Received: 15 September, 2011

IOTC-2011-WPNT01-14

CSIRO PUBLISHING

Marine and Freshwater Research, 2007, **58**, 376–397 www.publish.csiro.au/journals/mfr

Feeding dynamics, consumption rates and daily ration of longtail tuna (*Thunnus tonggol*) in Australian waters, with emphasis on the consumption of commercially important prawns

Shane P. Griffiths[A,B], *Gary C. Fry*[A], *Fiona J. Manson*[A] and *Richard D. Pillans*[A]

[A]CSIRO Division of Marine and Atmospheric Research, PO Box 120, Cleveland, Qld 4163, Australia.
[B]Corresponding author. Email: shane.griffiths@csiro.au

Abstract. The feeding ecology of longtail tuna was studied in northern and eastern Australia. Diet biomass data were used to estimate daily ration and consumption of individual prey taxa, particularly penaeids targeted by Australia's valuable Northern Prawn Fishery (NPF). Overall, the 497 stomachs contained 101 prey taxa. In both regions, small pelagic and demersal fishes comprised the majority of the diet biomass. Fish in both regions showed a marked increase in prey diversity, variation in prey composition and stomach fullness index in autumn and winter (March–August). This increase in apparently opportunistic feeding behaviour and feeding intensity showed an inverse relationship with reproductive activity, indicating a possible energy investment for gonad development. Daily ration decreased with increasing fish size, while annual consumption by fish increased with size. Total prey consumption in the Gulf of Carpentaria was estimated at 148 178 t year^{-1}. This includes 599 t year^{-1} of penaeids, equivalent to 11% of the annual NPF catch. This study demonstrated that longtail tuna play an important ecological role in neritic ecosystems. Their interaction with commercial fisheries highlights the need for targeted dietary studies of high order predators to better understand trophic pathways to facilitate ecosystem-based fisheries management.

Additional keywords: diet, ecosystem, fisheries management, pelagic, *Penaeus*, predation, trophodynamics.

Introduction

The growing worldwide interest in ecosystem approaches to fisheries management highlights a need for dietary information to populate ecosystem models. This is especially important for high-trophic-level predators – such as tunas – that can significantly influence the structure of pelagic systems (Essington *et al*. 2002). Such approaches are currently being explored for Australia's second most valuable fishery, the Northern Prawn Fishery (NPF) (see Okey 2006). Extensive research into the diets of demersal and estuarine fishes and their predation of commercially important prawns within the NPF (Brewer *et al*. 1991; Haywood *et al*. 1998; Salini *et al.* 1998) have provided valuable data for ecosystem models. However, the diet and consumption rates of large pelagic fishes in northern Australia are lacking, particularly in relation to predation of NPF target species. This lack of knowledge coupled with recent anecdotal accounts of pelagic fishes preying upon prawn aggregations in the NPF (Bienke 2004) initiated an interest in better understanding the feeding ecology and consumption rates of one of the region's largest and most prolific pelagic predators, longtail tuna *Thunnus tonggol* (Bleeker 1851).

Species of the *Thunnus* genera are well known to exhibit rapid growth rates and are physiologically characterised by high metabolic rates (Brill 1996). Close relatives of longtail tuna – yellowfin tuna *Thunnus albacares* and Atlantic bluefin tuna *Thunnus thynnus* – have among the highest metabolic rates of all fishes (Korsmeyer and Dewar 2001) and can consume in excess of 3 kg of prey per day (Maldeniya 1996; Aguado-Gimenez and Garcia-Garcia 2005). Therefore, longtail tuna are also likely to consume large quantities of prey in order to accommodate their high energy requirements for growth and metabolic function. As a consequence, they may exert a significant 'top-down' effect on tropical ecosystems, as has been demonstrated for other large tuna, such as yellowfin tuna in the eastern Pacific Ocean (Essington *et al*. 2002).

Preliminary observations of the diet of longtail tuna suggest that they are primarily piscivorous; however, they also consume a vast variety of prey types including crustaceans and cephalopods (Serventy 1942, 1956; Wilson 1981), which is likely to place them at a high trophic level similar to that of other tropical *Thunnus* species in other ecosystems (Maldeniya 1996; Ménard *et al*. 2000). Despite the economic and apparent ecological importance of longtail tuna in tropical coastal ecosystems (Yesaki 1993), few studies have investigated their feeding ecology in order to better understand their role in tropical ecosystems.

The specific aims of the present study were to (i) quantitatively assess the spatial, temporal and size-related variability in the diet composition and feeding intensity of longtail tuna in northern and eastern Australia, (ii) estimate the consumption rate and daily ration for three size classes of fish and (iii) estimate the annual biomass of prey consumed, particularly commercially important prawns, in the Gulf of Carpentaria within the NPF.

 10.1071/MF06197 1323-1650/07/040376

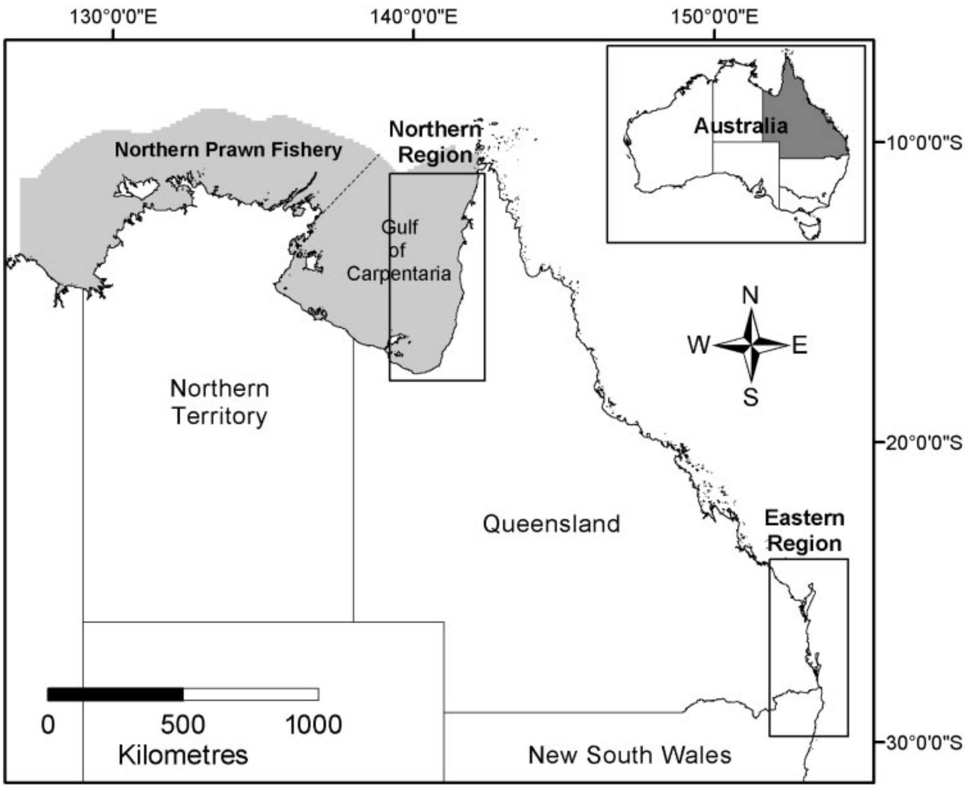

Fig. 1. Map of Australia showing the managed area of the Northern Prawn Fishery (NPF, shaded) and the northern and eastern regions where longtail tuna were collected for dietary analysis between February 2003 and April 2005. The dashed line in the NPF delineates the boundary of the Gulf of Carpentaria where annual prey consumption rates were estimated.

Methods and materials

Collection of specimens

Longtail tuna were collected monthly between February 2003 and April 2005 from two discrete regions in northern and eastern Australia using gillnets and rod and line (Fig. 1). In the northern region, specimens were collected from the eastern coast of the Gulf of Carpentaria from Weipa to Mornington Island, Queensland. In the eastern region fish were caught between Gladstone, Queensland and Iluka, New South Wales. In both regions, fish were captured within 27 nautical miles of the coast in depths of less than 30 m. Fish were put on ice upon capture and frozen as soon as possible, and freighted to the CSIRO Marine and Atmospheric Research laboratories in Cleveland for processing.

Regurgitation of stomach contents is common for some scombrids, when captured by rod and line (Begg and Hopper 1997), which can lead to potential bias when comparing diets of fish collected with other sampling methods. Conversely, the diets of fish captured in gillnets may be biased towards less-digestible prey if the gillnet sets are long (in this case 2–3 h), because digestion of stomach contents can continue after death (Ménard *et al*. 2000). We found no significant difference in the mean stomach fullness between fish captured by gillnet and rod and line (ANOVA: d.f. = 1, $F = 2.912$, $P = 0.094$); thus, collection method was ignored in subsequent dietary analyses.

Sample processing

In the laboratory, fish were weighed (0.01 g) and measured (fork length FL, mm) before the stomach was removed. Sex was determined macroscopically and gonads were removed, trimmed of fat and weighed (0.001 g) to calculate a gonadosomatic index (GSI) using the equation:

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

Upon examination of the stomach, prey items were removed and identified to the lowest possible taxon, counted, measured where possible (total length for all taxa, and additionally standard length for fish, carapace length for crustaceans, and mantle length for cephalopods), and a total wet weight was obtained for each prey type. Otoliths, cephalopod mandibles and backbones were noted but ignored in the analyses because they can accumulate in the stomach and be over-represented in the diet (Olson and Galvan-Magana 2002; Chipps and Garvey 2007). For each fish, each prey type was oven-dried at 60°C for 48 h and the dry weight measured. To investigate the intensity and timing of feeding, a quantitative measure of stomach fullness was obtained by dividing the wet weight of the stomach contents (0.01 g) by the wet weight of the eviscerated fish. Monthly changes in the stomach fullness index were also compared with monthly GSI data to investigate the possible effects of reproductive activity on feeding intensity.

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

$$\% \, DW_i = \left(\frac{DW_i}{\sum_{i=1}^{Q} DW_i} \right) \times 100 \tag{2}$$

$$\% \, FO_i = \left(\frac{F_i}{N} \right) \times 100 \tag{3}$$

where DW_i is the weight of prey type i, Q is the number of prey types, F_i is the number of fish stomachs containing prey type i, and N is the total number of fish stomachs containing prey. We primarily concentrated on describing the diet in terms of biomass, and we used dry weight in preference to wet weight so as to minimise the bias resulting from the consumption of prey items having a high moisture content.

Non-metric multidimensional scaling (nMDS) was used to examine differences in diet composition, in terms of biomass, among regions, seasons, and fish size classes. Seasons were defined as: spring (September–November), summer (December–February), autumn (March–May) and winter (June–August). The biomass of each prey taxon was represented as a percentage of the total prey biomass for each month (Eqn 2) in order to standardise the relative contributions of prey across all months. Data were left untransformed and a similarity matrix was constructed using the Bray-Curtis similarity coefficient (Clarke 1993). Analysis of similarities (ANOSIM) was used to test whether diet composition differed statistically among regions, seasons and size classes (Clarke 1993). Similarity percentages (SIMPER) were used to determine the prey items that made the greatest contribution to the similarity in samples within *a priori* groups (e.g. season), and the dissimilarity of samples between *a priori* groups. All multivariate analyses were conducted using the PRIMER (Plymouth Routines In Multivariate Ecological Research) package version 5.2.2.

Diel feeding

We assessed diel feeding periodicity by comparing the mean stomach fullness and the percentage of fish with stomachs containing prey between the day and night for each season sampled. This was only possible for autumn (March, April and May) and winter (June, July and August) in the northern region when day and night sampling was conducted concurrently. Because we obtained specimens opportunistically from commercial gillnet vessels, we were unable to determine the extent of feeding at discrete intervals over a 24-h period. Instead, we were only able to ascertain whether specimens were collected during the day or night.

Daily ration and prey consumption rates

We estimated daily consumption rates of prey by longtail tuna using the methods of Olson and Mullen (1986). This method predicts the feeding rate ($\hat{r}$, grams per hour) by dividing the mean wet weight of the stomach contents per predator ($\overline{W}_i$, in grams) by the average time required to evacuate the average proportion of prey type i (A_i). This can be represented in the following model for a predator that consumes a range of prey that are evacuated at different rates:

$$\hat{r} = \sum_{i=0}^{I} \frac{\overline{W}_i}{A_i} \tag{4}$$

where i refers to each of the prey types consumed by the predator. This represents the prey consumption per hour, so that $\hat{r}$ is multiplied by the number of hours per day in which the predator feeds to estimate the daily meal (*M*). Because longtail tuna primarily feed during the day (see 'Results'), we multiplied $\hat{r}$ by 12. Daily ration was then calculated by expressing the daily meal as a percentage of the average wet body weight of fish examined. We also investigated size-related variation in daily ration among three size classes: small (S, <800 mm), medium (M, 800 to 1000 mm) and large (L, >1000 mm).

Because we had no information on the evacuation times (A_i) for specific prey consumed by longtail tuna, we applied an estimate that most closely corresponded to the A_i values for particular prey experimentally determined by Olson and Boggs (1986) for yellowfin tuna. We felt that this approach was suitable for longtail tuna, because yellowfin tuna are a closely related species and the experiment of Olson and Boggs (1986) was undertaken in water temperatures (23.5–25.5°C) similar to that of the present study (21–28°C). They assigned values of A_i to squid (4.48), mackerel (*Scomber japonicus*) (5.29), smelt (*Hypomesus pretiosus*) (4.12) and nehu (*Stolephorus purpureus*) (2.24), and the mean for four experimental food types (3.77). Our estimates for each prey type were based on similarity of digestibility by taking into account the size and 'softness' of the prey type. This approach was successfully applied to dolphinfish (*Corypeanea hippurus*) in the eastern Pacific Ocean by Olson and Galvan-Magana (2002). We included all empty stomachs in the estimation of daily ration because they probably represent the true proportion of the population that may not have fed before the time of capture.

Annual prey consumption in the Gulf of Carpentaria

We were interested in estimating the annual consumption of prey species by longtail tuna, particularly penaeids that are commercially important in the NPF, which incorporates the northern study region (Fig. 1). Although we also aimed to estimate the annual consumption of prey for the eastern region and the entire NPF, this was not possible because we only had information on longtail tuna density for the Gulf of Carpentaria (GoC) (see Griffiths *et al.* in press). Longtail tuna apparently undertake an ontogenetic migration from the north-west to eastern Australia (Serventy 1956), and their density probably changes significantly across this spatial scale. Therefore, it is unrealistic to employ the GoC longtail tuna density for estimating consumption of fish in any area outside the GoC.

We initially aimed to estimate the annual biomass of prey consumed using the method of Pauly and Palomares (1987) and Brewer *et al.* (1991). This method was not considered suitable for longtail tuna because their model does not account for size-related changes in prey preference and daily ration. We modified the model to better account for these factors, which can be represented as:

$$B_i = 365T_i \sum_{j\varepsilon(\mathrm{S,M,L})} M_{ij}N_j \qquad (5)$$

where B_i is the total annual biomass of prey i consumed by longtail tuna of size class j ($j = \mathrm{S, M, L}$), T_i is the total area (km^2) where predation of the prey species can occur, M_{ij} is the daily meal of prey type i by fish in size class j (in terms of wet weight), N_j is the density of longtail tuna in size class j (fish km^{-2}) in area T_i. In the absence of size-specific density estimates for longtail tuna in the GoC, we used a value of 1.81 fish (s.d. $\pm$ 0.499) km^{-2} for all three size classes of longtail tuna in T_i (Griffiths *et al.* in press).

The annual consumption rate of each prey type was calculated for the entire GoC using a feeding area (T_i) of 397 700 km^2 (Zhou and Griffiths 2006). We did not want to overestimate the consumption rate of commercially important penaeids by longtail tuna. Most species of penaeids are more abundant close to the coast. Therefore, we assumed that predation was restricted to the commercial fishing grounds in the GoC comprising 206 804 km^2 (Zhou and Griffiths 2006). We recognise that prey, particularly prawns, may vary in their availability in space and time, and that the contribution of prey to the observed diet may be influenced by spatial or temporal variation in sampling intensity and predator consumption rates. In this model, we assumed that the contribution of prey to the overall diet was representative of the entire year since we collected samples monthly throughout each region. We also made a further assumption that the consumption rate of tuna did not vary spatially or temporally.

We incorporated uncertainty around our model parameters using a normal or uniform distribution depending on the data available. The A_i values used were point estimates without error estimates and should be considered minimum estimates. We used 10 000 Monte Carlo simulations in 'Crystal Ball Risk Analysis Software' (Decisioneering, Denver, CO) to obtain the mean biomass (B_i) of prey consumed in the GoC.

Results

Overall diet composition

A total of 497 longtail tuna stomachs were analysed, of which 168 (or 34%) were empty. The overall diet was diverse, consisting of 101 prey taxa (Table 1) with a total biomass of 5344 g and 22 423 g by dry and wet weight respectively. The contribution of each prey taxa (in terms of % DW and % FO) to the diet of fish from each region across seasons and fish sizes is given in Tables 2 to 4.

Overall, the relative importance of each prey category was remarkably similar for both regions in terms of biomass and frequency of occurrence. Pelagic fishes made the largest contribution to the diet of longtail tuna in terms of biomass and frequency of occurrence both in the northern region (90% DW, 73% FO) and the eastern region (93% DW; 65% FO) (Table 5). These were primarily represented by small schooling clupeids and engraulids including *Sardinella albella*, *Sardinella gibbosa*, *Stolephorous* spp. and *Sardinops* spp.

In terms of biomass, the next most important prey categories were similar for both regions: 4–5% for demersal fishes and 2–5% for cephalopods in the eastern and northern regions respectively. Other prey categories, including commercially important prawns, contributed <1% to the overall diet (Table 5). Demersal fishes were mainly represented by *Sillago* spp. (24%), *Pseudorhombus* spp. (16%), *Paramonacanthus filicauda* and *Nemipterus celebicus* (8%). Cephalopods were mainly represented by Teuthoidea sp. (72%), *Photololigo* spp. (11%) and *Sepia smithii* (10%).

In terms of frequency of occurrence, all prey categories contributed 3 to 8% to the overall diet, with commercially important prawns contributing 3% (Table 5). With respect to region, miscellaneous prey items (*Zostera* spp. and *Sargassum* spp.), crabs (portunids, *Charybdis* spp. and *Thalamita sima*) and cephalopods (Teuthoidea sp. and *Photololigo* spp.) made a slightly greater contribution to the diet in the eastern region. In contrast, demersal fishes (*Leiognathus splendens*, *Paramonacanthus filicauda* and *Centriscus scutatus*) and commercially important penaeids (*Penaeus* spp.) were more highly represented in the northern region.

Regional comparisons

The number of prey taxa consumed in the northern region (82 taxa) was nearly twice that of the eastern region (45 taxa). nMDS ordination showed no definitive difference in the taxonomic composition of diet with respect to region, because samples appeared widely dispersed (Fig. 2). However, ANOSIM indicated there was in fact a statistical difference in the diet composition between the two regions (Global $R = 0.181$, $P = 0.009$). SIMPER revealed that this difference resulted from greatest contributions of *Sardinella* spp., Teuthoidea sp. and *Selar boops* in the northern region, compared with greater contributions of Engraulidae sp., Clupeidae sp., Belonidae sp., *Scomber australasicus* and *Sardinops sagax* in the eastern region.

Seasonal comparisons

The number of prey taxa consumed differed markedly among seasons, but the pattern of seasonal variation was similar in both regions. In the northern region, fish had the most diverse diet in autumn and winter (47 and 27 taxa) and the least diverse diet in summer (7 taxa). The same trend was apparent in the eastern region, where fish had the most diverse diet in autumn and winter (29 and 17 taxa) and the least diverse diet in summer (7 taxa).

With respect to diet composition, nMDS ordinations showed a similar grouping of samples in both regions in that the proximity of samples in autumn and winter were far closer than those in summer and spring (Fig. 3). Because diets of individual fish were aggregated into monthly samples, there were too few possible sample permutations for ANOSIM to calculate a test statistic to determine whether diets statistically differed among seasons in each region. However, SIMPER revealed that the dissimilarity in diets among seasons was very high for both the northern region (73–92%) and the eastern region (69–80%).

In the northern region, *Sardinella* spp. and *Stolephorus* spp. contributed most to the diet biomass in each of the four seasons. The dissimilarity in diet composition among seasons was

Table 1. Prey taxa consumed (% dry weight) by longtail tuna in four seasons in northern and eastern Australia between February 2003 and April 2005

Fish with empty stomachs were excluded from the analysis. A_i is the average time (in hours) required to evacuate the average proportion of prey i present in the stomach, adopted from similar prey types examined by Olson and Galvan-Magana (2002). BC, benthopelagic crustaceans; Cep, cephalopods; Cra, crabs; DF, demersal fishes; Misc, miscellaneous; Pen, penaeids; PF, pelagic fishes

Family	Prey name	Category	A_i	Northern region					Eastern region					Total
				Spring	Summer	Autumn	Winter	Overall	Spring	Summer	Autumn	Winter	Overall	
Teleost														
Apogonidae	*Siphamia* spp.	DF	4.12				0.010	0.003						0.001
Belonidae	Belonidae sp.	PF	5.29				0.139	0.035	33.879		6.469		10.087	5.061
	Strongylura leiura	PF	5.29			1.774		0.444						0.222
Bregmacerotidae	*Bregmaceros* spp.	DF	4.12	0.033				0.008						0.004
Carangidae	*Alectis* sp.	PF	5.29								0.190		0.047	0.024
	Carangidae sp.	PF	5.29		4.345			1.086						0.543
	Carangoides spp.	PF	5.29	0.027				0.007						0.003
	Pantolobus radiatus	PF	5.29		9.131			2.283						1.141
	Scomberoides spp.	PF	5.29									1.795	0.449	0.224
	Scomberoides tol	PF	5.29			1.626	0.465	0.523						0.261
	Selar boops	PF	5.29				3.842	0.960						0.480
	Trachurus declivis	PF	5.29						1.542			0.536	0.520	0.260
Centriscidae	*Centriscus scutatus*	DF	5.29			0.025	0.076	0.025						0.013
Clupeidae	Clupeidae sp.	PF	2.24	4.108		2.454	0.757	1.830		29.128	4.863	1.718	8.927	5.379
	Dussumieria elopsoides	PF	4.12			4.819	7.021	2.960						1.480
	Herklotsichthys spp.	PF	2.24			1.184		0.296						0.148
	Hyperlophus vittatus	PF	2.24								4.684		1.171	0.585
	Nematalosa come	PF	4.12			12.707	1.084	3.448						1.724
	Nematalosa spp.	PF	4.12				0.905	0.226						0.113
	Pellona ditchella	PF	4.12				0.752	0.188						0.094
	Sardinella albella	PF	4.12			1.535		0.384						0.192
	Sardinella gibbosa	PF	4.12			3.377	9.938	3.329						1.664
	Sardinella spp.	PF	4.12	63.313	36.378	8.508	40.302	37.125		17.566	0.481	8.268	6.579	21.852
	Sardinops spp.	PF	4.12	4.482				1.120				43.280	10.820	5.970
Engraulidae	Engraulidae sp.	PF	2.24		5.778	19.951	1.012	6.685		47.704	43.859		22.891	14.788
Engraulididae	*Stolephorus* spp.	PF	2.24	0.217	31.927	12.408	6.259	12.703	0.022		14.169	5.152	4.836	8.769
	Thryssa hamiltoni	PF	4.12			4.353	1.090	1.361						0.680
	Thryssa setirostrus	PF	4.12				5.403	1.351						0.675
	Thryssa spp.	PF	4.12				0.381	0.095						0.048
Exocoetidae	*Cheilopogon* spp.	PF	4.12			1.994		0.498						0.249
	Exocoetidae sp.	PF	4.12			0.599	1.085	0.421						0.211
Haemulidae	*Pomadasys* spp.	DF	4.12				0.185	0.046						0.023
Hemiramphidae	Hemiramphidae sp.	PF	4.12	3.209				0.802	1.741		5.126	6.055	3.230	2.016
	Hemiramphus robustus	PF	4.12			3.819		0.955						0.477
	Hyporhamphus dussumieri	PF	4.12			4.103		1.026						0.513

Leiognathidae	Leiognathidae sp.	DF	4.12								0.184		0.046	0.023
	Leiognathus bindus	DF	4.12				0.128	0.032						0.016
	Leiognathus equillus	DF	4.12				1.226	0.306						0.153
	Leiognathus splendens	DF	4.12				3.246	0.812						0.406
	Leiognathus spp.	DF	4.12			2.223		0.556						0.278
Monacanthidae	Monacanthidae sp.	DF	3.77	2.121		0.007		0.532			0.100		0.025	0.279
	Paramonacanthus filicauda	DF	3.77	3.141				0.785						0.393
Mullidae	*Upeneus sulphureus*	DF	4.12				0.331	0.083						0.041
Nemipteridae	*Nemipterus celebicus*	DF	4.12				3.116	0.779						0.389
	Nemipterus spp.	DF	4.12			0.493		0.123						0.062
Ostraciidae	Ostraciidae sp.	BC	3.77	0.036		0.003		0.010			0.006		0.001	0.006
Paralichthyidae	*Pseudorhombus* spp.	DF	3.77									6.062	1.515	0.758
Platycephalidae	Platycephalidae sp.	DF	5.29				0.096	0.024						0.012
Plotosidae	Plotosidae sp.	DF	5.29				0.268	0.067						0.034
Scatophagidae	*Selenotoca multifasciata*	DF	3.37			0.294		0.074						0.037
Scombridae	*Scomber australasicus*	PF	5.29						55.875				13.969	6.984
	Scombridae sp.	PF	5.29	0.296				0.074						0.037
Scorpeinidae	Scorpeinidae sp.	DF	5.29				0.214	0.054						0.027
Serranidae	*Epinephalus* spp.	DF	5.29			0.003		0.001						0.000
Sillaginidae	*Sillago* spp.	DF	5.29									9.060	2.265	1.132
Sphyraenidae	*Sphyraena obtusata*	PF	5.29									1.243	0.311	0.155
Synodontidae	Synodontidae sp.	DF	3.77								1.198		0.300	0.150
Teleost	Teleost remains	PF	4.12	13.641		8.835	7.411	7.472	3.361	5.304	16.873	11.491	9.257	8.364
Terapontidae	*Terapon puta*	DF	5.29				1.008	0.252						0.126
Tetraodontidae	*Lagocephalus lunaris*	DF	3.77	0.306				0.077						0.038
	Tetraodontidae sp.	DF	3.77	2.084				0.521	0.367				0.092	0.306
Miscellaneous														
	Seagrass	Misc	2.24			0.024		0.006			0.001		0.000	0.003
Avies	Bird feather	Misc	2.24			0.001		0.000						0.000
Casuarinaceae	Cassurina plant remains	Misc	2.24			0.023		0.006						0.003
Hydrocharitaceae	*Halophila ovalis*	Misc	2.24								0.014		0.003	0.002
Hymenoptera	Hymenoptera	Misc	2.24			0.001		0.000						0.000
Sargassaceae	*Sargassum* spp.	Misc	2.24				0.007	0.002			0.015	0.292	0.077	0.039
Zosteraceae	*Zostera* spp.	Misc	2.24				0.004	0.001	0.583	0.062	0.152	0.007	0.201	0.101
Mollusca														
Bivalvia	Bivalve larvae	Misc	2.24			0.000		0.000						0.000
Loliginidae	*Photololigo* spp.	Cep	4.48	0.120			0.858	0.245				1.624	0.406	0.325
	Teuthoidea sp.	Cep	4.48	2.768	12.354	0.618	1.195	4.233	1.007		0.010	0.016	0.258	2.246
Sepiidae	*Sepia elliptica*	Cep	4.48									0.944	0.236	0.118
	Sepia plangon	Cep	4.48								0.485		0.121	0.061
	Sepia smithii	Cep	4.48									2.457	0.614	0.307
	Sepioidae sp.	Cep	4.48	0.032				0.008	0.201				0.050	0.029

(Continued)

Table 1. *(Continued)*

Family	Prey name	Category	A_i	Northern region					Eastern region					Total
				Spring	Summer	Autumn	Winter	Overall	Spring	Summer	Autumn	Winter	Overall	
Crustacea														
	Natantia	BC	2.24								0.001		0.000	0.000
Brachyura	Brachyuran megalopa	BC	3.37			0.002		0.000		0.014	0.014		0.007	0.004
Caridea	Caridae	BC	3.37			0.000		0.000						0.000
Crustacea	Crustacea remains	BC	3.37	0.006			0.003	0.002						0.001
Isopoda	Isopoda	BC	3.37	0.004		0.081	0.002	0.022	0.041		0.020		0.015	0.018
Palinuridae	*Panulirus phyllasoma*	BC	3.37			0.002		0.001						0.000
	Panulirus puerulus	BC	3.37			0.009		0.002						0.001
Penaeidae	*Metapenaeopsis novaeguinea*	Pen	2.24								0.629		0.157	0.079
	Metapenaeopsis palmensis	Pen	2.24						0.030				0.008	0.004
	Metapenaeopsis spp.	Pen	2.24	0.016		0.095	0.012	0.031			0.002		0.001	0.016
	Penaeus spp.[A]	Pen	2.24	0.012	0.087	0.273	0.006	0.095	0.448				0.112	0.103
	Penaeus esculentus[A]	Pen	2.24			0.158		0.040			0.319		0.080	0.060
	Penaeus merguiensis[A]	Pen	2.24			0.471		0.118						0.059
	Penaeus plebejus[A]	Pen	2.24	0.027				0.007			0.047		0.012	0.009
Portunidae	*Charybdis* spp.	Cra	5.29			0.069		0.017			0.014		0.004	0.010
	Charybdis truncata	Cra	5.29				0.166	0.042						0.021
	Charybdis yaldwini	Cra	5.29			0.051		0.013						0.006
	Portunus acerbiterminalis	Cra	5.29			0.161		0.040			0.031		0.008	0.024
	Portunus pelagicus	Cra	5.29			0.435		0.109						0.054
	Portunus rubromarginatus	Cra	5.29						0.275		0.041		0.079	0.040
	Portunus sanguinolentus	Cra	5.29			0.030		0.008						0.004
	Portunus spp.	Cra	5.29			0.053		0.013	0.403				0.101	0.057
	Thalamita sima	Cra	5.29						0.225	0.222			0.112	0.056
	Thalamita spp.	Cra	5.29			0.023		0.006						0.003
Sergestidae	Sergestidae sp.	BC	2.24	0.000				0.000						0.000
Squillidae	Stomatopoda larvae	BC	2.24	0.000		0.326		0.082						0.041
Number of prey taxa consumed				24	7	47	38	82	16	7	29	17	45	101
Number of stomachs examined				72	40	177	97	386	30	11	45	25	111	497
Number of empty stomachs				12	6	40	10	66	5	3	2	2	22	168
Average dry weight (g) of prey consumed per fish (excluding empty stomachs)				19.872	19.364	10.202	20.527	15.913	8.895	18.727	18.356	21.182	17.196	16.293

[A] Prey species of commercial importance to the Northern Prawn Fishery.

Table 2. Prey taxa consumed (% frequency of occurrence) by longtail tuna in four seasons in northern and eastern Australia between February 2003 and April 2005

Fish with empty stomachs were excluded from the analysis. BC, benthopelagic crustaceans; Cep, cephalopods; Cra, crabs; DF, demersal fishes; Misc, miscellaneous; Pen, penaeids; PF, pelagic fishes

Family	Species	Category	Northern region					Eastern region					Total
			Spring	Summer	Autumn	Winter	Overall	Spring	Summer	Autumn	Winter	Overall	
Teleost													
Apogonidae	*Siphamia* spp.	DF				1.351	0.676					0.000	0.253
Belonidae	Belonidae sp.	PF				1.351	0.676	31.579		8.889		10.117	7.841
	Strongylura leiura	PF			0.990		0.248					0.000	0.155
Bregmacerotidae	*Bregmaceros* spp.	DF	2.128				0.532					0.000	0.332
Carangidae	*Alectis* sp.	PF					0.000			2.222		0.556	0.417
	Carangidae sp.	PF		9.091			2.273					0.000	1.420
	Carangoides spp.	PF	2.128				0.532					0.000	0.332
	Pantolobus radiatus	PF		9.091			2.273					0.000	1.420
	Scomberoides spp.	PF					0.000				4.545	2.273	1.136
	Scomberoides tol	PF			2.970	1.351	1.418					0.000	0.717
	Selar boops	PF				1.351	0.676					0.000	0.253
	Trachurus declivis	PF					0.000	5.263			4.545	3.589	2.123
Centriscidae	*Centriscus scutatus*	DF			0.990	2.703	1.599					0.000	0.661
Clupeidae	Clupeidae sp.	PF	2.128		3.960	4.054	3.549		9.091	2.222	4.545	5.101	4.969
	Dussumieria elopsoides	PF			0.990	6.757	3.626					0.000	1.422
	Herklotsichthys spp.	PF			1.980		0.495					0.000	0.309
	Hyperlophus vittatus	PF					0.000			4.444		1.111	0.833
	Nematalosa come	PF			4.950	1.351	1.913					0.000	1.027
	Nematalosa spp.	PF				1.351	0.676					0.000	0.253
	Pellona ditchella	PF				1.351	0.676					0.000	0.253
	Sardinella albella	PF			2.970		0.743					0.000	0.464
	Sardinella gibbosa	PF			0.990	4.054	2.275					0.000	0.915
	Sardinella spp.	PF	23.404	63.636	18.812	35.135	44.031		36.364	4.444	18.182	19.293	35.324
	Sardinops spp.	PF	4.255				1.064				31.818	15.909	8.619
Engraulidae	Engraulidae sp.	PF		27.273	40.594	10.811	22.372		36.364	53.333		22.424	29.449
	Stolephorus spp.	PF	2.128	45.455	16.832	20.270	26.239	5.263		22.222	13.636	13.690	22.428
	Thryssa hamiltoni	PF			2.970	1.351	1.418					0.000	0.717
	Thryssa setirostrus	PF				6.757	3.378					0.000	1.267
	Thryssa spp.	PF				2.703	1.351					0.000	0.507
Exocoetidae	*Cheilopogon* spp.	PF			0.990		0.248					0.000	0.155
	Exocoetidae sp.	PF			0.990	1.351	0.923					0.000	0.408
Haemulidae	*Pomadasys* spp.	DF				1.351	0.676					0.000	0.253
Hemiramphidae	Hemiramphidae sp.	PF	10.638				2.660	5.263		6.667	18.182	12.073	8.445
	Hemiramphus robustus	PF			1.980		0.495					0.000	0.309
	Hyporhamphus dussumieri	PF			4.950		1.238					0.000	0.774
Leiognathidae	Leiognathidae sp.	DF					0.000			6.667		1.667	1.250
	Leiognathus bindus	DF				1.351	0.676					0.000	0.253
	Leiognathus equillus	DF				1.351	0.676					0.000	0.253
	Leiognathus splendens	DF				8.108	4.054					0.000	1.520
	Leiognathus spp.	DF			1.980		0.495					0.000	0.309

(Continued)

Table 2. ***(Continued)***

Family	Species	Category	Northern region					Eastern region					Total
			Spring	Summer	Autumn	Winter	Overall	Spring	Summer	Autumn	Winter	Overall	
Monacanthidae	Monacanthidae sp.	DF	4.255		0.990		1.311			4.444		1.111	1.653
	Paramonacanthus filicauda	DF	8.511				2.128					0.000	1.330
Mullidae	*Upeneus sulphureus*	DF				1.351	0.676					0.000	0.253
Nemipteridae	*Nemipterus celebicus*	DF				1.351	0.676					0.000	0.253
	Nemipterus spp.	DF			0.990		0.248					0.000	0.155
Ostraciidae	Ostraciidae sp.	BC	4.255		0.990		1.311			2.222		0.556	1.236
Paralichthyidae	*Pseudorhombus* spp.	DF					0.000				4.545	2.273	1.136
Platycephalidae	Platycephalidae sp.	DF				1.351	0.676					0.000	0.253
Plotosidae	Plotosidae sp.	DF				1.351	0.676					0.000	0.253
Scatophagidae	*Selenotoca multifasciata*	DF			0.990		0.248					0.000	0.155
Scombridae	*Scomber australasicus*	PF					0.000	21.053				5.263	3.947
	Scombridae sp.	PF	2.128				0.532					0.000	0.332
Scorpeinidae	Scorpeinidae sp.	DF				1.351	0.676					0.000	0.253
Serranidae	*Epinephalus* spp.	DF			0.990		0.248					0.000	0.155
Sillaginidae	*Sillago* spp.	DF					0.000				4.545	2.273	1.136
Sphyraenidae	*Sphyraena obtusata*	PF					0.000				4.545	2.273	1.136
Synodontidae	Synodontidae sp.	DF					0.000			2.222		0.556	0.417
	Teleost remains	PF	53.191		31.683	41.892	42.165	26.316	36.364	31.111	40.909	43.902	48.929
Terapontidae	*Terapon puta*	DF				1.351	0.676					0.000	0.253
Tetraodontidae	*Lagocephalus lunaris*	DF	2.128				0.532					0.000	0.332
	Tetraodontidae sp.	DF	2.128				0.532	5.263				1.316	1.319
Miscellaneous													
	Seagrass	Misc			0.990		0.248			2.222		0.556	0.571
Avies	Bird feather	Misc			1.980		0.495					0.000	0.309
Casuarinaceae	Cassurina plant remains	Misc			4.950		1.238					0.000	0.774
Hydrocharitaceae	*Halophila ovalis*	Misc					0.000			6.667		1.667	1.250
Hymenoptera	Hymenoptera	Misc			0.990		0.248					0.000	0.155
Sargassaceae	Sargassum spp.	Misc				2.703	1.351			2.222	13.636	7.374	4.333
Zosteraceae	*Zostera* spp.	Misc				1.351	0.676	21.053	27.273	28.889	4.545	21.576	15.867
Mollusca													
Bivalvia	Bivalve larvae	Misc			0.990		0.248					0.000	0.155
Loliginidae	*Photololigo* spp.	Cep	6.383			1.351	2.271				4.545	2.273	2.387
	Teuthoidea sp.	Cep	12.766	9.091	3.960	2.703	7.806	15.789		6.667	9.091	10.159	11.024

Sepiidae	*Sepia elliptica*	Cep					0.000				4.545	2.273	1.136
	Sepia plangon	Cep					0.000			2.222		0.556	0.417
	Sepia smithii	Cep					0.000				4.545	2.273	1.136
	Sepioidae sp.	Cep	2.128				0.532	5.263				1.316	1.319
Crustacea													
	Natantia	BC					0.000			2.222		0.556	0.417
Brachyura	Brachyuran megalopa	BC			1.980		0.495		9.091	2.222		2.828	2.431
Caridea	Caridae	BC			0.990		0.248					0.000	0.155
Crustacea	Crustacea remains	BC	2.128			1.351	1.208					0.000	0.586
Isopoda	Isopoda	BC	2.128		13.861	2.703	5.349	10.526		17.778		7.076	8.312
Palinuridae	*Panulirus phyllasoma*	BC			0.990		0.248					0.000	0.155
	Panulirus puerulus	BC			3.960		0.990					0.000	0.619
Penaeidae	*Metapenaeopsis novaeguinea*	Pen					0.000			4.444		1.111	0.833
	Metapenaeopsis palmensis	Pen					0.000	5.263				1.316	0.987
	Metapenaeopsis spp.	Pen	2.128		8.911	1.351	3.435			2.222		0.556	2.395
	Penaeus spp.[A]	Pen	2.128	9.091	3.960	2.703	5.146	5.263				1.316	3.865
	Penaeus esculentus[A]	Pen			0.990		0.248			2.222		0.556	0.571
	Penaeus merguiensis[A]	Pen			1.980		0.495					0.000	0.309
	Penaeus plebejus[A]	Pen	2.128				0.532			2.222		0.556	0.749
Portunidae	*Charybdis* spp.	Cra			1.980		0.495			2.222		0.556	0.726
	Charybdis truncata	Cra				1.351	0.676					0.000	0.253
	Charybdis yaldwini	Cra			0.990		0.248					0.000	0.155
	Portunus acerbiterminalis	Cra			4.950		1.238			2.222		0.556	1.190
	Portunus pelagicus	Cra			1.980		0.495					0.000	0.309
	Portunus rubromarginatus	Cra					0.000	5.263		2.222		1.871	1.404
	Portunus sanguinolentus	Cra			0.990		0.248					0.000	0.155
	Portunus spp.	Cra			2.970		0.743	5.263				1.316	1.451
	Thalamita sima	Cra					0.000	5.263	9.091			3.589	2.691
	Thalamita spp.	Cra			0.990		0.248					0.000	0.155
Sergestidae	Sergestidae sp.	BC	2.128				0.532					0.000	0.332
Squillidae	Stomatopoda larvae	BC	2.128		6.931		2.265					0.000	1.415
Number of prey taxa consumed			24	7	47	38	82	16	7	29	17	45	101
Number of stomachs examined			72	40	177	97	386	30	11	45	25	111	497
Number of empty stomachs			12	6	40	10	66	5	3	2	2	22	168
Average dry weight (g) of prey consumed per fish (excluding empty stomachs)			19.872	19.364	10.202	20.527	15.913	8.895	18.727	18.356	21.182	17.196	16.293
Average number of prey taxa consumed per fish (excluding empty stomachs)			1.389	1.200	1.709	1.660	1.583	1.500	1.636	2.422	1.800	1.955	1.667

[A]Prey species of commercial importance to the Northern Prawn Fishery.

Table 3. Prey taxa consumed (% dry weight) by small (<800 mm FL), medium (800–1000 mm FL) and large (>1000 mm FL) longtail tuna caught in northern and eastern Australia between February 2003 and April 2005

Fish with empty stomachs were excluded from the analysis. BC, benthopelagic crustaceans; Cep, cephalopods; Cra, crabs; DF, demersal fishes; Misc, miscellaneous; Pen, penaeids; PF, pelagic fishes

Family	Prey name	Category	Northern region			Eastern region		
			Small	Medium	Large	Small	Medium	Large
Teleost								
Apogonidae	*Siphamia* spp.	DF		0.016				
Belonidae	Belonidae sp.	PF	0.080				3.465	11.849
	Strongylura leiura	PF	0.681					
Bregmacerotidae	*Bregmaceros* spp.	DF	0.012					
Carangidae	*Alectis* sp.	PF						0.244
	Carangidae sp.	PF		0.925				
	Carangoides spp.	PF		0.025				
	Pantolobus radiatus	PF	0.738					
	Scomberoides spp.	PF					0.834	
	Scomberoides tol	PF	0.146	1.965				
	Selar boops	PF	2.219					
	Trachurus declivis	PF					0.249	0.407
Centriscidae	*Centriscus scutatus*	DF	0.053					
Clupeidae	Clupeidae sp.	PF	2.571	0.703			6.793	6.258
	Dussumieria elopsoides	PF	5.372	1.405				
	Herklotsichthys spp.	PF	0.455					
	Hyperlophus vittatus	PF						6.028
	Nematalosa come	PF	3.137	6.234				
	Nematalosa spp.	PF	0.523					
	Pellona ditchella	PF	0.434					
	Sardinella albella	PF	0.382	0.545				
	Sardinella gibbosa	PF	7.037					
	Sardinella spp.	PF	29.662	57.526	25.769		6.470	2.163
	Sardinops spp.	PF	1.591				13.424	10.447
Engraulidae	Engraulidae sp.	PF	6.126	6.808		27.936	37.631	11.989
	Stolephorus spp.	PF	9.723	3.462		37.065	10.784	3.800
	Thryssa hamiltoni	PF	1.199	2.902				
	Thryssa setirostrus	PF	2.704	1.098				
	Thryssa spp.	PF	0.220					
Exocoetidae	*Cheilopogon* spp.	PF	0.765					
	Exocoetidae sp.	PF	0.857					
Haemulidae	*Pomadasys* spp.	DF		0.282				
Hemiramphidae	Hemiramphidae sp.	PF	1.140				2.801	7.076
	Hemiramphus robustus	PF	1.466					
	Hyporhamphus dussumieri	PF	1.575					
Leiognathidae	Leiognathidae sp.	DF						0.237
	Leiognathus bindus	DF		0.194				
	Leiognathus equillus	DF		1.864				
	Leiognathus splendens	DF	0.919	2.516				
	Leiognathus spp.	DF	0.854					
Monacanthidae	Monacanthidae sp.	DF	0.010	1.965			0.082	
	Paramonacanthus filicauda	DF	0.863	0.664				
Mullidae	*Upeneus sulphureus*	DF	0.191					
Nemipteridae	*Nemipterus celebicus*	DF	1.800					
	Nemipterus spp.	DF	0.189					
Ostraciidae	Ostraciidae sp.	BC	0.008	0.014				0.008
Paralichthyidae	*Pseudorhombus* spp.	DF					2.817	
Platycephalidae	Platycephalidae sp.	DF	0.055					
Plotosidae	Plotosidae sp.	DF	0.155					
Scatophagidae	*Selenotoca multifasciata*	DF	0.113					
Scombridae	*Scomber australasicus*	PF						14.741
	Scombridae sp.	PF	0.105					
Scorpeinidae	Scorpeinidae sp.	DF	0.124					
Serranidae	*Epinephalus* spp.	DF	0.001					

(Continued)

Table 3. *(Continued)*

Family	Prey name	Category	Northern region			Eastern region		
			Small	Medium	Large	Small	Medium	Large
Sillaginidae	*Sillago* spp.	DF						6.576
Sphyraenidae	*Sphyraena obtusata*	PF					0.578	
Synodontidae	Synodontidae sp.	DF					0.987	
	Teleost Remains	PF	10.668	3.490	29.593	17.066	9.869	16.616
Terapontidae	*Terapon puta*	DF	0.582					
Tetraodontidae	*Lagocephalus lunaris*	DF	0.109					
	Tetraodontidae sp.	DF		1.948				0.097
Miscellaneous								
	Seagrass	Misc	0.009					0.002
Avies	Bird Feather	Misc	0.000	0.001				
Casuarinaceae	Cassurina Plant remains	Misc	0.008	0.004				
Hydrocharitaceae	*Halophila ovalis*	Misc					0.011	
Hymenoptera	Hymenoptera	Misc	0.000					
Sargassaceae	Sargassum spp.	Misc	0.004				0.148	
Zosteraceae	*Zostera* spp.	Misc			0.131	0.329	0.133	0.154
Mollusca								
Bivalvia	Bivalve Larvae	Misc	0.000					
Loliginidae	*Photololigo* spp.	Cep	0.538				0.755	
	Teuthoidea sp.	Cep	1.019	3.158	39.065	0.238	0.010	0.266
Sepiidae	*Sepia elliptica*	Cep					0.438	
	Sepia plangon	Cep				17.365		
	Sepia smithii	Cep					1.142	
	Sepioidae sp.	Cep	0.011					0.053
Crustacea								
	Natantia	BC					0.001	
Brachyura	Brachyuran megalopa	BC	0.001				0.003	0.018
Caridea	Caridae	BC	0.000					
Crustacea	Crustacea remains	BC	0.002	0.006				
Isopoda	Isopoda	BC	0.033	0.001			0.005	0.028
Palinuridae	*Panulirus phyllasoma*	BC	0.001					
	Panulirus puerulus	BC	0.004					
Penaeidae	*Metapenaeopsis novaeguinea*	Pen					0.443	0.118
	Metapenaeopsis palmensis	Pen					0.005	
	Metapenaeopsis spp.	Pen	0.035	0.036			0.002	
	Penaeidae sp.	Pen	0.099	0.053				0.118
	Penaeus esculentus	Pen	0.061					0.410
	Penaeus merguiensis	Pen	0.181					
	Penaeus plebejus	Pen	0.010					0.061
Portunidae	*Charybdis* spp.	Cra	0.004	0.058			0.012	
	Charybdis truncata	Cra			5.442			
	Charybdis yaldwini	Cra		0.052				
	Portunus acerbiterminalis	Cra	0.054	0.022			0.026	
	Portunus pelagicus	Cra	0.167					
	Portunus rubromarginatus	Cra					0.034	0.073
	Portunus sanguinolentus	Cra	0.012					
	Portunus spp.	Cra	0.011	0.025				0.106
	Thalamita sima	Cra					0.046	0.059
	Thalamita spp.	Cra		0.023				
Sergestidae	Sergestidae sp.	BC		0.000				
Squillidae	Stomatopoda Larvae	BC	0.121	0.011				
Total number of stomachs examined			272	97	17	19	53	39
Total number of prey taxa recorded			70	36	5	6	31	29

high (71–90%), indicating that the diet composition varied substantially among seasons; however, *Sardinella* spp. contributed between 18 and 35% to the dissimilarity among seasons. Several other species made reasonable contributions (>5%) to the dissimilarity of the diet among particular seasons, including *Paramonacanthus filicauda*, Teuthoidea sp., *Pantolobus radiatus*, *Nematalosa come*, *Selar boops* and *Nemipterus celebicus*.

Table 4. Prey taxa consumed (% frequency of occurrence) by small (<800 mm FL), medium (800–1000 mm FL) and large (>1000 mm FL) longtail tuna caught in northern and eastern Australia between February 2003 and April 2005

Fish with empty stomachs were excluded from the analysis. BC, benthopelagic crustaceans; Cep, cephalopods; Cra, crabs; DF, demersal fishes; Misc, miscellaneous; Pen, penaeids; PF, pelagic fishes

Family	Prey name	Category	Northern region			Eastern region		
			Small	Medium	Large	Small	Medium	Large
Teleost								
Apogonidae	*Siphamia* spp.	DF		2.632				
Belonidae	Belonidae sp.	PF	0.532				3.571	20.588
	Strongylura leiura	PF	0.532					
Bregmacerotidae	*Bregmaceros* spp.	DF	0.532					
Carangidae	*Alectis* sp.	PF						2.941
	Carangidae sp.	PF		2.632				
	Carangoides spp.	PF		2.632				
	Pantolobus radiatus	PF	0.532					
	Scomberoides spp.	PF					1.786	
	Scomberoides tol	PF	0.532	5.263				
	Selar boops	PF	0.532					
	Trachurus declivis	PF						2.941
Centriscidae	*Centriscus scutatus*	DF	1.596					
Clupeidae	Clupeidae sp.	PF	3.723	2.632			3.571	2.941
	Dussumieria elopsoides	PF	2.660	2.632				
	Herklotsichthys spp.	PF	1.064					
	Hyperlophus vittatus	PF						5.882
	Nematalosa come	PF	2.660	2.632				
	Nematalosa spp.	PF	0.532					
	Pellona ditchella	PF	0.532					
	Sardinella albella	PF	1.064	2.632				
	Sardinella gibbosa	PF	1.596					
	Sardinella spp.	PF	21.809	42.105	25.000		14.286	5.882
	Sardinops spp.	PF	1.064				8.929	5.882
Engraulidae	Engraulidae sp.	PF	22.872	10.526		40.000	39.286	5.882
	Stolephorus spp.	PF	14.362	21.053		20.000	12.500	14.706
	Thryssa hamiltoni	PF	1.596	2.632				
	Thryssa setirostrus	PF	2.128	2.632				
	Thryssa spp.	PF	1.064					
Exocoetidae	*Cheilopogon* spp.	PF	0.532					
	Exocoetidae sp.	PF	1.064					
Haemulidae	*Pomadasys* spp.	DF		2.632				
Hemiramphidae	Hemiramphidae sp.	PF	2.660				5.357	14.706
	Hemiramphus robustus	PF	1.064					
	Hyporhamphus dussumieri	PF	2.660					
Leiognathidae	Leiognathidae sp.	DF						8.824
	Leiognathus bindus	DF		2.632				
	Leiognathus equillus	DF		2.632				
	Leiognathus splendens	DF	2.128	5.263				
	Leiognathus spp.	DF	1.064					
Monacanthidae	Monacanthidae sp.	DF	1.064	2.632			3.571	
	Paramonacanthus filicauda	DF	1.596	2.632				
Mullidae	*Upeneus sulphureus*	DF	0.532					
Nemipteridae	*Nemipterus celebicus*	DF	0.532					
	Nemipterus spp.	DF	0.532					
Ostraciidae	Ostraciidae sp.	BC	1.064	2.632				2.941
Paralichthyidae	*Pseudorhombus* spp.	DF						2.941
Platycephalidae	Platycephalidae sp.	DF	0.532					
Plotosidae	Plotosidae sp.	DF	0.532					
Scatophagidae	*Selenotoca multifasciata*	DF	0.532					
Scombridae	*Scomber australasicus*	PF						11.765
	Scombridae sp.	PF	0.532					
Scorpeinidae	Scorpeinidae sp.	DF	0.532					

(Continued)

Table 4. *(Continued)*

Family	Prey name	Category	Northern region			Eastern region		
			Small	Medium	Large	Small	Medium	Large
Serranidae	*Epinephalus* spp.	DF	0.532					
Sillaginidae	*Sillago* spp.	DF						2.941
Sphyraenidae	*Sphyraena obtusata*	PF						2.941
Synodontidae	Synodontidae sp.	DF					1.786	
	Teleost remains	PF	36.170	28.947	75.000	40.000	26.786	44.118
Terapontidae	*Terapon puta*	DF	0.532					
Tetraodontidae	*Lagocephalus lunaris*	DF	0.532					
	Tetraodontidae sp.	DF		2.632				2.941
Miscellaneous								
	Seagrass	Misc	0.532					2.941
Avies	Bird feather	Misc	0.532					
Casuarinaceae	Casuarina plant remains	Misc	1.064					
Hydrocharitaceae	*Halophila ovalis*	Misc					5.357	
Hymenoptera	Hymenoptera	Misc	0.532					
Sargassaceae	Sargassum spp.	Misc	1.064				7.143	
Zosteraceae	*Zostera* spp.	Misc			25.000	20.000	26.786	11.765
Mollusca								
Bivalvia	Bivalve larvae	Misc	0.532					
Loliginidae	*Photololigo* spp.	Cep	2.128				1.786	
	Teuthoidea sp.	Cep	3.723	13.158	25.000	20.000	7.143	8.824
Sepiidae	*Sepia elliptica*	Cep					1.786	
	Sepia plangon	Cep				20.000		
	Sepia smithii	Cep					1.786	
	Sepioidae sp.	Cep	0.532					2.941
Crustacea								
	Natantia	BC					1.786	
Brachyura	Brachyuran megalopa	BC	1.064				1.786	2.941
Caridea	Caridae	BC	0.532					
Crustacea	Crustacea remains	BC	0.532	2.632				
Isopoda	Isopoda	BC	7.979	2.632			10.714	8.824
Palinuridae	*Panulirus phyllasoma*	BC	0.532					
	Panulirus puerulus	BC	2.128					
Penaeidae	*Metapenaeopsis novaeguinea*	Pen						2.941
	Metapenaeopsis palmensis	Pen					1.786	
	Metapenaeopsis spp.	Pen	4.787	5.263			1.786	
	Penaeidae sp.	Pen	3.191	5.263				2.941
	Penaeus esculentus	Pen	0.532					2.941
	Penaeus merguiensis	Pen	1.064					
	Penaeus plebejus	Pen	0.532					2.941
Portunidae	*Charybdis* spp.	Cra	0.532	2.632			1.786	
	Charybdis truncata	Cra			25.000			
	Charybdis yaldwini	Cra		2.632				
	Portunus acerbiterminalis	Cra	2.128	2.632			1.786	
	Portunus pelagicus	Cra	1.064					
	Portunus rubromarginatus	Cra					1.786	2.941
	Portunus sanguinolentus	Cra	0.532					
	Portunus spp.	Cra	1.064	2.632				2.941
	Thalamita sima	Cra					1.786	2.941
	Thalamita spp.	Cra		2.632				
Sergestidae	Sergestidae sp.	BC		2.632				
Squillidae	Stomatopoda larvae	BC	2.128	2.632				
Total number of stomachs examined			272	97	17	19	53	39
Total number of prey taxa recorded			70	36	5	6	31	29

Table 5. Percentage contribution (in terms of dry weight and frequency of occurrence) of eight prey categories to the diet of longtail tuna in northern and eastern regions in Australia

Prey category	% Dry weight			% Frequency of occurrence		
	Northern	Eastern	Overall	Northern	Eastern	Overall
Pelagic fishes	89.686	93.094	91.390	73.713	65.356	69.443
Demersal fishes	5.158	4.243	4.701	8.093	3.814	5.907
Cephalopods	4.486	1.686	3.086	4.596	7.818	6.242
Penaeids	0.289	0.369	0.329	4.270	2.244	3.235
Crabs	0.247	0.303	0.275	1.901	3.271	2.601
Benthopelagic crustaceans	0.119	0.024	0.071	5.477	4.569	5.013
Miscellaneous	0.015	0.281	0.148	1.950	12.929	7.559

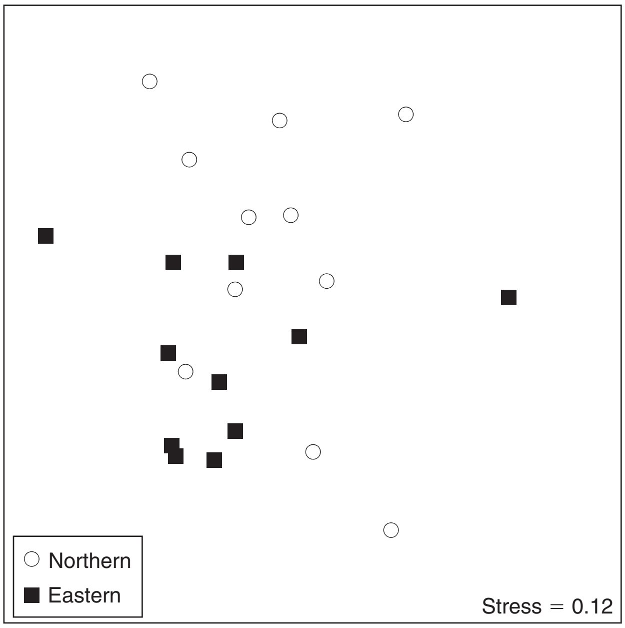

Fig. 2. nMDS ordination of diet biomass data for longtail tuna caught in northern and eastern Australian waters between February 2003 and April 2005. Stress value is shown.

In the eastern region, several prey taxa made substantial contributions to the diet biomass in each of the four seasons, including Engraulidae sp., *Stolephorus* spp. and Belonidae sp. The dissimilarity of the diet composition among seasons was high (89–99%), indicating that the diet composition varied substantially among seasons. Several species contributed greatly to the dissimilarity of diets among seasons, including Belonidae sp., *Scomber australasicus*, Clupeidae sp., Engraulidae sp., *Sardinops sagax* and *Pseudorhombus* spp.

Feeding periodicity

With respect to monthly variation in feeding intensity, the stomach fullness index varied considerably among months, being highest between April and July (0.34 ± 0.5 s.e.) and gradually declining to the lowest values between October and March (0.01 ± 0.0 s.e.). This pattern in the stomach fullness index showed a close inverse relationship with reproductive activity, with stomach fullness being highest in the months of lowest

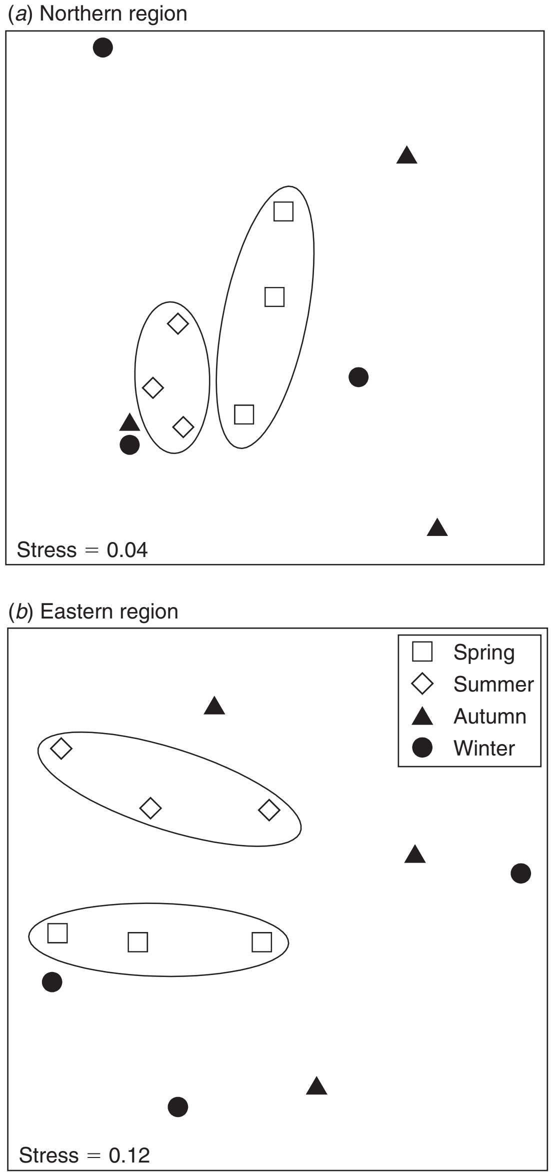

Fig. 3. MDS ordination of diet biomass data for longtail tuna caught in four seasons (spring, summer, autumn and winter) in (*a*) northern and (*b*) eastern Australian waters between February 2003 and April 2005. Stress values are shown.

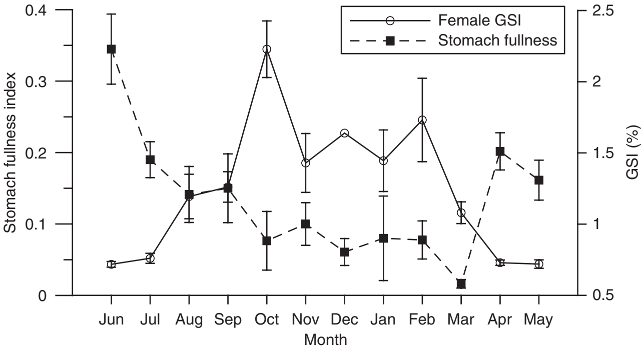

Fig. 4. Monthly mean (±s.e.) stomach fullness index and gonadosomatic index (GSI) showing the relationship between feeding intensity and reproductive activity. Both diet and GSI data from northern and eastern regions were combined.

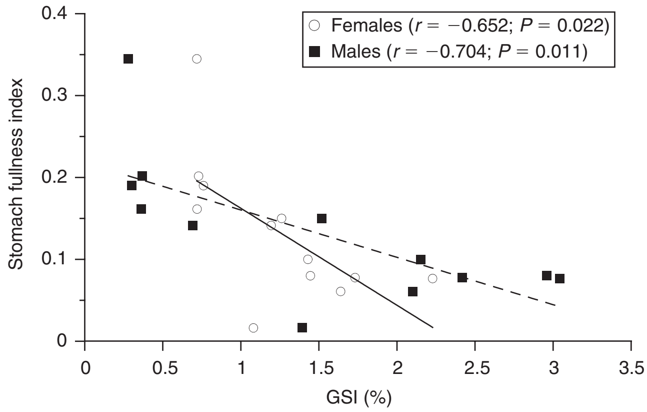

Fig. 5. Plot showing the relationship between reproductive activity (GSI) and feeding intensity (stomach fullness index) for longtail tuna caught in northern and eastern Australia between February 2003 and April 2005.

reproductive activity and lowest during the months of highest reproductive activity (Fig. 4). The relationship between GSI and stomach fullness index was negative and statistically significant for both males ($r = -0.704$, $P = 0.011$) and females ($r = -0.652$, $P = 0.022$) (Fig. 5).

An assessment of diel feeding periodicity was only possible for autumn and winter in the northern region, where day and night sampling was conducted concurrently in the same region. The proportion of stomachs containing prey was 2.4 to 3.8 times higher during the day than at night for autumn and winter, respectively. Although 23 and 40% of stomachs contained prey during the night during autumn and winter, stomach fullness was low (0.02 to 0.08) (Fig. 6). This result, coupled with the observation that most stomachs collected at night contained prey in advanced stages of digestion, indicates that fish probably did not feed during the night but had prey remaining in their stomachs from daytime meals. A two-way fixed-factor ANOVA revealed that mean stomach fullness was significantly higher during the day than at night in both autumn and winter (d.f. = 1, $F = 85.57$, $P < 0.0001$, Student-Newman-Keuls test; Fig. 6). However, mean stomach fullness was significantly higher during winter than during autumn (d.f. = 1, $F = 26.62$, $P < 0.0001$, Student-Newman-Keuls test; Fig. 6). A significant season × diel interaction (d.f. = 1, $F = 11.57$, $P < 0.001$) was also evident, owing to the mean stomach fullness being significantly different between autumn and winter during the day but not during the night (Student-Newman-Keuls test; Fig. 6).

Size-related comparisons

The number of prey taxa consumed by each size class differed markedly; however, diets of fish from the two regions showed a different pattern of variation among size classes. In the northern region, small fish had the most diverse diet (70 taxa), while large fish had the least diverse diet (5 taxa). In the eastern region, large fish had the most diverse diet (29 taxa) and small fish had the least diverse diet (6 taxa).

nMDS ordinations of diet biomass data (Fig. 7) and ANOSIM revealed a significant difference in the diets of the three size classes in the northern region (Global $R = 0.181$, $P = 0.009$) and the eastern region (Global $R = 0.181$, $P = 0.009$). Pair-wise comparisons revealed a consistent pattern in both regions in that the diets of large fish were significantly different to those of small and medium fish, whereas the diets of small and medium fish did not differ.

In the northern region, SIMPER revealed that this difference resulted from the consumption of cephalopods (Teuthoidea sp.),

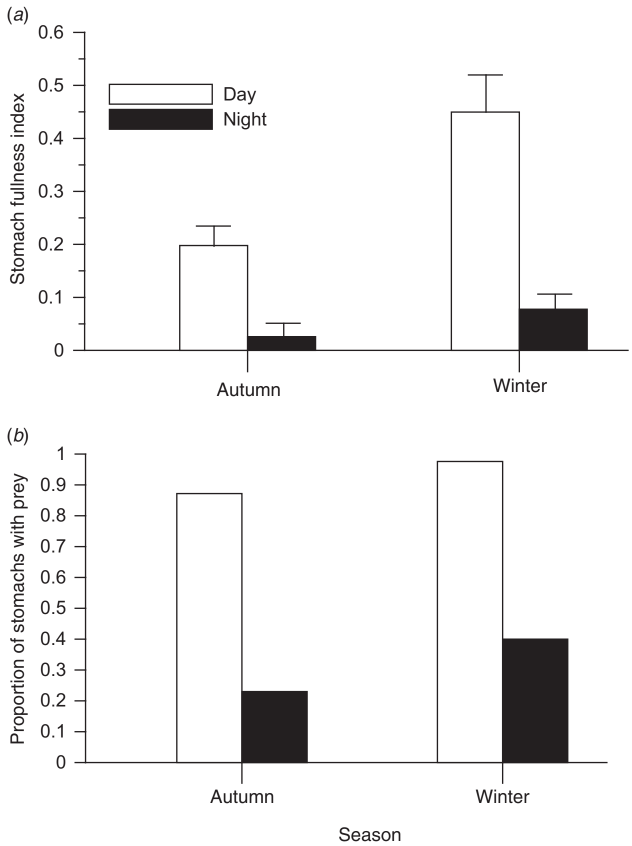

Fig. 6. (*a*) Mean (±s.e.) stomach fullness index and (*b*) proportion of stomachs with prey for longtail tuna caught during the day and night in autumn and winter in the Weipa region, northern Australia.

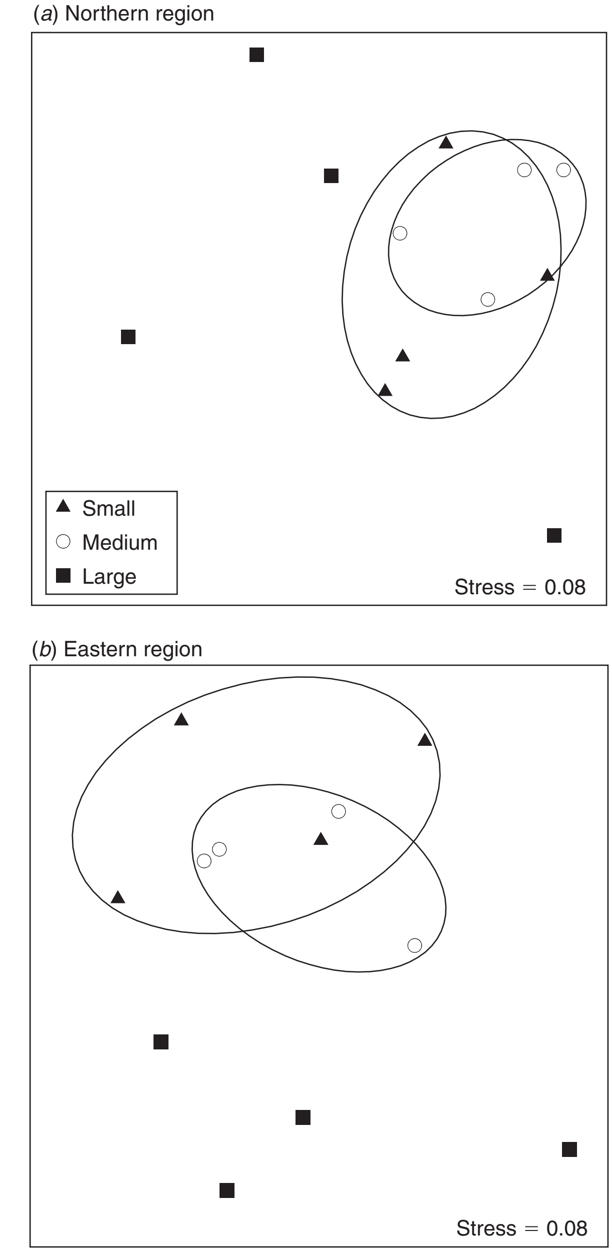

Fig. 7. nMDS ordination of diet biomass data for small (<800 mm FL), medium (800–1000 mm FL) and large (>1000 mm FL) longtail tuna caught in (*a*) northern and (*b*) eastern Australian waters between February 2003 and April 2005. Stress values are shown.

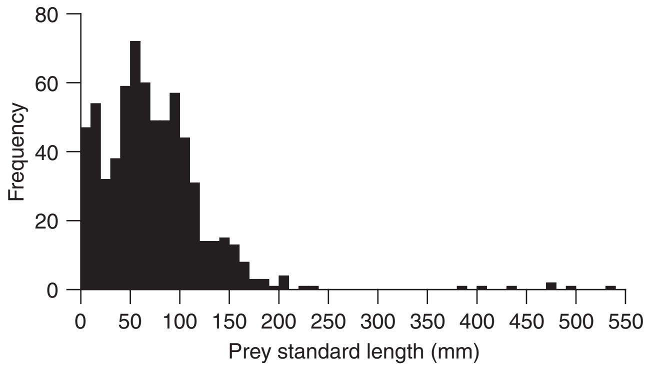

Fig. 8. Histogram showing the standard length (in 10 mm increments) of prey consumed by longtail tuna caught in (a) northern and (b) eastern Australia between February 2003 and April 2005.

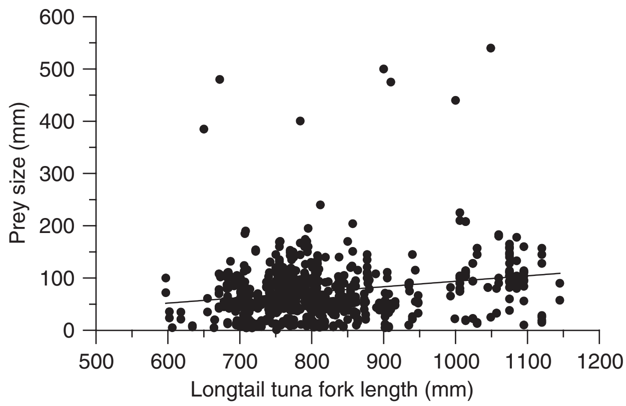

Fig. 9. Plot showing the relationship between longtail tuna fork length and the standard length (mm) of prey consumed. Data were combined for fish caught in northern and eastern Australia between February 2003 and April 2005.

Sardinella spp., teleost remains (mainly unidentifiable clupeids and engraulids) and *Charybdis truncata* by large fish, compared with the consumption of *Sardinella* spp., *Stolephorus* spp. and Engraulidae sp. by small and medium fish. In the eastern region, the difference resulted from the consumption of larger teleosts including *Scomber australasicus*, Belonidae sp., Hemiramphidae sp. and *Sillago* spp. by large fish, contrasting with the consumption of *Stolephorus* spp. Engraulidae sp., and teleost remains (mainly unidentifiable clupeids and engraulids) by small and medium fish.

After combining the data from both regions in order to investigate the relationship between fish size and prey size, it was clear that fish of all sizes primarily consumed prey of less than 120-mm total length (TL) (Fig. 8). There was no significant correlation between fish size and the size of prey consumed ($r = 0.042$, $P = 0.499$; Fig. 9). A small number of large prey (380–540 mm) – primarily belonids, hemiramphids and exocoetids – were consumed by a wide size range of fish (654–1055 mm FL).

Prey-consumption rates and daily ration

Evacuation rates (A_i) used for various prey taxa to estimate daily ration for longtail tuna are given in Table 1. The estimated mean (±s.e.) daily consumption averaged across all fish sizes was 159.39 ± 5.06 g, which translated into an estimated daily ration of $2.36 \pm 0.07\%$ of body weight per day (BW day^{-1}) (Table 6). Estimates of size-related variation in daily ration was undertaken by combining data from both regions, because digestion and evacuation rates are biologically controlled processes influenced by the ‘softness’ of the prey consumed rather than by diet

Table 6. Fork length (in mm), mean (±s.e.) body weight, daily consumption, ration, and estimated annual prey consumption for small, medium and large longtail tuna in Australia pooled for northern and eastern regions

Size class	Fork-length range (mm)	Weight (g)	Daily consumption (g day^{-1})	Daily ration (% BW day^{-1})	Annual consumption (kg year^{-1})
Small	597–799	5678 (101.41)	123.27 (4.35)	2.17 (0.08)	45.26 (0.23)
Medium	800–999	9413 (156.33)	212.77 (12.52)	2.26 (0.13)	77.14 (0.54)
Large	1000–1250	17 657 (589.06)	229.04 (12.92)	1.30 (0.07)	82.97 (0.55)
Overall	597–1120	8178 (142.36)	159.39 (5.06)	2.36 (0.07)	70.70 (0.25)

Table 7. Estimated annual consumption (tonnes year^{-1}) (±s.e.) of major prey categories by small, medium and large longtail tuna in the Gulf of Carpentaria (397 700 km^2)

Consumption estimates for commercially important penaeids were restricted to the trawl grounds (206 804 km^2) of the Gulf of Carpentaria. Consumption estimates were calculated using 10 000 Monte Carlo simulations of a consumption model and defining uncertainty around mean fish weight and daily ration for each size class and mean longtail tuna density in the region

Size class	Pelagic fishes	Demersal fishes	Cephalopods	Penaeids	Crabs	Benthopelagic crustaceans	Miscellaneous	Total
Small	25 396.98 (318.06)	5347.41 (66.97)	447.48 (5.60)	99.33 (2.16)	26.90 (0.34)	23.30 (0.29)	70.12 (0.88)	32 227.17 (89.71)
Medium	48 517.73 (1198.34)	5188.24 (128.14)	1403.47 (34.66)	28.51 (0.68)	114.81 (2.84)	14.32 (0.35)	0.19 (0.00)	56 105.11 (155.35)
Large	43 733.40 (934.14)	12 538.88 (267.83)	250.79 (5.36)	471.24 (9.89)	180.57 (3.86)	12.43 (0.27)	1.25 (0.01)	59 826.33 (166.07)
Overall	121 657.89 (1588.45)	23 953.11 (345.25)	2160.89 (32.40)	599.08 (10.12)	334.84 (5.15)	51.56 (0.67)	71.50 (1.71)	148 177.93 (244.41)

composition. Daily ration was similar for small ($2.17 \pm 0.08\%$ BW day^{-1}) and medium ($2.26 \pm 0.13\%$ BW day^{-1}) fish, and was lowest for large fish ($1.30 \pm 0.07\%$ BW day^{-1}) (Table 6). Estimated annual consumption rates for individual fish increased with fish size from 45.26 ± 0.23 kg year^{-1} for small fish to 82.97 ± 0.55 kg year^{-1} for large fish.

Annual prey consumption estimates in the Gulf of Carpentaria increased from $32\,227 \pm 90$ t year^{-1} for small fish to $59\,826 \pm 166$ t year^{-1} for large fish, resulting in an overall consumption rate of $148\,178 \pm 244$ t year^{-1} (Table 7). Pelagic and benthopelagic fishes contributed $121\,658 \pm 1588$ t year^{-1} and $23\,953 \pm 345$ t year^{-1}, respectively, to the total prey consumption. The next most important prey were commercially important cephalopods and penaeids, contributing 2161 ± 34 t year^{-1} and 599 ± 10 t year^{-1}, respectively. Also, large fish consumed at least four times the biomass of penaeids (471 ± 10 t year^{-1}) compared with small and medium fish. Crabs, benthopelagic crustaceans and miscellaneous prey items made smaller contributions (52–335 t year^{-1}) to the total prey consumption (Table 7).

Discussion

General diet description

Our results show that longtail tuna play an important ecological role in the neritic ecosystems of northern and eastern Australia by consuming a wide range of prey from both pelagic and demersal assemblages. Fish from both regions appear to consume a diverse suite of prey items during the daytime, not only from the pelagic realm in which they frequent, but also from demersal assemblages. Although the taxonomic composition of the diet differed significantly between regions, longtail tuna in both regions consumed small fishes when available, in particular small schooling pelagic clupeids and engraulids.

Although previous studies of longtail tuna feeding ecology have been based on small sample sizes, they complement the results of the present study that found that longtail tuna are predators that consume a variety of prey types, but primarily small pelagic fishes. For example, Wilson (1981) examined the stomachs of 26 longtail tuna from the Gulf of Papua and found fish to consume 31 prey taxa comprising a range of teleosts (85% by volume), crustaceans (8%) and cephalopods (6%), with engraulids the most predominant prey item overall. Serventy (1942, 1956) provided observational accounts of the stomach contents of a small number of longtail tuna caught throughout the Australian distribution of the species. He noted that a range of small pelagic fishes such as engraulids, clupeids, exocoetids, carangids, belonids and hemiramphids comprised the majority of diet, while other demersal prey including monacanthids, cephalopods and a range of crustaceans including penaeids were also commonly consumed. In Malaysia, Silas (1967) also found that longtail tuna consumed a diverse suite of teleosts from both pelagic and demersal habitats, including engraulids, clupeids, sygnathids and scombrids; however, in contrast to Australian studies, squids and crustaceans (stomatopods, mysids and megalopa) were the predominant prey in terms of frequency of occurrence.

The relatively high contribution of demersal and benthic prey (e.g. *Sillago* spp., Platycephalidae sp., *Upeneus sulphureus* and penaeids) in the diets of fish in this study demonstrates the large differences that can exist in the diets of similar-sized tuna species. Other tropical tunas have been documented to mainly consume prey from surface layers, such as small schooling pelagic fishes (e.g. engraulids, clupeids and scombrids), exocoetids and cephalopods (Maldeniya 1996; Bertrand *et al*. 2002; Olson and Galvan-Magana 2002). However, previous dietary studies in Australia (Serventy 1942, 1956; Wilson

1981) and Malaysia (Silas 1967) demonstrated that longtail tuna often consume demersal teleosts from families such as Sygnathidae, Blenniidae, Gobiidae, Mullidae, Platycephalidae and Callyonimidae. The high proportion of demersal prey in the diet may owe to their preference for relatively shallow neritic waters. Because water depths in the two regions where the fish were caught were less than 30 m, fish may easily target slower-moving demersal prey when their preferred pelagic fish prey is unavailable. Demersal prey are relatively uncommon in the diets of other large tunas, such as yellowfin and Atlantic bluefin tuna that inhabit deep oceanic waters, despite the fact that these predators having specialised retia to heat the brain, eyes and viscera that can enable fish to dive to the ocean floor in the deep, cool waters beyond continental shelves (Block *et al*. 2001; Brill *et al*. 2002). However, in an isolated case, Chase (2002) found over half of the prey in the diet of large Atlantic bluefin tuna (*Thunnus thynnus*) captured in the shallow waters (25 m) of Cape Cod bay, New England, to be comprised of benthic or demersal prey, including sessile sponges. He hypothesised that this was a result of opportunistic foraging in shallow waters.

Spatial and seasonal variation in diet

Longtail tuna played a similar ecological role in northern and eastern Australia by consuming a range of prey categories (e.g. pelagic and demersal fishes) in similar proportions. However, the diversity and composition of the diet varied significantly among regions, seasons and fish sizes. The diversity of prey in the northern region was nearly twice that of the eastern region, which probably reflects the higher diversity of fishes generally found in the tropical northern region (Blaber 2002). Also, the overall prey diversity, variation in diet composition and feeding intensity was highest during autumn and winter and decreased markedly in spring and summer. This pattern was consistent for both regions, despite fish in each region having significantly different diet composition. In the northern region, longtail tuna primarily consumed small schooling pelagic species such as *Sardinella* spp. and *Stolephorous* spp. during spring and summer, while *Stolephorous* spp., Clupeidae sp. and Engraulidae sp. were primarily consumed in the eastern region during this time.

There was a consistent pattern of seasonal variation in the diversity and composition of the diet of fish from the two regions, considering the vastly different environmental regimes of the two regions. In contrast to the subtle seasonal variation in water temperature in the subtropical-temperate climate of the eastern region (Ridgway and Godfrey 1997), the tropical northern region experiences a dynamic monsoonal climate with a 'wet' season between October and February and a 'dry' season between March and September. The numerous large estuaries in the region flood during the wet season and discharge large volumes of turbid freshwater into the Gulf of Carpentaria, significantly changing the salinity, temperature and turbidity regime of coastal waters (Blaber *et al*. 1995).

Tunas rely heavily on their high visual acuity to capture prey (Nakamura 1968), which probably explains why we found longtail tuna to feed primarily during the day. We assumed that longtail tuna would move further offshore during the wet season to avoid highly turbid waters, a behaviour known to occur in northern bluefin tuna (Brill *et al*. 2002; Lemos and Gomes 2004), yellowfin tuna and kawakawa (*Euthynnus affinis*) (Barry 1978). As a consequence, we expected a dramatic shift in the diet composition to reflect consumption of a greater variety of prey that is generally more abundant in offshore waters, such as exocoetids and cephalopods. However, our results indicated the contrary, with diets characterised by low prey diversity primarily being comprised of schooling pelagic species. This may indicate that longtail tuna may be more tolerant of turbid waters compared to other large tunas, thereby allowing them to remain within the coastal regime during the wet season to exploit locally abundant pelagic prey, such as *Sardinella* spp.

In contrast to the low prey diversity and feeding intensity during spring and summer, fish in both regions clearly increased feeding intensity and consumed a wider range of prey during autumn and winter; consuming a range of both pelagic and demersal prey items. In the northern region, fish consumed a vast array of demersal and benthic species including leiognathids, platycephalids, sillagids, mullids and nemipterids. Similarly, in the eastern region, the diet comprised numerous demersal species including *Psuedorohombus* sp., *Sillago* spp., penaeids and portunids. However, *Sardinops* spp. also made a large contribution to the diets of medium and large fish in the eastern region during autumn and winter. Serventy (1956) also found longtail tuna caught in south-eastern Australia during autumn to feed '. . . almost exclusively on pilchards (*Sardinops neopilchardus*)'. Ward *et al*. (2003) found *Sardinops sagax* to be most abundant along the eastern coast of Australia during autumn and winter months (June to August), when they migrate northward to spawn. Longtail tuna may therefore periodically target pilchard shoals as they migrate along the eastern coast.

Few studies of tuna have collected reproductive and dietary information concurrently in order to investigate the relationship between these two factors. Spotted mackerel (*Scomberomorus munroi*) and school mackerel (*S. queenslandicus*) from eastern Australia (Begg and Hopper 1997), and Spanish mackerel (*S. maculatus*) in Trinidad (Sturm 1978) were shown to have an inverse relationship between feeding intensity and reproductive activity. This was similar for longtail tuna, where temporal increases in feeding intensity in both regions showed a close inverse relationship with reproductive activity, as indicated by the gonadosomatic index (Figs 4 and 5). The fact that such a dramatic increase in apparently opportunistic feeding behaviour also occurs during the periods of highest feeding intensity may indicate that longtail tuna maximise consumption in the months leading up to the spawning season, in order to direct energy towards gonad development. The decline in stomach fullness during the spawning season may indicate that fish may actively reduce their feeding intensely and rely more on stored energy during this time. Fish may also be physically constrained to consume less prey during the spawning season because enlarged gonads, which can comprise up to 2.5% of body mass in females, occupy a large proportion of their visceral cavity.

Prey consumption rates and daily ration

Our study was able to provide the first information on prey consumption rates and daily ration for longtail tuna. Our annual prey consumption estimates clearly indicate that longtail tuna play an important role in structuring neritic ecosystems, consuming an estimated 148 000 t year^{-1} of prey in the Gulf of Carpentaria. It is important to note that our consumption estimates were based upon the gastric evacuation rates of yellowfin tuna. However, Olson and Galvan-Magana (2002) suggested that these gastric evacuation estimates are suitable for application to other tunas, billfishes and dolphinfishes based on their physiological similarities.

Estimated daily food consumption of longtail tuna (123–229 g day^{-1}) in the present study was similar or slightly lower than what has been recorded elsewhere for closely related tunas, whereas daily ration estimates (1.3–2.3% BW day^{-1}) were nearly half that of similar size classes of tropical tunas studied in other tropical regions (Olson and Boggs 1986; Maldeniya 1996; Ménard *et al*. 2000). Olson and Boggs (1986) estimated similar daily prey consumption rates (175–270 g day^{-1}), but much higher daily rations (3.8–9.6% BW day^{-1}) for yellowfin tuna. Similarly, Ménard *et al*. (2000) estimated that skipjack, bigeye and yellowfin tuna consume around 170 g day^{-1} and have a daily ration of 6.1% BW day^{-1}. In Sri Lankan waters, Maldeniya (1996) estimated that yellowfin tuna had a much higher daily prey consumption (275–539 g day^{-1}) and ration (2.3–5.5% BW day^{-1}) than longtail tuna in our study. The differences in daily ration and consumption rates between longtail tuna and other tropical tunas may be related to a difference in metabolic rates and water temperature that can influence prey evacuation rates (Durbin *et al*. 1983).

In contrast, our estimates of daily ration for longtail tuna were nearly twice that of southern bluefin tuna (*Thunnus maccoyii*) off Tasmania, Australia (Young *et al*. 1997). Small (<140 cm FL) and large (>140 cm FL) fish were reported to consume only 1.01% and 0.89% BW day^{-1}, respectively. This may owe to low water temperatures off Tasmania (<16°C), which may contribute to a decrease in gastric evacuation rate and therefore a lower daily ration (Durbin *et al*. 1983).

The pattern of size-related variation in the daily ration of longtail tuna was similar to that of other large pelagic fishes in that daily ration increased with body weight in small and medium size classes but then declined in the largest size class. In Sri Lankan waters, Maldeniya (1996) found that the daily ration of yellowfin tuna increased from 2.1% BW day^{-1} in small fish to 5.5% BW day^{-1} in medium fish, but then gradually declined to 1% BW day^{-1} for the largest size class. Brill (1987) found that the standard metabolic rate of two tunas, *T. albacares* and *Euthynnus affinis*, decreased with increasing body weight. We advocate that the decline in daily ration in large longtail tuna may be a result of a rapid decrease in growth rate at sizes greater than 100 cm FL (Wilson 1981), and thus a decrease in metabolic demand. Therefore, larger fish may only require proportionally smaller meals to meet their metabolic requirements.

Ecosystem and fishery interactions

Much research has been undertaken on the feeding ecology of demersal fishes in the NPF, mainly to identify significant natural mortality sources of commercially important prawns in order to improve prawn population models for management (Brewer *et al*. 1991; Salini *et al*. 1998; Haywood *et al*. 1998). More recently, results from such studies have become increasingly useful for populating ecosystem models for ecosystem approaches to fisheries management. However, the role of pelagic fishes in the neritic ecosystems of northern Australia and their interaction with commercial prawn fisheries in the region is poorly understood.

Our results indicate that longtail tuna prey on commercially important prawns, primarily *Penaeus merguiensis* and *P. esculentus*, but that the contribution of these prawns to the overall diet was relatively minor (1.2% by dry weight). Wilson (1981) also found penaeids to make a similar contribution to the diet of longtail tuna in the Gulf of Papua (1.8% by volume), while Serventy (1956) noted that penaeids were commonly consumed in Western Australia. By incorporating the consumption rates and daily ration of longtail tuna estimated in our study with information on their abundance in the region (Griffiths *et al*. in press), it is clear that they have a reasonable impact on penaeids, consuming around 600 t year^{-1} in the Gulf of Carpentaria. This equates to ~11.4% of the total annual commercial catch of prawns (5287 t) in the NPF during the time of sampling. However, considering that the GoC comprises about half of the NPF-managed area (Zhou and Griffiths 2006), the consumption of penaeids by longtail tuna is likely to exceed 1000 t year^{-1}.

It is important to note that although differential digestion rates of prey taxa were incorporated into our consumption model, the annual consumption estimates of penaeids are probably underestimated. First, these soft-bodied prey may be rapidly digested before inspection of the stomach. Haywood (1995) found that even in a slow-moving demersal fish, *Monacanthus chinensis*, penaeids are completely digested within 3 h of consumption. In the present study, most penaeids were found in advanced stages of digestion; therefore, their contribution to the diet biomass would have been greatly underestimated. Second, one species of commercially important penaeid, *Penaeus merguiensis*, forms dense aggregations for only a few months of the year as they migrate from the estuaries to the commercial trawl grounds between 10 and 20 m depth (Dell *et al*. in press). Unfortunately, the majority of our samples were collected from commercial gillnet vessels that generally fish beyond the depths of the trawl fishery in 25 to 40 m. In contrast, samples taken on rod and line from the sport fishery were restricted to inshore waters less than ~15-m depth. As a result, prawns were probably very much under-represented in our samples, if localised feeding had occurred near prawn aggregations as suggested by Bienke (2004).

Brewer *et al*. (1991) suggested that demersal fishes are the primary source of natural mortality of commercially important prawns in the NPF. They showed that 34 species of demersal fish consumed 2950 t year^{-1} of commercially important penaeids in Albatross Bay, a small region of the NPF (5788 km^2). This translates to an average consumption rate of around 88 t year^{-1} per species. In comparison, we estimated that longtail tuna consume around 17 t year^{-1} in this region. At least a dozen species of relatively large pelagic fishes occur in the region that are reputed or recorded to prey upon penaeids to varying degrees, such as spotted and school mackerel (*Scomberomorus queenslandicus* and *S. munroi*) (Begg and Hopper 1997). This highlights the need for more targeted dietary studies of high order predators in order to better understand and quantify the trophic linkages in ecosystems and their possible interactions with fisheries. This will help improve the realism of ecosystem models that may be employed to facilitate ecosystem-based fisheries management proposed for many fisheries worldwide.

Acknowledgements

We thank A. Vickers and crew from the FV 'Kundu', who provided samples from the Gulf of Carpentaria, and the numerous sport fishers who helped collect specimens. K. Davidson and Q. Dell are acknowledged for assistance with processing stomach samples. We are especially appreciative of constructive comments made on drafts of this manuscript by R. J. Olson (IATTC), S. J. M. Blaber and M. D. E. Haywood (CSIRO). This study was funded by CSIRO Division of Marine and Atmospheric Research.

References

Aguado-Gimenez, F., and Garcia-Garcia, B. (2005). Growth, food intake and feed conversion rates in captive Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus, 1758) under fattening conditions. *Aquaculture Research* **36**, 610–614. doi:10.1111/J.1365-2109.2005.01210.X

Barry, M. (1978). 'Behavioral Response of Yellowfin Tuna, *Thunnus albacares*, and Kawakawa, *Euthynnus affinis*, to Turbidity.' (NOAA/ERL/PMEL: Seattle, WA.)

Begg, G. A., and Hopper, G. A. (1997). Feeding patterns of school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*S. munroi*) Queensland east-coast waters. *Marine and Freshwater Research* **48**, 565–571. doi:10.1071/MF97064

Bertrand, A., Bard, F. X., and Josse, E. (2002). Tuna food habits related to the micronekton distribution in French Polynesia. *Marine Biology* **140**, 1023–1037. doi:10.1007/S00227-001-0776-3

Bienke, B.C. (2004). NPF late start a disaster. *Professional Fisherman* **August**, 6.

Blaber, S. J. M. (2002). Fish in hot water: the challenges facing fish and fisheries research in tropical estuaries. *Journal of Fish Biology* **61**, 1–20.

Blaber, S. J. M., Brewer, D. T., and Salini, J. P. (1995). Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. *Estuarine, Coastal and Shelf Science* **40**, 177–193. doi:10.1016/S0272-7714(05)80004-6

Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., *et al*. (2001). Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* **293**, 1310–1314. doi:10.1126/SCIENCE.1061197

Brewer, D. T., Blaber, S. J. M., and Salini, J. P. (1991). Predation on penaeid prawns by fishes in Albatross Bay, Gulf of Carpentaria. *Marine Biology* **109**, 231–240. doi:10.1007/BF01319391

Brill, R. W. (1987). On the standard metabolic rates of tropical tunas, including the effect of body size and acute temperature change. *Fishery Bulletin* **85**, 25–35.

Brill, R. W. (1996). Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphinfish. *Comparative Biochemistry and Physiology* **113A**, 3–15.

Brill, R., Lutcavage, M., Metzger, G., Bushnell, P., Arendt, M., Lucy, J., Watson, C., and Foley, D. (2002). Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*), in relation to oceanographic, conditions of the western North Atlantic, determined with ultrasonic telemetry. *Fishery Bulletin* **100**, 155–167.

Chase, B. C. (2002). Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. *Fishery Bulletin* **100**, 168–180.

Chipps, S. R., and Garvey, J. E. (2007). Quantitative assessment of food habits and feeding patterns. In 'Analysis and Interpretation of Freshwater Fisheries Data'. (Eds C. Guy and M. Brown.) Chapter 11. (American Fisheries Society: Bethesda, MD.)

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143. doi:10.1111/J.1442-9993.1993.TB00438.X

Dell, Q., Brewer, D. T., Heales, D. S., Griffiths, S. P., and Tonks, M. L. (in press). Comparison of bycatch impacts from two highly specialised trawl regimes in a tropical Australian penaeid fishery. *Fisheries Research*.

Durbin, E. G., Durbin, A. G., Langton, R. W., and Bowman, R. E. (1983). Stomach contents of silver hake, *Merluccius bilinearis*, and Atlantic cod, *Gadus morhua*, and estimation of their daily rations. *Fishery Bulletin* **81**, 437–454.

Essington, T. E., Kitchell, J. F., Boggs, C., Schindler, D. E., Olson, R. J., and Hilborn, R. (2002). Alternative fisheries and the predation rate of yellowfin tuna in the eastern Pacific Ocean. *Ecological Applications* **12**, 724–734.

Griffiths, S. P., Kuhnert, P. M., Venables, W. N., and Blaber, S. J. M. (in press). Estimating abundance of pelagic fishes using gillnet catch data in data-limited fisheries: a Bayesian approach. *Canadian Journal of Fisheries and Aquatic Sciences*.

Haywood, M.D.E. (1995). Rates at which post-larval prawns are digested by a small predatory fish and the implications for predation studies. *Journal of Fish Biology* **47**, 337–340.

Haywood, M. D. E., Heales, D. S., Kenyon, R. A., Loneragan, N. R., and Vance, D. J. (1998). Predation of juvenile tiger prawns in a tropical Australian estuary. *Marine Ecology Progress Series* **162**, 201–214.

Korsmeyer, K. E., and Dewar, H. (2001). Tuna metabolism and energetics. In 'Tuna Physiology, Ecology and Evolution'. (Eds B. A. Block and E. D. Stevens.) pp. 35–78. (Academic Press: San Diego, CA.)

Lemos, R. T., and Gomes, J. F. (2004). Do local environmental factors induce daily and yearly variability in bluefin tuna (*Thunnus thynnus*) trap catches? *Ecological Modelling* **177**, 143–156. doi:10.1016/J.ECOLMODEL.2004.02.005

Maldeniya, R. (1996). Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. *Environmental Biology of Fishes* **47**, 101–107. doi:10.1007/BF00002384

Ménard, F., Stéquert, B., Rubin, A., Herrera, M., and Marchal, E. (2000). Food consumption of tuna in the Equatorial Atlantic ocean: FAD-associated versus unassociated schools. *Aquatic Living Resources* **13**, 233–240. doi:10.1016/S0990-7440(00)01066-4

Okey, T. A. (2006). 'An Ecopath Model of Albatross Bay, Gulf of Carpentaria, Australia, for the Period 1986–1992: a Contribution to the FRDC 2004/024 Project Variation in Banana Prawn Catches at Weipa: a Comprehensive Regional Study.' (CSIRO Marine and Atmospheric Research: Cleveland, QLD.)

Olson, R. J., and Boggs, C. H. (1986). Apex predation by yellowfin tuna (*Thunnus albacares*): Independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 1760–1775.

Olson, R. J., and Galvan-Magana, F. (2002). Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean. *Fishery Bulletin* **100**, 279–298.

Olson, R. J., and Mullen, C. H. (1986). Recent developments for making gastric evacuation and daily ration determinations. *Environmental Biology of Fishes* **16**, 183–191. doi:10.1007/BF00005170

Nakamura, E. L. (1968). Visual acuity of two tunas, *Katsuwonus pelamis* and *Euthynnus affinis*. *Copeia* **1968**, 41–49. doi:10.2307/1441548

Pauly, D., and Palomares, L. (1987). Shrimp consumption by fish in Kuwait waters: a methodology, preliminary results and their implications for management and research. *Kuwait Bulletin of Marine Science* **9**, 101–125.

Ridgway, K. R., and Godfrey, J. S. (1997). Seasonal cycle of the East Australian Current. *Journal of Geophysical Research* **102**, 22 921–22 936. doi:10.1029/97JC00227

Salini, J. P., Brewer, D. T., and Blaber, S. J. M. (1998). Dietary studies on the predatory fishes of the Norman River Estuary, with particular reference to penaeid prawns. *Estuarine, Coastal and Shelf Science* **46**, 837–847. doi:10.1006/ECSS.1997.0319

Serventy, D. L. (1942). Notes on the economics of the northern tuna (*Kishinoella tonggol*). *Journal of the Council for Scientific and Industrial Research* **15**, 94–100.

Serventy, D. L. (1956). Additional observations on the biology of the northern bluefin tuna, *Kishinoella tonggol* (Bleeker), in Australia. *Australian Journal of Marine and Freshwater Research* **7**, 44–63.

Silas, E. G. (1967). Tuna fishery of the Tinnevelly coast, Gulf of Mannar. *Symposium Series of the Marine Biological Association of India* **1**, 1083–118.

Sturm, M.G. de L. (1978). Aspects of the biology of *Scomberomorus maculatus* (Mitchill) in Trinidad. *Journal of Fish Biology* **13**, 155–172. doi:10.1111/J.1095-8649.1978.TB03423.X

Ward, T. M., Staunton-Smith, J., Hoyle, S., and Halliday, I. A. (2003). Spawning patterns of four species of predominantly temperate pelagic fishes in the sub-tropical waters of southern Queensland. *Estuarine, Coastal and Shelf Science* **56**, 1125–1140. doi:10.1016/S0272-7714(02)00318-9

Wilson, M. A. (1981). The biology, ecology and exploitation of longtail tuna, *Thunnus tonggol* (Bleeker) in Oceania. MSc Thesis, Macquarie University, Sydney.

Yesaki, M. (1993). 'A Review of the Biology and Fisheries for Longtail Tuna (*Thunnus tonggol*) in the Indo-Pacific Region.' FAO Fisheries Technical Paper No. 336, Vol. 2. (FAO: Rome.)

Young, J. W., Lamb, T. D., Le, D., Bradford, R., and Whitelaw, A. W. (1997). Feeding ecology and interannual variations in diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. *Environmental Biology of Fishes* **50**, 275–291. doi:10.1023/A:1007326120380

Zhou, S., and Griffiths, S. P. (2006). Sustainability Assessment for Fishing Effects (SAFE): an application to diverse elasmobranch bycatch in a tropical Australian prawn trawl fishery. In'Design, Trial and Implementation of an Integrated, Long-term Bycatch Monitoring Program, Road Tested in the NPF. Final Report on FRDC Project 2004/024'. (Eds D. Brewer, S. Griffiths, D. Heales, S. Zhou, M. Tonks, Q. Dell, P. Kuhnert, S. Keys, W. Whitelaw, A. Burke, E. Raudzens.) pp. 179–207. (CSIRO: Cleveland, Qld.)

Manuscript received 20 October 2006, accepted 11 January 2007