Received: 15 September, 2011

IOTC–2011–WPNT01–24

# Temporal and size-related variation in the diet, consumption rate, and daily ration of mackerel tuna (*Euthynnus affinis*) in neritic waters of eastern Australia

Shane P. Griffiths, Petra M. Kuhnert, Gary F. Fry, and Fiona J. Manson

Griffiths, S. P., Kuhnert, P. M., Fry, G. F., and Manson, F. J. 2009. Temporal and size-related variation in the diet, consumption rate, and daily ration of mackerel tuna (*Euthynnus affinis*) in neritic waters of eastern Australia. – ICES Journal of Marine Science, 66: 720–733.

The diet, food consumption, and ration of mackerel tuna (*Euthynnus affinis*) were studied in Australian neritic waters. Overall, 43 prey taxa were identified from 271 stomachs. The diet was primarily pelagic clupeoids (78% by wet weight, WW; 71% by frequency of occurrence, FO) and demersal fish (19% WW; 32% FO). Multivariate regression tree analysis revealed that temporal differences, followed by fish size, explained most of the variation in the diet composition. Autumn diets differed from those in other seasons because tuna ate virtually only engraulids then. During other seasons, engraulids were still the dominant taxon in the diet, but fish also consumed a greater variety of other prey. Small tuna seemed to target small pelagic crustaceans and teleosts, and medium and large tuna to consume larger pelagic and demersal teleosts. Prey consumption increased with tuna size from 26.42 to 108.03 g d$^{-1}$ for small and large tuna, respectively. Conversely, daily ration decreased with increasing tuna size from 4.10 to 1.95% body weight per day for medium and large tuna, respectively. Mackerel tuna consumed an estimated 25 036 t year$^{-1}$ in the study region (170 990 km$^2$). Diet studies are becoming increasingly important in informing ecosystem models, and this study confirmed the need for sampling regimes to capture temporal and size-related variation in diet composition, to maximize the utility of data for use in such models.

**Keywords:** ecosystem models, kawakawa, multivariate regression trees, pelagic, western Pacific.

Received 11 March 2008; accepted 30 November 2008.

*S. P. Griffiths, G. F. Fry, and F. J. Manson: CSIRO Marine and Atmospheric Research, PO Box 120, Cleveland, QLD 4163, Australia. P. M. Kuhnert: CSIRO Mathematical and Information Sciences, PO Box 120, Cleveland, QLD 4163, Australia. Correspondence to S. P. Griffiths: tel: +61 7 3826 7364; fax: +61 7 3826 7222; e-mail: shane.griffiths@csiro.au.*

## Introduction

Mackerel tuna (or kawakawa; *Euthynnus affinis*) are medium-sized schooling pelagic fish distributed throughout the Indo-West Pacific between latitudes 35°N and 25°S, longitudes 40°E and 137°W, in water temperatures of 18–29°C (Froese and Pauly, 2007). They are one of four species representing the genus *Euthynnus*, and grow to a maximum weight of 14 kg and a total length of 100 cm fork length (FL; Froese and Pauly, 2007), though they are more commonly caught at less than half this size in most parts of their distribution. The species supports significant commercial and artisanal fisheries in many countries bordering the central, southwestern, and western Pacific Ocean and the eastern and western Indian Ocean. Since 1980, 32 countries have been reported to have taken a combined catch of >150 000 t year$^{-1}$ (FAO, 2003).

In addition to their economic importance, tuna play a key ecological role as high-level predators in oceanic pelagic ecosystems. This is largely a result of their occupying high trophic levels, and consuming vast quantities of prey to satisfy their high energy requirements (Brill, 1987; Korsmeyer and Dewar, 2001). For example, Olson and Boggs (1986) estimated that the yellowfin tuna (*Thunnus albacares*) population in the eastern Pacific Ocean consumes 4.3–6.4 million tonnes of prey between 1970 and 1972. Similarly, Watanabe *et al*. (2004) estimated that albacore (*Thunnus alalunga*) consumed 145 000–206 000 t d$^{-1}$ of the commercially important Japanese anchovy (*Engraulis japonicus*) over a 100-d period during their annual migration through the central North Pacific.

Less is known about the diets and consumption of neritic tuna and the role they play within nearshore ecosystems. Griffiths *et al*. (2007a) showed that longtail tuna (*Thunnus tonggol*) are notable predators in Australian coastal ecosystems, with the species estimated to consume 148 178 t year$^{-1}$ in the Gulf of Carpentaria. That study also showed that tuna can have a significant interaction with fisheries where the commercial target species and the prey of the predator are shared. In that case, it was estimated that longtail tuna consumed 599 t year$^{-1}$ of the same penaeids targeted by Australia's valuable northern prawn fishery, some 10% of the annual commercial catch. Such studies highlight the importance of understanding and quantifying the trophic linkages between fish and their ecosystem to inform and populate ecosystem models (e.g. Ecopath; Christensen and Pauly, 1992), which are being used increasingly to guide the emerging ecosystem management approaches pursued in many fisheries worldwide (Hall and Mainprize, 2004). Dietary studies of high-level predators, such as tuna, are particularly important for providing data for ecosystem models, because tuna can have a strong top-down influence on structuring ecosystems (Essington *et al*., 2002).

Although mackerel tuna are abundant in neritic and open ocean ecosystems throughout their distribution, very little is known of their biology and feeding ecology worldwide. This study focuses on understanding the feeding dynamics of the species in a discrete neritic Central Eastern Shelf Transition Bioregion in eastern Australia by (i) exploring the temporal and size-related variability in their diet composition and feeding intensity in the neritic regime of eastern Australia, (ii) estimating the consumption rate and daily ration for three size classes, and (iii) providing an estimate of the annual biomass of prey consumed.

## Material and methods

### Collection and processing of samples

In all, 271 mackerel tuna ranging from 284 to 809 mm FL were collected between January 2003 and May 2005 from eastern Australia using rod and line. Fish were caught within 10 nautical miles of the coast in a region of ~650 km between Gladstone, Queensland, and Tweed Heads, New South Wales (Figure 1). Fish were put on ice upon capture and transported to the CSIRO Marine and Atmospheric Research laboratories in Cleveland, where they were frozen and later processed.

In the laboratory, fish were weighed (to the nearest 0.01 g), measured (FL, mm), and their sex determined before removing the stomach. The gonads were removed and weighed (to the nearest 0.001 g) to calculate a gonadosomatic index (GSI) for each fish using the equation

$$\mathrm{GSI} = \left(\frac{\text{gonad weight (g)}}{\text{body weight (g)} - \text{gonad weight (g)}}\right) \times 100. \qquad (1)$$

Prey items were removed from the stomach and identified to the lowest possible taxon, counted, measured where possible (standard, carapace, and mantle lengths for fish, crustaceans, and cephalopods, respectively), and a total wet weight (WW) obtained for each prey type. Each prey type was allocated to a broad prey category to assist in the description of the overall diet and calculation of consumption rates. These groups were pelagic fish, demersal fish, bentho-pelagic crustaceans, molluscs, cephalopods, stomatopods, and miscellaneous. More specifically, pelagic fish are defined as fish that spend the majority of their lives in the pelagic zone, whereas demersal fish reside on or near the seafloor. Bentho-pelagic crustaceans are those taxa, or life stages, that utilize the region between the benthic and pelagic zones, often during diel vertical migrations. Molluscs are hard-shelled animals such as gastropods, and cephalopods in this study refer specifically to squids. The miscellaneous prey group contains a variety of items such as insects, inorganic matter, plastics, and seagrass. Although some prey taxa may ordinarily be classified in a particular manner (e.g. stomatopods as benthic because many reside in burrows as adults), we classified each prey in relation to the habitat it was likely to be utilizing at the life stage at which it was consumed by mackerel tuna. Hard parts, such as fish otoliths and backbones, and cephalopod mandibles were ignored because they can accumulate in the stomach and be over-represented in the diet (Olson and Galvan-Magana, 2002; Chipps and Garvey, 2007). A quantitative stomach fullness index was calculated for each fish to explore potential temporal variation in feeding intensity using the equation

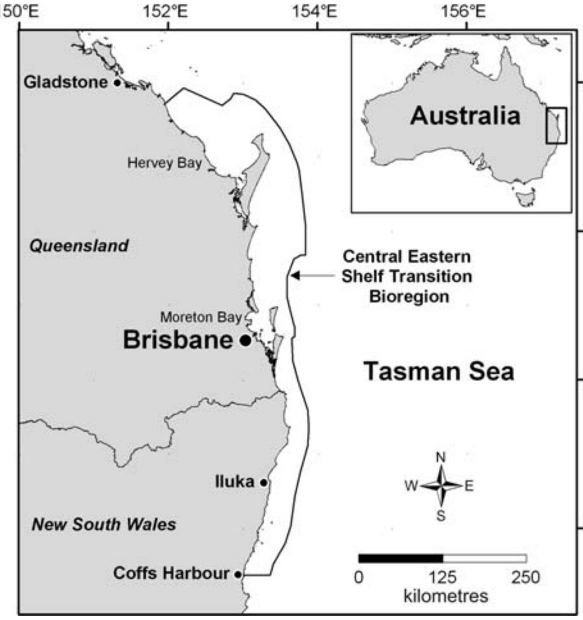

**Figure 1.** Map of the Central Eastern Shelf Transition Bioregion in eastern Australia where mackerel tuna were collected for dietary analysis between January 2003 and May 2005.

$$\text{Stomach fullness index} = \left(\frac{\text{stomach contents (g)}}{\text{body weight (g)} - \text{stomach contents (g)}}\right) \times 100. \qquad (2)$$

Mean monthly stomach fullness index values were also regressed with mean monthly GSI values to investigate the possible effects of reproductive activity on feeding intensity.

Diet was determined as the contribution of each prey type to the overall diet in terms of %WW and percentage frequency of occurrence (%FO) and was calculated only from fish stomachs containing prey. These two diet measures were calculated from

$$\%\mathrm{WW}_i = \left(\frac{\mathrm{WW}_i}{\sum_{i=1}^{Q} \mathrm{WW}_i}\right) \times 100, \qquad (3)$$

$$\%\mathrm{FO}_i = \left(\frac{F_i}{N}\right) \times 100, \qquad (4)$$

where $\mathrm{WW}_i$ is the WW of prey type $i$, $Q$ the number of prey types, $F_i$ the number of fish stomachs containing prey type $i$, and $N$ the total number of fish stomachs containing prey. Here, we primarily concentrate on describing the diet in terms of biomass, because such description has greater relevance for understanding trophic pathways. However, there is always the potential to introduce bias when using a single measure of diet (e.g. volume, number, biomass) owing to different digestion rates of particular prey types, though we account for these differences when estimating daily ration and prey consumption rates (see below). We did not use any compound diet indices in our analyses, such as the index of relative importance suggested by Cortés (1997) as a standardized reporting method for diets, because the addition or multiplication of individual diet measures represented as a percentage (i.e. the percentage contribution in terms of biomass, number, volume, or FO) produce dimensionless ratios that have no biological meaning (Bowen, 1996). Moreover, diet indices can be biased by the taxonomic resolution of the prey identified, so producing misleading results (Hansson, 1998).

To investigate the extent of dietary overlap between size classes of fish, diet biomass data were used to calculate Horn's overlap index ($R_o$; Horn, 1966):

$$R_o = \frac{\sum(p_{ij}+p_{ik})\log(p_{ij}+p_{ik}) - \sum p_{ij}\log p_{ij} - \sum p_{ik}\log p_{ik}}{2\log 2}, \tag{5}$$

where $p_{ij}$ is the proportion of prey type $i$ of the total biomass of prey consumed by size class $j$, and $p_{ik}$ is the proportion of prey type $i$ of the total biomass of prey consumed by size class $k$. Dietary overlap values of $\geq 0.6$ are considered to be biologically significant (Pianka, 1976). We assigned each fish to one of three size classes, small ($<$402 mm), medium (402–580 mm), or large ($>$580 mm), derived from the results of multivariate regression tree analysis, which showed that fish from these size categories have significantly different diets (see the Results section).

To investigate size-related shifts in prey-size preference, prey size was regressed against predator FL, and a Pearson's correlation coefficient used to explain the slope of the relationship.

## Multivariate regression tree analysis

We explored the effects of season, fish size, and sex on diet structure (i.e. taxonomic composition and their biomass) of mackerel tuna using multivariate regression tree analysis (De'ath, 2002), which is an extension of the univariate regression tree approach developed by Breiman *et al.* (1984). Seasons in this study were defined as spring (September–November), summer (December–February), autumn (March–May), and winter (June–August).

A Bray–Curtis distance matrix based on square-root transformed diet biomass data was constructed to derive a model that related the set of explanatory variables to distances between the diet composition of individual fish. Suitable transformations of assemblage data and distance metrics need to consider values of zero and the overall distribution of the data. We used a power transformation coupled with the Bray–Curtis dissimilarity metric. Here, the power transformation is of the form $x^{1/k}$, where $x$ represents the assemblage response, $1/k$ the power of the transformation, and $k$ takes on values of 2, 4, 8, or higher if required. As $k$ increases, the transformation behaves more like taking logarithms. This type of transformation is often used in conjunction with the Bray–Curtis dissimilarity metric in which $k$ is typically 2, resulting in the square root. We explored different values of $k$ and found that a square-root transformation was more than adequate for our diet data in terms of being able to partition prey weight assemblages into distinct groupings. We chose the Bray–Curtis metric because of its ability to handle the "double zero" problem (Faith *et al.*, 1987; Legendre and Gallagher, 2001), where a metric does not indicate a difference in diet between two fish simply because of the co-absence of a prey species.

The split criterion used to partition the data in the multivariate regression trees is based on the sum of squared distances, in which splits offer the greatest reduction in the sums of squares about the multivariate mean (i.e. Euclidean distance), which De'ath (2002) refers to as SS-MRT. Unlike standard implementations of SS-MRT presented by De'ath (2002), ours operated on an $n \times n$ distance matrix, where distances represent the dissimilarity between fish diet composition for each fish. Using the split criterion in this way, we were able to form partitions where fish with similar diet compositions (or equivalent distances) became grouped. The unique feature of this approach is that after the first split, the distance matrix is no longer symmetrical and represents a $k \times n$ matrix, where $k < n$. We found the additional distance information in this matrix to be useful in forming additional partitions of the data using SS-MRT, as opposed to treating the matrix as a dissimilarity matrix and using db-MRT, as described by De'ath (2002). Cross-validation was used to prune large trees back to a tree with the smallest cross-validated error rate. Pruning was achieved in a similar manner to that described for univariate regression trees (Breiman *et al.*, 1984), and it incorporated a tenfold cross-validation to snip branches of the tree back until the root node remains. The optimal model was chosen based on the tree yielding the minimum cross-validated error rate, although other smaller trees within 1 s.e. of the minimum can also be used. An advantage of the tree-based approach is that the length of the nodes provides a relative measure of the importance of each variable in explaining the variation in the data. We were interested in quantifying the importance of each explanatory variable to the diets of mackerel tuna, so we calculated variable importance rankings using the method described by Breiman *et al.* (1984) for univariate trees, but extended it to deal with multivariate data.

Predictions from the multivariate model are difficult to interpret unless the predicted distances are used in a subsequent analysis (e.g. clustering) to explore the partitioning in more detail. We used an alternative response (e.g. proportion contribution to the biomass) to obtain a pseudo-assemblage prediction, rather than an actual predicted distance for each specimen. In other words, our model was developed using the distance matrix as the response, but predicted using a more ecologically meaningful response variable, i.e. the proportional contribution in terms of biomass.

Tuna are often considered to be opportunistic predators, so the diet composition can vary markedly between individual fish (Chipps and Garvey, 2007). To obtain a measure of uncertainty around each prediction, we used bootstrapping to obtain prediction errors (Kuhnert and Mengersen, 2003) for each prey taxon by (i) computing the relevant distance matrix for each bootstrap sample, (ii) fitting an unpruned multivariate regression tree to the distance matrix, (iii) predicting to produce a set of "pseudo-" predictions for each prey taxon using "out-of-bag samples", and (iv) mapping the bootstrap predictions back to the original tree for interpretation. Here, the out-of-bag samples represent observations that were not included in the bootstrap sample. As pointed out by Efron and Tibshirani (1993), ~37% of data are not used in a bootstrap sample, thus constituting a valid test set that can be used to evaluate a model and predict accordingly. The process was repeated 1000 times to develop a bootstrap distribution of pseudo-predictions and 95% bootstrap confidence intervals.

Plots of a variable's partial dependence were then constructed to illustrate its relationship with the response variable, while averaging across all other variables in the model. These plots were constructed from the bootstrap pseudo-predictions constructed on the out-of-bag samples for a particular variable, while averaging across all other variables in the model, as described by Breiman (2001). The result is a step function (for continuous variables such as tuna size) showing the relationship between the variable and the pseudo-response. In our case, data were at equally spaced intervals to reduce the computational time required to form the predictions. As a result, our fitted curves do not appear smooth.

### Calculation of daily ration and prey consumption rates

Daily consumption rates of prey, or daily meal, $M$, were estimated using bootstrap techniques (Efron and Tibshirani, 1993) using the relationship of Olson and Mullen (1986). The expression for the bootstrap estimate of the daily consumption rate, $\hat{M}_B^*$ is

$$\hat{M}_B^* = 12\hat{r}_B^*, \tag{6}$$

where $\hat{r}_B^* = \frac{1}{N}\sum_{i=1}^{n_p}\left(\frac{1}{A_i}\right)\bar{\theta}_{iB}^*$ and $\bar{\theta}_{iB}^* = \frac{\sum_{b=1}^{B}\left[\sum_{j=1}^{n_j} w_{ij}^*(b)\right]}{B}$.

In this expression, $w_{ij}^*(b)$ represents a bootstrap sample, $b$, of WW for consumed prey type $i$ in g, $N$ the total number of predators (including empty stomachs) captured in size class $j$, $A_i$ the average time required to evacuate the average proportion of prey type $i$, $\bar{\theta}_{iB}^*$ the bootstrap plug-in estimate of the summed WW for prey type $i$, $B$ the number of bootstrap iterations, and $n_j$ and $n_p$ the number of stomachs for predator $j$ and number of prey types, respectively. Empty stomachs were included in the estimation of daily meals because they are likely to represent the true proportion of the population that may not have fed before the time of capture. In Equation (6), we multiply the mean hourly feeding rate, $\hat{r}_B$, by 12 because a closely related tuna (*T. tonggol*) of similar size feed mainly during the day in the same region (Griffiths *et al.*, 2007a). The corresponding estimate of the variance (assuming independence) is

$$\widehat{Var}\left(\hat{M}_B^*\right) = \frac{144}{N^2}\sum_{i=1}^{n_p}\frac{1}{A_i^2}\widehat{Var}\left(\theta_i^*\right) \text{ (iid)}, \tag{7}$$

where $\theta_i^* = \sum_{j=1}^{n_j} w_{ij}^*$.

As we lacked quantitative experimental data on evacuation times ($A_i$) for specific prey consumed by mackerel tuna, we used $A_i$ values for prey that were experimentally determined by Olson and Boggs (1986) for yellowfin tuna, a method successfully applied to species such as dolphinfish (*Coryphaena hippurus*; Olson and Galvan-Magana, 2002), bigeye (*Thunnus obesus*), yellowfin, skipjack (*Katsuwonus pelamis*; Ménard *et al.*, 2000), and longtail tuna (*T. tonggol*; Griffiths *et al.*, 2007a). The $A_i$ values used were point estimates without error estimates, so should be considered as minimum estimates.

Daily ration (% body weight consumed per day) was then calculated for each size class by expressing $M$ as a percentage of the average wet body weight of fish examined within each size class. In this calculation, we incorporated uncertainty around average body weight and $M$ by assuming a normal distribution for each parameter, then generated 10 000 Monte Carlo simulations in "Crystal Ball Risk Analysis Software" (Decisioneering Inc. Denver, Co.) to obtain the mean daily ration and a standard deviation for size class $j$ and all size classes combined.

### Annual estimates of prey consumption

We were interested in estimating the annual consumption of prey species by mackerel tuna in a discrete region off eastern Australia; the Central Eastern Shelf Transition Bioregion (Figure 1). To account for potential size-related differences in prey preference and daily ration, we used a modified version of the prey consumption model of Griffiths *et al.* (2007a) in conjunction with the bootstrap to estimate the total annual biomass of prey and the corresponding variance as outlined in Equation (7).

$$\begin{aligned}
\hat{B}_{iB}^* &= 365T\hat{\gamma}\sum_{j\in(S,M,L)}\hat{M}_{ijB}^*,\\
\widehat{Var}(\hat{B}_{iB}^*) &= [365T]^2\sum_{j\in(S,M,L)}\mathrm{Var}\left(\hat{M}_{ijB}^*\hat{\gamma}\right) \text{ (iid)}\\
&\approx [365T]^2\sum_{j\in(S,M,L)}\left\{(\hat{M}_{ijB}^*\hat{\gamma})^2\left[\frac{\widehat{Var}(\hat{M}_{ijB}^*)}{\hat{M}_{ijB}^{*2}}+\frac{\mathrm{Var}(\gamma)}{\hat{\gamma}^2}\right]\right\}
\end{aligned} \tag{8}$$

In Equation (8), $\hat{B}_{iB}^*$ is a bootstrap estimate of the total annual biomass of a prey $i$ consumed by mackerel tuna summed across size class $j$ ($j = S, M, L$), $T$ the total area (km$^2$) where prey species can be taken, $\hat{M}_{ijB}^*$ and Var($\hat{M}_{ijB}^*$) the bootstrap estimates of the daily meal and the corresponding variance of prey type $i$ by fish in size class $j$ (in terms of WW), and $\hat{\gamma}$ and Var($\gamma$) the estimated mean density and corresponding variance of mackerel tuna. In the absence of size-specific density estimates for mackerel tuna in eastern Australia, we used a value of 1.81 fish km$^{-2}$ for $\hat{\gamma}$ and 0.249 for Var($\gamma$) to represent all three size classes in $T$ estimated for longtail tuna off northern Australia (Griffiths *et al.*, 2007b), a species of comparable size and relative abundance to mackerel tuna.

The annual consumption rate of each prey type was calculated for the Central Eastern Shelf Transition Bioregion ($T$), a region covering an area of 170 990 km$^2$ from the coast to the edge of the continental shelf between Gladstone in Queensland and Coffs Harbour in New South Wales (Commonwealth of Australia, 2006). We recognize that prey may vary in their availability in space and time and that the contribution of prey to the diet observed may be influenced by spatial or temporal variation in sampling intensity and rates of predator consumption. Here, we assumed that the contribution of prey to the overall diet was representative of the entire year, because we collected samples monthly throughout the region. We also made a further assumption that the consumption rate of mackerel tuna did not vary spatially or temporally.

## Results

### Diet composition

Of the 271 stomachs analysed, 108 (or 40%) were empty. The overall diet consisted of 43 prey taxa, a total biomass of 7726 g. Taxonomic composition of prey and their percentage contribution to the diet in terms of biomass and FO for each season and fish size is given in Tables 1 and 2. Pelagic fish contributed most to the overall diet, in terms of biomass (78.45%) and FO (70.55%; Figure 2). The group primarily consisted of engraulids (21.9% by WW), *Sardinops sagax* (18.8%), *Trachurus declivis* (17.0%), and *Stolephorus* sp. (8.7%). Demersal fish made the second largest contribution to the diet in terms of biomass (18.75%) and FO (30.68%; Figure 2). That group primarily comprised carangids (12% by WW), monacanthids (2%), and *Priacanthus* sp. (1.6%).

All other prey groups contributed <2% of the diet by weight. However, in terms of FO, four groups constituted >5% of the diet:

**Table 1.** Contribution of prey (in terms of %WW) to the diet of small (<402 mm), medium (402–580 mm), and large (>580 mm) mackerel tuna caught over four seasons in eastern Australia between January 2003 and May 2005.

| | | | | | Spring | | | | Summer | | | | Autumn | | | | Winter | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Main taxon | Family or higher taxon | Prey name | Prey group | $A_i$ | Small | Medium | Large | Total | Small | Medium | Large | Total | Small | Medium | Large | Total | Small | Medium | Large | Total | Grand total |
| Teleost | Belonidae | Belonidae | PF | 5.29 | | | | | | | | | | | | | | | 12.429 | 10.482 | 4.259 |
| | Carangidae | Carangidae | DF | 5.29 | | | 4.710 | 4.100 | | | 18.529 | 4.744 | | | 8.253 | 4.199 | | 35.030 | 27.069 | 23.905 | 12.344 |
| | | *Trachurus declivis* | PF | 5.29 | | | 72.561 | 63.157 | | 10.595 | 2.277 | 8.278 | | | 13.247 | 6.740 | | | 11.266 | 9.501 | 16.977 |
| | Clupeidae | Clupeidae | PF | 2.24 | 12.947 | | | 1.146 | | 0.416 | | 0.302 | | 0.575 | 43.623 | 22.462 | 4.008 | | | 1.246 | 4.371 |
| | | *Hyperlophus vittatus* | PF | 2.24 | | | | | | | 12.635 | 3.235 | | | | | | | | | 0.903 |
| | | *Sardinella* sp. | PF | 4.12 | | | | | | | 9.032 | 2.313 | | | | | | | 0.441 | 0.372 | 0.797 |
| | | *Sardinops sagax* | PF | 4.12 | | | | | | 13.625 | | 9.895 | | | | | 9.894 | 20.445 | 44.714 | 39.435 | 18.788 |
| | Engraulidae | Engraulidae | PF | 4.12 | 20.146 | | 9.256 | 9.839 | 29.621 | 46.118 | 31.179 | 42.002 | 85.155 | 48.793 | 25.772 | 37.920 | 0.016 | 44.327 | 0.367 | 6.367 | 21.915 |
| | | *Encrasicholina* sp. | PF | 4.12 | | | | | | 8.567 | | 6.222 | | | | | | | | | 1.737 |
| | | *Stolephorus* sp. | PF | 2.24 | 23.562 | 99.959 | | 6.194 | | 16.481 | | 11.970 | | 49.642 | 5.177 | 25.876 | | | | 0.618 | 8.699 |
| | Dactylopteridae | Dactylopteridae | DF | 3.77 | 31.317 | | | 2.771 | | | | | | | | | | | | | 0.427 |
| | Gerreidae | *Gerres* sp. | DF | 4.12 | | | | | | | | | | | | | 37.283 | | 0.053 | 0.045 | 0.018 |
| | | *Pentaprion longimanus* | DF | 4.12 | | | 2.004 | 1.744 | | | | | | | | | | | | | 0.269 |
| | Monacanthidae | Monacanthidae | DF | 3.77 | | | | | 27.543 | 2.019 | 20.812 | 7.282 | | | | | | | | | 2.033 |
| | Mullidae | *Upeneus* sp. | DF | 4.12 | | | | | | 1.328 | 4.989 | 2.242 | | | | | | | | | 0.626 |
| | Ostraciidae | Ostraciidae | DF | 3.77 | | | | | | 0.023 | | 0.017 | | | | | | | | | 0.005 |
| | | *Lactoria gibbosus* | DF | 3.77 | | | | | | | | | | | 1.928 | 0.981 | | | | | 0.157 |
| | Plotosidae | Plotosidae | DF | 5.29 | | | 1.839 | 1.601 | | | | | | | | | | | | | 0.246 |
| | Priacanthidae | *Priacanthus* sp. | DF | 5.29 | | | 3.153 | 2.744 | | | | | | | | | | | 3.554 | 2.997 | 1.640 |
| | Scorpaenidae | Scorpaenidae | DF | 5.29 | | | | | | | | | | | | | 0.025 | | | 0.118 | 0.048 |
| | Synodontidae | *Saurida undosquamis* | DF | 3.77 | | | 6.106 | 5.314 | | | | | | | | | 0.137 | | | | 0.818 |
| | Tetraodontidae | *Arothron* sp. | DF | 3.77 | | | | | | 0.234 | | 0.170 | | | | | | | | | 0.047 |
| | | Tetraodontidae | DF | 3.77 | | | | | 1.868 | | | 0.033 | 11.582 | | | 0.267 | 0.535 | | | 0.013 | 0.057 |
| Elasmobranch | Dasyatidae | *Dasyatis* sp. | DF | 4.12 | | | 0.052 | 0.045 | | | | | | | | | | | | | 0.007 |
| Mollusca | Bivalvia | Bivalvia | Mol | 5.29 | | | | | | | | | | | | | 0.013 | | 0.107 | 0.090 | 0.037 |
| | Gastropoda | Gastropoda | Mol | 4.48 | | | | | | | | | | 0.005 | | 0.002 | | | | | 0.000 |
| | Teuthoidea | Teuthoidea | Cep | 4.48 | | | | | 40.915 | 0.011 | 0.510 | 0.861 | 3.263 | | 1.999 | 1.092 | | | | 0.024 | 0.426 |
| | Loliginidae | *Photololigo* sp. | Cep | 4.48 | | | | | | | | | | | | | | | | 0.002 | 0.001 |
| Crustacea | Brachyura | Brachyuran megalopa | BC | 3.37 | 11.516 | | 0.193 | 1.187 | | 0.511 | | 0.371 | | 0.671 | | 0.314 | | | | 0.505 | 0.542 |
| | | Crustacean zooplankton | BC | 2.24 | | | | | | | | | | | | | 8.719 | | | 0.002 | 0.001 |
| | Copepoda | Calanoid copepod | BC | 3.37 | | | | | | | 0.001 | 0.000 | | | | | | | | | 0.000 |
| | Isopoda | Isopoda | BC | 2.24 | | 0.041 | | 0.002 | | 0.013 | | 0.010 | | | | | | | | | 0.003 |
| | Natantia | Natantia | BC | 2.24 | | | | | | | | | | | | | 0.939 | | | 0.003 | 0.001 |
| | Paguridae | Paguridae | BC | 3.37 | | | | | | 0.017 | | 0.012 | | 0.061 | | 0.029 | | 0.050 | | 0.069 | 0.036 |
| | Penaeidae | *Metapenaeopsis novaeguinea* | BC | 2.24 | | | | | | | | | | 0.149 | | 0.070 | | | | | 0.011 |
| | Scyllaridae | *Thenus* sp. | BC | 3.37 | 0.428 | | | 0.038 | | | | | | | | | 4.907 | | | | 0.006 |
| | Sergestidae | Sergestidae | BC | 2.24 | | | | | 0.052 | | | 0.001 | | | | | 33.231 | | | | 0.000 |
| | Squillidae | *Odontodactylus cultifer* | Sto | 3.37 | | | | | | | | | | | | | | | | 0.017 | 0.007 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Squillidae larvae | Sto | 3.37 | | | | | | 0.011 | | 0.008 | | 0.035 | | 0.017 | 0.101 | 0.148 | | 4.189 | 1.707 |
| | Squillidae | Sto | 3.37 | | | | | | 0.010 | | 0.007 | | | | | 0.191 | | | | 0.002 |
| Miscellaneous | Sargassaceae | *Sargassum* sp. | Misc | 2.24 | | | | | 0.010 | | 0.007 | | | | | | | | | 0.002 |
| | Zosteraceae | *Zostera* sp. | Misc | 2.24 | 0.086 | | 0.127 | 0.118 | | 0.036 | 0.009 | | 0.069 | | 0.032 | | | | | 0.026 |
| | Miscellaneous | Unidentified matter | Misc | 5.29 | | | | | 0.012 | | 0.009 | | | | | | | | | 0.002 |
| Total WW (g) | | | | | 105.2 | 48.9 | 1 035.3 | 1 189.5 | 38.1 | 1 566.8 | 552.4 | 2 157.3 | 28.6 | 580.4 | 630.7 | 1 239.7 | 395.3 | 96.5 | 2 647.6 | 3 139.4 | 7 725.9 |
| Number of prey taxa | | | | | 7 | 2 | 10 | 15 | 5 | 18 | 10 | 25 | 3 | 9 | 7 | 14 | 14 | 5 | 9 | 21 | 43 |
| Total number of stomachs | | | | | 20 | 6 | 27 | 53 | 3 | 37 | 22 | 62 | 8 | 38 | 14 | 60 | 38 | 28 | 30 | 96 | 271 |
| Number of non-empty stomachs | | | | | 14 | 1 | 17 | 32 | 3 | 27 | 9 | 39 | 3 | 28 | 7 | 38 | 33 | 4 | 17 | 54 | 163 |

Fish with empty stomachs were not included. $A_i$ was used for calculating consumption rates and daily ration and is the average time (h) required to evacuate the average proportion of prey *i* present in the stomach. A description of the prey groups is provided in the "Material and methods" section and abbreviated as pelagic fish (PF), demersal fish (DF), bentho-pelagic crustaceans (BC), molluscs (Mol), cephalopods (Cep), stomatopods (Sto), and miscellaneous prey (Misc).

bentho-pelagic crustaceans (28.8%), stomatopods (19%), cephalopods (6.1%), and miscellaneous prey (5.5%; Figure 2).

## Seasonal and size-related variation in diet

The total number of prey taxa consumed by tuna differed between seasons, with fish having the most diverse diet in winter and summer (21 and 25 taxa, respectively) and the least diverse diet in autumn and spring (14 and 15 taxa, respectively). There was significant dietary overlap between small and medium-sized fish ($R_o = 0.657$), but not between small and large fish ($R_o = 0.392$) or between medium and large fish ($R_o = 0.547$).

Multivariate regression tree analysis based on diet biomass data revealed that season explained the greatest amount of variation in the diet (relative variable importance rank = 100). The first split in the tree separated the autumn diets from the three other seasons (Figure 3). This was primarily due to engraulids dominating the overall diet (median of bootstrap samples = 52%) in autumn. In the other seasons, engraulids still made a reasonable contribution (median = 25%), but other taxa such as stomatopod larvae, *T. declivis*, and carangids were predicted by the model each to have contributed some 10% to the overall diet (Figure 3).

Fish size was the second most important variable (relative variable importance rank = 72.5), but its influence on the diet was not consistent among seasons. Although autumn diets did not differ by fish size, which may have been because we only had 14 stomachs with prey for those months, the diets in the three other seasons were separated into three size groupings; <402 mm; 402–580 mm, and >580 mm, with the most important split at 580 mm (Figure 3). These splits were because fish >580 mm consumed larger pelagic teleost prey such as carangids, *T. declivis*, *S. sagax*, and belonids, and also several large demersal teleosts including plotosids, *Priacanthus* sp., and *Saurida undosquamis* (Figure 3). In contrast, fish <402 mm mainly consumed small pelagic crustaceans (stomatopod larvae and brachyuran megalopa), and larval fish (dactylopterids and monacanthids), and fish of 402–580 mm consumed mainly schooling pelagic fish such as engraulids (41%), *Stolephorus* sp. (16%), and *S. sagax* (8%; Figure 3).

Partial dependence plots from bootstrapped diet biomass data demonstrated a clear size-related shift in the prey most commonly consumed. Figure 4 shows the successive shift in diet, first dominated by small pelagic prey such as stomatopod larvae and dactylopterids in fish <500 mm, to increasing proportions of larger prey including engraulids and *Stolephorus* sp., and a final shift in fish of approximately >600 mm to large teleost prey including *T. declivis*, carangids, and belonids.

## Prey size and feeding intensity

Mackerel tuna consumed prey ranging in size from 0.6 to 220 mm, but nearly all prey were <80 mm (Figure 5). Four main modes were clearly evident in the prey size frequency distribution (Figure 5). These generally represented four broad prey categories: (i) planktonic crustaceans and larval fish (e.g. brachyuran megalopa and larval dactylopterids), (ii) small pelagic schooling clupeids and engraulids, (iii) demersal fish (e.g. carangids, monacanthids, and *Priacanthus* sp.), and (iv) larger pelagic fish (e.g. *T. declivis*, *S. sagax*, and belonids). There was a significant positive correlation between fish size and the size of prey consumed (Figure 6; $r = 0.235$, $p < 0.0001$).

Mean stomach fullness index was highest between May and September (0.035 ± 0.007 s.e.) and lowest between October and

**Table 2.** Contribution of prey (in terms of %FO) to the diet of small (<402 mm), medium (402–580 mm), and large (>580 mm) mackerel tuna caught over four seasons in eastern Australia between January 2003 and May 2005.

| | | | | Spring | | | | Summer | | | | Autumn | | | | Winter | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Main taxon** | **Family or higher taxon** | **Prey name** | **Prey group** | **Small** | **Medium** | **Large** | **Total** | **Small** | **Medium** | **Large** | **Total** | **Small** | **Medium** | **Large** | **Total** | **Small** | **Medium** | **Large** | **Total** | **Grand total** |
| Teleost | Belonidae | Belonidae | PF | | | | | | | | | | | | | | | 17.647 | 5.556 | 1.840 |
| | Carangidae | Carangidae | DF | | | 23.529 | 12.500 | | | 44.444 | 10.256 | | | 14.286 | 2.632 | | 25.000 | 41.176 | 14.815 | 10.429 |
| | | *Trachurus declivis* | PF | | | 52.941 | 28.125 | | 3.704 | 11.111 | 5.128 | | | 14.286 | 2.632 | | | 17.647 | 5.556 | 9.202 |
| | Clupeidae | Clupeidae | PF | 14.286 | | | 6.250 | | 7.407 | | 5.128 | | 3.571 | 14.286 | 5.263 | 9.091 | | | 5.556 | 5.521 |
| | | *Hyperlophus vittatus* | PF | | | | | | | 22.222 | 5.128 | | | | | | | | | 1.227 |
| | | *Sardinella* sp. | PF | | | | | | | 11.111 | 2.564 | | | | | | | 11.765 | 3.704 | 1.840 |
| | | *Sardinops sagax* | PF | | | | | | 11.111 | | 7.692 | | | | | 3.030 | 25.000 | 17.647 | 9.259 | 4.908 |
| | Engraulidae | Engraulidae | PF | 14.286 | | 17.647 | 15.625 | 66.667 | 33.333 | 22.222 | 33.333 | 100 | 67.857 | 28.571 | 63.158 | 33.333 | 50.000 | 5.882 | 25.926 | 34.356 |
| | | *Encrasicholina* sp. | PF | | | | | | 3.704 | | 2.564 | | | | | | | | | 0.613 |
| | | *Stolephorus* sp. | PF | 14.286 | 100.000 | | 9.375 | | 18.519 | | 12.821 | | 17.857 | 14.286 | 15.789 | 12.121 | | | 7.407 | 11.043 |
| | Dactylopteridae | Dactylopteridae | DF | 42.857 | | | 18.750 | | | | | | | | | | | | | 3.681 |
| | Gerreidae | *Gerres* sp. | DF | | | | | | | | | | | | | | | 5.882 | 1.852 | 0.613 |
| | | *Pentaprion longimanus* | DF | | | 5.882 | 3.125 | | | | | | | | | | | | | 0.613 |
| | Monacanthidae | Monacanthidae | DF | | | | | 33.333 | 11.111 | 22.222 | 15.385 | | | | | | | | | 3.681 |
| | Mullidae | *Upeneus* sp. | DF | | | | | | 3.704 | 11.111 | 5.128 | | | | | | | | | 1.227 |
| | Ostraciidae | Ostraciidae | DF | | | | | | 3.704 | | 2.564 | | | | | | | | | 0.613 |
| | | *Lactoria gibbosus* | DF | | | | | | | | | | | 42.857 | 7.895 | | | | | 1.840 |
| | Plotosidae | Plotosidae | DF | | | 5.882 | 3.125 | | | | | | | | | | | | | 0.613 |
| | Priacanthidae | *Priacanthus* sp. | DF | | | 11.765 | 6.250 | | | | | | | | | | | 11.765 | 3.704 | 2.454 |
| | Scorpaenidae | Scorpaenidae | DF | | | | | | | | | | | | | 3.030 | | | 1.852 | 0.613 |
| | Synodontidae | *Saurida undosquamis* | DF | | | 5.882 | 3.125 | | | | | | | | | | | | | 0.613 |
| | Tetraodontidae | *Arothron* sp. | DF | | | | | | 3.704 | | 2.564 | | | | | | | | | 0.613 |
| | | Tetraodontidae | DF | | | | | 33.333 | | | 2.564 | 33.333 | | | 2.632 | 6.061 | | | 3.704 | 2.454 |
| Elasmobranch | Dasyatidae | *Dasyatis* sp. | DF | | | 5.882 | 3.125 | | | | | | | | | | | | | 0.613 |
| Mollusca | Bivalvia | Bivalvia | Mol | | | | | | | | | | | | | | | 5.882 | 1.852 | 0.613 |
| | Gastropoda | Gastropoda | Mol | | | | | | | | | | 3.571 | | 2.632 | | | | | 0.613 |
| | Teuthoidea | Teuthoidea | Cep | | | | | 66.667 | 3.704 | 11.111 | 10.256 | 33.333 | | 28.571 | 7.895 | 6.061 | | | 3.704 | 5.521 |
| | Loliginidae | *Photololigo* sp. | Cep | | | | | | | | | | | | | 3.030 | | | 1.852 | 0.613 |
| Crustacea | Brachyura | Brachyuran megalopa | BC | 35.714 | | 11.765 | 21.875 | | 14.815 | | 10.256 | | 3.571 | | 2.632 | 27.273 | | | 16.667 | 12.883 |
| | | Crustacean zooplankton | BC | | | | | | | | | | | | | 6.061 | | | 3.704 | 1.227 |
| | Copepoda | Calanoid copepod | BC | | | | | | | 11.111 | 2.564 | | | | | | | | | 0.613 |
| | Isopoda | Isopoda | BC | | 100.000 | | 3.125 | | 25.926 | | 17.949 | | | | | | | | | 4.908 |
| | Natantia | Natantia | BC | | | | | | | | | | | | | 6.061 | | | 3.704 | 1.227 |
| | Paguridae | Paguridae | BC | | | | | | 7.407 | | 5.128 | | 3.571 | | 2.632 | 18.182 | 25.000 | | 12.963 | 6.135 |
| | Penaeidae | *Metapenaeopsis novaeguinea* | BC | | | | | | | | | | 3.571 | | 2.632 | | | | | 0.613 |
| | Scyllaridae | *Thenus* sp. | BC | 7.143 | | | 3.125 | | | | | | | | | | | | | 0.613 |
| | Sergestidae | Sergestidae | BC | | | | | 33.333 | | | 2.564 | | | | | | | | | 0.613 |
| | Squillidae | *Odontodactylus cultifer* | Sto | | | | | | | | | | | | | 6.061 | | | 3.704 | 1.227 |
| | | Squillidae larvae | Sto | | | | | | 3.704 | | 2.564 | | 3.571 | | 2.632 | 75.758 | 25.000 | | 48.148 | 17.178 |
| | | Squillidae | Sto | | | | | | 3.704 | | 2.564 | | | | | | | | | 0.613 |

| | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Miscellaneous | Sargassaceae | *Sargassum* sp. | Misc | | | | | | 3.704 | | 2.564 | | | | | | | | | 0.613 |
| | Zosteraceae | *Zostera* sp. | Misc | 7.143 | | 5.882 | 6.250 | | | 11.111 | 2.564 | | 14.286 | | 10.526 | | | | | 4.294 |
| | Miscellaneous | Unidentified matter | Misc | | | | | | 3.704 | | 2.564 | | | | | | | | | 0.613 |
| Total WW (g) | | | | 105.3 | 48.9 | 1 035.3 | 1 189.5 | 38.1 | 1 566.8 | 552.4 | 2 157.2 | 28.6 | 580.4 | 630.7 | 1 239.7 | 395.3 | 96.5 | 2 647.6 | 3 139.4 | 7 725.8 |
| Number of prey taxa | | | | 7 | 2 | 10 | 15 | 5 | 18 | 10 | 25 | 3 | 9 | 7 | 14 | 14 | 5 | 9 | 21 | 43 |
| Total number of stomachs | | | | 20 | 6 | 27 | 53 | 3 | 37 | 22 | 62 | 8 | 38 | 14 | 60 | 38 | 28 | 30 | 96 | 271 |
| Number of non-empty stomachs | | | | 14 | 1 | 17 | 32 | 3 | 27 | 9 | 39 | 3 | 28 | 7 | 38 | 33 | 4 | 17 | 54 | 163 |

Fish with empty stomachs were not included.

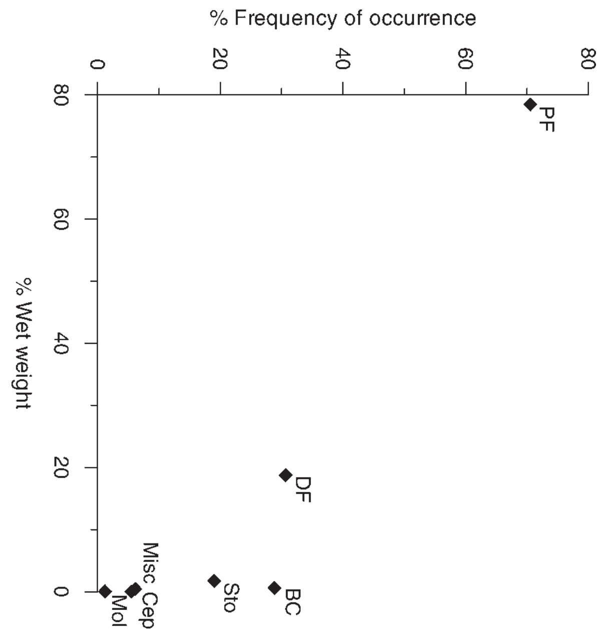

**Figure 2.** Prey importance plot showing percentage contribution of major prey categories in terms of WW and FO to the diet of mackerel tuna caught in eastern Australia between January 2003 and May 2005. Abbreviations of prey categories are pelagic fish (PF), demersal fish (DF), stomatopods (Sto), bentho-pelagic crustaceans (BC), cephalopods (Cep), molluscs (Mol), and miscellaneous prey (Misc).

April (0.008 ± 0.001). Feeding intensity was inversely related to reproductive activity, with stomach fullness lowest during the peak spawning period (October–March) and highest when gonads were in a resting or developing stage (range of mean monthly GSI, 0.65–0.93; Figure 7).

## Estimates of prey consumption and daily ration

Estimated mean (±s.d.) daily consumption for individual fish increased with fish size from 26.42 ± 3.25 g $d^{-1}$ for small fish to 87.17 ± 9.17 g $d^{-1}$ for medium-sized fish and 108.03 ± 14.33 g $d^{-1}$ for large fish. The daily consumption averaged across all fish sizes was 73.87 ± 8.92 g $d^{-1}$, translating to a daily ration of 2.18 ± 0.26% body weight per day (BW $d^{-1}$; Table 3). Daily ration decreased with increasing fish size from 4.10 ± 0.53 %BW $d^{-1}$ for medium-sized fish to 1.95 ± 0.28 %BW $d^{-1}$ for large fish (Table 3).

Annual prey consumption estimates for the Central Eastern Shelf Transition Bioregion increased from 2985 ± 1203 t $year^{-1}$ for small fish to 12 204 ± 4999 t $year^{-1}$ for large fish, resulting in an overall consumption rate of 25 036 ± 6134 t $year^{-1}$ (Table 4). Pelagic and demersal fish contributed 20 035 ± 4134 and 3368 ± 934 t $year^{-1}$, respectively, to the total prey consumption. The next most important prey items were stomatopods and bentho-pelagic crustaceans: 1183 ± 381 and 338 ± 127 t $year^{-1}$, respectively. Cephalopods, molluscs, and miscellaneous prey items made lesser contributions (5.50–94.35 t $year^{-1}$) to total prey consumption (Table 4).

## Discussion

In the relatively shallow neritic waters off eastern Australia, mackerel tuna are primarily epipelagic predators that consume a variety of epipelagic prey including fish, crustaceans, and cephalopods, although the relative proportions of these prey types change

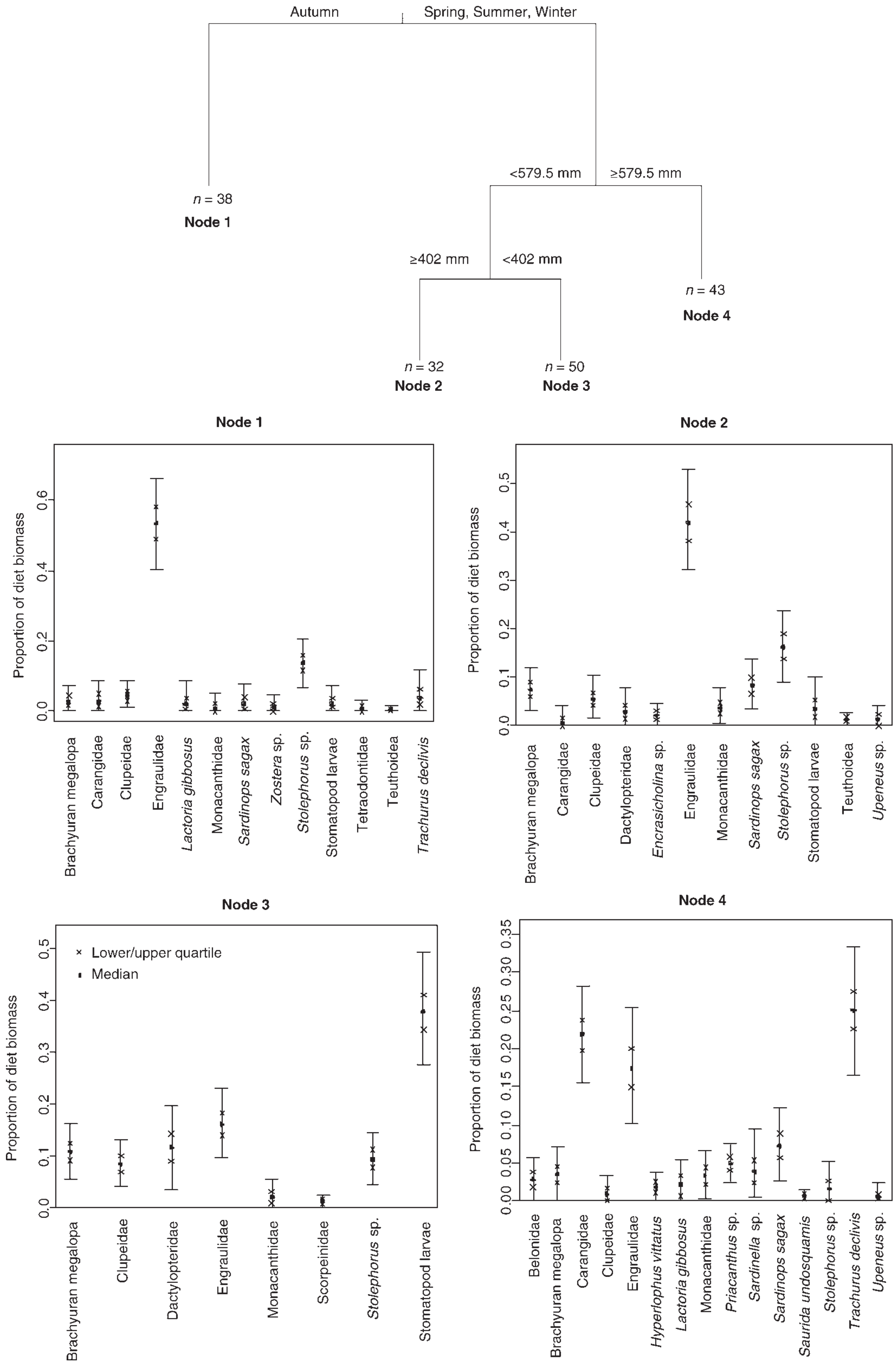

**Figure 3.** Multivariate regression tree of the Bray–Curtis similarity measure using square-root transformed diet biomass data from individual fish with non-empty stomachs ($n = 163$). Factors included in the analysis were FL, season, and sex. *CV* error = 0.931. For each terminal node, graphs show bootstrap predictions (from 1000 samples) of the proportion contribution of important prey taxa to the diet biomass. The median is shown with lower and upper quartiles and 95% confidence intervals.

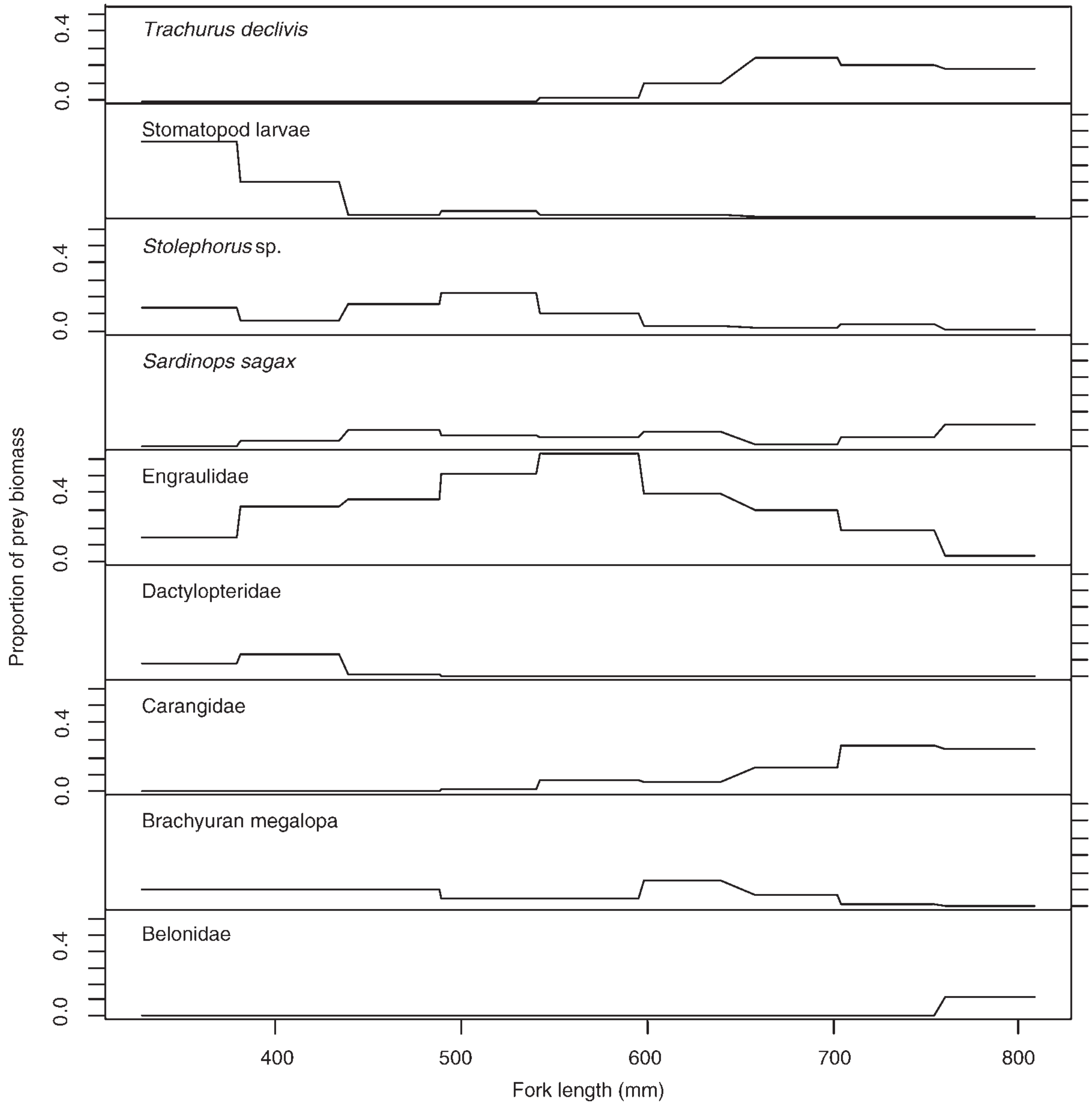

**Figure 4.** Partial dependence plots showing the predicted proportion of important prey taxa (in terms of biomass) in the diet of mackerel tuna with respect to predator size based on 1000 bootstrap samples.

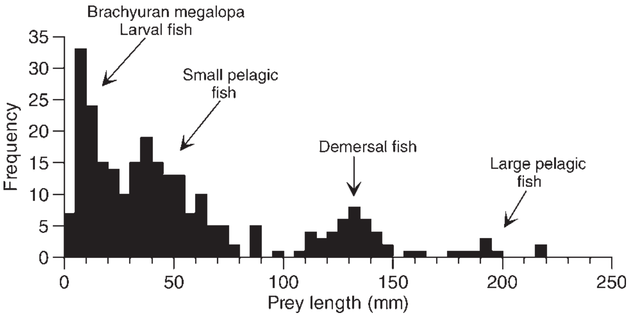

**Figure 5.** Prey size frequency histogram showing the length of prey (in 5-mm increments) consumed by mackerel tuna caught in eastern Australia between January 2003 and May 2005. Prey types consisting of four distinct prey size modes are shown.

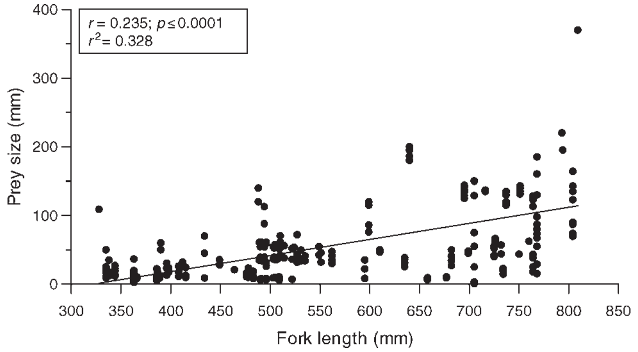

**Figure 6.** Plot of relationship between mackerel tuna FL and the length (mm) of prey consumed in eastern Australia between January 2003 and May 2005.

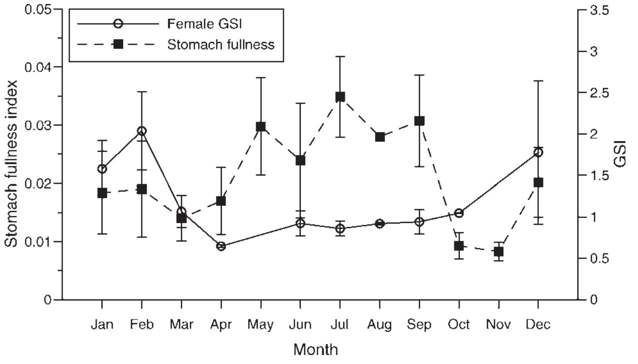

**Figure 7.** Monthly mean (±s.e.) stomach fullness index and GSI for female mackerel tuna, showing the relationship between feeding intensity and reproductive activity.

with fish size. Overall, small schooling pelagic clupeoids dominated the diet in terms of %WW and %FO. However, the species also consumed demersal prey, demonstrating that it may feed opportunistically during periods when epipelagic prey are less abundant.

Few studies have investigated the feeding ecology of mackerel tuna. Blaber *et al.* (1990) and Chiou and Lee (2004) both recorded 21 prey taxa from the stomachs of mackerel tuna caught around the Solomon Islands and Taiwan and found fish prey to constitute >90% of the overall prey biomass. Of those fish prey, most were *Stolephorus* sp. In the present study, the diversity of prey was more than double those of previous studies (43 taxa), perhaps indicating that fish in the present study fed more opportunistically than in other regions, or that sampling intensity was higher. However, the diet was similar in that *Stolephorus* sp. was also the most frequently encountered prey overall, although it constituted just 8.7% of the diet in terms of biomass. This was because larger prey such as *T. declivis*, carangids, and *S. sagax* were common in the diets of larger fish, but were not well represented in terms of FO across the entire size spectrum of specimens caught.

Tropical tuna of similar size to mackerel tuna that frequent oceanic habitats beyond continental shelves have been shown to primarily consume epipelagic fish, crustaceans, and cephalopods. For example, Graham *et al.* (2007) found juvenile yellowfin tuna (<50 cm FL) around the Hawaiian Islands to feed nearly exclusively in the upper mixed layer, consuming larval stomatopods, decapod crustaceans, and teleosts. In the western tropical Indian Ocean (Potier *et al.*, 2004) and the western Pacific Ocean (Bertrand *et al.*, 2002), yellowfin tuna mainly consumed epipelagic fish, crustaceans, and cephalopods.

Given that mackerel tuna are widely regarded as epipelagic predators in other regions of their distribution (Chiou and Lee, 2004), it is of note that several demersal and even benthic prey taxa were recorded in the diet in the present study, especially in larger fish. Similar results were obtained for mackerel tuna around Taiwan (Chiou and Lee, 2004), and for the closely related little tunny (*Euthynnus alletteratus*), which consumed demersal prey such as priacanthids, dactylopterids, and triglids off western Africa (Bahou *et al.*, 2007), synodontids, sciaenids, and bothids in the southeastern United States (Manooch *et al.*, 1985), and cephalopods, crustaceans, and teleosts (caproids, macrorhamphosids) in the central Mediterranean (Falautano *et al.*, 2007).

This difference in diet composition between mackerel tuna and other tropical tuna in open ocean habitats may in part be explained by water depth and physiology. In deep oceanic waters, the depth of the foraging niche of tuna is constrained by their physiological ability to withstand colder water temperature at depth. Although tuna such as bigeye can dive as deep as 1500 m where temperatures can reach 3°C (Schaefer and Fuller, 2002), most species forage at or above the thermocline (Brill *et al.*, 1999; Marcinek *et al.*, 2001), so their diets rarely contain demersal or benthic prey. Small tuna, such as mackerel tuna, may more likely be restricted to warmer surface waters owing to their higher surface area to volume ratio than that of larger tuna, meaning that they would lose proportionally more body heat to the environment during dives to cooler water at depth (Graham and Dickson, 2001). As a result, their diet would be expected to be primarily epipelagic prey. However, in our study region, mackerel tuna were generally found in waters shallower than 100 m, where they should be able to forage throughout the entire water column and to consume demersal prey (e.g. *Upeneus* sp., *S. undosquamis*), which may be less accessible in deeper oceanic habitats. Although demersal feeding by tuna is not common, such opportunistic feeding has been recorded for Atlantic bluefin tuna (*T. thynnus*; Chase, 2002), little tunny (Manooch *et al.*, 1985), and longtail tuna (Griffiths *et al.*, 2007a), when sampling was conducted in shallow coastal waters.

## Temporal variation in diet composition

Season was the most important factor in explaining the variation in the diet of mackerel tuna. Autumn diets, however, comprised fewer (14) prey taxa than other seasons and were dominated by engraulids. This is probably the consequence of higher local abundances of that prey in autumn; Ward *et al.* (2003) suggest that several small pelagic clupeoids, including *E. australis*, migrate to the warm waters of southeastern Queensland before spawning in winter and spring. In contrast, diets in the other seasons were generally more diverse (25 and 21 taxa in summer and winter, respectively). Small schooling pelagic teleosts such as engraulids, *Stolephorus* sp., and clupeids still contributed most to the WW of the diet, but relatively large teleosts including *T. declivis* and *S. undosquamis*, as well as many small prey such as larval dactylopterids, were well represented. It should be noted that the diversity of prey consumed during each season may also be in part attributable to different numbers of fish representing each size category during each season. For example, a larger number of medium-sized mackerel tuna was caught in autumn. Therefore, perhaps a

**Table 3.** Fork length range, mean (±1 s.d.) body weight, daily consumption, and daily ration for small (<402 mm), medium (402–580 mm), and large (>580 mm) mackerel tuna.

| Size class | Fork length (FL) range (mm) | Body weight (g) | Daily consumption (g $d^{-1}$) | Daily ration (% BW $d^{-1}$) |
|---|---|---|---|---|
| Small | 284–401 | 946.02 (720.14) | 26.42 (3.25) | 2.86 (0.34) |
| Medium | 402–579 | 2 146.72 (583.18) | 87.17 (9.17) | 4.10 (0.53) |
| Large | 580–809 | 5 362.77 (1 254.93) | 108.03 (14.33) | 1.95 (0.28) |
| All size classes | 284–809 | 3 455 (2 103.03) | 73.87 (8.92) | 2.18 (0.26) |

**Table 4.** Estimated mean annual consumption (t $\text{year}^{-1}$, $\pm 1$ s.d.) of major prey categories by small ($<402$ mm), medium (402–580 mm), and large ($>580$ mm) mackerel tuna in the Central Eastern Shelf Transition Bioregion (170 990 $\text{km}^2$) of eastern Australia.

| Size class | Pelagic fish | Demersal fish | Stomatopods | Bentho-pelagic crustaceans | Cephalopods | Molluscs | Miscellaneous | Total |
|---|---|---|---|---|---|---|---|---|
| Small | 1 206.46 (434.15) | 342.42 (112.52) | 1 154.00 (380.12) | 274.81 (124.92) | 5.81 (2.48) | – | 1.24 (0.34) | 2 984.74 (1 203.45) |
| Medium | 9 477.97 (88.81) | 245.22 (88.81) | 27.70 (20.02) | 38.52 (18.78) | 53.74 (44.12) | – | 4.16 (1.27) | 9 847.31 (582.03) |
| Large | 9 350.92 (922.97) | 2 780.26 (922.97) | 0.94 (0.26) | 24.92 (10.69) | 34.80 (11.68) | 5.50 (1.52) | 6.71 (4.00) | 12 204.05 (4 998.68) |
| All size classes | 20 035.34 (4 133.70) | 3 367.89 (934.04) | 1 182.64 (380.65) | 338.25 (126.78) | 94.35 (45.71) | 5.50 (1.52) | 12.11 (4.21) | 25 036.1 (6 134.23) |

coincidental change in prey preference by a particular size class of tuna during a particular season could have biased our results.

The feeding intensity of mackerel tuna varied considerably over time, and unexpectedly declined during the warmer months (October–April), a period when the standard metabolic rate for the species would be expected to increase with increasing water temperature (Brill, 1987), and hence demand greater prey consumption. This variation in feeding intensity may be explained in part by the clear relationship with reproductive activity, because feeding intensity was lowest during the period of greatest reproductive activity. The same pattern has been observed for other scombrids, including spotted mackerel (*Scomberomorus munroi*) and school mackerel (*Scomberomorus queenslandicus*; Begg and Hopper, 1997), Spanish mackerel (*Scomberomorus maculates*; Sturm, 1978), and longtail tuna (Griffiths *et al.*, 2007a). It may therefore be a strategy to maximize energy investment towards gonad development for spawning.

## Size-related variation in diet composition

Although season was the most important variable influencing the diets of mackerel tuna, fish size played an important role in determining diet composition. An exception was during autumn where engraulids contributed $>25\%$ of the WW of all three size classes, which may be due to opportunistic predation on engraulids that are locally abundant then (Ward *et al.*, 2003). However, focusing on the data from the other three seasons, it was clear that the diet of fish changed markedly with increasing size. The diets of fish approximately $<400$ mm were primarily small pelagic crustaceans (e.g. stomatopod larvae and brachyuran megalopa) and larval fish (engraulids, dactylopterids, monacanthids, and tetraodontids). The diet of medium-sized fish (400–580 mm) was primarily the same prey taxa consumed by smaller fish, especially for pelagic clupeoids and engraulids. This explains the significant dietary overlap between these two size classes ($R_o = 0.657$). However, the actual competition between these two size classes is unlikely to be significant, because prey size significantly increased with fish size. In particular, medium-sized fish consumed mainly adults of the shared pelagic fish prey species, which are often spatially segregated from their early life in Australian waters (Ward *et al.*, 2003; Dimmlich and Ward, 2006). In contrast, large fish ($>580$ mm) consumed mainly larger specimens of a different suite of teleost prey, including carangids, *T. declivis*, belonids, and *S. sagax*.

Similar ontogenetic shifts in diet composition have been noted for the closely related little tunny off western Africa by Bahou *et al.* (2007) and off the southeastern United States by Manooch *et al.* (1985), small fish primarily consuming small crustaceans and larger fish progressively more, and larger, teleost prey. However, in the Mediterranean Sea, fish showed the reverse behaviour, consuming mainly teleosts as juveniles, and proportionally more crustaceans and cephalopods as adults (Falautano *et al.*, 2007).

## Consumption and daily ration

Estimated annual prey consumption in the present study indicates that mackerel tuna play an important role in this neritic ecosystem, consuming an estimated 25 000 t $\text{year}^{-1}$ of prey in the Central Eastern Shelf Transition Bioregion. The estimated daily food consumption of mackerel tuna (26–108 g $\text{d}^{-1}$) in this study was similar to that of tropical tuna of similar size, such as skipjack (24–157 g $\text{d}^{-1}$), juvenile bigeye tuna (40–134 g $\text{d}^{-1}$; Ménard *et al.*, 2000), juvenile yellowfin tuna (18–136 g $\text{d}^{-1}$; Maldeniya, 1996), and longtail tuna (123 g d$^{-1}$; Griffiths *et al.*, 2007a). In contrast, daily ration estimates for mackerel tuna (1.95–4.10% BW d$^{-1}$) were generally lower than for bigeye tuna (4.82% BW d$^{-1}$) and skipjack (5.51% BW d$^{-1}$) of similar size in the Equatorial Atlantic Ocean (Ménard *et al.*, 2000), and yellowfin tuna in Sri Lankan waters (2.1–5.5% BW d$^{-1}$; Maldeniya, 1996) and in captivity (3.8–9.6% BW d$^{-1}$; Olson and Boggs, 1986). However, in the subtropical region where the present study was undertaken, the daily ration of mackerel tuna was higher than for longtail tuna (1.30–2.26% BW d$^{-1}$; Griffiths *et al.*, 2007a) and southern bluefin tuna (*Thunnus maccoyii*; 0.89–1.01% BW d$^{-1}$; Young *et al.*, 1997).

Mackerel tuna daily ration decreased with increasing size, particularly between medium-sized and large fish, which is a similar pattern found in other studies of tuna. For example, Maldeniya (1996) found the daily ration of yellowfin tuna in the tropical waters of Sri Lanka to decline from 4.2% BW d$^{-1}$ in small fish (<60 cm FL) to 1% BW d$^{-1}$ for large fish (>130 cm FL). Similarly in subtropical Australian waters, the daily ration of longtail tuna decreased from 2.17% BW d$^{-1}$ in small fish (<80 cm FL) to 1.30% BW d$^{-1}$ in large (>100 cm FL) fish (Griffiths *et al.*, 2007a).

Water temperature and fish size may play an important role in influencing the prey consumption rate and daily ration of mackerel tuna. A decrease in water temperature can result in decreased gastric evacuation rate (Temming *et al.*, 2002) and metabolic rate (Korsmeyer and Dewar, 2001) in scombrids. Brill (1987) showed that the standard metabolic rate of mackerel tuna decreased with increasing body weight. Moreover, Dickson *et al.* (2000) determined that heat production and retention in red muscle tissue of black skipjack tuna (*Euthynnus lineatus*) increased with size. Therefore, mackerel tuna in our subtropical study region may have a lower gastric evacuation rate and standard metabolic rate than in tropical regions. This effect, coupled with a decline in metabolic rate with increasing size, suggests that larger mackerel tuna may be required to consume proportionally smaller daily meals to maintain their standard metabolic rate.

### Implications for ecosystem models

Many fisheries worldwide are moving towards ecosystem-based fisheries management (Hall and Mainprize, 2004; Scandol *et al.*, 2005). This approach may be supported by ecosystem models, such as Ecopath (Christensen and Pauly, 1992), which can be useful for understanding the complex ecological relationships among species within an ecosystem to disentangle natural and anthropogenic effects on the system. Dietary studies are crucial for providing data for these models in terms of the direction and magnitude of trophic flows between ecological functional groups (Marasco *et al.*, 2007), which can only be achieved by quantifying the diet composition and the consumption/biomass ratio ($Q/B$), the latter being based on daily ration. However, our study has highlighted the fact that diet composition and daily ration can vary markedly with season and fish size, so future dietary studies of high trophic level pelagic fish need to be designed to capture the potentially high spatial, temporal, and ontogenetic variability commonly encountered in the diets of pelagic fish. This may improve the realism of ecosystem models and enhance their utility as tools for managing fisheries from an ecosystem perspective.

## Acknowledgements

We thank the numerous sportfishers who helped collect mackerel tuna, K. Davidson, Q. Dell, and R. Pillans for assistance in processing stomach samples, and D. Peel and R. Pillans for critically reviewing earlier drafts. The study was funded by the CSIRO Division of Marine and Atmospheric Research.

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doi:10.1093/icesjms/fsp065