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Marine Biology

International Journal on Life in Oceans and Coastal Waters

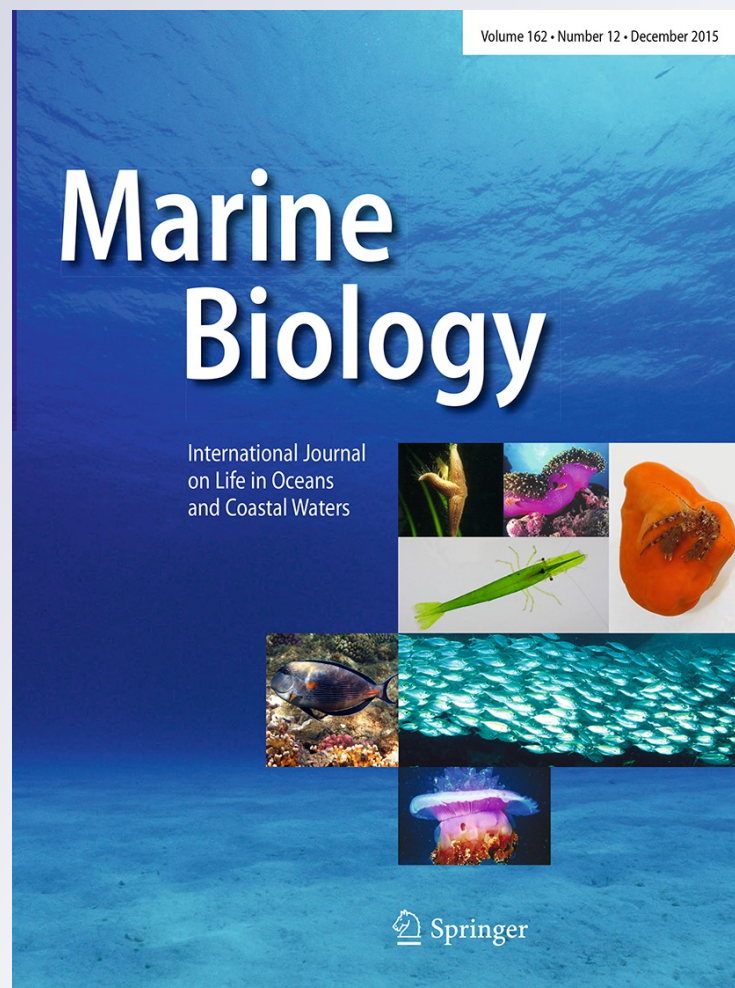
ISSN 0025-3162

Volume 163

Number 2

Mar Biol (2016) 163:1-8

DOI 10.1007/s00227-015-2790-x



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Temperate marine herbivorous fishes will likely do worse, not better, as waters warm up

Elizabeth D. L. Trip^{1,2,3} · Kendall D. Clements¹ · David Raubenheimer⁴ · J. Howard Choat⁵

Received: 13 May 2015 / Accepted: 16 November 2015
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Abstract Increased temperatures are associated with reduced body sizes, life spans, and reproductive outputs in shallow water marine fishes, reflecting the pervasive effects of temperature on metabolic rates in ectotherms. Herbivorous fishes have been seen as an exception to this trend, based on the hypothesis that physiological and demographic processes in these species are constrained by the inability to digest algae at low temperatures. It is thus argued that increased temperatures deliver a net benefit to herbivorous fishes. This study examines an alternative argument, that warming temperatures can have increasingly inimical effects on temperate piscine herbivores. We

consider the hypothesis that herbivores experience greater oxidative stress at warmer temperatures, a consequence of temperature-related increases in metabolic rates. We use the age pigment lipofuscin to examine the rate of oxidative damage accumulation in populations of a temperate marine herbivorous fish, *Odax pullus* (Labridae), at different latitudes (temperatures) across New Zealand (175.3°E, 36.3°S–167.9°E, 47°S). We show a 55 % faster rate of oxidative damage accumulation in shorter-lived fish living at warmer latitudes. In these populations, it took 33–50 % fewer years to accumulate similar amounts of oxidative damage than in those living at colder latitudes, indicating greater oxidative stress in fish living at warmer temperatures. We conclude that at least some temperate piscine herbivores will be exposed to negative demographic impacts at their low-latitude range margins as temperatures increase.

Responsible Editor: H. Pörtner.

Reviewed by undisclosed experts.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-015-2790-x) contains supplementary material, which is available to authorized users.

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Introduction

Increases in temperature have pervasive and predictable effects on the physiology and demography of ectotherms. These include reductions in mean body size, earlier maturation, and increased initial growth rates, and may be summarized as the temperature–size rule (TSR) (Atkinson 1994; Kingsolver and Huey 2008), with effects manifested most clearly in aquatic ectotherms (Forster et al. 2012). Demographic variation consistent with the TSR is detectable in reef fishes as spatial patterns distributed over latitudinal gradients of temperature (Trip et al. 2014), and as temporal patterns linked to fluctuations in sea surface temperature over time (Neuheimer et al. 2011). However, studies on herbivorous fishes, a key group of aquatic ectotherms that target marine macrophytes and macroscopic algae, have generated contrasting views on the impact of increasing

temperatures on physiological and demographic processes (Clements et al. 2009).

One view that has an extended history of support in the literature (Gaines and Lubchenco 1982; Horn 1989; Harmelin-Vivien 2002, Floeter et al. 2005; Poore et al. 2012; Bates et al. 2014) argues that herbivorous aquatic ectotherms will benefit from warming temperatures due to a presumed incapacity to process and digest plant and algal material at low temperatures. This hypothesis of a physiological constraint on digestive processes in piscine herbivores, referred to as the temperature constraint hypothesis (TCH), generates two predictions: (1) constraints on the capacity to digest plant and algal components of diet will impose nutritional penalties on somatic and reproductive growth at low temperatures resulting in reduced abundances of piscine herbivores at higher, colder, latitudes ($>30^\circ$), and (2) herbivorous fish taxa will benefit from increased temperatures, with enhanced demographic performance at their low-latitude range margins and abundances that track increasing temperature profiles. These predictions, however, conflict with the responses predicted by the TSR, in which ectotherms will have larger body sizes, achieved through longer periods of indeterminate growth, associated with increased lifetime reproductive outputs.

A direct comparison of growth in herbivorous and carnivorous southern hemisphere ectotherms over a significant latitudinal gradient of temperature (Trip et al. 2014) strongly supports an interpretation based on the TSR. In this example, populations of the target herbivorous species *Odax pullus* manifested reduced growth rates, smaller size, reduced lifetime reproductive output and lower mean abundances at the northern, warmer limits of the geographic range. Although this study confirmed reductions in size, reproductive outputs, and abundance associated with temperature increases, the extent to which these are detrimental and lead to reproductively non-viable populations is unclear. Indeed, increased juvenile growth, early sexual maturation, and reduced life expectancies accelerate population turnover rates (Stearns 1992), and arguably represent life history strategies that can facilitate adaptation to changing environments, including global warming (Ramos et al. 2014). In this case, it might be argued that “Hotter is better” (Kingsolver and Huey 2008), with the fitness benefits of a faster generation turnover outweighing the physiological costs incurred by a fast pace of life.

Although the concept of “Hotter is better” may have beneficial demographic effects under some circumstances (Kingsolver and Huey 2008), the assumed benefits to piscine herbivores of increasing temperatures do not account for the possibility that global warming may generally be detrimental to temperate water fish faunas (e.g., Baudron et al. 2014). The reasons for this are twofold. First, the impacts of increasing temperature may be more severe on

species with an evolutionary history restricted to temperate waters, which refers to many temperate water herbivores that have evolved in Southern hemisphere cold water environments (Brix et al. 1998). Second, higher metabolic rates and increased oxidative stress at warmer temperatures intensify the rate of physiological aging (Finkel and Holbrook 2000). The cumulative costs of living associated with higher and more variable temperatures may be quantified by measuring compounds that naturally accumulate in animals as a consequence of physiological trade-offs and oxidative damage (Gagliano et al. 2011). Lipofuscin is one such compound that is recognized as a widespread signature of physiological aging (Brunk and Terman 2002; Terman and Brunk 2004). In this context, physiological aging is characterized by the progressive change in tissues and organs of the body, associated with a decrease in physiological function (Gagliano et al. 2011). Under these circumstances, we may predict that northern populations of the herbivorous *O. pullus* will show a greater rate of accumulation of lipofuscin than southern low-temperature populations. This is indicative of the exposure of a species with a long evolutionary history in cold water environments (Alfaro et al. 2009; Clements et al. 2004) to increased and fluctuating temperatures at the northern range margin (Sutton and Roemmich 2001). Our prediction is that populations exposed to higher temperatures would exhibit greater rates of lipofuscin accumulation, indicative of higher levels of oxidative stress and physiological aging than those in southern regions. The alternative prediction is that, if increased temperatures benefit the herbivorous *O. pullus*, we would expect the opposite trend, with southern, colder-water populations experiencing greater physiological (oxidative) stress resulting from constraints on the digestion and assimilation of algae at low temperatures (TCH).

Materials and methods

Study species

Odax pullus is a percomorph fish, family Labridae (Clements et al. 2004), that is endemic to the New Zealand, where it occupies shallow rocky reef beds covered with assemblages of laminarian and fucoid algae (Francis 2012). *O. pullus* is herbivorous throughout its geographical range, feeding exclusively as an adult on the macroalgal species *Ecklonia radiata*, *Carpophyllum* spp., *Lessonia* spp., and *Macrocystis* spp. (Clements and Choat 1993).

Sampling design

Sampling was designed to reflect latitudinal differences in life span of *O. pullus*. Fish were collected from two broad

Table 1 Coordinates and mean annual sea surface temperature (SST, in degrees Celsius) of sampling locations, and demographic parameters of populations sampled [N is number of samples collected, Maxage is maximum age in years (years), and T_{\max} is mean maximum age (life span) in years]

Region	Location	Longitude/latitude	SST (°C) ^a	N	Max age (years)	T_{\max} (years) (\pm SE)	Age range of 40 % oldest individuals (years)
Northern	Hauraki G.	175.3°E, 36.3°S	17.6	276	11	7.5 (\pm 0.2)	6–10
	D'Urville Is.	173.9°E, 40.7°S	14.7	81	11	7.9 (\pm 0.3)	7–11
Southern	Fiordland	166.9°E, 45.5°S	13.7	41	17	14.8 (\pm 0.5)	11–17
	Stewart Is.	167.9°E, 47°S	12.1	101	19	13.5 (\pm 0.3)	12–17

^a See (Trip et al. 2014) for details of how SST estimates were obtained

geographical regions of New Zealand, north of 42°23'S (maximum age range 9–11 years), and south of this point (maximum age range of 17–19 years) (Trip et al. 2014). A total of 499 *O. pullus* individuals were collected from two locations within each of the two regions (Table 1). For each fish, the forebrain was dissected and formalin-fixed (Hammer and Braum 1988), the sagittal pair of otoliths was removed and stored dry, and fish length (Fork Length, FL) was recorded to the nearest mm. Sampling spanned 11° of latitude and a 5.5 °C difference in mean annual sea surface temperature (Table 1) and covered ~85 % of the geographical range of the study species.

Estimation of chronological age, life span, and growth

A further 432 *O. pullus* individuals, which had previously been collected in Trip et al. (2014), were included in the analyses of estimation of age, size, and growth ($N_{\text{Hauraki Gulf}} = 161$; $N_{\text{D'Urville Island}} = 39$; $N_{\text{Fiordland}} = 12$; $N_{\text{Stewart Island}} = 220$). Chronological age of each fish was estimated from sectioned sagittal otoliths using standard and validated techniques (Trip et al. 2011). Maximum age was estimated from the oldest individual sampled at each location. Mean maximum age (life span) and size were calculated as the mean age in years of the 10 % oldest individuals (T_{\max}) and the mean length (in mm) of the 10 % largest individuals (L_{\max}) at each location (Trip et al. 2014). Growth was modelled for all four populations sampled from the relationship between age and size, using the re-parameterized equation of the von Bertalanffy growth function (rVBGF) as described in Trip et al. (2011). The 95 % confidence ellipses were estimated around parameters T_{\max} , L_{\max} , and rVBGF parameters of mean size-at-age 1 year (L_1) and mean size-at-age 5 years (L_5) for each population sampled, using a bootstrapping procedure (Moore et al. 2007).

Estimation of oxidative damage

The amount of oxidative damage was estimated for each fish using the auto-fluorescing age pigment lipofuscin.

Lipofuscin is a non-degradable cellular waste mixture that accumulates in non-mitotic cells (e.g., neurons), and which is composed of oxidized proteins, lipids, carbohydrates, and traces of metals (mainly iron) (Terman and Brunk 2006). Lipofuscin has previously been used as a marker of oxidative stress and aging in fish (Valenzano et al. 2006; Terzibasi et al. 2008; Gagliano et al. 2011).

Amount of lipofuscin was quantified from histological sections of forebrain tissue using fluorescence microscopy and image analysis. At each location, five individuals within the 40 % oldest fish were randomly selected to allow comparing amounts of oxidative damage over equal proportions of life span across populations of fish with different maximum ages. Lipofuscin auto-fluorescence was detected using blue excitation (450–490 nm) and green emission (500–550 nm) wavelengths (Brunk and Terman 2002). Sections were photographed at 100× magnification, and a binary image of each photograph was obtained using image analysis software ImageJ 1.43 g (Fig. S1, Electronic Supplementary Material). Total area of lipofuscin fluorescence was expressed as a proportion of total brain area analyzed for each section examined (% lipofuscin) (Gagliano et al. 2011). The average amount of % lipofuscin for each fish was calculated from the mean of five equidistant sections (separated by ~50 μm) taken for each individual (mean % lipofuscin, MPL). The presence of lipofuscin material in the auto-fluorescence identified was validated using lipophilic Sudan black B staining (Sheehy et al. 1996) (Appendix S1, Fig. S2, Electronic Supplementary Material).

Statistical analysis

Analysis was designed to determine whether lipofuscin accumulated at different rates in populations of fish with different life spans living at different latitudes. We used analysis of covariance (homogeneity-of-slopes model) to compare the slopes of the relationship between MPL and chronological age between fish sampled in the northern and southern regions, with sampling locations nested within regions (Quinn and Keough 2002). Our hypothesis

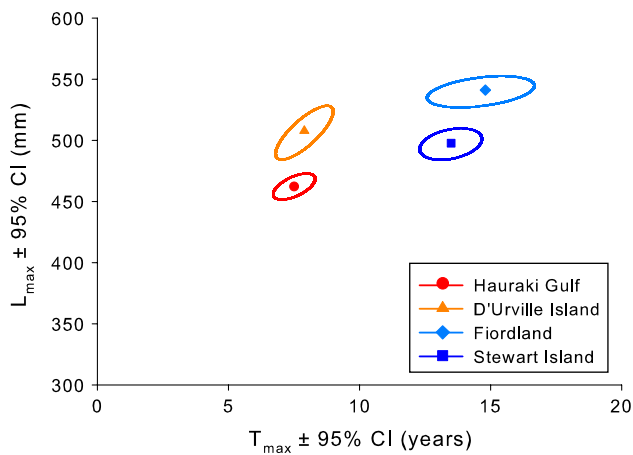


Fig. 1 Relationship between life span (mean maximum age T_{max} , in years) and adult body size (mean maximum size L_{max} , Fork Length in mm) in four populations of *Odax pullus* across New Zealand. Ellipses show 95 % confidence regions around T_{max} and L_{max} for the northern, warmer locations (red: Hauraki Gulf; orange: D'Urville Island) and southern, colder locations (light blue Fiordland, dark blue Stewart Island)

predicted significant differences in the slope of the relationship between lipofuscin and age between populations with different life spans, with significantly reduced slopes in populations with greater life spans at higher latitudes. No transformations of the data were required.

Results

Maximum age recorded at the sampling locations increased from 11 years in the northern region (Hauraki Gulf, D'Urville Island) to 17 and 19 years in the southern region (Fiordland, Stewart Island). There was no difference in mean maximum age (life span) between the two locations sampled within each region, but life span was significantly greater in the southern region ($X \pm SE = 14.8 \pm 0.5$ years in Fiordland, $n = 6$, and 13.5 ± 0.3 years at Stewart Island $n = 33$) than in the northern region (7.5 ± 0.2 years in the Hauraki Gulf, $n = 44$, and 7.9 ± 0.6 years at D'Urville Island, $n = 12$) (Fig. 1). Regional differences in demographic parameters were also evident in terms of body size, with individuals reaching significantly greater mean maximum sizes in the southern region ($X \pm SE = 541.2 \pm 3.0$ mm FL in Fiordland, $n = 6$, and 497.6 ± 3.2 mm FL at Stewart Island, $n = 33$) than in the northern region (462.3 ± 2.9 years in the Hauraki Gulf, $n = 44$, and 507.8 ± 5.6 years at D'Urville Island, $n = 12$) (Fig. 1). Smaller mean maximum sizes at the northern locations were associated with faster somatic growth rates over the first 25–45 % of life spans (Fig. 2a), resulting in greater mean sizes at ages 1

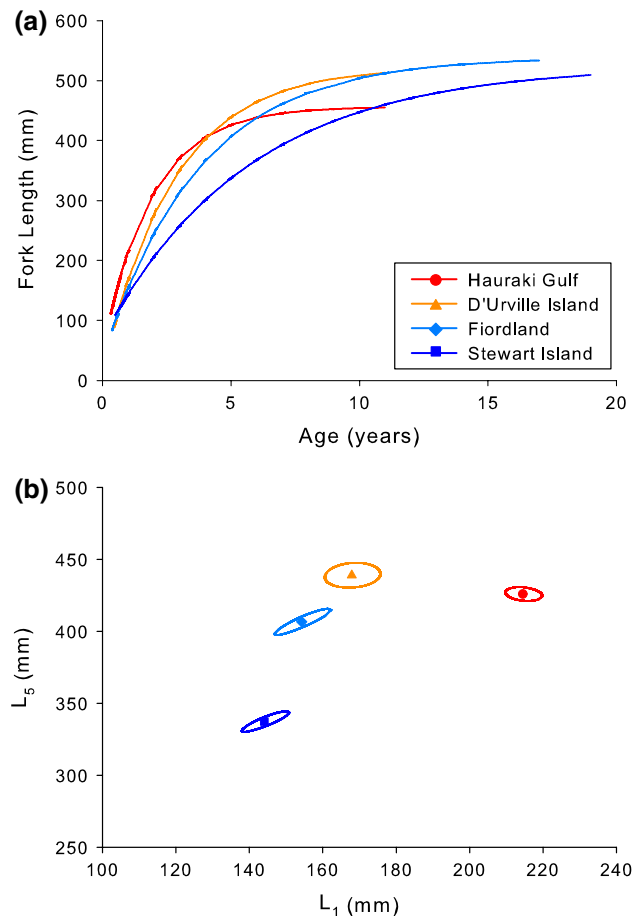


Fig. 2 Growth of *Odax pullus* across New Zealand. **a** Growth curves shown are re-parameterized von Bertalanffy Growth Functions (rVBGF) fitted to size (Fork Length, in mm) and age (in years) of individuals living in the northern, warmer locations (red Hauraki Gulf; orange D'Urville Island) and southern, colder locations (light blue Fiordland, dark blue Stewart Island). **b** Mean size-at-ages 1 (L_1) and 5 (L_5) years with 95 % confidence regions L_1 and L_5 are rVBGF parameter estimates for the growth curves shown in (a)

and 5 years in fish from the northern than from the southern populations (Fig. 2b).

At all four locations sampled, MPL (mean percent lipofuscin, hereafter referred to as 'lipofuscin') increased linearly with age (Fig. 3; Table 2), showing that lipofuscin accumulated with age with older individuals displaying greater amounts of lipofuscin than younger ones, and confirming lipofuscin as a reliable marker of age in the study species. Where fish displayed similar life spans (within geographical regions), there was no difference in either the amount of lipofuscin accumulated at any given age or the rate of accumulation (slope of the relationship between lipofuscin and age) (Fig. 3; Table 2).

In contrast, there were significant differences in lipofuscin accumulation between regions, where SST differed by 3.25 °C (Table 1). The slope of the relationship

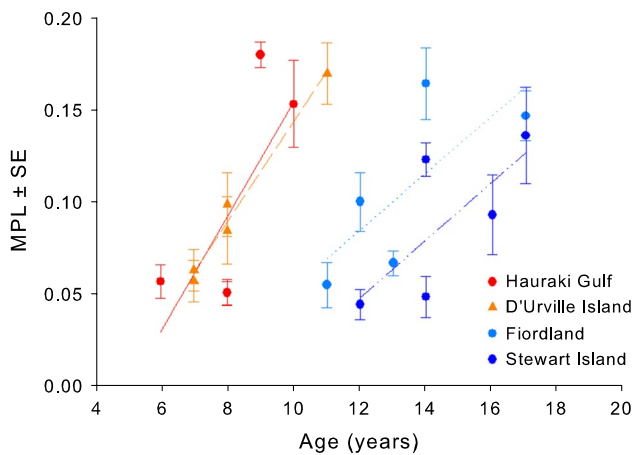


Fig. 3 Oxidative damage accumulation in *Odax pullus* across New Zealand. Symbols show mean percent lipofuscin (MPL) with standard error (SE) of individual fish of different ages for two populations living at northern, warmer locations (red Hauraki Gulf; orange D'Urville Island) and two populations living at southern, colder locations (light blue Fiordland, dark blue Stewart Island). MPL is the mean calculated over 5 replicate sections taken for each individual examined

Table 2 Analysis of covariance (ANCOVA) results, comparing the slopes of the relationship between mean percent lipofuscin (MPL) and chronological age over two spatial scales: on a broad latitudinal scale that reflects significant differences in life span ("Region", i.e., northern vs. southern regions), and on a local spatial scale ("Location(region)", i.e., across locations sampled)

Effect	SS	df	F	p
Intercept	0.00706	1	57.36	<0.001
Region	0.00005	1	0.43	0.53
Location (region)	0.00012	2	0.05	0.95
Age	0.02455	1	179.49	<0.001
Age × Region	0.00227	1	16.57	<0.01
Age × Location (region)	0.00007	2	0.03	0.97
Error	0.01456	12		

Bold p values are significant at the 0.05 level

between lipofuscin and age differed significantly between the northern and southern regions (Age × Region interaction, Table 2), with lipofuscin accumulating 55 % faster at the northern (SST = 16.2 °C) than the southern locations (SST = 12.9 °C) (Fig. 3). These regional differences in the rate of lipofuscin accumulation were associated with significant differences in the amount of lipofuscin accumulated at any given age (over the last 40 % of life span). Fish aged 6 and 7 years at the northern locations showed similar amounts of lipofuscin as fish aged 11 and 12 years from the southern locations (Fig. 3). Similarly, fish aged 10 and 11 years from the northern locations showed similar amounts of lipofuscin as fish aged 17 years from the

southern locations, indicating that it took 33–50 % fewer years for individuals of the northern populations to accumulate similar amounts of lipofuscin as the southern ones.

Discussion

The core issue in the present study was the capacity of *O. pullus* populations at their northern range margin to maintain reproductively viable populations in the face of increasing temperature. The demographic data confirmed a positive association between latitude and a number of key parameters in *O. pullus* sampled over their full latitudinal distribution. The main correlated trends were greater mean life spans and mean adult sizes at higher, colder latitudes, which contrasted with lower mean life spans and mean adult sizes at lower, warmer latitudes. Reduced life spans and smaller sizes of females may result in reduced reproductive outputs and lower abundances in high-temperature regions. This was confirmed for *O. pullus* in Trip et al. (2014), in which species populations at the northern range margin had fewer age classes contributing to annual reproduction, and an order of magnitude lower density than that recorded at the southern range margin. Although there were clear demographic signatures associated with temperature, the extent to which these might lead to significant changes in abundance and latitudinal distribution in populations subject to further temperature increases is unclear.

We identify three reasons that suggest that northern populations of the herbivorous *O. pullus* are at the limits of their physiological and ecological capacity to respond to increasing temperatures. Firstly, the herbivorous clade of the odacine labrids, which contains *O. pullus*, has a cold water evolutionary history (Clements et al. 2004), a fact reflected in the structure of the hemoglobin (Brix et al. 1998; Wells 1999). A consequence of this is sensitivity of *O. pullus* hemoglobin oxygen affinity at high temperatures, leading Brix et al. (1998) to suggestion that the northern populations are at the limits of their physiological capacity to respond to increasing temperatures. Secondly, the lipofuscin levels observed in the present study in populations of *O. pullus* at the northern range limit complement this conclusion. The increased rate of lipofuscin accumulation in northern populations suggests an increase in the cumulative costs of living (Terman and Brunk 2004), and populations at warmer latitudes experience faster rates of oxidative damage accumulation and higher levels of oxidative stress. The demographic differences between the northern and southern populations and their association with different accumulation rates of lipofuscin are striking. Individuals of the two southern populations lived 42 % longer and showed a rate of lipofuscin accumulation that was 45 % slower relative to northern populations. This was associated

with differences in the amount of lipofuscin accumulated at given ages, with individuals of the longer-lived southern populations taking 35–50 % longer to accumulate similar amounts of lipofuscin as those of the shorter-lived northern populations. The resulting pattern emerging for this cold-adapted species is that of a reduction in the capacity of *O. pullus* to supply oxygen to tissues (Brix et al. 1998) and meet the increasing demands for oxidative metabolism (greater levels of oxidative stress) at warmer temperatures, a pattern that coincides with the hypothesis of oxygen limitation as a unifying principle underlying the responses of ectothermic animals to rising temperatures (Pörtner and Knust 2007; Pörtner and Farrell 2008).

In addition to intrinsic factors impacting somatic and reproductive growth, populations of *O. pullus* may be further impacted by extrinsic factors that modify food resources and habitat structure. This species is an obligate herbivore with an adult diet dominated by laminarian algae (Choat and Clements 1992; Clements and Choat 1993) and strong associations with high algal cover (Meekan and Choat 1997). Laminarian algae are the primary food source of *O. pullus* over the entire geographic distribution (Johnson 2011). However, over this distributional range the biomass of dietary algae varies from relatively sparse and patchy cover at lower latitudes to continuous algae beds at higher latitudes (Choat and Schiel 1982; Schiel 1990; Shears and Babcock 2007), with a concomitant increase in dietary algae diversity (Johnson 2011). It is now evident that growth, reproductive potential and early development in southern temperate laminarian algae are negatively impacted by rising temperatures (Wernberg et al. 2011; Bearham et al. 2013; Mabin et al. 2013). In addition, laminarian algae can show fluctuations in abundance at a scale relevant to *O. pullus* foraging at the northern limits of the range, where summer die-off events occur (Cole and Babcock 1996; Cole and Syms 1999). Increasing temperatures are also reflected in major changes in habitat structure, accelerating latitudinal shifts in species distributions (Johnson et al. 2011). It is also noteworthy that juvenile *O. pullus*, which in northern populations manifest high initial growth rates, have a greater component of animal matter in the diet than those at the southern margins (Johnson 2011). This suggests that populations exposed to high temperatures must supplement dietary protein with animal matter to maintain elevated juvenile growth in the face of increased metabolic rates.

The analysis of physiological markers, demographic, and abundance data fails to support the hypothesis that herbivorous fish are negatively affected at lower temperatures (Gaines and Lubchenco 1982; Harmelin-Vivien 2002; Behrens 2005; Floeter et al. 2005; Behrens and Lafferty 2007). In contrast, *O. pullus* life span, reproductive output and abundance increased with latitude and declined with

increasing temperatures, which were in turn associated with higher levels of oxidative stress, as quantified by rates of lipofuscin accumulation. Indeed, the information to date suggests that this herbivorous species may be at greater risk of increasing coastal temperatures than a phylogenetically related labrid fish species that feeds on invertebrates (Trip et al. 2014). Further, the continental structure of the Australasian region provides only limited opportunities for latitudinal migration following reductions in the abundance of dietary and habitat forming algae. For the southwestern Australian coast, the southeastern Australian coast and New Zealand, latitudinal limits are reached at 35, 43, and 47°S, respectively. Finally, these results deal with species endemic to temperate regions. Recently, it has been suggested that tropical grazing fishes, including acanthurids and scarine labrids, will take advantage of increasing temperatures to invade temperate environments and modify habitat structures by consuming algae endemic to these regions (Verges et al. 2014). Although there are records of these tropical taxa recruiting into temperate environments (Feary et al. 2013), the extent to which they can form viable populations in non-carbonate reef environments dominated by macroscopic algae is presently unclear.

Acknowledgments We thank J.S. Johnson, Leigh marine lab, Catamaran Sailing Charters, and Jewel Charters for help with sample collection; M. Sheehy for advice on lipofuscin histology; J.S. Johnson and A. Hickey for discussion of ideas. Samples were collected under New Zealand Ministry of Fisheries Permit 385, and work was conducted under The University of Auckland Animal Ethics Committee Approval #AEC/03/2006/R456. This study and E.D.L.T. were supported by a Royal Society of New Zealand Marsden grant to K.D.C., D.R. and J.H.C.

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