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

Matthew D. Taylor\textsuperscript{A,B,D} and Debashish Mazumder\textsuperscript{C}

\textsuperscript{A}Sydney Institute of Marine Science, Building 22, Chowder Bay Road, Mosman, NSW 2088, Australia.
\textsuperscript{B}Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Science, University of New South Wales, NSW 2052, Australia.
\textsuperscript{C}Institute for Environmental Research, Australian Nuclear Science and Technology Organisation, Lucas Heights, NSW 2234, Australia.
\textsuperscript{D}Corresponding author. Email: mattytaylor@unsw.edu.au

Abstract. Carbon and nitrogen stable isotope ratios were analysed for hatchery-reared, recaptured and wild mulloway, \textit{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\textsuperscript{-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.

Introduction

The chemical compositions of various tissues are often used to investigate trophic and spatial aspects of the ecology of estuarine fishes (Hesslein \textit{et al}. 1991). The stable nitrogen and carbon isotopic composition of fish muscle tissue (Jardine \textit{et al}. 2005) can indicate patterns of movement and energy transfer (Logan \textit{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 \textit{et al}. 2005). Fish reared under hatchery conditions may have unique carbon and nitrogen isotope compositions compared with wild conspecifics (Grey \textit{et al}. 2004), which are determined by rearing location and food source (Kennedy \textit{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 \textit{et al}. 2003).

Trophic interactions form the basis of predator and prey dynamics (Dickmann \textit{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 \textit{et al}. 2002). Stable isotopes indicate ontogenetic changes in dietary sources (Fry \textit{et al}. 1999; Badalamenti \textit{et al}. 2002). However, there are few examples of research that combine isotopic analysis with stomach contents analysis in fish (Dittel \textit{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, \textit{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 \textit{et al}. 2006b), 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\textsuperscript{-1} in Australia (Henry and Lyle 2003), with most targeting larger adult fish whose
removal adversely affects recruitment (Taylor et al. 2005a). 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. 2006a). This switch coincides with an increase in home range and foraging activity (Taylor et al. 2006b). 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. 2005b; 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 15N and 13C 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 km² 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. 2005a) 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, 1 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 cm³ 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. 2005a) 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 cramped 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 δ15N 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...
Analytical precision was determined to be 0.072‰ (one s.d.) for both δ¹⁵N and δ¹³C. The δ¹⁵N values in all stocked fish increased to 186 days after release (Fig. 1), forming a positive linear relationship with time-after-release (δ¹⁵N = 0.16 · Time + 13.57; \( r^2 = 0.88, F_{1,19} = 130.91, P < 0.01 \)). The δ¹³C values for stocked fish decreased rapidly after release, forming a significant negative logarithmic regression with time (δ¹³C = −0.51 · ln(Time) − 18.05; \( r^2 = 0.85, F_{1,19} = 98.76, P < 0.01 \)).

There were significant relationships between growth trajectories and Δδ¹⁵N after release (Fig. 2a, b). This included significant linear relationships between Δδ¹⁵N to 200 days after release with mass (g) increase (Δδ¹⁵N = 0.03 · ΔMass + 0.84; \( r^2 = 0.36, F_{1,14} = 7.2, P = 0.02 \)) and length increase (Δδ¹⁵N = 0.15 · ΔTL + 0.64; \( r^2 = 0.20, F_{1,14} = 4.46, P = 0.05 \); Fig. 2b). Older fish were provided as 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.

**Results**

**Isotopic composition and growth of released mulloway**

Analytical precision was determined to be 0.072‰ (one s.d.) for both δ¹⁵N and δ¹³C. The δ¹⁵N values in all stocked fish increased to 186 days after release (Fig. 1), forming a positive linear relationship with time-after-release (δ¹⁵N = 0.16 · Time + 13.57; \( r^2 = 0.88, F_{1,19} = 130.91, P < 0.01 \)). The δ¹³C values for stocked fish decreased rapidly after release, forming a significant negative logarithmic regression with time (δ¹³C = −0.51 · ln(Time) − 18.05; \( r^2 = 0.85, F_{1,19} = 98.76, P < 0.01 \)).

There were significant relationships between growth trajectories and Δδ¹⁵N after release (Fig. 2a, b). This included significant linear relationships between Δδ¹⁵N to 200 days after release with mass (g) increase (Δδ¹⁵N = 0.03 · ΔMass + 0.84; \( r^2 = 0.36, F_{1,14} = 7.2, P = 0.02 \)) and length increase (Δδ¹⁵N = 0.15 · ΔTL + 0.64; \( r^2 = 0.20, F_{1,14} = 4.46, P = 0.05 \); Fig. 2b). Older fish were provided as 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.
Trophodynamic changes in mulloway

Marine and Freshwater Research

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 $\delta^{15}N$ and $\delta^{13}C$ occurred through wild fish in Groups 4–6, and $\delta^{15}N$ 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, $\Delta$TL and $\Delta$Mass, which indicated that the isotopic composition of hatchery-reared mulloway is rapidly altered after their release into natural systems, and that $\delta^{15}N$ 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: $\delta^{13}C = \delta^{13}C_0 + (\delta^{13}C_0 - \delta^{13}C_m) \cdot e^{-(k+m)\cdot t}$, where $\delta^{13}C_0$ and $\delta^{13}C_m$ 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 ($W_0$, 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): $k = ln(W/W_0^t)$ - 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. 2006a), 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 $\delta^{15}N$ 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 ocellatus*) 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. 2006a).

**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 δ¹⁵N and δ¹³C 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 ¹⁵N and ¹³C over longer temporal scales, but the time-specific storage of isotopes in this tissue has yet to be determined.

The δ¹³C 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 δ¹³C 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. (2006a), however, did not detect a difference in the diets between wild and stocked fish of this size. The high variability in the δ¹³C 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 δ¹³C signature relative to smaller wild fish (Group 4), which may reflect a shift towards food webs dominated by producers using a C₄ 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 δ¹³C and δ¹⁵N 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 δ¹⁵N, 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 ¹⁵N and ¹³C 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. ¹⁵N and ¹³C stable isotopes in wild mulloway reflect a dietary shift to increasing piscivory with size. However, further investigations of changes in δ¹⁵N and δ¹³C 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).

**Acknowledgements**

We wish to thank I. Suthers, S. Fielder, H. El Hassan and Sydney recreational anglers for help and cooperation during the study. We also wish to thank two anonymous reviewers and A. Boulton for their valuable and constructive comments on this manuscript. This project was undertaken using funds provided the New South Wales Recreational Saltwater Fishing Trust and the Australian Research Council. Animals were collected under a NSW Department of Primary Industries Scientific Collection Permit (P03/0086) and handled under Animal Care and Ethics approval from the University of New South Wales (approval # 02/115). This manuscript was prepared while M. Taylor was a visiting scientist to the New South Wales Department of Primary Industries Cronulla Fisheries Research Centre of Excellence. This manuscript is contribution number 0022 from the Sydney Institute of Marine Science.

**References**


Manuscript received 23 January 2009, accepted 6 August 2009

http://www.publish.csiro.au/journals/mfr