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Fishing constrains phenotypic responses of marine fish to climate variability

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Abstract

1. Fishing and climate change are profoundly impacting marine biota through unnatural selection and exposure to potentially stressful environmental conditions. Their effects, however, are often considered in isolation, and then only at the population level, despite there being great potential for synergistic selection on the individual.
2. We explored how fishing and climate variability interact to affect an important driver of fishery productivity and population dynamics: individual growth rate. We projected that average growth rate would increase as waters warm, a harvest-induced release from density dependence would promote adult growth, and that fishing would increase the sensitivity of somatic growth to temperature.
3. We measured growth increments from the otoliths of 400 purple wrasse (*Notolabrius funicola*), a site-attached temperate marine reef fish inhabiting an ocean warming hotspot, to generate nearly two decades of annually resolved growth estimates from three populations spanning a period before and after the onset of commercial fishing. We used hierarchical models to partition variation in growth within and between individuals and populations, and attribute it to intrinsic (age, individual-specific) and extrinsic (local and regional climate, fishing) drivers.
4. At the population scale, we detected predictable additive increases in average growth rate associated with warming and a release from density dependence. A fishing-warming synergy only became apparent at the individual scale where harvest resulted in the 50% reduction of thermal-growth reaction norm diversity. This phenotypic change was primarily caused by the loss of larger individuals showing a strong positive response to temperature change after the onset of size-selective harvesting.
5. We speculate that the dramatic loss of individual-level biocomplexity is caused by either inadvertent fisheries selectivity based on behaviour, or the disruption of social

hierarchies resulting from the selective harvesting of large, dominant and resource-rich individuals. Whatever the cause, the removal of individuals that display a positive growth response to temperature could substantially reduce species' capacity to adapt to climate change at temperatures well below those previously thought stressful.

Keywords: Climate change, fish growth, fisheries selectivity, multiple stressors, otolith biochronology, reaction norm, time series; fisheries induced evolution

Introduction

A growing body of work has documented how fishing-induced loss of 'biocomplexity', such as life history variation, demographic and stock structure, can increase the sensitivity of populations to environmental variability (Hilborn *et al.* 2003). Termed the 'portfolio effect', the dynamics of aggregated stocks rich in biocomplexity are less variable than those of their individual constituents (Schindler *et al.* 2010). Current work in this space adopts a population-level focus reflecting the argument that fishing is unlikely to alter the sensitivities of individual fish to the environment because harvested individuals are no longer alive to respond (Perry *et al.* 2010). Instead, the selective harvesting of certain phenotypes results in populations dominated by fewer and younger age classes (Ottersen, Hjermann & Stenseth 2006) and depauperate of life history diversity (Law 2000), that in turn display an amplified environmental response (Hsieh *et al.* 2006; Hidalgo *et al.* 2011; Rouyer *et al.* 2011).

Fishing increases overall mortality rates and can select against certain sized fish, and life-history theory predicts that this elevated mortality should select for 'faster' life histories characterised by rapid juvenile growth, early maturation, smaller body size and reduced life span (Roff 1992; Law 2000). Fishing can also affect individuals across their lifetime through environmentally sensitive labile traits such as somatic growth (Morrongiello & Thresher 2015; Audzijonyte *et al.* 2016). Indeed, growth is an ideal candidate with which to explore additive and synergistic impacts of fishing and environmental variability on individuals as it is the phenotypic manifestation of interacting intrinsic (within individual) and extrinsic (environmental or ecological) components that affect the acquisition and allocation of resources (Enberg *et al.* 2012). Growth not only influences individual fitness insofar as it is related to body size, behaviour, reproductive output and mortality rates, but also contributes, along with other factors like reproduction and survival, to a range of population-level metrics such as recruitment success, generation time, and stock biomass. Whilst fishing can selectively remove fast (or slow) growers from a population (Sinclair, Swain & Hanson 2002; Enberg *et al.* 2012), it can also affect the growth of remaining fish through alterations to density dependent processes (Lorenzen & Enberg 2002), social context (Buston 2003), habitat (Rooper *et al.* 2011) or food webs (Audzijonyte *et al.* 2013). Importantly, the impact of these fishing-related changes on the individual is dependent on the environmental context (Crozier *et al.* 2010; Waples & Audzijonyte 2016).

Here, we developed 19-year growth biochronologies (1980-1999) for three south-east Australian populations of a site-attached temperate reef fish, *Notolabrus fucicola* (Richardson 1840; purple wrasse) (Fig. 1a-b), using the individual-based and annually-resolved growth information naturally archived in otoliths. Otolith growth increments are analogous to tree rings in that they are periodically deposited, and their width reflects somatic growth (Campana 2001; Morrongiello, Thresher & Smith 2012). The south-east Australian purple wrasse commercial fishery is nascent, beginning in the early 1990s (Fig. 1d) and targeting adults (8+ years of age, >280 mm) using baited fish traps for the live fish trade (Lyle & Hodgson 2001). We used annually resolved estimates of population-level and individual growth 10 years prior to, and nine years after, the onset of harvesting to assess the potentially interacting effects of harvest and environmental variation on growth rates. The marine environment of south-east Australia has undergone significant change over the last decade to millennia attributable to increased fishing activity (Tilzey & Rowling 2001), natural climatic variability (Thresher 2002), and a warming trend 3-4 times the global average (Hobday & Pecl 2014), the last associated with a strengthening of the East Australian Current (Ridgway 2007).

We used mixed effects models to partition individual growth variation amongst its intrinsic and extrinsic components. These statistical models can be readily extended from their common population-level focus to estimate individual-based reaction norms and persistent between-individual effects due to environmental variability (Fig. 2) (van de Pol & Wright 2009; Morrongiello & Thresher 2015). Such model innovations allowed for the concurrent assessment of fishing and climatic effects at the population, between-individual, and within-individual levels. Adopting a hierarchical approach, we hypothesised that: 1) average individual growth rates will be positively related to warming conditions, in accordance with other shallow water fishes in the region (e.g. Thresher *et al.* 2007; Neuheimer *et al.* 2011) and because sampled reefs in this study are at the poleward range limit and therefore unlikely to be close to critical upper thermal limits; 2) the advent of commercial fishing halfway through our study period will result in an increase in average adult growth due to release from density dependence (Lorenzen & Enberg 2002); 3) the sensitivity of somatic growth to temperature will change after fishing at a population level due to the selective removal of larger individuals (Perry *et al.* 2010); and 4) the sensitivity of individual-level growth to temperature will change after fishing as an indirect outcome of a shift in the balance between biotic (e.g. competition) and abiotic (e.g. temperature) controlling factors of growth across a fish's lifetime. We demonstrate that harvesting can affect the sensitivity of individual fish to climate variability via their thermal reaction norms. Whilst fishing relaxed density dependent constraints on growth, it halved the expression of phenotypic diversity within populations through either inadvertent selection or the disruption of social hierarchies.

Materials and methods

Study species

Purple wrasse are a secondarily gonochoristic species, with all fish starting as females and some changing sex to males before maturity at 2-3 years of age and ~120 mm in length (Barrett 1995a; Denny & Schiel 2002). They inhabit the shallow (<25m) coastal waters of south-east Australia and New Zealand (Russell & Gomon 1994), displaying fidelity to the reef on which they settle (Barrett 1995b). Individuals can reach 600 mm in length and live ≥ 25 years (Denny & Schiel 2002), with a maximum age of 20 observed in the study region (Ewing *et al.* 2003). Peak growth occurs during the austral spring and summer (Welsford & Lyle 2005).

Fish collection and annual growth estimation

Otolith samples were collected as part of fishery independent surveys in 1999-2002 from three near shore reefs on the east coast of Tasmania, Australia: Point Bailey (PB, n=134), Eaglehawk Neck (EHN, n=132) and Hen and Chicken Rocks (HCR, n=134 fish (Fig 1a&b). All reefs have been subjected to commercial fishing since 1990 (Fig. 1c). Fish were caught using baited fish traps and sampled when total length was >130 mm (see Ewing *et al.* 2003 for additional sampling details). The formation of annual growth increments in purple wrasse otoliths has been validated (Ewing *et al.* 2003) and ageing precision (calculated using average percent error (APE), Beamish & Fournier 1981) is high (0.8% within readers, 2.6% among readers; Ewing *et al.* 2003).

Sagittal otolith sections were viewed under 100x magnification, images taken using a Leica camera (MZ16FA) and increment measurements made using Leica Application Suite (Version 4, Leica Microsystems Ltd) along an axis from the primordium to the other edge of the ventral lobe. Otolith growth was a strong indicator for somatic growth: larger purple wrasse (in length and weight) had wider otolith radii (OLS regression: n=216 fish with length data, R^2= 0.759, P<0.001; n=376 fish with weight data [log transformed to account for allometric relationship], R^2= 0.725, P<0.001; see Fig. S1 in supporting information). We therefore used otolith increment widths as a proxy for annual somatic growth. We did not perform back calculation as our response variable of interest was growth rate, not size at age (see Enberg *et al.* 2012 for discussion of difference).

Fish used in this study were between 2 and 19 years of age at the time of capture (see Fig. S2 for age distribution and size at age plots) with an obvious skew towards older fish contributing growth information in earlier years (Fig. 1b). Such non-random samples are a common issue when using historical collections, including otoliths, to recreate past biological patterns (Pyke & Ehrlich 2010; Morrongiello, Thresher & Smith 2012). We countered the possibility of non-random samples introducing spurious growth patterns in three ways. First, we adopted a stratified sampling regime whereby we maximised the age spread of fish representing each cohort to ensure where possible we had data from young and old fish for each year (Morrongiello, Thresher & Smith 2012). Second, we included a bias-correction term in our models that identified the presence of any directional trend in growth associated with skewed age distributions, and corrected annual growth estimates accordingly (age-at-capture, see below; Morrongiello & Thresher 2015). Third, to ensure the age-related growth measured in pre- and post-fishery periods were comparable and to facilitate the meaningful estimation of any interactions among age-dependent growth and the environment, we truncated increment data to that associated with ages 2-11 within fish (i.e. increments associated with the 2nd to 11th year of an individual's life) which is the extent available data in the pre-fishery period.

Growth predictors

Purple wrasse growth variation was related to a series of intrinsic and extrinsic covariates. Intrinsic variables included fish age in years corresponding to a particular increment (*age*) and *age-at-capture* which controlled for age-dependent biases or differential selectivity in the data (Morrongiello & Thresher 2015) and is similar in purpose to the length term in Hagen and Quinn's otolith-based growth model (1991). Extrinsic variables included *site* (PB, EHN, HCR), average annual southern oscillation index (*SOI*), average annual sea surface temperature (SST) over the fish growth year (*annualSST*, 1 October to 30 September), average warm period SST (*warmSST*, 1 October to 31 March), and the presence or absence of commercial fishing operations (*fishery*). *Sex* was not considered due to uncertainty around when fish sex-changed to males and evidence from von Bertalanffy growth models indicating minimal sex-specific differences in growth (Ewing *et al.* 2003).

We used SynTS (Ridgway *et al.* 2006) to provide localised estimates of SST for each site (Fig. 1c). SynTS is a spatially (0.2° to 0.25° resolution) and temporally resolved product that models temperature-at-depth and is available semi-daily for the period 1993-2011 for Australian waters. We extended *SST* estimates for each site back to 1980 (Figure 1d) by regressing available SynTS data (19 years) with the coarser modelled estimates of annual SST from the HadISST1 1° latitude-longitude grid product (Rayner *et al.* 2003).

A commercial fishery for purple wrasse (and the related blue throat wrasse *Notolabrus tetricus*) commenced in the early 1990s (Lyle & Hodgson 2001) but the quality of commercial catch data was poor prior to 1998 due to fisher over-reporting and a lack of consistency in distinguishing catch by species (Ziegler, Haddon & Lyle 2006). We therefore considered commercial fishery impacts (*fishery*) as a categorical variable with two levels: no fishing (1980-1989) and fishing (1990-2001).

Statistical analyses

Average individual growth

A series of mixed effects models were developed through a two-stage process (Morrongiello & Thresher 2015) to investigate intrinsic and extrinsic drivers of purple wrasse *annual growth* (otolith annuli width in mm) within and across the three sites. Analyses were performed using the lme4 package in R 3.0.2. These models assume a compound symmetric correlation structure among increments within an individual, which has previously been shown to be appropriate for otolith growth analyses where within-group time series are short and autocorrelation minimal (Weisberg, Spangler & Richmond 2010; Morrongiello *et al.* 2011). We assumed an exponential decay function to model growth-increments as a function of age (e.g. Helser & Lai 2004). Otolith increment and age data where log-log transformed to linearize this relationship and ensure homogeneity of variance, and all covariates mean-centred to facilitate model convergence and interpretation of interaction terms.

Stage one involved partitioning growth variation into its specific intrinsic, and pooled extrinsic, components. Initially we compared four models with varying random effect structures and the interactive intrinsic fixed effects *site*age* and *site*age-at-capture.* This maximal fixed effect structure allowed for age-specific effects on growth that could vary among sites and site-specific differences in potential sampling bias (Biro 2013) or differential growth selectivity e.g. faster growers have lower survival (Ricker 1969; Morrongiello, Thresher & Smith 2012). The most complex model can be represented by:

$$y_{ijk} = \alpha_k + \alpha_i^F + \alpha_{k,l}^Y + \beta_j x_{j(k)} + b_{ij}^F x_{ij} + b_{jk,l}^Y x_{j(k),l} + f(\cdot) + \varepsilon_{ijk}$$

$$\begin{bmatrix} \alpha_i^F \\ b_{1i}^F \end{bmatrix} \sim N(0,\Sigma_i),\ \begin{bmatrix} \alpha_{k,l}^Y \\ b_{1k,l}^Y \end{bmatrix} \sim N(0,\Sigma_{k,l}),\ \varepsilon_{ijk} \sim N(0,\sigma^2) \qquad \text{(Eq. 1)}$$

where y_{ijk} is the annual growth for the ith fish at age j from site k, α_k is the fixed (population average) annual growth intercept, $\alpha^{Y}_{k,l}$ is the random extrinsic effect for *site k* at year l (l=1980,…,1999), $\beta_{j(k)}$ describes the age-dependent (j= 2,…,11) decline in growth specific to each *site k* (k= 1,2,3), α^{F}_{i} is the random intrinsic fish effect (i=1,…,400), b_{ij} is the random slope of *age* for fish i, $b_{jk,l}$ is the random slope of *age* for *site k* at year l and $f(\cdot)$ denotes additional fixed effects (e.g. *age-at-capture, annualSST, fishery* and their interactions). This model allows each individual fish to have a unique random intercept (higher or lower growth than average) and random growth by age slope (individual specific differences in age-dependent growth). It also allows a random intercept for each year within each site to reflect pooled extrinsic sources of variation (good or poor growth years, independent within and between sites) and for these random intercepts to have their own unique age slope (time and space varying interactions between age-dependent growth and extrinsic effects). The three simpler models sequentially dropped the random age slopes for individual fish, site-year combinations, or both (Table S1).

The four random effect structures were fit with restricted maximum likelihood (REML) and compared using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002). These values were rescaled as the difference between each model and the model with the lowest $\mathrm{AIC_c}$ ($\Delta\mathrm{AIC_c}$). We then applied the best random effect structure to models of increasing intrinsic fixed effect complexity using maximum likelihood (ML) and compared their performance using $\mathrm{AIC_c}$. The optimal annual growth model was re-analysed using REML to produce unbiased parameter estimates.

Stage two involved extending the optimal annual growth model determined above to relate patterns in inter-annual growth variation to extrinsic variables. We developed and compared models that included combinations of *fishery* and one of *SOI*, *annualSST* or *warmSST* due to collinearity among environmental variables. The maximal models included four way interactions among *age, site*, *fishery* and *SOI*, *annualSST*, or *warmSST*; these complex terms allowed for the additive or synergistic effects of fishery and environmental variation to be age and/or site dependent. Simpler models included different combinations of these terms. Models were fit with ML, compared using $\mathrm{AIC_c}$ as above, and the optimal model refit with REML.

<u>Average thermal reaction norms</u>

Equation 1 and its extrinsic effect derivations assess how the average individual's growth responds to environmental change and fishing activity. This average growth response (Fig. 2a) could be derived from within-individual phenotypic plasticity whereby an individual's growth varies depending on the experienced conditions (reaction norm; Fig. 2b-c), between-individual effects that reflect persistent environmental or genetic differences (Fig. 2d) or a combination of both (Fig. 2e-f). We partitioned the average temperature growth response into its within- and between-individual components using the method outlined by Morrongiello and Thresher (2015) that employs within subject centring (van de Pol & Wright 2009). We calculated the average annual temperature experienced by individuals across their lifetime $\bar{x}_{SST,}$, then the deviation of each annual temperature experienced by a fish from this mean ($x_{SSTi(l)} - \bar{x}_{SSTi}$). The linear mixed effect model (based on the 'best' average individual growth model from above) that accounts for within- and between-individual temperature effects is then specified as:

$$\begin{aligned} y_{ijk} = \alpha_k + \alpha_i^F + \alpha_{k,l}^Y + \beta_j x_{j(k)} + b_{ij}^F x_{ij} + b_{jk,l}^Y x_{j(k),l} + \beta_W (x_{SSTi(l)} - \bar{x}_{SSTi}) + b_{Wi}^F (x_{SSTi(l)} - \bar{x}_{SSTi}) \\ + \beta_A \bar{x}_{SSTi} + \beta_j x_{j(m)} + \varepsilon_{ijk} \\ \begin{bmatrix} \alpha_i^F \\ b_{ji}^F \\ b_{Wi}^F \end{bmatrix} \sim N(0, \Sigma_i),\ \begin{bmatrix} \alpha_{k,l}^Y \\ b_{jk,l}^Y \end{bmatrix} \sim N(0, \Sigma_{k,l}),\ \varepsilon_{ijk} \sim N(0, \sigma^2) \end{aligned} \qquad \text{(Eq. 2)}$$

where β_W is the average within-individual temperature slope (average thermal reaction norm), b_{Wi}^F is the random within-individual temperature slope for fish *i* (individual-specific thermal reaction norm), β_A is the between-individual temperature slope and $\beta_{j(m)}$ is a *fishery*age* interaction to account for age-dependent fishery effects on growth (see results). Equation 2 can be extended to include $\beta_{W(A)}$, an interaction of within- and between-individual slopes that tests whether individual growth responses are dependent on average thermal conditions experienced (e.g. Fig. 2d), and the terms $\beta_{W(k)}$ and $\beta_{W(m)}$ that are average thermal reaction norms for each *site* (*k*) and *fishery* period (*m*) respectively and capture potential spatial and temporal differences in average phenotypic plasticity. Models of increasing fixed effect complexity were fit with ML and compared using AIC$_c$.

Thermal reaction norm variation

We compared phenotypic variation in predicted thermal reaction norms (b_{Wi}^F, derived from the best equation 2 formulation) before and after the onset of fishing for all fish combined and separately for each site. Fish were assigned to either the pre-fishery or post-fishery period based on which period they spent most of their life in. Predicted estimates of individual-specific thermal reaction norms are sensitive to the number of underlying data points: values for fish with little growth data are 'shrunk' closer to the average reaction norm (β_W) than those from fish with lots of growth observations. We therefore only compared reaction norms from fish with at least six growth measurements (range 6-10), resulting in 45 pre-fishery and 224 post-fishery individuals in total. We then estimated the ratio of variance using 10,000 bootstrapped samples for all the pre-fishery reaction norms and a random selection of the same number post-fishery reaction norms. Finally, we compared patterns of size-dependent reaction norm expression across both periods to test for social hierarchy-dependent fishing effects on thermal sensitivity.

Results

We detected a hierarchy of attributable biological response, with considerable within- and between-individual growth variation becoming manifest as population-level differences in average growth rate through time. The data support three of our four hypotheses: average growth rate increased as water warmed (1); adults grew faster after the onset of fishing (2); and the sensitivity of growth to temperature increased with harvesting, but, critically, only at the individual level (4).

Intrinsic and extrinsic sources of growth variation

The best supported random effect structure for average individual growth was the most complex (Table S1) and included random age slopes and intercepts for individual fish and each site by year combination. Using this random effect structure, the best supported intrinsic fixed covariate model included additive terms for *age* and *site* (Table S2a). This model did not include the *age-at-capture* term, meaning we did not detect any evidence for biases in growth rates through time or across sites associated with our sampling regime. Growth declined with age (Fig. 3a) and on average Eaglehawk Neck (EHN) fish grew 7% and 12% faster than those from Point Bailey (PB) and Hen and Chicken Rocks (HCR), respectively (Table 1; Fig. 3b). Extrinsic patterns in annual growth rates across sites (Fig. 3c) were all significant ($p<0.016$) and strongly correlated (EHN vs. PB [n=18]: r=0.74, EHN vs. HCR [n=17]: r=0.57; PB vs. HCR [n=17]: r=0.77). Annual growth was lowest in the mid-1980s and rapidly increased post ≈1995, just after the period of maximum fishery catch (Fig. 1d).

Older fish had relatively higher growth compared to younger fish in 'good' growth years (0.73 correlation between year random intercept and random age slope; Table 2, Fig. S3a). This result indicates that whilst all fish grow faster in good years, older fish have relatively higher growth compared to younger fish (Fig. S3b).

All models including additional extrinsic parameters performed better than the intrinsic covariate model (Table S2b). The best overall model included average annual sea surface temperature (*annualSST*) and different growth~age relationships before and after the onset of commercial fishing *(age * fishery*) (Table 1). The growth of older fish was proportionally higher after the onset of commercial fishing (Fig. 4a); 2-year olds grew 7.4% slower (overlapping 95% CIs), but 5-year-olds grew 10.3% and 10-year-olds 26% faster in the latter period. Average growth rates across all ages increased by 6.6% per °C (Fig. 4b). The magnitude of spatial growth variation among sites remained relatively constant despite the addition of environmental data (Table 1). There were, however, declines in the variance associated with both the site-specific year random intercept (-18.2%) and age slope (-23.8%) in the extrinsic effect model (Table 2) indicating that the addition of *annualSST* and *fishery* explained some, but not all, of the inter-annual age-dependent growth variability. We found no evidence for a temperature by fishing interaction affecting average individual growth, as measured at the population scale.

Within- versus between-individual growth variation

There was little support for spatial or temporal variation in average thermal reaction norms (Table S2c). Further, we found negligible evidence that the positive population-averaged temperature response (Fig. 4b) was due to a temporal warming trend resulting in some fish spending all their lives in warmer waters (β_A t statistic 1.85; Fig. 2d-f). Mean water temperatures did not differ before and after the commencement of fishing (Welch two sample t-test, $t_{16.98} \leq 1.03$, $P = 0.318$) (Fig. 1), and variance in annual temperature did not change through time (3-year moving window; linear trend $p > 0.730$). Instead, the observed temperature-growth relationship was predominantly attributable to within-individual phenotypic plasticity (β_W t statistic 3.00; Fig. 2c), There was a 50% decline in thermal reaction norm phenotypic variation after the onset of fishing (variance ratio: 2.002 [95% CI: 1.273, 3.147], $p <0.001$; Fig. 5a). This result was robust to various ways of generating the underlying data (ratio range: 1.508-2.642, Appendix S1). The relationship between fish size and reaction norm slope differed markedly across pre- and post-fishing periods (ANCOVA, fish length * fishery $F_{1,265}$= 4.97, p=0.027). It was strongly positive prior to the onset of fishing, and non-significant thereafter (Fig. 5b).

Discussion

To the best of our knowledge, this is the first study to document harvest-induced changes in the distribution of thermal reaction norms in marine or terrestrial systems. Empirical evidence for climate and fishing synergies is rare and primarily focussed on how lost biocomplexity changes the functioning of higher levels of biological organisation (Hilborn *et al.* 2003; Perry *et al.* 2010; Planque *et al.* 2010; Kjesbu *et al.* 2014; Le Bris *et al.* 2018). Further, whilst climate impacts are usually couched in terms of increased and sometimes unsustainable physiological demands at temperatures that exceed the species' optimum (e.g. Rummer *et al.* 2014), our data indicate that the ability of individuals to respond to temperature variation can be compromised before these upper limits are reached. Here, we found that harvesting did not have a major impact on shaping the relationship between population-average growth and temperature. Rather, harvesting affected individual thermal sensitivities (reduction in reaction norm variation), as well as driving a shift in the size-dependent expression of thermally-dependent growth. Available data strongly suggest that the observed reduction in phenotypic diversity is the result of a change in biotic rather than abiotic conditions or an artefact of recreating past growth rates from more contemporary samples. We found no evidence of between-individual (β_A) growth changing through time, which was mirrored in similar mean water temperature before and after the commencement of fishing and stable food availability over the study period (see Stuart-Smith *et al.* 2010). Further, our bias correcting term (*age-at-capture*) was not present in the best model indicating that there was no systematic difference in estimated growth rates caused by older fish predominantly contributing information to earlier years.

Two hypotheses can explain our observed fishing-induced homogenisation of individual thermal sensitivity. First, the fish traps used to catch purple wrasse could indirectly select on thermal phenotype and thus cause fisheries-induced evolution in this trait. It is well documented that fishing gears can be size selective (Law 2000) and drive reductions in size and age at maturity and increases in juvenile growth (Swain 2011; Audzijonyte *et al.* 2016). Our results are, however, counter to theoretical expectations in that it was average adult growth that increased post fishing. Further, it is unclear how any selection driving potential changes in maturation would then cause a homogenisation of thermal sensitivities. Only recently have other forms of selection, such as on behaviour, been considered. In general, behaviour and physiology can play important roles in determining an individual's encounter rate with passive fishing gears such as traps (Pauli & Sih 2017). Bolder individuals and those with higher underlying metabolisms often take more risks or spend more time foraging, increasing their likelihood of being caught (Biro & Post 2008; Olsen *et al.* 2012). Thermal performance has strong links to behaviour and physiology (Angilletta Jr *et al.* 2003; Portner & Farrell 2008), so changing frequencies of thermal phenotypes could be an indirect response to fishing selectivity mediated through another parameter, such as activity level. Further work is needed to explore the behavioural response of purple wrasse to fishing gear and test whether behaviour is indeed related to thermal tolerance.

A second alternative hypothesis, that we believe is more biologically plausible, is suggested by the observed relaxation of density dependent growth in purple wrasse. The growth rate of sexually mature older fish (>5 years older) increased dramatically (10-28%) after the onset of the commercial fishery, although changes for young fish (≤ 2 years) were negligible. The biggest increase in average growth rate occurred in 1995, just after the maximum fisheries catch (178 tonnes) in 1994. Purple wrasse are long-lived, have strong fidelity to the rocky reef on which they settle (Barrett 1995b; Welsford 2003), and have a social system based on overlapping home ranges (Barrett 1995b). Studies of an ecologically similar congeneric species suggest that home ranges increase with body size and that there is a social hierarchy underpinned by agonistic interactions predominantly among similar sized individuals (Shepherd & Clarkson 2001). The presence of a similar social structure, coupled with known low adult natural mortality rates (Barrett 1995b), would imply that smaller purple wrasse, with small home ranges and low status, may have limited resources with which to positively respond to warmer temperatures, i.e., grow faster (Ohlberger 2013). Conversely, larger dominant individuals could readily maximise their growth in warmer years because of their access to larger foraging areas and potential surplus resources. A key assumption underpinning this mechanism, that experienced temperatures do not exceed upper thermal limits for purple wrasse, is supported as our study area is close to its poleward range limit (Russell & Gomon 1994). Among small individuals, the effect of warming temperatures on growth rate was, in fact, predominantly negative, consistent with increased physiological demands (Clarke & Johnston 1999) coupled with resource limitation. The relatively weaker phenotypic response of younger, but not older fish to “good” growth years also suggests they are resource limited.

In such a scenario, size-dependent access to resources, possibly reinforced by stable pre-fishing social hierarchies, leads to both wide variation in thermal reaction norms among individuals while accounting for the correlation we observed between body size and the slope of the thermal reaction norm. Harvesting not only lowers purple wrasse density on reefs, but also selectively removes larger individuals (Lyle & Hodgson 2001; Ziegler, Haddon & Lyle 2006). This combination steepens the distribution of thermal reaction norms at the lower end by allowing subordinate individuals access to more resources, but also truncates it at the upper end by removing the large dominants that could, pre-fishing, optimise their thermal growth responses in the presence of surplus resources. Coincident disruption of social hierarchies, we suggest, further flattens the correlation between body size and the slope of the thermal reaction norm, as the benefits of being big are diminished. In turn this contributes to the homogenisation of expressed reaction norms across the population after the onset of fishing. The release from density dependence is therefore not confined only to fish within the same cohort (e.g. Bacheler, Buckel & Paramore 2012; Whitten *et al.* 2013), but instead manifests across all age and size classes.

A counter argument to the density dependent hypothesis outlined above can be based on the observation that the impacts of size differences in a population are relative (e.g. Ross, Losey & Diamond 1983). In the post-fishery period, there would be new dominant fish (even if smaller) and these individuals should have surplus resources to maximise growth in warm years. The fact that such a pattern was not observed could be the result of: prolonged size selectivity (demographic or evolutionary) continually removing fish with strong thermal responses (hypothesis 1), size-dependent differences in purple wrasse growth (Denny & Schiel 2001) whereby smaller individuals cannot access high quality prey (unlikely), or some temperature-mediated shift in the allocation of resources away from growth to reproduction (Pankhurst & Munday 2011) in the post-fishery period. Evidence for these alternate mechanisms is currently lacking for purple wrasse, but it is possible that they are working in concert with density dependent processes to drive the observed growth changes at the individual and population level.

Fishing and climate change are having profound impacts on the trajectory and variability of marine populations (Harley *et al.* 2006; Audzijonyte *et al.* 2016). However, despite the wealth of work undertaken in marine environments on the causes of longer-term biological change, the effects of these two drivers have traditionally been considered in isolation, and when in concert only at the population scale (e.g. Perry *et al.* 2010; Planque *et al.* 2010; Kjesbu *et al.* 2014; Le Bris *et al.* 2018). Here, we show that fishing can induce shifts in purple wrasse individual-level biocomplexity, namely the expression of growth thermal reaction norms. Across all individuals, the mean slope of the thermal reaction norm is relatively unchanged by harvesting primarily due, we argue, to the improved performance of small, and potentially resource-limited subordinate individuals. However, lower density populations and targeted removal of larger, resource-rich individuals with their strong phenotypic responses to temperature implies that fishing can erode the adaptive capacity of a species to deal with climate change by selecting against those phenotypes with the capacity to respond to warming waters. The loss of these thermally high performing individuals may well be removing important buffers against the impacts of climate variations and change.

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Authorship contributions

JRM and RET designed the study and PCS developed methods and collected data. JRM performed statistical analyses and led the writing of the manuscript. All authors contributed substantially to revisions.

Data accessibility

Data for this study are available from Figshare at: https://doi.org/10.26188/5c4227cb49476 (Morrongiello 2019).

References

Angilletta Jr, M.J., Wilson, R.S., Navas, C.A. & James, R.S. (2003) Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology & Evolution,* **18,** 234-240.

Audzijonyte, A., Fulton, E., Haddon, M., Helidoniotis, F., Hobday, A.J., Kuparinen, A., Morrongiello, J., Smith, A.D.M., Upston, J. & Waples, R.S. (2016) Trends and management implications of human-influenced life-history changes in marine ectotherms. *Fish Fish,* **17,** 1005-1028.

Audzijonyte, A., Kuparinen, A., Gorton, R. & Fulton, E.A. (2013) Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. *Biol. Lett,* **9**.

Bacheler, N.M., Buckel, J.A. & Paramore, L.M. (2012) Density-dependent habitat use and growth of an estuarine fish. *Canadian Journal of Fisheries and Aquatic Sciences,* **69,** 1734-1747.

Barrett, N.S. (1995a) Aspects of the biology and ecology of six temperate reef fishes (Families: Labridae and Monacanthidae). PhD, University of Tasmania.

Barrett, N.S. (1995b) Short and long term movement patterns of six temperate reef fishes (Families Labridae and Monacnthidae). *Marine and Freshwater Research,* **46,** 853-860.

Beamish, R.J. & Fournier, D.A. (1981) A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences,* **38,** 982-983.

Biro, P.A. (2013) Are most samples of animals systematically biased? Consistent individual trait differences bias samples despite random sampling. *Oecologia,* **171,** 339-345.

Biro, P.A. & Post, J.R. (2008) Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences,* **105,** 2919-2922.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Inference: a Practical Information-Theoretic Approach,* second edn. Springer-Verlag, New York, USA.

Buston, P. (2003) Social hierarchies: Size and growth modification in clownfish. *Nature,* **424,** 145-146.

Campana, S.E. (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology,* **59,** 197-242.

Clarke, A. & Johnston, N.M. (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology,* **68,** 893-905.

Crozier, L.G., Zabel, R.W., Hockersmith, E.E. & Achord, S. (2010) Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. *Journal of Animal Ecology,* **79,** 342-349.

Denny, C.M. & Schiel, D.R. (2001) Feeding ecology of the banded wrasse *Notolabrus fucicola* (Labridae) in southern New Zealand: prey items, seasonal differences, and ontogenetic variation. *New Zealand Journal of Marine and Freshwater Research,* **35,** 925-933.

Denny, C.M. & Schiel, D.R. (2002) Reproductive biology and population structure of the banded wrasse, *Notolabrus fucicola* (Labridae) around Kaikoura, New Zealand. *New Zealand Journal of Marine and Freshwater Research,* **36,** 555-563.

Enberg, K., Jorgensen, C., Dunlop, E.S., Varpe, O., Boukal, D.S., Baulier, L., Eliassen, S. & Heino, M. (2012) Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. *Marine Ecology,* **33,** 1-25.

Ewing, G.P., Welsford, D.C., Jordan, A.R. & Buxton, C. (2003) Validation of age and growth estimates using thin otolith sections from the purple wrasse, *Notolabrus fucicola*. *Marine and Freshwater Research,* **54,** 985-993.

Hagen, P.T. & Quinn, T.J. (1991) Long-term dynamics of young Pacific halibut: evidence of temperature-induced variation. *Fisheries Research,* **11,** 283–306.

Harley, C.D.G., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L. & Williams, S.L. (2006) The impacts of climate change in coastal marine systems. *Ecology Letters,* **9,** 228-241.

Helser, T.E. & Lai, H.-L. (2004) A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, Micropterus salmoides. *Ecological Modelling,* **178,** 399-416.

Hidalgo, M., Rouyer, T., Molinero, J.C., Massut, E., Moranta, J., Guijarro, B. & Stenseth, N.C. (2011) Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series,* **426,** 1-12.

Hilborn, R., Quinn, T.P., Schindler, D.E. & Rogers, D.E. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences,* **100,** 6564-6568.

Hobday, A.J. & Pecl, G.T. (2014) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. *Rev Fish Biol Fish,* **24,** 415-425.

Hsieh, C.-h., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M. & Sugihara, G. (2006) Fishing elevates variability in the abundance of exploited species. *Nature,* **443,** 859-862.

Kjesbu, O.S., Bogstad, B., Devine, J.A., Gjøsæter, H., Howell, D., Ingvaldsen, R.B., Nash, R.D.M. & Skjæraasen, J.E. (2014) Synergies between climate and management for

Atlantic cod fisheries at high latitudes. *Proceedings of the National Academy of Sciences,* **111,** 3478-3483.

Law, R. (2000) Fishing, selection, and phenotypic evolution. *Ices Journal of Marine Science,* **57,** 659-668.

Le Bris, A., Mills, K.E., Wahle, R.A., Chen, Y., Alexander, M.A., Allyn, A.J., Schuetz, J.G., Scott, J.D. & Pershing, A.J. (2018) Climate vulnerability and resilience in the most valuable North American fishery. *Proceedings of the National Academy of Sciences,* **115,** 1831-1836.

Lorenzen, K. & Enberg, K. (2002) Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proceedings of the Royal Society B-Biological Sciences,* **269,** 49-54.

Lyle, J.M. & Hodgson, K. (2001) Tasmanian scalefish fishery assessment- 2000. Technical Report 19. Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, Hobart.

Morrongiello, J.R., Crook, D.A., King, A.J., Ramsey, D.S. & Brown, P. (2011) Impacts of drought and predicted effects of climate change on fish growth in temperate Australian lakes. *Global Change Biology,* **17,** 745-755.

Morrongiello, J.R. & Thresher, R.E. (2015) A statistical framework to explore ontogenetic growth variation among individuals and populations: a marine fish example. *Ecological Monographs,* **85,** 93-115.

Morrongiello, J.R., Thresher, R.E. & Smith, D.C. (2012) Aquatic biochronologies and climate change. *Nat. Clim. Change,* **2,** 849-857.

MORRONGIELLO, JOHN (2019): Morrongiello etal 2019 Journal of Animal Ecology-purple wrasse otolith increments.csv. University of Melbourne. Dataset. https://doi.org/10.26188/5c4227cb49476

Neuheimer, A.B., Thresher, R.E., Lyle, J.M. & Semmens, J.M. (2011) Tolerance limit for fish growth exceeded by warming waters. *Nature Climate Change,* **1,** 110-113.

Ohlberger, J. (2013) Climate warming and ectotherm body size – from individual physiology to community ecology. *Functional Ecology,* **27,** 991-1001.

Olsen, E.M., Heupel, M.R., Simpfendorfer, C.A. & Moland, E. (2012) Harvest selection on Atlantic cod behavioral traits: implications for spatial management. *Ecology and evolution,* **2,** 1549-1562.

Ottersen, G., Hjermann, D.A.G.Ø. & Stenseth, N.C. (2006) Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (Gadus morhua) stock. *Fisheries Oceanography,* **15,** 230-243.

Pankhurst, N.W. & Munday, P.L. (2011) Effects of climate change on fish reproduction and early life history stages. *Marine and Freshwater Research,* **62,** 1015-1026.

Pauli, B.D. & Sih, A. (2017) Behavioural responses to human-induced change: Why fishing should not be ignored. *Evolutionary Applications,* **10,** 231-240.

Perry, R.I., Cury, P., Brander, K., Jennings, S., Mollmann, C. & Planque, B. (2010) Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. *J Marine Syst,* **79,** 427-435.

Planque, B., Fromentin, J.M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I. & Kifani, S. (2010) How does fishing alter marine populations and ecosystems sensitivity to climate? *J Marine Syst,* **79,** 403-417.

Portner, H.O. & Farrell, A.P. (2008) Physiology and climate change. *Science,* **322,** 690-692.

Pyke, G.H. & Ehrlich, P.R. (2010) Biological collections and ecological/environmental research: A review, some observations and a look to the future. *Biological Reviews,* **85,** 247–266.

Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent, E.C. & Kaplan, A. (2003) Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research-Atmospheres,* **108,** D14.

Ricker, W.E. (1969) Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *Journal of the Fisheries Research Board of Canada,* **26,** 479-541.

Ridgway, K.R. (2007) Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophysical Research Letters,* **34**.

Ridgway, K.R., Dunn, J.R., Cahill, M. & Griffin, D. (2006) SynTS: a 3D ocean observational analysis for the Australian region. *Proceedings of the 15-years Progress in Altimetry, ESA Symposium*. Venice.

Roff, D.A. (1992) *The evolution of life histories; theory and analysis*. Chapman and Hall, London.

Rooper, C.N., Wilkins, M.E., Rose, C.S. & Coon, C. (2011) Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. *Continental Shelf Research,* **31,** 1827-1834.

Ross, R.M., Losey, G.S. & Diamond, M. (1983) Sex change in a coral-reef fish: dependence of stimulation and inhibition on relative size. *Science,* **221,** 574-575.

Rouyer, T., Ottersen, G., Durant, J.M., Hidalgo, M., Hjermann, D.O., Persson, J., Stige, L.C. & Stenseth, N.C. (2011) Shifting dynamic forces in fish stock fluctuations triggered by age truncation? *Global Change Biology,* **17,** 3046-3057.

Rummer, J.L., Couturier, C.S., Stecyk, J.A.W., Gardiner, N.M., Kinch, J.P., Nilsson, G.E. & Munday, P.L. (2014) Life on the edge: thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. *Global Change Biology,* **20,** 1055-1066.

Russell, B.C. & Gomon, M.F. (1994) Purple wrasse, *Notolabrus funicola*. *The Fishes of Australia's South Coast* (eds M.F. Gomon, C.J.M. Glover & R.H. Kuiter), pp. 992. State Print, Adelaide.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A. & Webster, M.S. (2010) Population diversity and the portfolio effect in an exploited species. *Nature,* **465,** 609-612.

Shepherd, S.A. & Clarkson, P.S. (2001) Diet, feeding behaviour, activity and predation of the temperate blue-throated wrasse, *Notolabrus tetricus*. *Marine and Freshwater Research,* **52,** 311-322.

Sinclair, A.F., Swain, D.P. & Hanson, J.M. (2002) Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. *Canadian Journal of Fisheries and Aquatic Sciences,* **59,** 372-382.

Stuart-Smith, R.D., Barrett, N.S., Stevenson, D.G. & Edgar, G.J. (2010) Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. *Global Change Biology,* **16,** 122-134.

Swain, D. (2011) Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). *Evol Appl.,* **4,** 18-29.

Thresher, R.E. (2002) Solar correlates of Southern Hemisphere mid-latitude climate variability. *International Journal of Climatology,* **22,** 901-915.

Thresher, R.E., Koslow, J.A., Morison, A.K. & Smith, D.C. (2007) Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proc. Natl. Acad. Sci. U.S.A.,* **104,** 7461-7465.

Tilzey, R.D.J. & Rowling, K.R. (2001) History of Australia's South East Fishery: a scientist's perspective. *Marine and Freshwater Research,* **52,** 361-375.

van de Pol, M.V. & Wright, J. (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour,* **77,** 753-758.

Waples, R.S. & Audzijonyte, A. (2016) Fishery-induced evolution provides insights into adaptive responses of marine species to climate change. *Front. Ecol. Environ.,* **14,** 217-224.

Weisberg, S., Spangler, G. & Richmond, L.S. (2010) Mixed effects models for fish growth. *Canadian Journal of Fisheries and Aquatic Sciences,* **67,** 269-277.

Welsford, D.C. (2003) Early life-history, settlement dynamics and growth of the temperate wrasse, *Notolabrus fucicola* (Richardson 1840), on the east coast of Tasmania. PhD, University of Tasmania.

Welsford, D.C. & Lyle, J.M. (2005) Estimates of growth and comparisons of growth rates determined from length- and age-based models for populations of purple wrasse (*Notolabrus fucicola*). *Fishery Bulletin,* **103,** 697-711.

Whitten, A.R., Klaer, N.L., Tuck, G.N. & Day, R.W. (2013) Accounting for cohort-specific variable growth in fisheries stock assessments: A case study from south-eastern Australia. *Fish Res,* **142,** 27-36.

Ziegler, P.E., Haddon, M. & Lyle, J.M. (2006) *Sustainability of small-scale, data poor commercial fisheries : developing assessments, performance indicators and monitoring strategies for temperate reef species*. Tasmanian Aquaculture and Fisheries Institute. Marine Research Laboratories, Fisheries Research and Development Corporation (Australia), Hobart.

Tables and figures

Table 1: Fixed effect parameter estimates for the best intrinsic and extrinsic covariate models. Note *growth* and *age* are natural-log transformed.

fixed effects	**intrinsic covariate model**	**extrinsic covariate model**
parameter	**estimate** **(95% CI)**	**estimate** **(95% CI)**
Intercept	-3.149 (-3.180, -3.118)	-3.255 (-3.308, -3.198)
Age	-0.780 (-0.820, -0.745)	-0.931 (-0.998, -0.864)
site (HCR)	-0.128 (-0.172, -0.086)	-0.100 (-0.164, -0.050)
site (PB)	-0.073 (-0.116, -0.026)	-0.102 (-0.143, -0.053)
annualSST	-	0.064 (0.024, 0.101)
fishery (present)	-	0.125 (0.069, 0.175)
*age * fishery*	-	0.191 (0.122, 0.274)

Table 2: Random effect variance components for the best intrinsic and extrinsic covariate models outlined in table 1. Random *age* slopes for each random intercept are denoted by |. Corr is correlation is between random intercept and respective random slope.

random effects	**intrinsic covariate model**		**extrinsic covariate model**	
variance component	**Std. Dev**	**corr.**	**Std. Dev**	**Corr.**
ID	0.111		0.112	
age|ID	0.128	-0.17	0.127	-0.16
site:year	0.044		0.036	
age|site:year	0.105	0.73	0.080	0.50
Residual	0.215		0.214	

Figure captions

Figure 1: a) Map illustrating locations of study sites on east coast of Tasmania, Australia. b) Temporal extent of increment data used in analyses. Lines and line length represent individual fish and the number of years available; stepping on the left hand side of lines indicate cohorts sampled and the right-hand ends the three sampling years. c) Temporal variation in sea surface temperature (SST) by site. d) Historical record of purple wrasse commercial catches for the state of Tasmania, illustrating the onset of the wrasse fishery in 1990. Note, site-specific catch data is not available prior to 1995 and quality catch data not available prior to 1998.

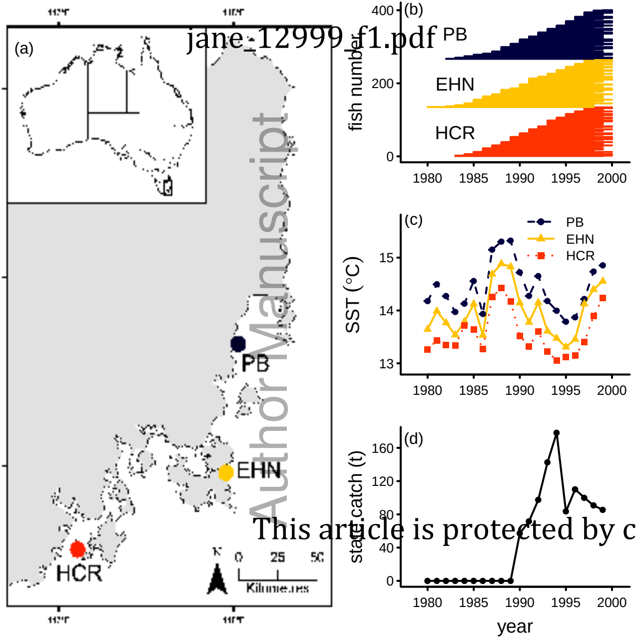
Figure 2: Hypothetical average population growth response (β_p; solid red line) along an environmental gradient (a) can be caused by a number of within- and between- individual patterns (dashed lines).Examples include: (b) consistent phenotypic plasticity between individuals in how they respond to environmental variation (within-individual reaction norms β_W); (c) phenotypic plasticity is present in the population, but individuals differ in the slope of their reaction norms (β_{Wj}); (d) persistent environmental or genetic effects that cause shifts in between-individual overall growth (β_A) depending on the environmental context, but no evidence for phenotypic plasticity; (e) changes in the environment that cause similar within- and between-individual variation in growth ($\beta_P = \beta_W + \beta_A$); and (f) an interaction of within- and between-individual responses whereby an individual's reaction norm is dependent on the environmental conditions they inhabit.

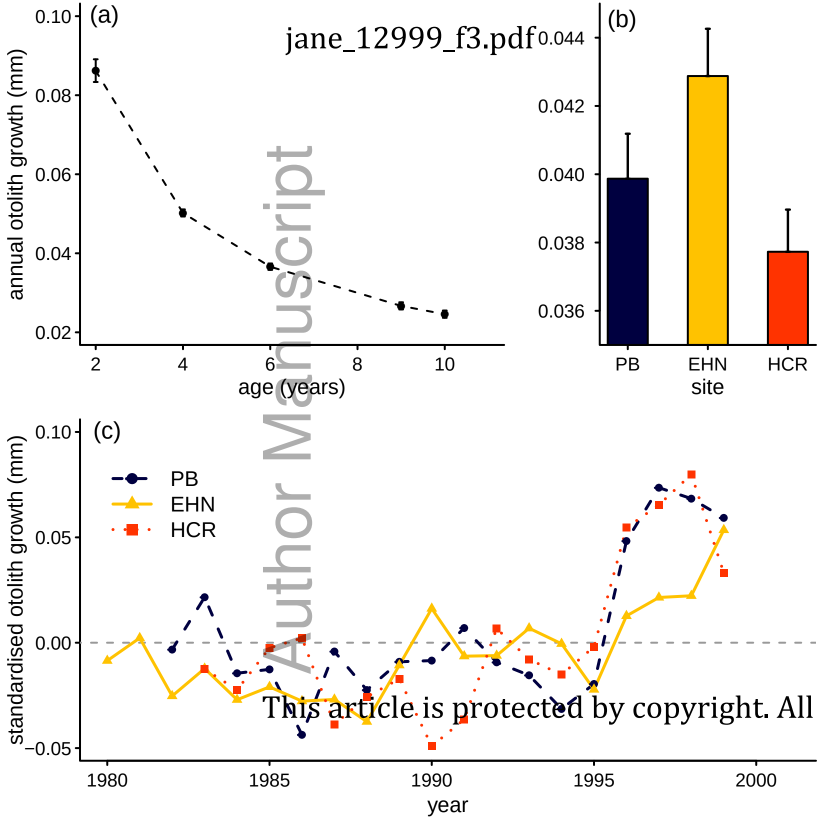
Figure 3: Annual otolith growth variation (mm of otolith growth, ±95% CI) in purple wrasse back-transformed to the original scale. (a) age effect; (b) site effect (EHN: Eagle Hawk Neck; HCR: Hen and Chicken Rocks; PB: Point Bailey); and (c) standardised mean annual otolith growth across three sites, predicted by site-specific *Year* random effect conditional modes (best linear unbiased predictors BLUPs) from the best intrinsic effect model in Table 1. Horizontal dotted line represents the long-term average (fixed effect intercept), with points above this line indicative of good growth years whilst those below poor growth years. Note: in (a) CIs for older ages may be smaller than plotted point size and are not shown in (c) to improve clarity.

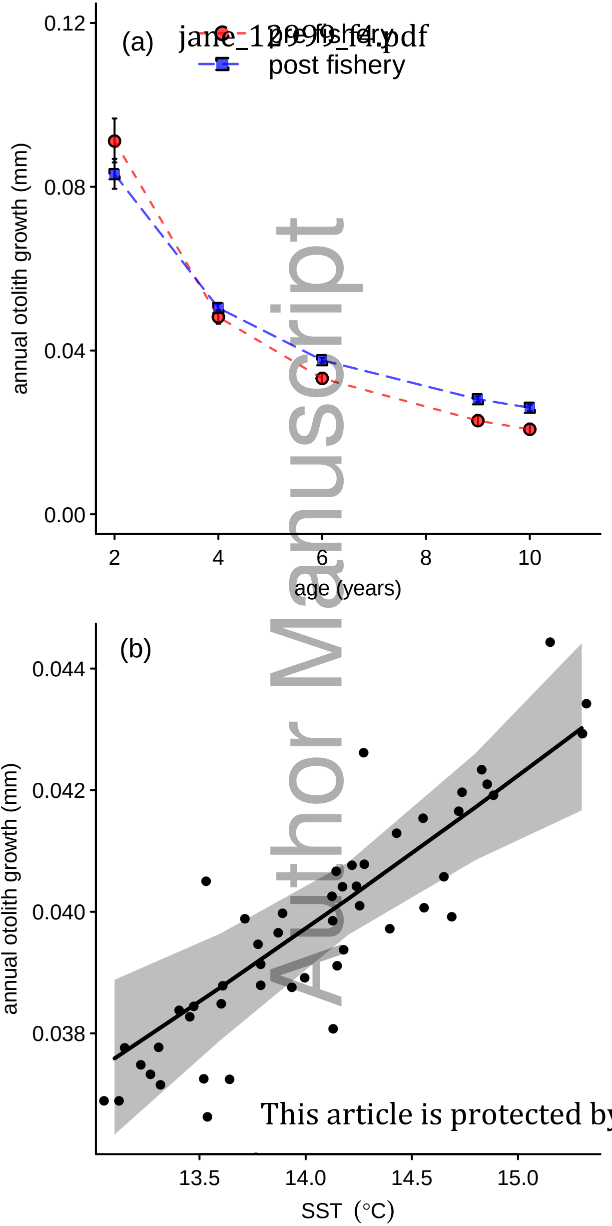
Figure 4: Purple wrasse annual otolith growth (annuli width mm ± 95% CI, back-transformed to the original scale) as a function of extrinsic factors. (a) Age-dependent annual otolith growth by fishery status (circles: pre-fishery 1980-1989; squares: post-fishery 1990-1999); and (b) annual otolith growth as a function of sea surface temperature (SST). Note: in (a) CIs for older ages may be smaller than plotted point size; in (b) data points indicate annual growth rates after accounting for fixed and random effects.

Figure 5: Variation in individual thermal reaction norms. (a) Density plot of observed thermal reaction norms in the pre- and post-fishery periods, with sample averages and β_W

(±95% CI) provided for reference. (b) Observed relationship between an individual's thermal phenotype (reaction norm slope) and body size (length at capture) as a function of fishery status.


(a)
PB
EHN
HCR
N
0
25
50
Kilometres
(b)
fish number
400
200
0
PB
EHN
HCR
1980
1985
1990
1995
2000
(c)
SST (°C)
15
14
13
PB
EHN
HCR
1980
1985
1990
1995
2000
(d)
stat. catch (t)
160
120
80
40
0
1980
1985
1990
1995
2000
year


(a)
annual otolith growth (mm)
0.10
0.08
0.06
0.04
0.02
2
4
6
8
10
age (years)
(b)
0.044
0.042
0.040
0.038
0.036
PB
EHN
HCR
site
(c)
standardised otolith growth (mm)
0.10
0.05
0.00
−0.05
PB
EHN
HCR
1980
1985
1990
1995
2000
year


(a)
pre fishery
post fishery
annual otolith growth (mm)
0.12
0.08
0.04
0.00
2
4
6
8
10
age (years)
(b)
annual otolith growth (mm)
0.044
0.042
0.040
0.038
13.5
14.0
14.5
15.0
SST (°C)

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