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Stable isotopes reveal post-release trophodynamic and ontogenetic changes in a released finfish, mulloway (*Argyrosomus japonicus*)

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Abstract. Carbon and nitrogen stable isotope ratios were analysed for hatchery-reared, recaptured and wild mulloway, *Argyrosomus japonicus*, to investigate temporal and growth-related changes in isotopic composition for stocked fish after release, and to evaluate changes in isotopic composition in terms of ontogenetic dietary switches. $\delta^{13}C$ and $\delta^{15}N$ values decreased and increased, respectively, after release. The isotope composition of released fish was distinct from wild fish until 200 days after release, but after 200 days post-release fish did not differ significantly from wild fish of similar or greater sizes. Abrupt dietary transitions from crustaceans to teleost fish (>50 cm total length (TL)) were evident in a rapid $\delta^{13}C$ and $\delta^{15}N$ change in wild mulloway, and $\delta^{15}N$ was significantly greater in wild fish >65 cm TL compared with wild fish <50 cm TL. Multivariate carbon and nitrogen isotopic data were suitable for separating stocked and wild fish for up to 200 days after release, but did not separate wild fish grouped according to dietary composition. Carbon and nitrogen isotopic composition closely reflected dietary transitions and rapid adaptation by stocked mulloway to wild diets, which was evident in a high tissue turnover rate of up to 0.017 day^{-1}. Stable isotopes are a useful tool for examining the integration of released fish into stocked ecosystems and can be used to describe convergence in the diets of wild and released fish.

Additional keywords: back calculation, diet, ontogeny, otolith growth, Sciaenidae.

Introduction

The chemical compositions of various tissues are often used to investigate trophic and spatial aspects of the ecology of estuarine fishes (Hesslein *et al*. 1991). The stable nitrogen and carbon isotopic composition of fish muscle tissue (Jardine *et al*. 2005) can indicate patterns of movement and energy transfer (Logan *et al*. 2006), particularly when fishes are exposed to complex assemblages of prey. Fractionation of these isotopes through trophic levels can indicate the origin of dietary carbon and nitrogen sources, and allows the construction of trophic relationships (Trueman *et al*. 2005). Fish reared under hatchery conditions may have unique carbon and nitrogen isotope compositions compared with wild conspecifics (Grey *et al*. 2004), which are determined by rearing location and food source (Kennedy *et al*. 2005). Tissue turnover will alter the unique isotopic composition of hatchery-reared fish after release to eventually reflect that of the wild stock, and the rate of isotopic change can be related back to the rate at which wild diets are adopted (Tominaga *et al*. 2003).

Trophic interactions form the basis of predator and prey dynamics (Dickmann *et al*. 2007) and much of our understanding of fish communities. Identifying dietary sources is central to these concepts; however, quantifying the relative importance of prey items beyond the appearance of prey in stomach contents is often difficult (Bosley *et al*. 2002). Stable isotopes indicate ontogenetic changes in dietary sources (Fry *et al*. 1999; Badalamenti *et al*. 2002). However, there are few examples of research that combine isotopic analysis with stomach contents analysis in fish (Dittel *et al*. 2006). Isotopic data are useful in substantiating dietary information from stomach contents, which provide an instantaneous snapshot of dietary contents, with an indication of diet over the preceding months. Concomitant analysis of these two data sources can increase our understanding of dietary relationships and can aid the interpretation of isotopic composition in trophic studies.

Mulloway, *Argyrosomus japonicus* (Sciaenidae), is an apex predator in the coastal ecosystems of southern Australia, South Africa and China. This species is a fast-growing estuarine resident until sexual maturity at 50–75 cm total length (TL) (Taylor *et al*. 2006*b*), reaching a maximum age and length of ~24 years and 132 cm respectively (Silberschneider and Gray 2008). The iconic sportfish status of the species means that recreational anglers harvest up to 975 t $year^{-1}$ in Australia (Henry and Lyle 2003), with most targeting larger adult fish whose

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removal adversely affects recruitment (Taylor *et al*. 2005*a*). Mulloway undergo substantial changes in diet as late juveniles, rapidly switching from a benthic crustacean diet to a piscivorous diet between 50 and 65 cm (Taylor *et al*. 2006*a*). This switch coincides with an increase in home range and foraging activity (Taylor *et al*. 2006*b*). The scarcity of information on the trophic dynamics of Sciaenidae in general is surprising, considering their potential contribution to top-down control of marine ecosystems (Christensen and Pauly 1998) and substantial interest in stock enhancement of member species throughout the world (Taylor *et al*. 2005*b*; Liu and Sadovy 2008). In particular, there are few studies that incorporate stable isotope composition of late-juvenile or adult stages, with most work focusing on larvae (e.g. Deudero *et al*. 2004; Rowell *et al*. 2008; Suzuki *et al*. 2008). Ideally, investigations of the trophic interactions of Sciaenidae should involve a combination of traditional dietary analyses and stable isotope analyses.

The objective of the present study was to conduct a preliminary investigation into the trophic relationships of released and wild mulloway, *A. japonicus*, using ^{15}N and ^{13}C stable isotopes. The present study aimed to evaluate changes in the isotopic composition of released mulloway with time after release, individual growth trajectories, and in the context of ontogenetic dietary changes in late-juvenile mulloway, and to compare the isotopic composition of released mulloway with wild conspecifics. We tested the following hypotheses: (*i*) there would be no change in the isotopic composition of stocked mulloway after release; (*ii*) there would be no difference in isotopic composition between stocked and wild mulloway; and (*iii*) there would be no difference in isotopic composition among wild mulloway of different sizes.

Materials and methods

Study site

The Georges River (33°59′S, 151°9′E) is the major estuary in the Sydney metropolitan area, extending 50 km inland through a primarily urbanised catchment. The river has a waterway area of 12 km^2 and discharges into a large open embayment (Botany Bay; 33°59′S, 151°12′E) before flowing into the Tasman Sea. The Georges River has been heavily impacted by urban and industrial development (Gibbs 2001; Haworth 2002), with significant shore modification, saltmarsh and mangrove destruction, and heavy urban pollution inputs.

Fish rearing and stocking

Juvenile mulloway were grown to 7.9 ± 3.5 cm (mean ± s.e.) at Port Stephens Fisheries Centre (PSFC) in polyvinyl-lined 1-ha ponds with a continual supply of fresh estuarine water (Fielder and Bardsley 1999). Fish fed on natural copepod blooms in the ponds, but their diet was heavily supplemented with commercial 1–2 mm pellets (Ridleys Aquafeed, Deception Bay, Queensland, Australia). Fish were marked with oxytetracycline hydrochloride (OTC) as previously described (Taylor *et al*. 2005*a*) and released into the Georges River on 9 May 2003, as part of an *Argyrosomus japonicus* stocking trial.

Sampling

Released and wild mulloway were sampled from around the release site using an otter trawl (6-m mouth, 12-m length, 0.6-mm cod-end mesh size) and bottom-set monofilament gillnets (100-m length, 2-m hang, 57-mm mesh). Each sampling event included three 20-min trawls and a 2-h deployment of the gillnet. Sampling was conducted during the evening on 3 July 2003, 7 August 2003, 17 August 2003, 14 September 2003, 11 November 2003 and 28 June 2004 (the samples were provided from the recreational fishery on this date). Captured mulloway were killed in an ice slurry and transferred to a freezer for holding. Fish were measured for length and weight, the otoliths were removed for detection of the OTC mark, and 0.5 cm^3 of white dorsal muscle tissue was removed for stable isotope analysis. Otoliths (or fin spines for the 28 June 2004 samples) were sectioned and the marks were visualised as described previously to determine the origin of the fish (Taylor *et al*. 2005*a*) using an Olympus BH-2 microscope with a reflected fluorescence attachment (Olympus, Tokyo, Japan).

Otolith back calculation

Individual growth rates were calculated for recaptured mulloway using the Biological Intercept method (Campana 1992; Vigliola *et al*. 2000) because recaptured mulloway were still in their linear growth phase. Otolith images under fluorescent excitation (490 nm) at 4× magnification were digitalised using a Spot Flex 64 MP camera (Diagnostic Instruments, Sterling Heights, MI, USA). The cross-sectional radius of the otoliths was measured to both the OTC mark and to the exterior of the section, along a line from the core to the proximal edge of the sulcus acusticus using Image Pro Plus v 4.5 (Media Cybernetics, Silver Spring, MD, USA). Size at stocking was calculated using the formula:

$$L_s = L_{cpt} + \frac{(R_s - R_{cpt})(L_{cpt} - L_0)}{(R_{cpt} - R_0)}$$

where L_s and R_s are the length and radius at the time of stocking (time of marking), L_{cpt} and R_{cpt} are the length and radius at the time of capture, and L_0 and R_0 are the length and radius at the biological intercept. L_0 and R_0 were measured using 14-day-old larvae obtained from the PSFC hatchery.

Chemical analysis

Samples were dried at 65°C for 72 h and then ground to a fine powder with a mortar and pestle. Dry powder (500 μg) from each sample was loaded into tin capsules and manually compacted to minimise internal air space, and the capsules were crimped and placed into 96-well microplates. The samples were analysed using a IsoPrime EA/IRMS continuous flow stable isotope mass spectrometer (GV Instruments, Wythenshawe, Manchester, UK).

Data analysis

Temporal and growth-related changes in tissue isotopic composition were tested for significance using linear regression analysis; assumptions of normality, homogeneity of variance and linearity were assessed through graphical examination of the residuals. The mean δ^{15}N values at stocking were determined from hatchery-reared fish and changes in the values were expressed as a function of: (*i*) individual, post-release length increase (Δcm) determined from back-calculated individual growth trajectories; and (*ii*) a gross increase in mass (Δg) since release

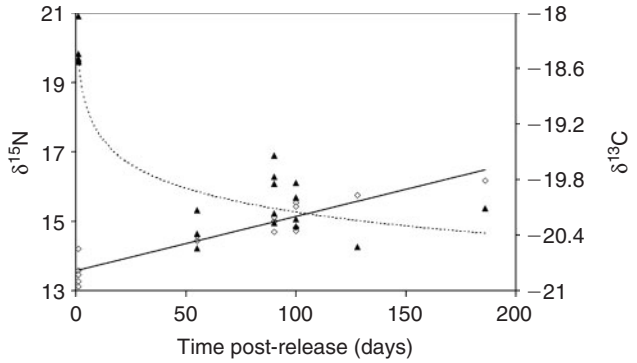

Fig. 1. $\delta^{15}N$ (◊) and $\delta^{13}C$ (▲) values 200 days after release. $\delta^{15}N$ and $\delta^{13}C$ formed a positive linear (solid line) and negative logarithmic (dashed line) relationship, respectively, with increasing time after release.

calculated by converting the back-calculated length-at-release to a mass estimate using the standard length–weight relationship (Silberschneider *et al*. 2009).

Taylor *et al*. (2006*a*) produced several size groupings on the basis of dietary data for mulloway, including fish <50 cm TL with diets dominated by mysid and decapod crustaceans (Group 4 in the results), fish 50–65 cm TL with a transitory diet including both decapod crustaceans and teleost fish (Group 5 in the results), and fish >65 cm TL with diets dominated by teleost fish and cephalopods (Group 6 in the results). An analysis of similarity (ANOSIM) was carried out on a Bray–Curtis dissimilarity matrix of untransformed multivariate isotopic data to determine differences in isotopic composition among these size groupings for wild fish and hatchery-reared fish (Group 1), released fish recaptured 50–200 days after stocking (Group 2) and released fish recaptured >200 days after stocking (Group 3). The $\delta^{15}N$ values for wild fish grouped by diet were tested for homogeneity of variance using Levene's test and evaluated using a single factor ANOVA. All parametric tests were carried out in SPSS v. 11 (SPSS, Chicago, IL, USA) and the multivariate analyses were done in PRIMER v. 5.2.2 (PRIMER-E, Plymouth, UK).

Results

Isotopic composition and growth of released mulloway

Analytical precision was determined to be 0.072‰ (one s.d.) for both $\delta^{15}N$ and $\delta^{13}C$. The $\delta^{15}N$ values in all stocked fish increased to 186 days after release (Fig. 1), forming a positive linear relationship with time-after-release ($\delta^{15}N = 0.16 \cdot \text{Time} + 13.57$; $r^2 = 0.88$, $F_{1,19} = 130.91$, $P < 0.01$). The $\delta^{13}C$ values for stocked fish decreased rapidly after release, forming a significant negative logarithmic regression with time ($\delta^{13}C = -0.51 \cdot \ln(\text{Time}) - 18.05$; $r^2 = 0.85$, $F_{1,19} = 98.76$, $P < 0.01$).

There were significant relationships between growth trajectories and $\Delta\delta^{15}N$ after release (Fig. 2*a*, *b*). This included significant linear relationships between $\Delta\delta^{15}N$ to 200 days after release with mass (g) increase ($\Delta\delta^{15}N = 0.03 \cdot \Delta\text{Mass} + 0.84$; $r^2 = 0.36$, $F_{1,14} = 7.2$, $P = 0.02$) and length increase ($\Delta\delta^{15}N = 0.15 \cdot \Delta\text{TL} + 0.64$; $r^2 = 0.20$, $F_{1,14} = 4.46$, $P = 0.05$; Fig. 2*b*). Older fish were provided as

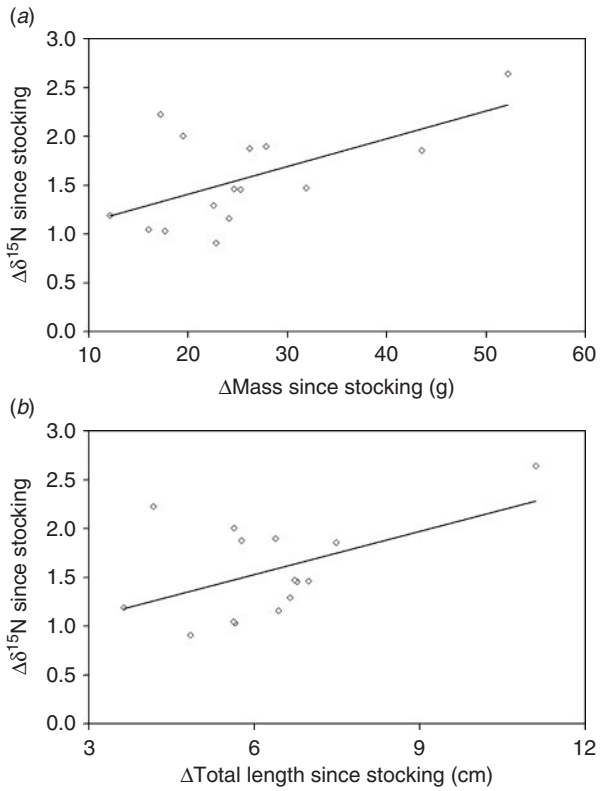

Fig. 2. $\Delta\delta^{15}N$ with individual post-release growth trajectories for *Argyrosomus japonicus*. Growth trajectories are calculated in terms of (*a*) mass (g) increase after release and (*b*) total length increase after release.

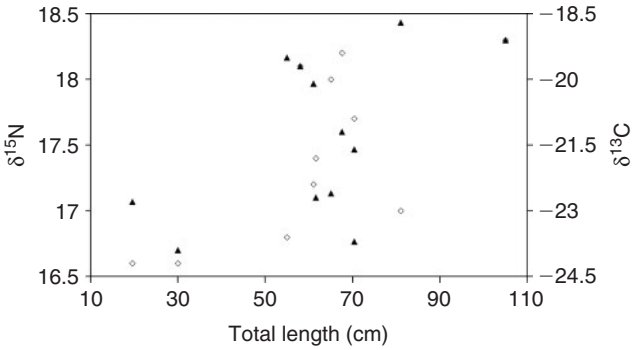

Fig. 3. Size-related changes in $\delta^{15}N$ (◊) and $\delta^{13}C$ (▲) composition for wild mulloway captured in the Georges River.

filleted carcasses from the recreational fishery without otoliths and could not be included in these analyses.

Isotopic composition and dietary ontogeny

Mulloway became enriched in both nitrogen and carbon with increasing size, with the greatest rate of enrichment occurring between 55 and 65 cm TL (Fig. 3). This increase occurred in a jackknife fashion across this size range; however, there were insufficient data points at higher and lower sizes to produce a good model fit.

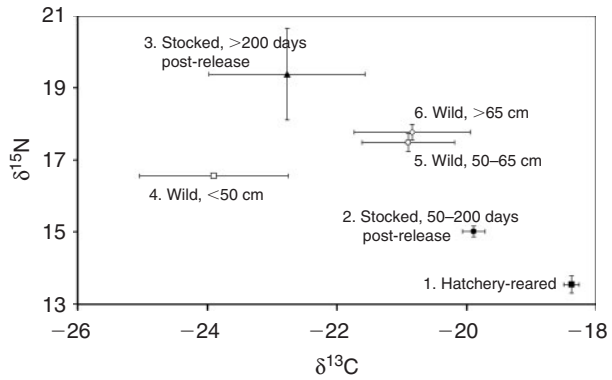

Fig. 4. $\delta^{15}N$ and $\delta^{13}C$ values (mean ± s.e.) grouped for stocked (black markers) and wild (white markers) mulloway in the Georges River. Mulloway have been grouped as hatchery-reared (Group 1, $n = 4$, ■), stocked 50–200 days after release (Group 2, $n = 17$, ●), stocked >200 days after release (Group 3, $n = 2$, ▲), wild <50 cm (Group 4, $n = 2$, □), wild 50–65 cm (Group 5, $n = 5$, ◯) and wild >65 cm (Group 6, $n = 5$, ◇).

Isotopic composition of released and wild mulloway

Enrichment of ^{15}N and $\delta^{13}C$ occurred through wild fish in Groups 4–6, and ^{15}N enrichment occurred in hatchery-reared fish after stocking (Fig. 4). The ANOSIM revealed that hatchery-reared fish (Group 1) had a significantly different ($P < 0.01$) isotopic composition at the time of stocking to fish 50–200 days (Group 2) and >200 days (Group 3) after stocking, and to wild fish <50 cm TL (Group 4), 50–65 cm TL (Group 5) and >65 cm TL (Group 6). In addition, fish recaptured 50–200 days after stocking (Group 2) had a significantly different ($P < 0.01$) isotopic composition to fish recaptured >200 days after stocking (Group 3), and to wild fish (Groups 4–6). The isotopic composition of hatchery-reared fish recaptured >200 days after stocking (Group 3) was not significantly different from wild fish (Group 4, $r = 0.75$, $P = 0.33$; Group 5, $r = 0.29$, $P = 0.24$; Group 6, $r = 0.11$, $P = 0.29$); however, this comparison was based on only two data points for Group 3. The ANOSIM indicated no significant differences between the multivariate isotopic data of wild fish (Groups 4–6). A single factor ANOVA on the $\delta^{15}N$ values of wild fish in these groupings did indicate a significant difference between grouped wild fish ($F_{2,11} = 4.41$, $P < 0.05$), with Group 6 having a significantly greater $\delta^{15}N$ than Group 4 fish (Hochbergs, $P < 0.05$; Figs 3 and 4).

Discussion

Isotopic composition and growth of released mulloway

This is the first study to evaluate changes in isotopic composition with back-calculated growth trajectories in released fish. We were fortunate that the hatchery food source used resulted in hatchery-reared fish with an isotopic composition considerably different to that of wild fish. This is likely to have resulted from the use of ingredients in the pellets that were not found in the stocked system as observed in previous studies (Hurd *et al*. 2008). This isotopic separation facilitated the evaluation of changes in tissue composition and turnover in terms of time, ΔTL and ΔMass, which indicated that the isotopic composition of hatchery-reared mulloway is rapidly altered after their release into natural systems, and that ^{15}N increases at a rate of 0.03‰ g^{-1} of body tissue for released mulloway <200 days after release. Hatchery-reared mulloway have a high $\delta^{13}C$ composition relative to most wild conspecifics and released fish, but this rapidly depletes in the muscle tissue within 55 days after stocking. This points to a marked shift in the source of organic carbon in the diet (Fry 1988). The relationship in Fig. 1 shows rapid depletion in $\delta^{13}C$ towards an asymptotic equilibrium, and a longer time series of data would confirm this trend. Interpretation of these changes in isotopic composition in the context of individual growth trajectories could potentially be extended to estimate the daily ration of individual fish and the growth rate after release, allowing the direct use of isotopic signatures to make inferences regarding release strategies such as site, season and size at release (Tominaga *et al*. 2003).

Hesslein *et al*. (1993) developed an exponential tissue turnover model describing the $\delta^{13}C$ value at any time after the switch from old to new food: $\delta^{13}C = \delta^{13}C_n + (\delta^{13}C_0 - \delta^{13}C_n) \cdot e^{-(k+m)\cdot t}$, where $\delta^{13}C_n$ and $\delta^{13}C_0$ are the $\delta^{13}C$ values in equilibrium with the new food and old food respectively; t is time (days) and m is the metabolic turnover constant (day^{-1}). The growth rate of each fish (k) is described as a function of the weight at capture (W, g), the weight at the commencement of the experiment (W_0, taken as the back-calculated weight at stocking) and the time elapsed (t, days): $k = \ln(W \cdot W_0^{-1}) \cdot t^{-1}$. Solving for m using these relationships, our data equate to a tissue turnover rate of 0.017 day^{-1} for released mulloway, based on the assumption that $\delta^{13}C$ has reached equilibrium for the new 'wild' diet within 200 days after release. A metabolic turnover of this magnitude points to rapid adaptation and effective exploitation of 'wild' diets after release, and the resultant addition of new tissue. This value was an order of magnitude greater than that reported for whitefish *Coregonus nasus* muscle (5–21 cm TL; Hesslein *et al*. 1993).

Isotopic composition and dietary ontogeny

The only other study to examine the isotopic composition of a mature sciaenid used *Sciaena umbra* (Deudero *et al*. 2004); most previous studies on members of Sciaenidae have focussed on fish <8 mm (Herzka and Holt 2000; Herzka *et al*. 2001, 2002; Dorval *et al*. 2005). *Sciaena umbra* had $\delta^{15}N$ values ~10‰ lower than *A. japonicus*; however, $\delta^{15}N$ and $\delta^{13}C$ increased with size in both *S. umbra* (28.7–44.5 cm TL; Deudero *et al*. 2004) and *A. japonicus* (19–105 cm TL; the present study). The lower $\delta^{15}N$ reflects that fact that *S. umbra* individuals were not piscivorous through the size range analysed. Clear ontogenetic changes in *A. japonicus* diet occur within the size range analysed (Taylor *et al*. 2006*a*), with an abrupt transition at ~55 cm TL from a diet dominated by mysid and decapod crustaceans to a predominantly piscivorous diet, including juvenile conspecifics. The transition was apparent in the rapid increase in both $\delta^{15}N$ and $\delta^{13}C$ from 55 to 65 cm TL. The lack of a significant difference in multivariate isotopic composition data for wild mulloway grouped by dietary composition was not surprising given the high $\delta^{13}C$ variability among these groups; however, there was a significant difference in $\delta^{15}N$ values between mysid/decapod consumers (Group 4) and piscivores (Group 6). This result confirms that ^{15}N provides a good indication of increasing piscivory in mulloway, and

supports existing dietary data. Analysis of the isotopic composition of similar-sized red drum (*Sciaenops occelatus*) would provide an interesting comparison to these observations, given that similar dietary trends to *A. japonicus* are evident from stomach contents analyses (Llanso *et al*. 1998; Taylor *et al*. 2006*a*).

Isotopic composition of released and wild mulloway

Fish reared under hatchery conditions had a unique isotopic composition compared with those of wild conspecifics, which provides a mechanism to differentiate stocked from wild individuals after recapture. Hatchery-reared mulloway in the present study were discernable from wild mulloway on the basis of their $\delta^{15}N$ and $\delta^{13}C$ values; however, the hatchery-specific isotopic composition appeared to converge with the wild isotopic composition after 200 days. Isotopic signatures have been used previously to differentiate between hatchery-reared and wild salmonid species (Dempson and Power 2004; Kennedy *et al*. 2005). However, non-salmonid examples are limited to Japanese flounder *Paralichthys olivaceus* (Watanabe *et al*. 2005) and the present study. Dempson and Power (2004) classified escaped hatchery-reared *Salmo salar* on the basis of their isotopic signature and the technique was broadened to classify farmed salmon by rearing location (Kennedy *et al*. 2005). The rapid changes in isotopic composition with time after release shown in the present study indicate that, although this technique may provide a useful tool to identify hatchery-reared mulloway after recapture, suitability is limited until ~200 days after release. The clear benefit of this technique is that it not only allows identification, but also provides additional trophic and bioenergetic information after release. Kennedy *et al*. (2005) suggested the use of more stable structures, such as scales, for post-release identification using ^{15}N and ^{13}C over longer temporal scales, but the time-specific storage of isotopes in this tissue has yet to be determined.

The $\delta^{13}C$ values were highly variable within Groups 4–6, relative to variation within the hatchery-reared and early release groups (Groups 1 and 2). The low $\delta^{13}C$ variability within Groups 1 and 2 reflects the stability of the hatchery environment and associated food sources. Group 3 fish, which had been at large >200 days, displayed large within-group variation similar to the wild groups. Although not statistically significant, the enriched trophic position of Group 3 fish relative to Group 4 fish suggests that Group 3 fish may be consuming Group 4 fish or other fish of a similar trophic position to Group 4 fish. Taylor *et al*. (2006*a*), however, did not detect a difference in the diets between wild and stocked fish of this size. The high variability in the $\delta^{13}C$ values in Groups 3–6 indicates that these size classes may be relying on food webs that use a range of energy sources (Post 2002). In addition, the largest wild fish (Groups 5 and 6) have an enriched $\delta^{13}C$ signature relative to smaller wild fish (Group 4), which may reflect a shift towards food webs dominated by producers using a C_4 pathway (Kremer and Küppers 1977; Descolas-Gros and Fontugne 1985).

The isotopic composition observed both in the present study and in Kennedy *et al*. (2005) changed rapidly after release, and fish adopt $\delta^{13}C$ and $\delta^{15}N$ values similar to wild conspecifics as they consume a 'wild' rather than a 'pellet' diet and tissue turnover takes place. Based on the change in $\delta^{15}N$, stocked *A. japonicus* may progress through the equivalent of two trophic levels in less than 1.5 years after release (assuming ~3.4‰ per trophic level; Post 2002). This, coupled with the high tissue turnover rate calculated above, confirms that stocked mulloway may exert considerable predation pressure on forage fish soon after release. Consequently, care should be taken in estimating an appropriate stocking density based on available ecosystem resources when releasing predators into estuarine systems because overstocking will likely have adverse affects on prey populations, competitors and conspecifics. This is particularly relevant for red drum *Sciaenops ocellatus* stocking in the southern USA, where over 30 million fish can be released annually (Gold 2004).

In conclusion, we have demonstrated the utility of ^{15}N and ^{13}C stable isotopes for release experiments and in differentiating stocked and wild mulloway for short periods (<200 days) after release. Hatchery-reared mulloway show a similar isotopic composition to wild mulloway soon after release, confirming that hatchery-reared fish adopt wild feeding habits. ^{15}N and ^{13}C stable isotopes in wild mulloway reflect a dietary shift to increasing piscivory with size. However, further investigations of changes in $\delta^{15}N$ and $\delta^{13}C$ with size in Sciaenidae are required to aid our understanding of the role of these species in the trophic dynamics of the wider ecosystem. Analysis of stable isotopes has the potential to improve stock enhancement programs for sciaenids by validating predatory impact estimates and consumption rates for stocked estuarine predators (Taylor and Suthers 2008). Overall, stable isotopes are a useful tool for examining the integration of released fish into stocked ecosystems, and can be used to describe convergence in the diets of wild and released fish and to estimate rates of tissue turnover. Future applications of this technique would benefit from an assessment of tissue turnover in controlled environments for a range of food sources to estimate the rate of change in the isotopic composition of fish tissues following a dietary shift (Herzka and Holt 2000).

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References

Badalamenti, F., D'Anna, G., Pinnegar, J. K., and Polunin, N. V. C. (2002). Size-related trophodynamic changes in three target fish species recovering from intensive trawling. *Marine Biology* **141**, 561–570. doi:10.1007/S00227-002-0844-3

Bosley, K. L., Witting, D. A., Chambers, R. C., and Wainright, S. C. (2002). Estimating turnover rates of carbon and nitrogen in recently metamorphosed winter flounder *Pseudopleuronectes americanus* with

stable isotopes. *Marine Ecology Progress Series* **236**, 233–240. doi:10.3354/MEPS236233

Campana, S. E. (1992). Analysis of otolith microstucture data. In 'Otolith Microstructure and Analysis'. (Eds D. K. Stevenson and S.E. Campana.) pp. 73–100. (Department of Fisheries and Oceans: Ottawa.)

Christensen, V., and Pauly, D. (1998). Changes in models of aquatic ecosystems approaching carrying capacity. *Ecological Applications* **8**, S104–S109.

Dempson, J. B., and Power, M. (2004). Use of stable isotopes to distinguish farmed from wild Atlantic salmon, *Salmo salar. Ecology of Freshwater Fish* **13**, 176–184. doi:10.1111/J.1600-0633.2004.00057.X

Descolas-Gros, C., and Fontugne, M. R. (1985). Carbon fixation in marine phytoplankton: carboxylase activities and stable carbon-isotope ratios: physiological and paleoclimatological aspects. *Marine Biology* **87**, 1–6. doi:10.1007/BF00396999

Deudero, S., Pinnegar, J. K., Polunin, N. V. C., Morey, G., and Morales-Nin, B. (2004). Spatial variation and ontogenic shifts in the isotopic composition of Mediterranean littoral fishes. *Marine Biology* **145**, 971–981. doi:10.1007/S00227-004-1374-Y

Dickmann, M., Mollmann, C., and Voss, R. (2007). Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival. *Marine Ecology Progress Series* **342**, 277–289. doi:10.3354/MEPS342277

Dittel, A. I., Epifanio, C. E., and Fogel, M. L. (2006). Trophic relationships of juvenile blue crabs (*Callinectes sapidus*) in estuarine habitats. *Hydrobiologia* **568**, 379–390. doi:10.1007/S10750-006-0204-2

Dorval, E., Jones, C. M., Hannigan, R., and van Montfrans, J. (2005). Can otolith chemistry be used for identifying essential seagrass habitats for juvenile spotted seatrout, *Cynoscion nebulosus*, in Chesapeake Bay? *Marine and Freshwater Research* **56**, 645–653. doi:10.1071/MF04179

Fielder, D. S., and Bardsley, W. J. (1999). A preliminary study on the effects of salinity on growth and survival of mulloway *Argyrosomus japonicus* larvae and juveniles. *Journal of the World Aquaculture Society* **30**, 380–387. doi:10.1111/J.1749-7345.1999.TB00689.X

Fry, B. (1988). Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography* **33**, 1182–1190.

Fry, B., Mumford, P. L., Tam, F., Fox, D. D., Warren, G. L., Havens, K. E., and Steinman, A. D. (1999). Trophic position and individual feeding histories of fish from Lake Okeechobee, Florida. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 590–600. doi:10.1139/CJFAS-56-4-590

Gibbs, P. J. (2001). Monitoring of natural recolonisation of seagrass and transplant success of *Zostera capricorni* at the Sydney Airport third runway in Botany Bay. Sydney Airports Corporation, Final Report to Sydney Airports Corporation Limited and Sydney Ports Corporation, Sydney.

Gold, J. (2004). Stock structure and effective size of red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico and implications relative to stock enhancement and recruitment. In 'Stock Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities'. (Eds K. Leber, S. Kitada, H. L. Blankenship and T. Svåsand.) pp. 353–370. (Blackwell: Oxford.)

Grey, J., Waldron, S., and Hutchinson, R. (2004). The utility of carbon and nitrogen isotope analyses to trace contributions from fish farms to the receiving communities of freshwater lakes: a pilot study in Esthwaite Water, UK. *Hydrobiologia* **524**, 253–262. doi:10.1023/B:HYDR.0000036144.49795.DD

Haworth, R. (2002). Changes in mangrove/salt-marsh distribution in the Georges River estuary, Southern Sydney, 1930–1970. *Wetlands (Australia)* **20**, 80–103.

Henry, G. W., and Lyle, J. M. (2003). 'The National Recreational and Indigenous Fishing Survey.' (Australian Government Department of Agriculture, Fisheries and Forestry: Canberra.)

Herzka, S. Z., and Holt, G. J. (2000). Changes in isotopic composition of red drum (*Sciaenops ocellatus*) larvae in response to dietary shifts: potential applications to settlement studies. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 137–147. doi:10.1139/CJFAS-57-1-137

Herzka, S. Z., Holt, S. A., and Holt, G. J. (2001). Documenting the settlement history of individual fish larvae using stable isotope ratios: model development and validation. *Journal of Experimental Marine Biology and Ecology* **265**, 49–74. doi:10.1016/S0022-0981(01)00324-0

Herzka, S. Z., Holt, S. A., and Holt, G. J. (2002). Characterization of settlement patterns of red drum *Sciaenops ocellatus* larvae to estuarine nursery habitat: a stable isotope approach. *Marine Ecology Progress Series* **226**, 143–156. doi:10.3354/MEPS226143

Hesslein, R. H., Hallard, K. A., and Ramlal, P. (1993). Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2071–2076. doi:10.1139/F93-230

Hesslein, R. H., Capel, M. J., Fox, D. E., and Hallard, K. A. (1991). Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 2258–2265. doi:10.1139/F91-265

Hurd, T. M., Jesic, S., Jerin, J. L., Fuller, N. W., and Miller, D., Jr (2008). Stable isotope tracing of trout hatchery carbon to sediments and foodwebs of limestone spring creeks. *The Science of the Total Environment* **405**, 161–172. doi:10.1016/J.SCITOTENV.2008.06.036

Jardine, T. D., Gray, M. A., McWilliam, S. M., and Cunjak, R. A. (2005). Stable isotope variability in tissues of temperate stream fishes. *Transactions of the American Fisheries Society* **134**, 1103–1110. doi:10.1577/T04-124.1

Kennedy, B. P., Chamberlain, C. P., Blum, J. D., Nislow, K. H., and Folt, C. L. (2005). Comparing naturally occurring stable isotopes of nitrogen, carbon, and strontium as markers for the rearing locations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 48–57. doi:10.1139/F04-184

Kremer, B. P., and Küppers, U. (1977). Carboxylating enzymes and pathway of photosynthetic carbon assmilation in different marine algae – evidence for the C_4 pathway? *Planta* **133**, 191–196. doi:10.1007/BF00391918

Liu, M., and Sadovy, Y. (2008). Profile of a fishery collapse: why mariculture failed to save the large yellow croaker. *Fish and Fisheries* **9**, 219–242. doi:10.1111/J.1467-2979.2008.00278.X

Llanso, R., Bell, S., and Vose, F. (1998). Food habits of red drum and spotted seatrout in a restored mangrove impoundment. *Estuaries* **21**, 294–306. doi:10.2307/1352476

Logan, J., Haas, H., Deegan, L., and Gaines, E. (2006). Turnover rates of nitrogen stable isotopes in the salt marsh mummichog, *Fundulus heteroclitus*, following a laboratory diet switch. *Oecologia* **147**, 391–395. doi:10.1007/S00442-005-0277-Z

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**, 703–718.

Rowell, K., Flessa, K. W., Dettman, D. L., Roman, M. J., Gerber, L. R., and Findley, L. T. (2008). Diverting the Colorado River leads to a dramatic life history shift in an endangered marine fish. *Biological Conservation* **141**, 1138–1148. doi:10.1016/J.BIOCON.2008.02.013

Silberschneider, V., and Gray, C. A. (2008). Synopsis of biological, fisheries and aquaculture-related information on mulloway *Argyrosomus japonicus* (Pisces : Sciaenidae), with particular reference to Australia. *Journal of Applied Ichthyology* **24**, 7–17.

Silberschneider, V., Gray, C. A., and Stewart, J. (2009). Age, growth, maturity and the overfishing of the iconic sciaenid, *Argyrosomus japonicus*, in south-eastern Australia. *Fisheries Research* **95**, 220–229. doi:10.1016/J.FISHRES.2008.09.002

Suzuki, K. W., Kasai, A., Ohta, T., Nakayama, K., and Tanaka, M. (2008). Migration of Japanese temperate bass *Lateolabrax japonicus* juveniles within the Chikugo River estuary revealed by delta C-13 analysis. *Marine Ecology Progress Series* **358**, 245–256. doi:10.3354/MEPS07300

Taylor, M. D., and Suthers, I. M. (2008). A Predatory Impact Model and targeted stocking approach for optimal release of mulloway (*Argyrosomus japonicus*). *Reviews in Fisheries Science* **16**, 125–134. doi:10.1080/10641260701727293

Taylor, M. D., Fielder, D. S., and Suthers, I. M. (2005*a*). Batch marking of otoliths and fin spines to assess the stock enhancement of mulloway, *Argyrosomus japonicus*. *Journal of Fish Biology* **66**, 1149–1162. doi:10.1111/J.0022-1112.2005.00678.X

Taylor, M. D., Fielder, D. S., and Suthers, I. M. (2006*a*). Spatial and ontogenetic variation in the diet of wild and stocked mulloway (*Argyrosomus japonicus*, Sciaenidae) in Australian estuaries. *Estuaries and Coasts* **29**, 785–793.

Taylor, M. D., Palmer, P. J., Fielder, D. S., and Suthers, I. M. (2005*b*). Responsible estuarine finfish stock enhancement: an Australian perspective. *Journal of Fish Biology* **67**, 299–331. doi:10.1111/J.0022-1112.2005.00809.X

Taylor, M. D., Laffan, S. D., Fielder, D. S., and Suthers, I. M. (2006*b*). Key habitat and home range of mulloway (*Argyrosomus japonicus*) in a south-east Australian estuary: finding the estuarine niche to optimise stocking. *Marine Ecology Progress Series* **328**, 237–247. doi:10.3354/MEPS328237

Tominaga, O., Uno, N., and Seikai, T. (2003). Influence of diet shift from formulated feed to live mysids on the carbon and nitrogen stable isotope ratio in dorsal muscles of juvenile Japanese flounders *Paralichthys olivaceus*. *Aquaculture* **218**, 265–276. doi:10.1016/S0044-8486(02)00496-9

Trueman, C. N., McGill, R. A. R., and Guyard, P. H. (2005). The effect of growth rate on tissue–diet isotopic spacing in rapidly growing animals. An experimental study with Atlantic salmon (*Salmo salar*). *Rapid Communications in Mass Spectrometry* **19**, 3239–3247. doi:10.1002/RCM.2199

Vigliola, L., Harmelin-Vivien, M., and Meekan, M. G. (2000). Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of *Diplodus* from the Mediterranean Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 1291–1299. doi:10.1139/CJFAS-57-6-1291

Watanabe, Y., Seikai, T., and Tominaga, O. (2005). Estimation of growth and food consumption in juvenile Japanese flounder *Paralichthys olivaceus* using carbon stable isotope ratio delta C-13 under laboratory conditions. *Journal of Experimental Marine Biology and Ecology* **326**, 187–198. doi:10.1016/J.JEMBE.2005.05.020

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