Geographic and sex-specific variation in growth of yellow-eyed mullet, *Aldrichetta forsteri*, from estuaries around New Zealand

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Abstract
Survival and reproductive rates in fish are often a function of body size. Consequently, spatial- and sex-specific variation in somatic growth rates can have important consequences for population growth and resilience. We used otolith-based approaches to estimate geographic- and sex-specific growth rates of yellow-eyed mullet (*Aldrichetta forsteri*) collected from 14 estuaries and harbours around New Zealand. *Aldrichetta forsteri* is an abundant and dominant component of New Zealand’s estuarine fish fauna. We extracted otoliths from 511 fish, validated daily and annual increments, and prepared transverse thin sections of otoliths to determine age. “Size-at-age” relationships were estimated using both linear- and non-linear (von Bertalanffy) growth models, and model performance was evaluated using Akaike’s Information Criterion. Because growth rates of sampled fish were best approximated by linear functions, we used ANCOVA to test the null hypothesis that growth rates of *A. forsteri* were homogeneous between sexes and among geographic locations around New Zealand. Our analyses suggest heterogeneous growth rates between sexes and among locations. Interestingly, relative growth rates between sexes appeared to vary across separate latitudinal gradients for North Island and South Island. Within each island (but not across islands), female *A. forsteri* generally grew faster than males at the lowest latitudes; relative growth rates of females declined progressively below males with increasing latitude.

INTRODUCTION
Body sizes and growth rates of teleost fish have long been recognised as important determinants of their reproductive capacity and longevity (Wootton 1990). For a broad range of organisms, body size and growth rates vary across latitudinal gradients (e.g., Mayr 1956; Ashton et al. 2000; Ashton 2001; Garvey et al. 2003). Additionally, for many animals, sexual selection and/or reproductive costs lead to differential growth rates and/or divergent maximum body sizes between males and females (Rensch 1950; Andersson 1994; Love et al. 1990). Across species, relationships between growth- and body size parameters are generally assumed to result from trade-offs that maximise reproductive success (Pianka 1970). Particularly for fish, such parameters are often estimated using the von Bertalanffy growth function (VBGF), and relationships between parameters are used as surrogates for life-history patterns (Beverton & Holt 1957; Ricker 1975). For example, species with relatively fast growth rates are often characterised by low ages and small sizes at sexual maturity, high reproductive outputs, short life-spans, and low asymptotic lengths (Roff 1984; Stearns & Crandall 1984; Stearns 1992).

Although body size and growth for a given species may vary predictably across latitudes and between sexes, few studies have examined how patterns of sex-specific growth might vary across latitudinal gradients for any species (but see Defeo & Cardoso 2002). This is surprising because such geographic variation in the relative patterns of somatic growth between sexes might set limits on...
growth rates of populations, and therefore determine boundaries for species ranges (e.g., Zaidan et al. 2003). Furthermore, sexual dimorphism that varies among spatially segregated populations may indicate gradients in selective regimes that can promote diversity (e.g., Arnqvist 1992).

Here, we examine sex-specific patterns of growth of the yellow-eyed mullet, Aldrichetta forsteri, and explore how these patterns vary among sites that are arrayed across c. 10 degrees of latitude in New Zealand. Known biology of A. forsteri is reviewed by Taylor & Paul (1998), and by Sullivan et al. (2005): A. forsteri is typically a schooling species, and is common and abundant in estuaries and harbours throughout New Zealand and southern Australia. Adults are generally omnivorous, feeding upon algae, diatoms, benthic invertebrates, detritus, fish eggs, and small fish. Females begin developing eggs in July, with egg maturation by late December; spawning generally occurs from late December to mid March, possibly in coastal waters. In New Zealand, the species is regularly targeted by recreational fisheries and occasionally by commercial fisheries (Taylor & Paul 1998; Sullivan et al. 2005). Previous studies suggest that A. forsteri have a maximum lifespan of c. 7 years, and exhibit growth rates that vary among sites (Lenanton & Potter 1987; Potter et al. 1990) and between sexes (Thompson 1957).

MATERIALS AND METHODS

We used four standardised gill nets to sample A. forsteri from 14 permanently open estuaries from around New Zealand (Kaipara, Parengarenga, Waikare, Manakau, Thames, Waitemata, Tauranga, Raglan, Golden Bay, Porirua, Whanganui, Havelock, Avon-Heathcote, Blueskin Bay). Two nets consisted of three 20-m-long ¥ 2-m-high panels; adjoining net panels comprised either 50.8-mm mesh (n = 2 panels) or 63.5-mm mesh (n = 1 panel). The remaining two nets also contained three panels as described, with the exception that the single panel with 50.8-mm mesh measured 12 m in length. All sampling was completed between December 2000 and February 2001, and sampling duration and intensity at individual sites was strictly regulated by the New Zealand Ministry of Fisheries (MFish). Consequently, sampled fish from some neighbouring estuaries were pooled to facilitate statistical estimates of geographic variation in growth (pooled sites indicated in Fig. 1, shown geographically in Fig. 2). As far as possible, attempts were made to pool samples from nearby sites that were located at similar latitudes, and from estuaries with similar geomorphologies. Within each sampled estuary, fish were collected from areas of similar habitat (e.g., mudflats, mangroves) in nearshore shallow waters (<3.0 m depth). We recorded total length (TL, measured to nearest mm) and sex (determined from gonad inspection) for all sampled fish, and we extracted and prepared sagittal otoliths (following methods of Secor et al. 1992) for subsequent analyses in the laboratory.

We embedded sagittal otoliths from 511 fish in a clear epoxy resin and cut samples along 0.5 mm transverse sections with an isomet low-speed diamond saw, to obtain otolith cross-sections that contained the entire growth axis. We then ground and polished both sides of the samples with carborundum (400–1200 grade), 30 µm lapping film (3M Imperial, New Zealand), and 0.3 µm alumina paste. Otolith thin-sections were examined under a stereo microscope to estimate number of “annual” rings, and under higher power (400¥) with transmitted light to determine the number of “daily” rings between presumed annual bands for a subsample of otoliths (for validation of annual rings, see below). Otolith increments were counted separately by two readers to obtain independent estimates of age. All discrepancies were re-examined, and if a consensus was not reached, the otolith was excluded from the study (n = 33). A total of 20 A. forsteri were captured alive using rod and line and held in a sea-aquaria under semi-natural conditions (natural photoperiod, flow-through sea water under ambient temperature and salinity regimes) for an initial 2-day acclimatisation period. Fish were then transferred to a tank containing an unbuffered solution of 400 mg litre–1 Alizarin red S (ARS) in sea water for 24 h to facilitate marking of otoliths (Tsukamoto 1988), and subsequently returned to sea-aquaria. Fish were killed after 7 days and sagittal otoliths were extracted and prepared for examination following methods described above. Otolith sections were viewed with a UV light microscope fitted with block filters (band-pass filter 450–490 nm) to highlight the ARS marks; the number of daily increments following the mark were recorded by two readers to validate daily increment formation (e.g., confirmation of seven increments following ARS mark); annual rings were validated by confirming c. 365 daily increments present between annual rings, as detailed above.
Fig. 1 Length-age plots for *Aldrichetta forsteri* sampled from seven regional populations spanning c. 10 degrees of latitude. Fitted lines estimated from ANCOVA (see Table 2); slopes reflect growth rates (cm length accrual per year), and are heterogeneous between males (closed symbols and solid lines) and females (open symbols and dashed lines) and among regions (A–G). Symbol keys in A–D denote sites that were pooled within regions to facilitate parameter estimates. Note that *y* axis begins at 10 cm.
We constructed size-at-age plots for *A. forsteri*, stratified by sex and geographic location, to facilitate estimates of growth rates, and their patterns of variation between sexes and among regions. To determine whether patterns of growth for *A. forsteri* were better described by linear versus non-linear growth functions, we plotted age estimates (years) against TL (cm) of individuals sampled from different geographic locations, and estimated growth rates with competing models. Growth rate was estimated separately for males and females at each geographic location by fitting linear regressions of length on age (using PROC REG, SAS version 8.02; units of growth rate = cm length accrual/year). Similarly, we fitted a von Bertanlaffy growth function (VBGF) to size-at-age, partitioned by sex and geographic location:

\[ L_t = L_\infty [1 - e^{-K(t-t_0)}] \]

where \( L_t \) is mean length at age \( t \), \( L_\infty \) is the mean asymptotic length, \( K \) is the growth coefficient that describes the rate at which the asymptotic size \( L_\infty \) is approached, and \( t_0 \) is the theoretical age at which length equals zero does not vary substantially among populations or sexes. We used least-squares non-linear regression with a Gauss-Newton algorithm (PROC NONLIN, SAS version 8.02) to fit the VBGF (SAS Institute 1999).

We used Akaike’s Information Criterion (AIC) to compare the fits of linear models and VBGF, and to determine the “best” underlying model that described patterns of growth for *A. forsteri* (Akaike 1992). AIC evaluates model performance based upon both the likelihood of the model given the data and the number of model parameters; the approach is particularly useful for comparisons among non-nested models (Quinn & Keough 2002). Models with the smallest AIC values were deemed the best models.

Because patterns of growth of *A. forsteri* (at least for the sizes encompassed by our samples) were best described by linear growth models, we used an analysis of covariance (ANCOVA) (PROC GLM, SAS version 8.02) to test the null hypothesis that growth rates of *A. forsteri* were homogeneous between sexes and among geographic locations around New Zealand (SAS Institute 1999). We tested the main effects of “location” and “sex”, and the effect of the covariate “age” on total length of *A. forsteri*, and we used a full ANCOVA model that included all possible interaction terms.
RESULTS

An ARS concentration of 400 mg litre⁻¹ produced clearly discernible yellow marks (enhanced by UV illumination) on otoliths of treated fish, and did not cause any mortality or obvious adverse effects on *A. forsteri*. Both otolith readers consistently scored seven clearly formed increments following the chemical mark, suggesting that the increments at this scale are formed daily. Counts of these validated daily increments within a presumed annual band confirmed the presence of c. 365 increments. We interpreted this evidence that our annual banding could be accurately used to age *A. forsteri* to the nearest half-year.

VBGF predicted mean asymptotic lengths and growth coefficients for *A. forsteri* that were poorly estimated (see standard errors of estimates) and largely unrealistic (Table 1). This was because the relationships between size and age of *A. forsteri* partitioned among geographic locations and sexes were predominately linear (Fig. 1). Patterns showed little evidence of asymptotic growth (L-infinity) from the size distributions of fish that were sampled. Comparisons of AIC scores (Table 1) suggested that the linear model gave a better relative fit of growth patterns than the VBGF in 13 of 14 instances (only males from Northland were slightly better described by the VBGF). Consequently, we used ANCOVA to conduct formal statistical tests of heterogeneity in growth rates between sexes and among sites.

The ANCOVA model used to partition variation in growth rates (described by the relationship between the dependent variable length and the...
covariate age) among geographic location and sex indicated a significant 3-way interaction between age, region, and sex (Table 2). This interaction suggests that patterns of growth may vary between sexes in an inconsistent pattern across regions (i.e., the slopes of the relationships between length and age appear heterogeneous between males/females across geographic locations; Fig. 1). The estimated slopes of these relationships indicate females grew faster than males in Northland and Havelock regions, but not elsewhere in New Zealand (Fig. 2). Growth rates of females relative to males varied across separate latitudinal gradients for North Island and South Island (Fig. 2).

DISCUSSION

For many fish, survival and fecundity are a function of body size. Larger individuals are often subject to lower predation rates (e.g., Baily & Houde 1989), larger females often produce more eggs (e.g., Trella 1998), and larger males may gain fertilisation access to more females (e.g., Warner 1975). Geographic variation in growth rates, therefore, can have large and important consequences for reproductive output, longevity, and hence the dynamics of spatially segregated populations.

Our results suggest _A. forsteri_ sampled from populations around New Zealand had heterogeneous patterns of growth, both between sexes and across geographic locations. Our sampling efforts captured fish 12–38 cm in length, and for this distribution of sizes (similar, overlapping distributions were sampled at all sites), growth was best approximated by a linear model. We note that more intensive sampling (e.g., using a wider range of net mesh sizes to capture larger and/or smaller individuals) may have facilitated better estimates of VBGF parameters. Nonetheless, although growth patterns of many fish follow the VBGF (Wootton 1990), our data suggest that _A. forsteri_ appear to maintain relatively constant growth rates throughout their lives (supported statistically by AIC comparisons). Because previous studies suggest that _A. forsteri_ have a maximum lifespan of c. 7 years (Lenanton & Potter 1987; Potter et al. 1990), and this is within the age range of the largest individuals that we regularly sampled from our sites, we believe that the observed pattern of non-asymptotic growth may be real (i.e., not simply an artefact of limited sampling). _A. forsteri_ may simply maximise lifetime fitness through continued, high energetic investment to somatic growth.

Growth rates estimated from the linear models did, however, vary between sexes in an inconsistent pattern across geographic locations. Our analyses suggest that females grew faster than males in Northland (lowest latitude sampled on North Island) and Havelock (lowest latitude sampled exclusively on South Island), whereas at all other regions, rates of growth were either similar or else males grew faster. Relative growth rates of females declined with increasing latitude, in separate, parallel gradients for North Island and South Island. Females sampled from Cook Strait populations (comprising individuals pooled from both islands) had relative growth rates that were “intermediate” to the island-specific latitudinal trends.

Geographic variation in patterns of sexual dimorphism is rarely the subject of investigation by biologists (reviewed in Issac 2005), though the rapidly growing discipline of “macroecology” provides a valuable forum in which to explore and interpret such emergent patterns (Brown 1995). We believe the latitudinal clines in relative growth rates between sexes of _A. forsteri_ signal the operation of fundamental, unexplored macroecological processes that may have important implications for population dynamics, range distributions, and patterns and rates of evolution. Disparities in growth rates among populations of _A. forsteri_ may reflect phenotypic plasticity arising from energetic constraints that vary as a function of local environmental conditions (e.g., temperature), coupled with differential energetic investment strategies between the sexes. For example, the observation that female _A. forsteri_ appeared to exhibit faster growth than males in lower latitude (i.e., warmer) conditions, with a reversal of this pattern at higher latitudes, may indicate an increase in the relative costs of reproduction to females found at progressively higher latitudes. Alternatively, such patterns may arise from sexual selection (e.g., Clutton-Brock & Harvey 1977) or natural selection (e.g., Colwell 2000) that favours larger sizes for one sex over another, which varies with environmental conditions (e.g., as a function of latitude). Although we could find no studies from marine systems that explore this concept, terrestrial biologists have noted similar patterns for Indian fruit bats, where females attained larger sizes in lower latitudes, and males grew larger at higher latitudes (Storz et al. 2001).

Growth rates of many organisms are known to be a product of environmental conditions (Houde 1989) and genotype (Roff 1992). Syntheses by Conover & Schultz (1995), and more recently by Garvey et al.
(2003), highlight the potential importance of interactions between environmental conditions and genotypes for generating among-population variability in somatic growth rates. For species with broad geographic distributions, genotypes and environmental conditions may be expected to vary spatially (e.g., across latitudinal gradients), and the pattern of covariance between these factors can affect phenotypic variation. For example, “countergradient variation” (sensu Levins 1969) describes a spatial pattern of variation in genotypes that opposes (or compensates for) environmental gradients, and their effects on phenotypes (e.g., growth rates). Likewise, “co-gradient variation” can result in spatial patterns of genotypes that intensify environmental effects on phenotypes (Garvey et al. 2003). This framework establishes an expectation that gradients in phenotypes may arise from the interaction between genotypic and environmental variation, and we speculate that genotypic heterogeneity may explain the repeated latitudinal trend in relative growth rates of A. forsteri: i.e., the separate, disjointed latitudinal gradients for North Island and South Island may arise from covariance in genotypes and environmental gradients compounded by limited gene flow across Cook Strait. Testing of this hypothesis will require additional sampling of A. forsteri populations, environmental conditions and patterns of genetic structure among populations.

Regardless of the mechanism(s) responsible, we expect that the spatial variation in sex-specific growth rates that we have observed for A. forsteri will result in geographic variation in intrinsic rates of population growth (r) that can: (1) contribute to latitudinal range boundaries of the species (e.g., Zaidan et al. 2003); and (2) affect source-sink/metapopulation dynamics of a regional stocks (e.g., Hanski 2002) if local populations from separate estuaries are connected by migrations of larvae or adults. Similarly, we expect that such patterns may have evolutionary implications dependent upon rates of gene flow: if gene flow is restricted across regions, then we would predict that the latitudinal gradients in sexual dimorphism may promote genetic diversity (e.g., Arnqvist 1992). Alternatively, if gene flow is relatively high among regions, we might predict that environmental gradients promote phenotypic plasticity as a mechanism to maximise fitness (Warner 1991). Overall, we believe the macroecological patterns we document here for A. forsteri are intriguing and suggest the operation of relatively unexplored processes in biology and, consequently, warrant further exploration.

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