (S-DOV) before deploying bioassays of kelp filmed with remote underwater videos (RUV). Three or four 25 × 5 m S-DOV transects were sampled along the ecotone between reef and seagrass, separating each transect by a minimum of approximately 10 m to ensure independence of replicates and ignoring fish appearing from behind the cameras to avoid double counting [45]. Using EventMeasure software (SeaGIS Pty Ltd), all individual fish were counted, measured (fork length) and identified to the lowest taxonomic level possible. Fish known to be consumers of kelp were classified by climatic affinity (tropical: rabbitfish *S. fuscescens*; temperate: silver drummer *K. sydneyanus* and herring cale *O. cyanomelas*). Herbivory on kelp was assessed through tethered bioassays consisting of a cluster of at least nine individual approximately 15 cm long lateral blades of *E. radiata* attached to 0.5 m rods simulating kelp canopy. One cluster was deployed per reef at each sampling day, representing one independent sampling unit. Tethers were deployed within the typical feeding time frame of diurnal herbivorous fish, from the morning until the afternoon (8.00–16.00 h) [46] and filmed for 3–4 h with GoPro cameras to identify the species responsible for the consumption of kelp, their relative abundances (MaxN), their bite rates on kelp (bites h^{-1}) and defecation rates (faeces h^{-1}). During winter of 2018 (September), we deployed additional kelp tethers for 3 days to test if consumption rates would increase under a higher timeframe of exposure. In addition to herbivory on tethered kelps, bites on other macrophytes attached to the substratum and drifting in the water column were also registered during RUV analyses (e.g. kelp, seagrass, *Sargassum* spp., *Ulva* spp., *Hypnea* spp.). We identified the species of fish feeding and classified their herbivory modes as: browsing (substrate-attached macrophytes, including kelp tethers), kelp browsing (attached *E. radiata*), drifting (non-attached macrophytes) and total herbivory (browsing + drifting consumption).

Kelp lateral blades of bioassays were pressed between a white background and a Perspex glass and photographed before and after deployment. The photographs of kelp were analysed using the software IMAGEJ (rsb.info.nih.gov/ij/) to calculate the area consumed per time ($cm^2\ h^{-1}$) [23,44,47]. This was transformed to biomass ($g\ h^{-1}$) using a linear area–weight regression. Herbivory and defecation rates were standardized for each species of the main kelp consumers (tropical rabbitfish: *S. fuscescens* and temperate silver drummers: *K. sydneyanus*). Bite rates estimates were multiplied by weight-specific bite sizes (cm^2), calculated from bite size-weight regressions using bite measures from specimens of both species donated by the Department of Primary Industries and Regional Development (Fisheries Research) and recreational fishermen (electronic supplementary material), while defecation rates were multiplied by the mean weight of each species calculated from the corresponding S-DOV carried out immediately before each herbivory assay [48]. Underwater temperature data for each reef were recorded *in situ* during the fish and herbivory surveys using HOBO data loggers. The full dataset used for analyses is accessible from the Dryad Digital Repository [49].

(c) Statistical analyses

We used mixed-effects linear regression analyses to evaluate (i) the effect of temperature on the abundance (S-DOV and MaxN) of tropical and temperate herbivorous fish, and the effect of both temperature and herbivorous fish abundance on (ii) kelp consumption rates, (iii) drift consumption rates and (iv) defecation rates of *S. fuscescens* and *K. sydneyanus*. Changes in fish abundance were evaluated with negative binomial generalized linear mixed models using the R package glmmTMB [50]. Fish herbivory and defecation rates were analysed with linear mixed-effects models (LMEM) with the R package nlme [51]. Since the effect of multiple unmeasured factors in the natural environment can affect the phenomena of interest and increase the frequency of low values, masking the true effect of explanatory variables, we applied linear quantile mixed-effects regressions (LQMM) to the 90th percentile of the response distribution using the R package lqmm in addition to regressions based on the conditional mean of the response variables [52]. The use of quantile regression in ecological studies has increased since it is a more robust technique than the more common ordinary least-squares approach and it allows a more complete analysis of the relationships between variables [53]. In all regressions, we included random intercepts based on reefs and years, but for herbivory and defecation rates, we also included random slopes based on herbivorous fish abundance. Models with different structure of the random components were compared and the best was chosen based on AIC, BIC, likelihood-ratio test and graphical examination of predictions versus observations. Overdispersion, normality and homogeneity of the residuals of LMEM were assessed with histograms and fitted versus predicted scatterplots. When assumptions were not met, data were log transformed. In the case of statistically significant effects of explanatory variables, we used the R package sjPlot to graph the model predictions [54]; temperature was plotted as the moderator variable based on mean (18.59°C) and ±s.e. values (20.85 and 16.33°C). The R code of these analyses is provided in electronic supplementary material.

3. Results

(a) Persistence during winter

Rabbitfish were present at temperate reefs in all surveys. There was no significant relationship between herbivorous fish abundance and temperature (figure 1). However, all herbivorous fish species were present in higher average abundances during summer, with tropical rabbitfish being the most abundant (MaxN: 25.8 ± 8.1; S-DOV: 12 ± 4 individuals $125\ m^{-2}$, mean ± s.e.), followed by silver drummers (MaxN: 10.2 ± 4.4, S-DOV: 3.5 ± 1.4 individuals $125\ m^{-2}$) and herring cale (MaxN: 0.4 ± 0.6, S-DOV: 0.4 ± 0.2 individuals $125\ m^{-2}$). Rabbitfish remained present during winter in waters as cold as 16°C, forming schools (MaxN: 17.3 ± 7.2, S-DOV: 5.8 ± 2.7 individuals $125\ m^{-2}$) of similar abundance as silver drummers (MaxN: 7 ± 3.1, S-DOV: 4.1 ± 1.4 individuals $125\ m^{-2}$) but greater than herring cale (MaxN: 0.3 ± 0.1, S-DOV: 0.25 ± 0.2 individuals $125\ m^{-2}$) (figure 1). Rabbitfish average fork length was 28.5 ± 1.5 cm (min: 20.5 cm and max: 38.5 cm), while silver drummer average length was 43.2 ± 9.1 cm (min: 18 cm and max: 72.5 cm). Silver drummers had larger bite area than rabbitfish by three times within their comparable weight range (i.e. 200–400 g) and six times larger at bigger sizes (approx. 7300 g) (electronic supplementary material).

(b) Primary consumption rates

Temperate and tropical herbivorous fish consumed kelp at higher rates in the warmest temperatures of summer (max T: 22°C) than in the lower temperatures in winter (min T: 16°C). Rabbitfish total consumption rate during summer was $244 \pm 65\ cm^2\ h^{-1}$ (mean ± s.e.) from 18 092 total bites (426 bites h^{-1}), while in winter, the average rate was $7.4 \pm 7.4\ cm^2\ h^{-1}$ from 979 total bites (15.3 bites h^{-1}). In comparison, silver drummers consumed macrophytes at a rate of $45.6 \pm 22\ cm^2\ h^{-1}$ in summer (715 bites: 21.2 bites h^{-1}) and $1.7 \pm 1.6\ cm^2\ h^{-1}$ in winter (69 bites: 1.1 bites h^{-1}). Herring cale had the lowest consumption rates with only 83 bites (1.6 bites h^{-1}) in all summer surveys and zero consumption during winter (figure 2).

Rabbitfish browsing was 37 times higher during summer ($223 \pm 64\ cm^2\ h^{-1}$) than during winter ($6 \pm 5.9\ cm^2\ h^{-1}$). Similarly, although at lower rates, browsing by silver drummer was 26 times higher during summer ($42 \pm 22\ cm^2\ h^{-1}$) than in winter ($1.7 \pm 1.6\ cm^2\ h^{-1}$). Herring cale browsing was equivalent to their total consumption (electronic supplementary material). Browsing was observed in seagrass, *Sargassum* and kelp. Seagrass was only consumed by rabbitfish in summer ($4.6 \pm 2.7\ cm^2\ h^{-1}$). Short thalli of *Sargassum* were mainly consumed by rabbitfish during both seasons (summer: $36.4 \pm 22.4\ cm^2\ h^{-1}$, winter: $0.15 \pm 0.15\ cm^2\ h^{-1}$), while silver drummer ($0.8 \pm 0.8\ cm^2\ h^{-1}$) and herring cale (45 bites: 0.8 ± 0.8 bites h^{-1}) only consumed it during summer at lower rates. Consumption of kelp (tethered *E. radiata*) accounted for 82% of the total browsing. Rabbitfish bit kelp 13 020 times and on average consumed 32 times more in summer ($182 \pm 67\ cm^2\ h^{-1}$) than during winter ($5.7 \pm 5.6\ cm^2\ h^{-1}$). Silver drummer bit kelp 616 times and consumed 24 times more kelp in summer ($41 \pm 23.5\ cm^2\ h^{-1}$) than in winter ($1.7 \pm 1.6\ cm^2\ h^{-1}$). Herring cale were rarely seen and only bit kelp 35 times during one survey in summer (0.75 ± 0.75 bites h^{-1}). In terms of biomass, total consumption of tethered kelp in summer amounted to 529.5 g, equivalent to $10.4 \pm 3.1\ g\ h^{-1}$ (mean ± s.e.); while in winter, total consumption was 37.7 g, equivalent to $0.6 \pm 0.5\ g\ h^{-1}$. This was further confirmed with the results of 3-day tether deployments during winter of 2018 that yielded consumption values of $2.3\ g\ h^{-1}$.

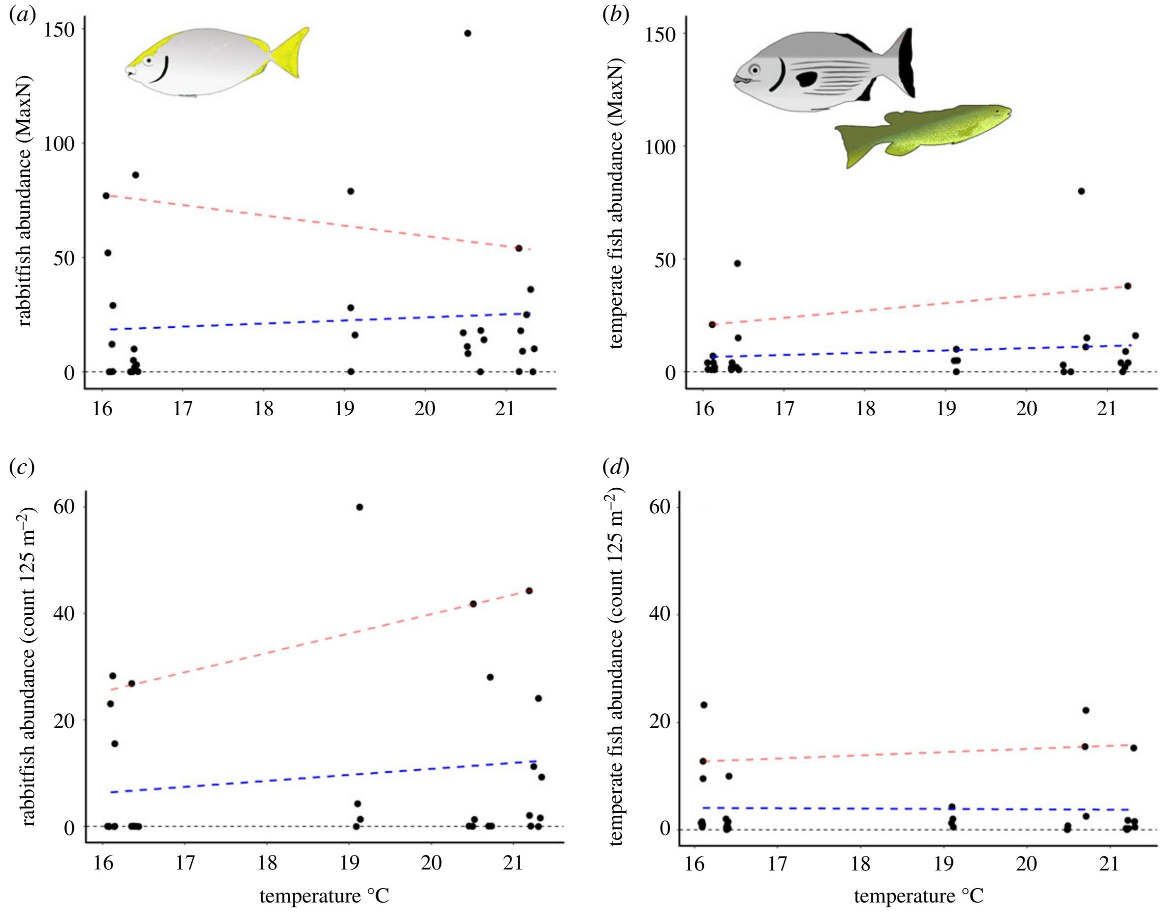

Figure 1. Relationship between the abundance of (*a*,*c*) tropical (*S. fuscescens*) and (*b*,*d*) temperate herbivorous fish (*O. cyanomelas* and *K. sydneyanus*) and temperature changes through the year from (*a*,*b*) RUV and (*c*,*d*) S-DOV. Regressions to the 0.9 quantile (upper dashed line) and the mean (lower dashed line) were non-statistically significant ($p > 0.5$). (Online version in colour.)

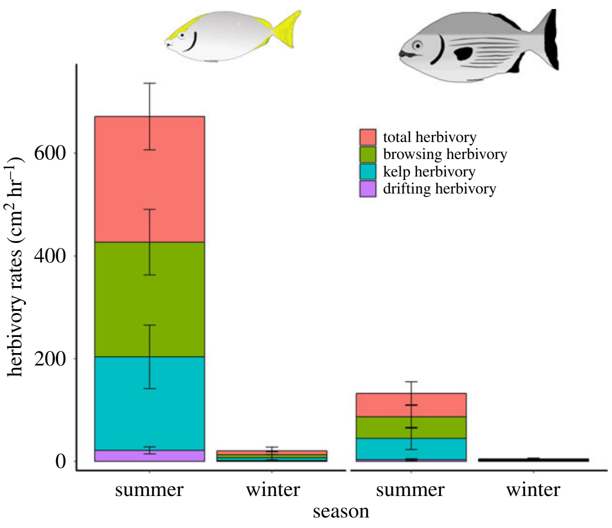

Figure 2. Rates of different modes of herbivory (mean ± s.e.) by tropical (*S. fuscescens*) and temperate (*K. sydneyanus*) herbivorous fish during winter (17–16°C) and summer (19–21°C) in temperate reefs of southwestern Australia. (Online version in colour.)

Kelp consumption rates were correlated with rabbitfish abundance with a significant interaction with temperature (figure 3*a*; LQMM$_{0.9}$, $p < 0.0001$; LMEM, $t_{28} = 5.18$, $p < 0.0001$). Kelp consumption at 16°C during winter was low despite the presence of abundant rabbitfish schools of up to 50–80 individuals, registering a maximum consumption of 119 cm^2 h^{-1}. By contrast, similar rabbitfish abundance in summer (19–21°C) was associated with kelp consumption rates of 782 cm^2 h^{-1} (figure 3*a*). Consumption by silver drummers was not correlated with their abundance or with temperature, although the higher rates of consumption occurred at higher temperatures (figure 3*b*). Thus, although temperate herbivores consumed more kelp biomass per bite, they had lower net consumption rates than tropical rabbitfish, which had fivefold higher bite rates and up to threefold higher net consumption (figure 3).

While browsing accounted for most of the total herbivory registered during all surveys (89%), we also registered a considerable number of bites on seaweeds drifting in the water column, a behaviour and ecological function generally disregarded in the ecological literature of fish herbivory. This accounted for 11% of the total primary consumption, with rabbitfish largely responsible for this mode of herbivory, consuming green, red and brown seaweed (i.e. *Ulva* spp., *Hypnea* spp., *Sargassum* spp., *Dictyopteris* spp. and kelp). Neither rabbitfish abundance nor temperature were significantly correlated with drift consumption, although most of the consumption was observed in summer (LQMM$_{0.9}$, $p = 0.9148$; LMEM, $t_{28} = 0.33$, $p = 0.7418$). In contrast with browsing, the highest rates of drift consumption were recorded when abundances of rabbitfish were low; the total number of bites recorded in summer were 1942 bites (21.4 ± 7 cm^2 h^{-1}), in contrast with 202 bites during winter (1.5 ± 1.5 cm^2 h^{-1}; figure 3*c*). No significant interaction was found between silver drummer abundance and temperature on their drifting

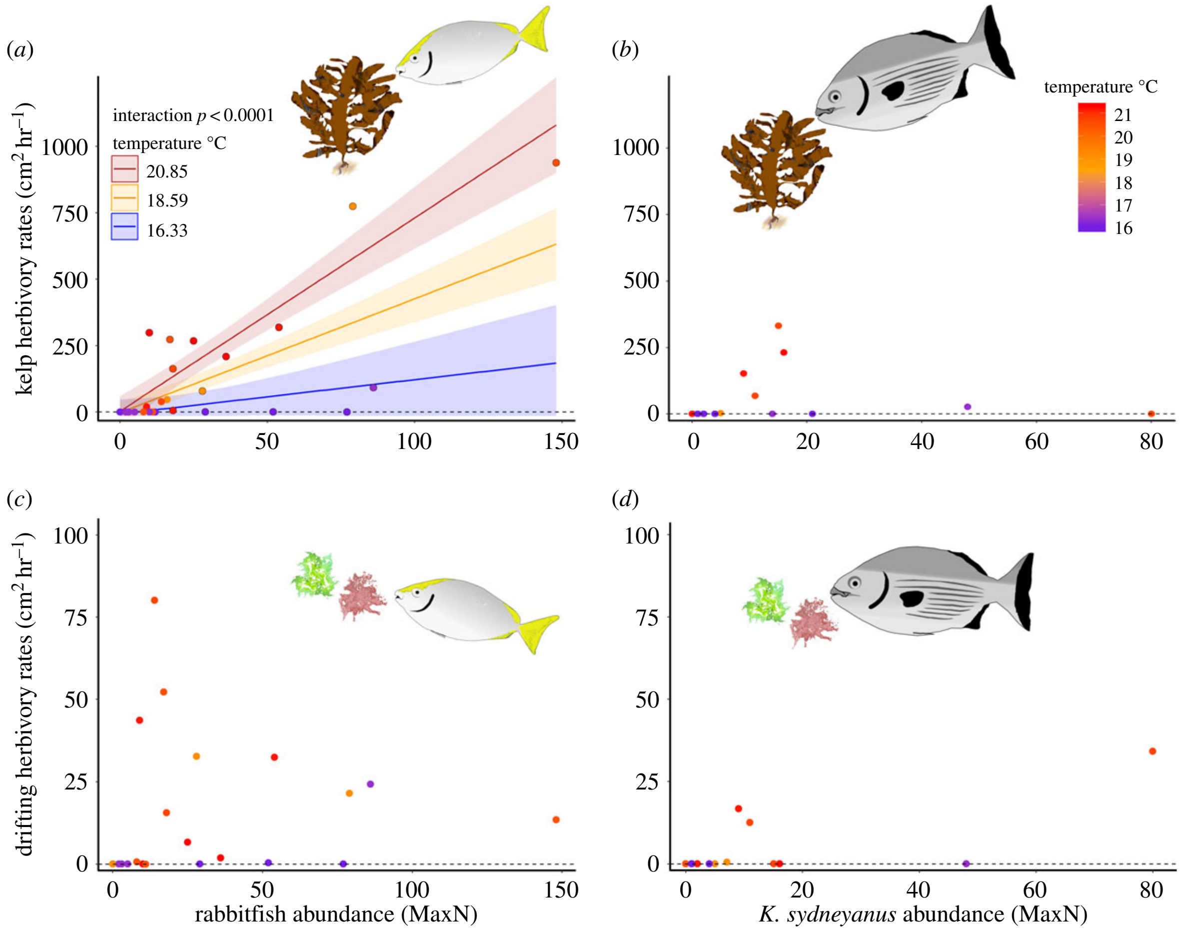

Figure 3. Relationship between (*a*,*b*) kelp consumption and (*c*,*d*) drifting herbivory rates (e.g. *Ulva* spp. and *Hypnea* spp.) with temperature and abundances of herbivorous fish. (*a*) Regressions (CI = 95%) of kelp consumption based on a significant interaction between abundance of tropical rabbitfish (*S. fuscescens*) and temperature (mean ± s.e.). (*b*) Relationship between kelp consumption, abundance of temperate silver drummers (*K. sydneyanus*) and temperature. (*c*) Relationship between drifting herbivory, rabbitfish abundance and temperature. (*d*) Relationship between drifting herbivory, abundance of silver drummers and temperature. (Online version in colour.)

herbivory rates ($LQMM_{0.9}$, $p = 0.1098$; LMEM, $t_{28} = 2.0$, $p = 0.055$); their consumption was only observed during summer at low frequency (3.4 ± 2 cm^2 h^{-1}: 87 bites).

(c) Defecation rates

Defecation during summer accounted for 94.5% (i.e. 294) of all the observed defecations during our study, with the majority of these being from rabbitfish (97%) and the rest from silver drummer (2.3%), with no faeces registered from herring cale. Defecation rates of rabbitfish had a significant interaction between their abundances and temperature (figure 4*a*; $LQMM_{0.9}$, $p < 0.0001$; LMEM, $t_{28} = 3.85$, $p = 0.0006$), and were strongly correlated with their total bite rates ($p < 0.001$). Defecation rates of silver drummers were not related with their abundances, but were correlated with temperature (figure 4*b*; $LQMM_{0.9}$, $p = 0.005$) and bite rates ($p < 0.001$). Thus, as bite rates decreased with temperature during winter we registered less defecations from all species (figure 4*c*,*d*). Defecation rates weighted by fish biomass showed that rabbitfish produced eight times more faeces on average (2.75 ± 0.6 faeces kg h^{-1}, 6 ± 1.27 faeces h^{-1}) than silver drummers in warm conditions (0.34 ± 0.17 faeces kg h^{-1}: 0.2 ± 0.1 faeces h^{-1}). In winter, defecation rates were lower; however, rabbitfish still produced five times more detritus (0.07 ± 0.07 faeces kg h^{-1}; 0.23 ± 0.23 faeces h^{-1}) than silver drummers (0.014 ± 0.014 faeces kg h^{-1}, 0.01 ± 0.01 faeces h^{-1}).

4. Discussion

Our study investigated the ecological functions of tropical rabbitfish in their new temperate ecosystems (consumption of macrophytes and its transformation to detritus biomass) relative to native temperate herbivores and analysed its variability through time according to key biological (abundance) and environmental variables (temperature). We found that rabbitfish persisted through the years, even during temperatures as low as 16°C, overwintering in similar abundance as their most important temperate competitors, silver drummers. Highly mobile fish species can relocate to more favourable thermal environments if they are suffering from thermal stress (i.e. behavioural thermoregulation) [38]. However, rabbitfish did not seem to migrate to warmer environments and did not suffer significant declines in population size. Although not reported elsewhere, this could be the same case for populations of rabbitfish inhabiting temperate reefs in Japan (*S. fuscescens* [55,56]), the Mediterranean Sea (*Siganus luridus* and *Siganus rivulatus* [24]) and eastern Australia (*S. fuscescens* [57]), where their distributions have expanded.

Rabbitfish populations seem to be well established in the kelp forests of Western Australia. However, their persistence in the future will depend on their recruitment success. *Siganus fuscescens* has expanded its distribution polewards in Western Australia since 2011, aided by an extreme marine heatwave that intensified the transport of tropical waters

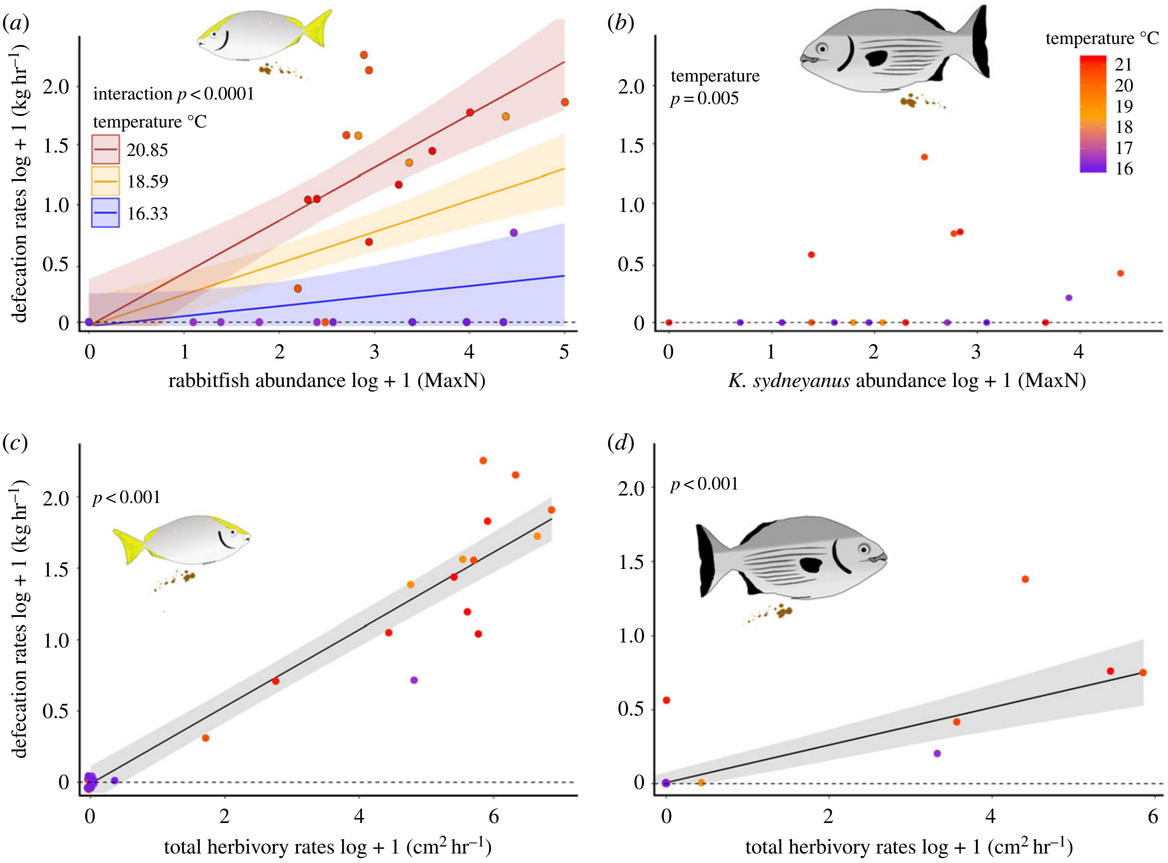

Figure 4. Relationship between defecation rates, abundance, temperature and total herbivory rates of (*a*,*c*) tropical and (*b*,*d*) temperate herbivorous fish. (*a*) Regressions (CI = 95%) of defecation rates of tropical rabbitfish (*S. fuscescens*) with a significant interaction between their abundance and temperature (mean ± s.e.). (*b*) Relationship between defecation rates of temperate silver drummers (*K. sydneyanus*), their abundance and temperature. (*c*) Relationship between total herbivory rates and defecation rates of rabbitfish. (*d*) Relationship between total herbivory rates and defecation rates of silver drummers.

towards higher latitudes [58]. Their presence in temperate environments has been reported during summers of subsequent years, including schools of juveniles, suggesting successful reproduction and recruitment events in their new temperate habitats [59]. All the rabbitfish observed during our S-DOV and RUV surveys were mature individuals (greater than 20 cm FL). However, on two occasions during the summer of 2016, we observed schools of juveniles roaming through seagrass and kelp beds adjacent to our survey sites (electronic supplementary materials). Breeding activity of tropical species in temperate ecosystems has been reported for some species, but currently, it is considered uncommon in a global context [60]. To our knowledge, rabbitfish are the only group of tropical herbivores documented as reproductively active at high latitudes [61]. *Siganus fuscescens* can recruit to kelp forests [62], indicating that temperate reefs are suitable for juveniles. Nevertheless, thermal tolerance is narrower in juvenile stages and extreme low temperatures can cause high rates of mortality [42,43]. For instance, many juvenile tropical fish appear during the summer in temperate reefs of eastern Australia, but most of them are not able to overwinter in the southernmost regions (e.g. Merimbula) [63]. High mortality caused by cold spells has been reported for rabbitfish populations; however, well-established and interconnected populations seem to be highly resilient, recovering in a short period of time when warmer conditions return [64].

Primary consumption and detritus production rates have been increased by rabbitfish throughout the year. The metabolic rates and energetic requirements of ectotherm organisms follow a positive exponential relationship with the environmental temperature [38]. Accordingly, consumption of macrophytes by fish fluctuates through the seasons of the year [40,41] and along latitudinal thermal gradients (18–27°C) [12]. Feeding trials in aquarium experiments have shown that low temperatures decrease consumption rates (e.g. surgeonfish, 20–24°C) [65–67] until a threshold is reached and individuals cease to feed (e.g. damselfish, 17–18.6°C) [39]. Herbivory by rabbitfish was higher in summer and although it decreased during winter, it remained fivefold higher than silver drummers, their most important local competitors. Similarly, we found that tropical rabbitfish were the main producers of faeces, having five- to eightfold higher defecation rates than silver drummers during winter and summer. Despite having smaller bite sizes than temperate herbivores, rabbitfish achieved a higher consumption efficiency as a function of higher bite rates. Although the bigger size of silver drummers suggest a high food intake for maintenance, larger animals tend to have lower feeding rates [68], as has been constantly described for this species in the region [44,47]. Similarly, herbivory rates by odacids have been lower than tropical fish in past studies, agreeing with our results regarding herring cale [69]. In contrast with past studies of rabbitfish herbivory in the Mediterranean Sea, where the native fish *Sarpa salpa* had a bigger impact on macrophytes during summer [19], our results suggest that rabbitfish can exert higher ecological impacts in temperate reefs throughout the year despite the reductions in herbivory during winter, since although net production of kelp in the region is positive during summer, kelp forests lose biomass during winter due to high rates of erosion [29].

Siganus fuscescens had the most flexible diet and was the most important herbivorous fish on all feeding modes. Rabbitfish browsed the most on kelp and sargassum, was the only species that consumed seagrass, and in addition to macrophytes, they can be avid consumers of cnidarians [70,71]. While they are usually categorized within one functional group, it is now known that they can be browsers [57,72] and grazers [16,19]. Our research adds an additional category to their feeding flexibility: drifting herbivory. We showed that 11% of herbivory was on detached macrophytes, demonstrating that herbivory by fish is more complex in temperate reefs than has generally been described. In tropical reefs, drifting herbivory has rarely been considered [73], probably because detached macrophytes are either small or rare and the process itself might not be critical for reef resilience [74]. By contrast, consumption of detached macrophytes is recognized as an important process on temperate reefs [27,47] and temperate seagrass beds [44]. Here, we observed rabbitfish consuming significant amounts of a diverse array of drifting seaweed in the water column, a herbivory mode not previously associated with them [74]. The ecological implications of drifting herbivory are important, since it implies that consumption of standing stock seaweed is reduced, alleviating the impact on the habitat structure, and retaining biomass that otherwise would have been transported elsewhere, reducing the export of biomass and nutrients to inter-connected ecosystems [75].

Our study quantitatively modelled the interactions between changes in temperature, abundance of tropical herbivores and their rates of herbivory and defecation in temperate reefs. Based on our models and evidence of poleward migrations of tropical species [17], future increases in temperature and abundance of tropical herbivores due to climate change could further accelerate the transformation of macrophyte standing stocks to detritus biomass, altering historical ecological patterns and functioning of temperate reefs [26]. For instance, these analyses imply that a rise in temperature of 2°C, as predicted for the region of study by the end of the century under a business as usual scenario [76], could increase consumption and defecation rates of abundant schools of rabbitfish threefold on average. Currently, herbivory-mediated detritus of kelp in temperate reefs is low compared with erosion-generated detritus [28] and is mainly produced by sea urchins [27] with herbivorous fish playing a secondary role [69]. The increase in rates of herbivory and defecation by rabbitfish observed in our study suggest that this paradigm is already changing in temperate ecosystems with tropicalized herbivorous communities. Rabbitfish faeces sink to the seafloor within the vegetation, where the nutrients are likely to be recycled by a myriad of organisms. Marine herbivores shred macrophytes and enrich them in organic nutrients and minerals in their passage through the digestive system [30,34], and once released, these could enter the microbial food web and be consumed by detritivorous organisms and higher trophic levels [31,33,77,78]. Further research into the detailed pathways that tropical fish faeces could follow in temperate foodwebs is necessary to assess their specific impact in the ecosystem.

Through seasonal surveys and feeding assays across 3 years, our study provides new knowledge about the persistence of range-expanding tropical rabbitfish and their capacity to modify trophic processes in temperate reefs. We showed that rabbitfish populations in southwestern Australia are able to withstand winter temperatures, remaining in the area with approximately similar abundances as in summer months. Rabbitfish consumed more kelp, fed from more species of macrophytes on all feeding modes and produced more faeces throughout the year than their temperate competitors. Rabbitfish browsed intensively in abundant schools but when they roved in small groups, they also consumed multiple drifting seaweeds, a novel herbivory mode for this tropical herbivores. We report rabbitfish defecation rates for the first time in temperate ecosystems and found that they are accelerating significantly the herbivory-derived detritus in the ecosystem, a function usually attributed to sea urchins. Our study highlights that the ecological implications of herbivory in kelp forests go beyond the sole process of reducing the cover of primary producers, representing the transformation of the ecological function of macrophyte biomass from habitat providers to nutrient sources for other trophic groups as detritus. Predicted warming and increases in abundance and diversity of tropical herbivorous fish in the future due to climate change are likely to accelerate this process, with the potential to gradually drive temperate reefs to canopy-free states. This will depend on the specific relationship through time between the net primary consumption and net primary production of temperate reefs in different parts of the world.

Ethics. Permits for seaweed collection and operation within Marine Parks of Western Australia were granted by the Department of Biodiversity, Conservation and Attractions (SW019107) and the Department of Primary Industries and Regional Development (Exemption No. 3050). Ethics approval to conduct fieldwork involving animals was granted by the University of Western Australia (F77574).

Data accessibility. The full dataset used for analyses is accessible from the Dryad Digital Repository: https://doi.org/10.5061/dryad.tx95x69sg [49].

Authors' contributions. S.Z.-P. and T.W. conceived the study and acquired the funding; S.Z.-P. and T.W. collected the field data; S.Z.-P. analysed the data and wrote the paper. All authors contributed to drafting the manuscript and gave final approval for publication.

Competing interests. We declare we have no competing interests.

Funding. This work was funded by the Australian Research Council (grant no. DP170100023); the Hermon Slade Foundation (grant no. HSF13-13) and the Holsworth Wildlife Research Endowment (grant no. RA/1/411/101).

Acknowledgements. We thank N. Bosch, S. Bell, H. Denham, M. Moustaka, Y. Mulders, A. Pessadorrona, F. Ribeiro and H. Zu for assistance in field operations and the anonymous reviewers whose criticism and suggestions greatly improved this manuscript.

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