

# Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient

Elizabeth D. L. Trip<sup>1\*†</sup>, Kendall D. Clements<sup>1</sup>, David Raubenheimer<sup>2</sup> and J. Howard Choat<sup>3</sup>

<sup>1</sup>School of Biological Sciences, University of Auckland, Auckland, New Zealand; <sup>2</sup>Faculty of Veterinary Science and School of Biological Sciences, Charles Perkins Centre, The University of Sydney, Sydney, Australia; <sup>3</sup>School of Marine and Tropical Biology, James Cook University, Townsville, Australia

## Summary

1. In ectotherms, growth rate, body size and maturation rate covary with temperature, with the direction and magnitude of variation predicted by the Temperature-Size Rule (TSR). Nutritional quality or availability of food, however, may vary over latitudinal gradients, resulting in ambiguous effects on body size and maturation rate. The Temperature-Constraint Hypothesis (TCH) predicts that marine herbivorous ectotherms are nutritionally compromised at latitudes exceeding 30°. This provides an opportunity to resolve the contrasting demographic responses of ectotherms to variation in temperature and nutritional status over latitudinal gradients.

2. This study uses analysis of demographic rates to evaluate the predictions of the TSR in a marine herbivorous ectotherm sampled over a significant latitudinal gradient.

3. The direction and magnitude of demographic variation was established in the marine herbivorous fish, *Odax pullus* (the butterfish), and compared with that of a phylogenetically related but trophically distinct species, the carnivorous *Notolabrus fucicola* (the banded wrasse). Both species were sampled at three locations across the length of New Zealand covering latitudes between 35°S and 49°S. Growth rate, mean size-at-age, age- and size-at-maturity, life span and abundance were estimated for each species at each location.

4. Demographic traits of both taxa varied with latitude. Both species showed slower initial growth rates, and matured later at a larger body size at higher latitudes than populations sampled at lower latitudes. In addition, abundances increased significantly at higher latitudes in both species.

5. These results were consistent with the TSR but not with the TCH, confirming that nutritional ecology (herbivore vs. carnivory) did not determine demographic patterns over a biologically significant latitudinal gradient. Results from this study suggest that the absence of herbivorous reef fishes from the higher latitudes of the Northern Hemisphere may not reflect a general physiological mechanism as suggested by the TCH and highlights the need to clarify the evolutionary histories of the marine biota of each hemisphere.

**Key-words:** Berrigan-Charnov life-history puzzle, biogeography, herbivory, Labridae, marine ectotherm life-history traits, smooth-joining two-phase growth model

## Introduction

Temperature has a pervasive influence on the demography of aquatic ectotherms, including shallow water fishes.

Growth rate, body size and reproductive schedules of fishes vary with temperature over gradients of latitude (Conover 1992; Heibo, Magnhagen & Vollestad 2005; Robertson *et al.* 2005; Ruttenberg *et al.* 2005; Trip *et al.* 2008). The magnitude and direction of this variation is predicted by the Temperature-Size Rule (TSR), whereby reduced temperatures result in lower initial growth rate and delayed maturation at a larger body size (Atkinson

\*Correspondence author. E-mail: elizabeth.lamantrip@gmail.com

†Present address: Institute of Natural and Mathematical Sciences, Massey University, Auckland, New Zealand

1994). Physiological analyses in fishes indicate that this reflects the influence of temperature on metabolic rates (Clarke 2003; Portner & Farrell 2008; Munch & Salinas 2009).

The predictions of the TSR, including demographic responses over gradients of temperature, are well supported in the literature (Kingsolver & Huey 2008). Resource availability, however, will also drive demographic variation in ectotherms, whereby reduced food availability or increased nutrient stress results in lower initial growth rate and delayed maturity at a smaller adult body size (Stearns 1992). For this reason, the interpretation of demographic variation in ectotherms over latitudinal gradients will be complex, as variation due to increased nutrient stress (delayed maturity at a smaller size) yields contrasting predictions to the TSR (later maturity at a larger size) with increasing latitude.

An opportunity to resolve the contrasting demographic responses of ectotherms to variation in temperature and nutritional status over latitudinal gradients is provided by Gaines and Lubchenco (1982). Their hypothesis, henceforth identified as the Temperature-Constraint Hypothesis (TCH), argues that nutrition in aquatic ectothermic herbivores may be compromised at higher latitudes due to a presumed inability to process and assimilate plant food at low temperatures. Indeed, a recent evaluation of the TCH (Floeter *et al.* 2005) argues that this constraint significantly inhibits food processing and digestion in aquatic ectothermic herbivores living at latitudes exceeding 30°. A corollary of this is that, at higher latitudes, ectothermic herbivores will be subject to increasing nutrient stress resulting in reduced abundances at higher latitudes (Horn 1989; Harmelin-Vivien 2002; Behrens 2005; Floeter *et al.* 2005; Behrens & Lafferty 2007, 2012).

The predictions of the TCH, however, are challenged by the presence of a number of unequivocally herbivorous fishes in coastal environments extending beyond 35° of latitude into cold-temperate waters, especially in the Southern Hemisphere (Clements, Raubenheimer & Choat 2009). To investigate the contrasting predictions of the TSR and the TCH, this study focuses on a Southern Hemisphere marine fish, *Odax pullus* (Forster), a wrasse (F. Labridae) endemic to New Zealand with a distribution spanning a 14° latitudinal gradient of temperate coastal habitat between latitudes of 35°S and 49°S. The diet of *O. pullus* is explicitly herbivorous, with subsequent processing by fermentative digestion. To provide a clearer resolution of the relative importance of temperature versus nutritional constraints, we compared the response variables with those of a phylogenetically related but trophically distinct carnivorous labrid, *Notolabrus fucicola* (Richardson). *N. fucicola* was selected for its similarities to *O. pullus* in habitat association, body size range and latitudinal distribution (Francis 2012). The two species have established phylogenetic affinities (Westneat & Alfaro 2005).

This study has two main objectives. (i) To determine whether the responses in growth rate, body size and

maturation rate of *O. pullus* to latitude conform to the predictions of the temperature (TSR) or nutritional resources (TCH) hypotheses. Berrigan and Charnov (1994) used size-at-age plots to illustrate different demographic consequences of a reduction in initial growth rates due to reduced nutrient availability as opposed to reduced temperature, with the former resulting in smaller body size at maturation and the latter in larger body size at maturation. The form of their growth curves provides a means to predict the shape of the reaction norm for size- and age-at-maturity. If growth and development are primarily driven by temperature (i.e. consistent with the TSR), then we would expect crossed growth curves (Arendt 2010) and reaction norms for size- and age-at-maturity with a positive slope in both the herbivorous and the carnivorous species (Fig. 1a). However, if growth and development of the herbivorous species are reduced at higher latitudes as predicted by the TCH, we would expect contrasting families of growth curves, nested in the herbivorous taxon with the reaction norms generating a negative slope (Fig. 1b), but crossed in the carnivorous taxon (Fig. 1a). (ii) A number of studies (Harmelin-Vivien 2002; Floeter *et al.* 2005; Mora 2008; Poore *et al.* 2012) have argued that a consequence of the TCH is that a physiological process, the reduced capacity to digest plant material at higher latitudes, will influence the geographic distribution of herbivorous reef fishes. The second objective of this study is therefore to determine the pattern and magnitude of changes in abundance in the two study species across the latitudinal gradient. If herbivorous fishes are unable to meet metabolic demands at low temperatures (TCH), abundances of *O. pullus* will be reduced at higher, relative to lower latitudes (Floeter *et al.* 2005). In contrast, increased abundances of the herbivorous and carnivorous taxa at higher latitudes would be inconsistent with the TCH.

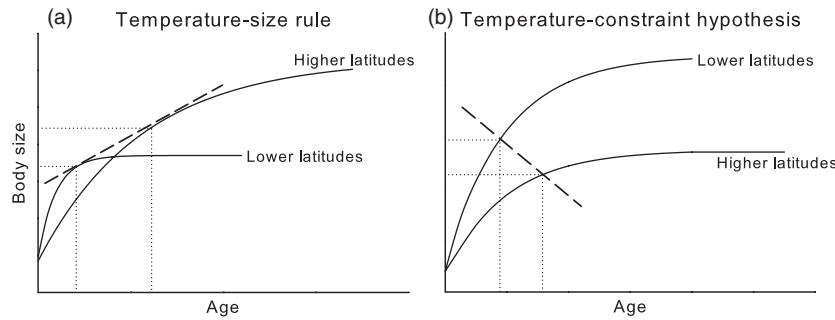
## Materials and methods

### STUDY SPECIES

*Odax pullus* (odacines) and *Notolabrus fucicola* (pseudolabrids) are nested within the Labridae (Westneat & Alfaro 2005) and are representative of clades of labrid fishes endemic to the Southern Hemisphere, have similar size ranges and occupy similar shallow habitats (Gomon, Bray & Kuitert 2008). *O. pullus* is herbivorous feeding preferentially on the phaeophytes *Ecklonia radiata*, *Carpophyllum* spp., *Lessonia* spp. and *Macrocystis* spp. (Clements & Choat 1993). *N. fucicola* is carnivorous, feeding on invertebrates including bivalves, crabs, isopods and amphipods (Denny & Schiel 2001).

### SAMPLING

Sampling was carried out over 11° of latitude (Fig. 2), which covers 80% of the species' New Zealand distributional range. Each species was sampled for demographic characteristics and abundance at the northern and southern regions of their distributional range, and at a geographically intermediate locality. Demographic and abundance data were sampled at the three



**Fig. 1.** Theoretical growth trajectories and maturation reaction norms in response to latitude (a) as predicted by the Temperature-Size Rule (TSR) as seen in the majority of ectotherms (Atkinson 1994; Berrigan & Charnov 1994) and (b) as predicted by the Temperature-Constraint Hypothesis (TCH) for ectothermic herbivores (Gaines & Lubchenco 1982; Floeter *et al.* 2005). Note that (b) refers specifically to the hypothesis that the digestion of algal foods in marine piscine herbivores is constrained by temperature at higher latitudes (TCH). Continuous lines are growth trajectories, and dashed lines show the shape of the reaction norm in size- and age-at-maturity.

locations; seasonal considerations precluded collection of maturation data from the intermediate location. The three sampling locations varied in latitude and mean annual sea surface temperature (SST), spanning a gradient of 11° in latitude with a mean annual SST difference of 5.5 °C (Table 1). The three locations are referred to as the northern (Hauraki Gulf), intermediate (D'Urville Island) and southern (Stewart Island) locations (Fig. 2). There were no differences amongst locations in the detectability of the two study species, and all sampling was performed by all four authors. The environmental features of the northern and southern limits of the sampling gradient have defined patterns of oceanic circulation, with the northern limits subject to subtropical and the southern limits to subantarctic currents, a pattern that has been consistent since the last glacial maximum (Marr *et al.* 2013).

A total of 902 individuals of *O. pullus* and 279 individuals of *N. fucicola* were sampled by spearing at the three locations. Fork Length (FL) was recorded to the nearest millimetre. The sagittal pair of otoliths was removed, rinsed in 70% ethanol and stored dry. Gonad tissue was collected for a subsample of 546 *O. pullus* and 178 *N. fucicola* individuals, weighed to the nearest gram and formalin-fixed for histology. Abundances were recorded along 30 × 10 m belt transects on Scuba at all three locations. At least 15 replicate belt transects were conducted by the same author (JHC) within each location to obtain mean density estimates.

#### ESTIMATION OF AGE

Age of *O. pullus* and *N. fucicola* was estimated from transverse sections of sagittal otoliths. Preparation of otolith sections and

methodology used for enumeration of age are described in Trip *et al.* (2011b). Ageing methods were validated in Trip *et al.* (2011b) for *O. pullus* and Ewing *et al.* (2003) for *N. fucicola*.

#### MEAN SIZE-AT-AGE

Estimates of mean size-at-age were obtained by modelling the growth of the two species at all sampling locations separately. Specifically, the relationship between size and age was modelled using the reparameterized von Bertalanffy growth function (rVBGF) (Francis 1988), which specifically generates model parameter estimates of expected mean size-at-age, thereby allowing for intraspecific comparison of mean size-at-age across populations. The form of the rVBGF function is detailed in Trip *et al.* (2008). The rVBGF function was fitted to observe size-at-age data of *O. pullus* and *N. fucicola* at each location following a smooth-joining two-phase (SJ2P) model approach and using the rVBGF function for both phases of growth (McMahon *et al.* 2011) (see Appendix S1, Supporting Information). To construct the SJ2P, the two growth phases are required to have the same slope at age Critage (the age at which growth switches from one phase to the other). Using the rVBGF function, having the same slope at age Critage required that:

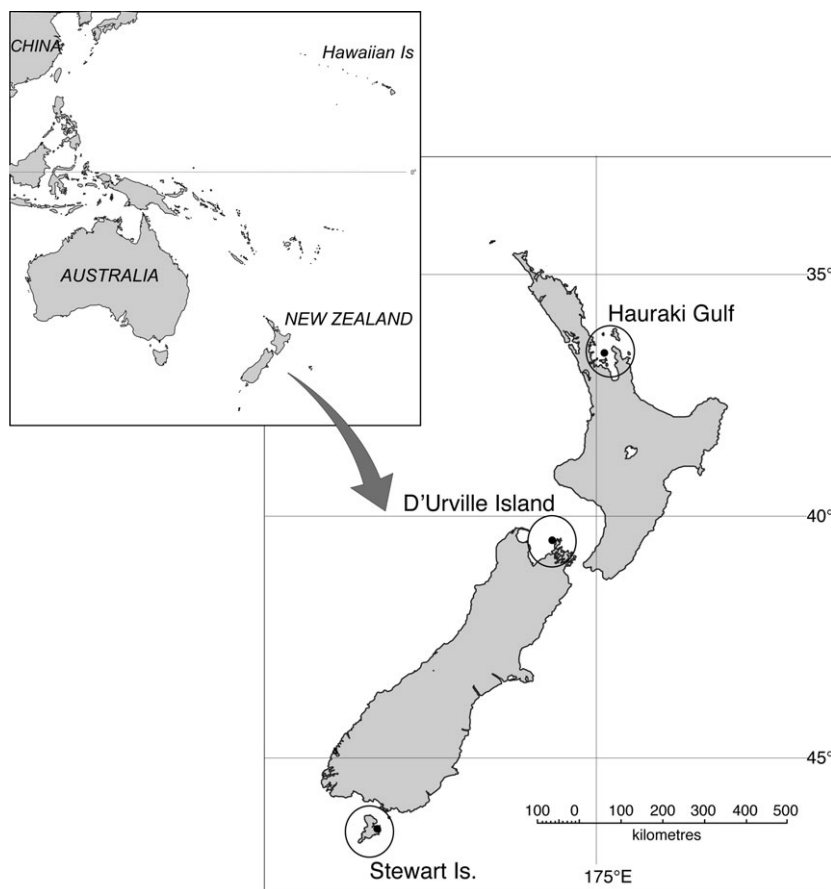
$$\frac{dL(\text{Criteage})}{dt} = \left( \frac{L_{\mu} - L_{\tau}}{1 - r^2} \right) * \left\{ \left( -r^{-2\tau/\mu - \tau} \right) * \left( \frac{2}{\mu - \tau} * r^{2 * \text{Criteage}/\mu - \tau} * \ln(r) \right) \right\}, \quad \text{eqn1}$$

with parameters  $L_{\mu}$ ,  $L_{\omega}$ ,  $L_{\tau}$  representing mean size-at-ages  $\mu$ ,  $\omega$  and  $\tau$ , and  $r = \frac{L_{\tau} - L_{\omega}}{L_{\mu} - L_{\omega}}$  (eqn 2) (Francis 1988). Ages  $\mu$  and  $\tau$  are

**Table 1.** Sampling details of *Odax pullus* and *Notolabrus fucicola* across New Zealand: latitude/longitude coordinates, mean annual sea surface temperature (SST, degrees Celsius), mean minimum monthly SST (Min SST, °C), mean maximum monthly SST (Max SST, °C), amplitude of mean monthly temperature difference between the warmest and coldest months ( $\Delta$ SST, °C), sample size (N), and number of gonad samples collected (in brackets).

| Location      | Lat/Long        | Mean SST | Min SST | Max SST | $\Delta$ SST | N total (N gonad samples) |                    |
|---------------|-----------------|----------|---------|---------|--------------|---------------------------|--------------------|
|               |                 |          |         |         |              | <i>O. pullus</i>          | <i>N. fucicola</i> |
| Hauraki G.    | 175.3°E, 36.3°S | 17.6     | 14.7    | 21.0    | 6.4          | 447 (319)*                | 75 (60)*           |
| D'Urville Is. | 173.9°E, 40.7°S | 14.7     | 12.4    | 17.7    | 5.3          | 125 (104)                 | 68 (63)            |
| Stewart Is.   | 167.9°E, 47°S   | 12.1     | 10.4    | 14.0    | 3.6          | 325 (123)*                | 136 (55)*          |

\*indicates presence of active females in the sample, showing samples for which size- and age-at-maturity could be estimated



**Fig. 2.** Map of sampling locations of *Odax pullus* and *Notolabrus fucicola* across New Zealand.

arbitrary ages selected to represent the earlier and later parts of the growth trajectory, respectively, while age  $\omega$  is the mean of  $\mu$  and  $\tau$ . Ages  $\mu$ ,  $\omega$  and  $\tau$  were 0.5, 0.7 and 0.9 year for the first phase of growth, yielding rVBGF parameters  $L_{0.5}$ ,  $L_{0.7}$  and  $L_{0.9}$  and providing estimates of mean size-at-ages 6, 8.5 and 11 months, and were 1, 6 and 11 years for the second growth phase, generating parameters  $L_1$ ,  $L_6$  and  $L_{11}$  and providing estimates of mean size-at-ages 1, 6 and 11 years.

All models were fitted by minimizing the negative log of the likelihood, assuming a normal probability distribution of size-at-age  $t$  ( $L_t$ ), with mean  $L_t$  and standard deviation  $\sigma$  (Haddon 2001). The number of individuals aged 1 year or less sampled at each location ranged from 36 to 78 for *O. pullus*. In contrast, few *N. fucicola* individuals aged 1 year or less were collected (1–3 fish) (Fig. S1, Table S1, Supporting Information). Therefore, an estimate value of size-at-settlement (*i.e.* size at theoretical age zero) of 15.5 mm FL (based on settlement data in Welsford, Jordan & Smolenski 2004) was used as a constraint to model growth of *N. fucicola* (see Berumen 2005 for the importance of juveniles in modelling growth). As a constraint was used to model the growth of *N. fucicola*, SJ2P parameters generated for the first phase of growth ( $L_{0.5}$ ,  $L_{0.7}$  and  $L_{0.9}$ ) of *N. fucicola* were not used in our analyses for comparison with *O. pullus*.

To compare estimates of mean size-at-age (parameters  $L_{0.5}$ ,  $L_1$ ,  $L_6$  and  $L_{11}$ ) across locations within each study species, variance around SJ2P parameters was estimated using a bootstrapping technique (Gotz *et al.* 2008). Comparison of 95% confidence intervals (CI) has been shown to provide comparatively more conservative results relative to standard significance testing methods (Schenker & Gentleman 2001; Welsford & Lyle 2005).

#### ADULT SIZE AND LIFE SPAN

Mean maximum age  $T_{max}$  (life span) and mean maximum body size  $L_{max}$  (adult body size) were calculated for each population as the average age (in years) of the 10% oldest individuals for *O. pullus* and 25% oldest individuals for *N. fucicola* and as the average body size (fork length, in mm) of the 10% largest individuals found within each sample of *O. pullus* and 25% largest individuals of *N. fucicola*, respectively (adapted from Trip *et al.* 2008). Mean maximum age and size were calculated on a greater proportion of the sample in *N. fucicola* to account for comparatively lower sample sizes than that in *O. pullus* (Claisse *et al.* 2009). CIs around  $T_{max}$  and  $L_{max}$  were estimated to compare  $T_{max}$  and  $L_{max}$  across locations for each species.

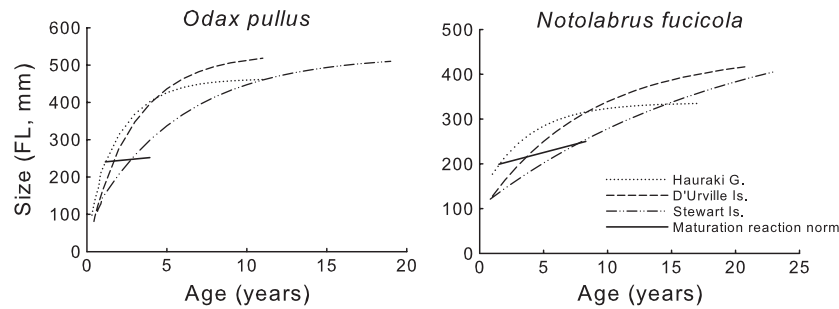
#### SIZE- AND AGE-AT-MATURITY

Size- ( $L_{50}$ ) and age-at-maturity ( $T_{50}$ ) of female *O. pullus* and *N. fucicola* were estimated as detailed in Trip *et al.* (2011a). As no reproductively active females were found at the Intermediate location (D'Urville Island) at the time of sampling (Table 1),  $L_{50}$  and  $T_{50}$  were not estimated at that location. Estimates of size- and age-at-maturity were compared for each species across locations by plotting  $L_{50}$  and  $T_{50}$  with bootstrapped CIs (Schenker & Gentleman 2001).

#### TEMPERATURE

Mean monthly sea surface temperature (SST) data were obtained from satellite-derived temperatures spanning from January 1985





**Fig. 3.** Growth trajectories (dashed and dotted lines) and maturation reaction norms (continuous lines) in *Odax pullus* and *Notolabrus fucicola* across New Zealand. Growth trajectories displayed are reparameterized von Bertalanffy growth functions fitted using a smoothing two-phase (SJ2P) model. Maturation reaction norms were constructed from estimates of size- and age-at-maturity obtained at the northern (Hauraki Gulf) and southern (Stewart Island) locations sampled.

to December 2007 (Smale & Wernberg 2009). Satellite-SST data were retrieved from the National Oceanographic and Atmospheric Administration (NOAA) CoastWatch Program 'Bloom-Watch 360' (data provided by NOAA Southwest Fisheries Science Center, Environmental Research Division). Four SST measures were considered: mean annual SST, mean monthly minimum SST (Min SST), mean monthly maximum SST (Max SST) and amplitude of difference in mean SST between warmest and coldest months ( $\Delta$ SST). All four SST measures showed significant pairwise correlations. Therefore, mean annual SST was retained as the only measure of temperature. Mean annual SST decreased significantly with latitude (Correlation analysis;  $R = 0.97$ ,  $P < 0.001$ ).

## Results

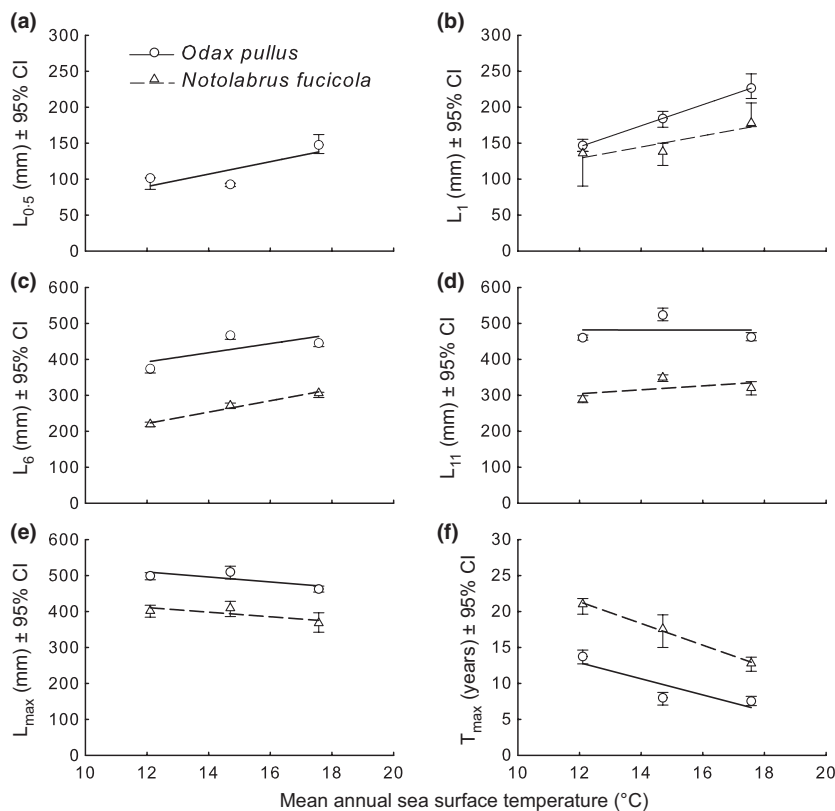
### GROWTH, BODY SIZE AND LIFE SPAN

Growth curves and associated demographic traits differed between locations in a similar fashion for each species (Fig. 3, and Fig. S1, Supporting Information). Four main trends were observed: (i) populations at the northern location (Hauraki Gulf) showed faster initial growth rates than those of the Southern location (Stewart Island); (ii) rapid juvenile growth at the Northern location was associated with asymptotic growth curves in which mean maximum size was achieved at  $\sim 50\%$  of the life span in each species; (iii) populations at the Southern location displayed significantly slower initial growth rates, indeterminate growth curves and a mean maximum size achieved only in the last 10% of the life span, with mean maximum sizes for *O. pullus* and *N. fucicola* significantly greater at the Southern as opposed to the Northern location; (iv) mean maximum ages in the Southern location were approximately double those estimated for populations in the Northern location. At the Intermediate location (D'Urville Island), populations displayed similar initial growth rates to the Northern location. However, in contrast to the asymptotic growth displayed at the Northern location, fish at the Intermediate location continued to grow at a slower rate over the second half of the life span, reaching larger mean maximum sizes than at the Northern location.

Details of age-specific growth patterns are shown in Fig. 4 and Table 2. Higher growth rates of juvenile *O. pullus* at the Northern location resulted in significantly larger mean size-at-age after 6 months ( $L_{0.5}$ ) than in juveniles from the Intermediate and Southern locations (Fig. 4a). SST accounted for 64% of the variation in mean size-at-age 6 months of *O. pullus* across locations, although the effect of SST on  $L_{0.5}$  was not significant (simple linear regression,  $F_{1,1} = 1.79$ ;  $P = 0.409$ ). A similar pattern of mean size increasing significantly with SST was retrieved for 1-year-old fish of both species (Fig. 4b, Table 2).

In older fish, the comparison of growth rates in populations of both species at 6 and 11 years ( $L_6$  and  $L_{11}$ , respectively) revealed a more complex picture. In both species, individual comparisons showed that populations from the Southern location had a significantly smaller mean size-at-age 6 years than those from the Northern location (Fig. 4c). However, *O. pullus* populations at the Intermediate location were significantly larger than those of the Northern location, a reflection of the asymptotic growth curve of *O. pullus* (Fig. 3). ANCOVA identified no significant effect of temperature on mean size-at-age 6 years and no species-specific temperature effects (Table 2). In 11-year-old *O. pullus*, the size difference between the Northern and Southern locations had disappeared, although individuals at the Intermediate location remained significantly larger than those at the other two locations. A similar result was seen in *N. fucicola*, with the exception that fish from the Southern location were significantly smaller at age 11 years than those of the Northern location (Fig. 4d), a reflection of the species-specific differences in the growth curves across the three sampling locations (Fig. 3). Again, there was no significant overall effect of temperature on  $L_{11}$ , and this was consistent between the two species (Table 2).

Analysis of mean maximum size and age for both species (Figs 4e,f) summarized the overall life-history patterns for each species. In *O. pullus*, significantly greater maximum sizes and ages were recorded from the Southern location when compared to the Northern location



**Fig. 4.** Relationship between demographic traits of *Odax pullus* and *Notolabrus fucicola* and temperature. Each plot shows the relationship between mean annual sea surface temperature and (a) mean size-at-age 6 months ( $L_{0.5}$ ) (*O. pullus* only), (b) 1 year ( $L_1$ ), (c) 6 years ( $L_6$ ), (d) 11 years ( $L_{11}$ ), (e) mean maximum size (adult size,  $L_{max}$ ) and (f) mean maximum age (life span,  $T_{max}$ ). Mean size-at-ages 0.5, 1, 6 and 11 years are best-fit reparameterized von Bertalanffy growth function parameters estimated using a smooth-joining two-phase (SJ2P) model. Adult size ( $L_{max}$ ) and life span ( $T_{max}$ ) are mean maximum size and age based on the 10% (*O. pullus*) and 25% (*N. fucicola*) largest and oldest individuals, respectively. Means are bias-adjusted and presented with 95% confidence intervals (CI).

(Fig. 4e). *N. fucicola* also showed a trend in decreasing size with increased temperature, but these differences were not significant (Fig. 4e). ANCOVA revealed no significant effect of SST on mean maximum size and no difference in the response of each species to temperature (Table 2). A significant intercept term (Table 2) identified species-specific differences, a reflection of *O. pullus* achieving a greater mean maximum size than *N. fucicola* at all locations.

Maximum ages and life span (mean maximum age) varied significantly across a north-to-south gradient. Maximum ages of *O. pullus* ranged from 11 years at the Northern and Intermediate locations to 19 years at the Southern location, showing an almost twofold increase in the duration of maximum life span of *O. pullus*. Similarly, in *N. fucicola* maximum ages recorded ranged from 17 years in the Northern location to 21 years at the Intermediate location and 23 years at the Southern location (Fig. 3). There was a significant negative effect of SST on mean maximum age of both *O. pullus* and *N. fucicola* (Fig. 4f), and this effect was consistent across the two species (Table 2). A significant intercept term reflected species-specific differences in life span, with *N. fucicola* achieving significantly greater mean maximum ages at all locations (Table 2).

#### SIZE- AND AGE-AT-MATURITY

In *O. pullus*, females were sexually mature at 240.7 mm FL (228.7–264.8) and 1.2 years (1.1–1.5) at the Northern

location, and at 252.1 mm FL (246.4–264.7) and 3.9 (3.6–4.3) years at the Southern location. In *N. fucicola*, females were sexually mature at 199.0 mm FL (136.6–165.0) and 1.5 years (1.4–1.6) at the Northern location, and at 250.0 mm FL (225.0–272.9) and 8.3 years (7.3–8.7) at the Southern location. These results indicated that (i) in both species, females matured significantly later at the Southern location relative to those living at the Northern location, and (ii) whilst there was no significant difference in size-at-maturity between the Northern and Southern locations in *O. pullus*, *N. fucicola* matured at a larger size at the Southern location relative to those living at the Northern location, resulting in a positive slope of the thermal reaction norm for size- and age-at-maturity.

#### GEOGRAPHICAL ABUNDANCE PATTERNS

Density of *O. pullus* and *N. fucicola* increased sixfold to tenfold from the Northern to the Southern location (Fig. 5). In both species, there was a strong positive relationship between density and latitude. For *O. pullus*, the relationship was exponential (nonlinear regression;  $y = -11.5 \cdot \exp^{0.0676 \cdot x}$ ;  $R^2 = 0.34$ ;  $P < 0.001$ ); for *N. fucicola*, the relationship was linear (simple linear regression;  $y = 0.8 \cdot x - 25.7$ ;  $R^2 = 0.31$ ;  $P < 0.001$ ).

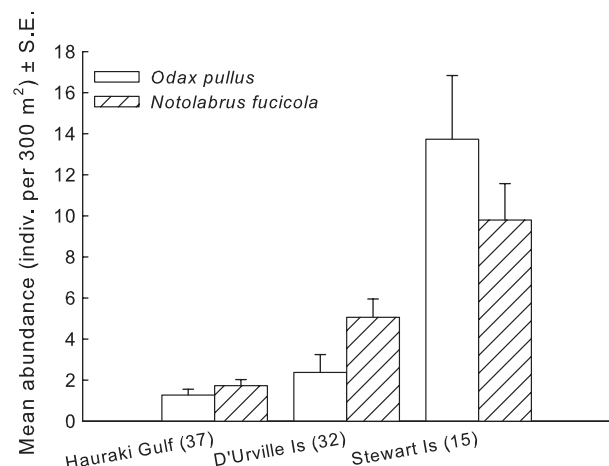
#### Discussion

Demographic responses to the prevailing temperatures at each location generated characteristic patterns of growth

**Table 2.** Effect of temperature on growth rate, mean size-at-age, adult body size and life span of *Odax pullus* and *Notolabrus fucicola*. Results of ANCOVA (homogeneity-of-slopes model) testing (i) for an effect of mean annual sea surface temperature (SST) on mean size-at-ages 1, 6, 11 years ( $L_1$ ,  $L_6$ , and  $L_{11}$ , respectively), mean maximum size ( $L_{max}$ ) and mean maximum age ( $T_{max}$ ) within each species, and (ii) whether the effect of SST on the demographic variables differed between the two species (SST\*species interaction term).

| Parameter | Effect      | SS       | d.f. | F      | P            |
|-----------|-------------|----------|------|--------|--------------|
| $L_1$     | Intercept   | 0.82     | 1    | 0.008  | 0.938        |
|           | Species     | 144.42   | 1    | 1.359  | 0.364        |
|           | SST         | 3756.42  | 1    | 35.352 | <b>0.027</b> |
|           | SST*species | 346.63   | 1    | 3.262  | 0.213        |
|           | Error       | 212.52   | 2    |        |              |
| $L_6$     | Intercept   | 2341.00  | 1    | 1.987  | 0.294        |
|           | Species     | 1343.81  | 1    | 1.140  | 0.397        |
|           | SST         | 6127.83  | 1    | 5.200  | 0.150        |
|           | SST*species | 65.14    | 1    | 0.055  | 0.836        |
|           | Error       | 2356.91  | 2    |        |              |
| $L_{11}$  | Intercept   | 17375.21 | 1    | 8.770  | 0.098        |
|           | Species     | 1979.47  | 1    | 0.999  | 0.423        |
|           | SST         | 217.40   | 1    | 0.110  | 0.772        |
|           | SST*species | 227.07   | 1    | 0.115  | 0.767        |
|           | Error       | 3962.57  | 2    |        |              |
| $L_{max}$ | Intercept   | 38920.60 | 1    | 86.731 | <b>0.011</b> |
|           | Species     | 365.32   | 1    | 0.814  | 0.462        |
|           | SST         | 1316.92  | 1    | 2.935  | 0.229        |
|           | SST*species | 1.71     | 1    | 0.004  | 0.956        |
|           | Error       | 897.50   | 2    |        |              |
| $T_{max}$ | Intercept   | 144.22   | 1    | 54.176 | <b>0.018</b> |
|           | Species     | 5.76     | 1    | 2.163  | 0.279        |
|           | SST         | 51.55    | 1    | 19.363 | <b>0.048</b> |
|           | SST*species | 1.13     | 1    | 0.425  | 0.581        |
|           | Error       | 5.32     | 2    |        |              |

Significant results are shown in bold ( $P < 0.05$ ). Separate ANCOVAs were performed for each demographic variable



**Fig. 5.** Geographical distribution of abundance patterns of *Odax pullus* and *Notolabrus fucicola*. Density estimates are expressed in number of individuals per 300 m<sup>2</sup> with standard error (SE). Number of transects performed at each location are presented in brackets.

and reaction norms in both study species. Crossed growth curves were generated over a broad north-to-south gradient by a pattern of increased initial growth rates and earlier maturation at smaller body size at warmer temperatures. The combinations of growth and reproductive responses resulted in a pattern of larger body size at higher latitudes as predicted by the Temperature-Size Rule (TSR). This response pattern and the greater densities at higher latitudes were consistent between the herbivorous species and the carnivorous species, arguing against nutritional stress due to inhibition of digestion of dietary plant material at low temperatures, a key assumption of the Temperature-Constraint Hypothesis (TCH).

A critical feature of this interpretation was the incorporation of age structure and life span in the analysis. This enabled a more comprehensive interpretation of the impacts of latitude (temperature) on demography. The increased life span at higher latitudes observed in both species was consistent with the influence of metabolic rates on age structure in ectotherms under the influence of varying temperatures (Munch & Salinas 2009). Reduction in mean age at lower latitudes was particularly striking in *O. pullus*, where the maximum age in the lower and intermediate latitude populations was only 58% of that in the higher latitude population. In *O. pullus*, truncated life span resulted in growth curves that barely cross or do not cross, crossing being one criterion for invoking the TSR (Arendt 2010). While the growth trajectory of fish from the Northern population confirms that crossing will occur, the growth curves of the Intermediate and Southern populations indicate that crossing would occur over equivalent life spans. These results illustrate and emphasize the need to obtain estimates of age and life span when testing for the predictions of the TSR. Comparisons of age structures at each location also provided information on reproductive tactics in both species. Extended life span and greater size associated with delayed maturity at higher latitudes suggested a trade-off with the compensation for delayed reproduction in these populations, achieved through an increase in spawning opportunities, a doubling of the adult life span and greater fecundities (larger body size) (Fig. S2, Supporting Information).

Analysis of abundances in each species over the latitudinal gradient revealed that the higher latitude location (Stewart Island) supported densities of *O. pullus* eight times higher than those recorded from the Northern, lower latitude location (Hauraki Gulf), a trend also seen in *N. fucicola*. The geographic pattern of abundance in *O. pullus* strongly ramped to the southern limit of their distribution is in direct contrast with the predictions of the TCH. Such a differential in density might have been expected to generate increased intraspecific competition at higher latitudes reflected in reduced size at maturation relative to low-density populations (Stearns 1992). However, growth and maturation schedules did not support such an interpretation. These results confirm that, in terms of growth rates, maturation schedules and abundance

patterns, herbivorous fish at higher latitudes were similar to fish from another trophic group.

Although the Intermediate location was intermediate in latitude (and temperature) to the Northern and Southern locations, it did not reveal an intermediate demographic response between the patterns found at the two extremities of the range. This suggested the possibility that locality-specific factors might also be influencing latitudinal demographic and abundance profiles and hence that the demographic patterns would reflect local environmental conditions, not temperature. However, our sampling effort covered >80% of the species' geographical range and spanned from the northern to the southern extremities of their distributions, and the demographic responses seen in the two study species matched that seen in a majority of ectotherms over similar gradients of latitude (TSR) (Atkinson 1994). The most likely scenario is that the responses seen in the demographic parameters of *O. pullus* and *N. fucicola* reflect a response over a broad north-to-south scale. However, it will be essential for future investigations to survey a greater number of localities over the latitudinal gradient and include estimates of local environmental and biological effects on the response of demographic traits to disentangle the effects of temperature (latitude) from that of local environmental factors.

As *O. pullus* is subject to a commercial fishery that targets individuals in the larger size classes (see online Supporting Information for a detailed description of the *O. pullus* fishery), it is possible that the demographic and abundance patterns observed may reflect the size-selective removal of older and larger individuals, resulting in faster growth, earlier maturity, smaller adult size and reduced abundance at locations with greater fishing pressure (Hutchings 2004; Hamilton *et al.* 2007; Enberg *et al.* 2012). Data on landings from the *O. pullus* fishery, however, show that the fishery is concentrated on the Southern populations with landings at Stewart Island exceeding those of the Hauraki Gulf by a factor of 12 (Appendix S2 and Fig. S3, Supporting Information). In addition, the restricted inshore distribution of *O. pullus* at the northern localities (Meekan & Choat 1997) and the relatively few predators that occur in this habitat (Choat & Ayling 1987) argues against predation as a factor driving the size and abundance patterns.

The TCH has a long tenure in the literature (Gaines & Lubchenco 1982) and is still frequently invoked to explain biogeographic patterns (Harmelin-Vivien 2002; Floeter *et al.* 2005; Cheal *et al.* 2012; Litsios *et al.* 2012; Poore *et al.* 2012). The TCH would predict ectothermic herbivores at higher latitudes to be smaller and far less abundant than their conspecifics at lower latitudes. The results of this study, however, suggest the opposite as the patterns of slower initial growth, delayed maturation and greater body size for *O. pullus* and *N. fucicola* all support an alternative hypothesis, the TSR. The trends observed in both study species represent common responses to a temperature regime and were not accounted for by nutritional ecology.

In particular, analysis of the nutritional ecology of the herbivorous taxon over a temperature range of 10.7° of latitude showed no evidence of a temperature-related constraint on digestion of plant material. The positive relationship between latitude and *O. pullus* abundance also refutes a major argument of the TCH, that is, that physiological processes restrict the abundances of ectothermic herbivores to warmer waters. One reason for the disparity between the predictions of the TCH and the present results appears to reflect the different geological and oceanographic histories of the Northern and Southern Hemisphere temperate and polar shallow water environments. However, while the Southern Hemisphere includes groups of herbivorous fishes at high latitudes (Gomon, Bray & Kuiter 2008; Last *et al.* 2011) that are absent from the Northern Hemisphere, the Northern Hemisphere also supports a number of unique herbivorous taxa, for example the stichaeids (Horn 1989). Clearly, additional work is required to clarify the evolutionary histories of fishes at higher latitudes in each hemisphere. Whilst the results from this study demonstrate clear differences between populations at the latitudinal extremes of their range, which support the TSR, the status of populations at Intermediate locations identifies these as areas where additional studies should be carried out. In particular, information on the reproductive and demographic status of *O. pullus* populations at intermediate latitudes is required to clarify the impact of temperature on the nutritional ecology and demography of ectothermic herbivores over significant latitudinal gradients.

### Data accessibility

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.f1c11>.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Modelling of growth in fish, and the Smooth-Joining Two-Phase model

**Appendix S2.** Variation in fishing effort for *Odax pullus* across sampling locations

**Figure S1.** Growth trajectories and size-at-age data of *Odax pullus* (left hand panel) and *Notolabrus fucicola* (right hand panel) across New Zealand, showing the difference between using a single reparameterised Von Bertalanffy Growth Function (rVBGF; continuous line) and using the smooth-joining two-phase model (SJ2P; dashed line) to model growth of the study species.

**Figure S2.** Size-specific fecundity of reproductively active females *Odax pullus*, showing a similar relationship between ovary weight and body size in the Hauraki Gulf (continuous line) and Stewart Island (dashed line).

**Figure S3.** Fishing effort for *O. pullus* at the three sampling locations.

**Table S1.** Akaike Weights comparing the goodness-of-fit of the smooth-joining two-phase (SJ2P) model and fitting a single reparameterised von Bertalanffy growth function (rVBGF) to the size-at-age data.