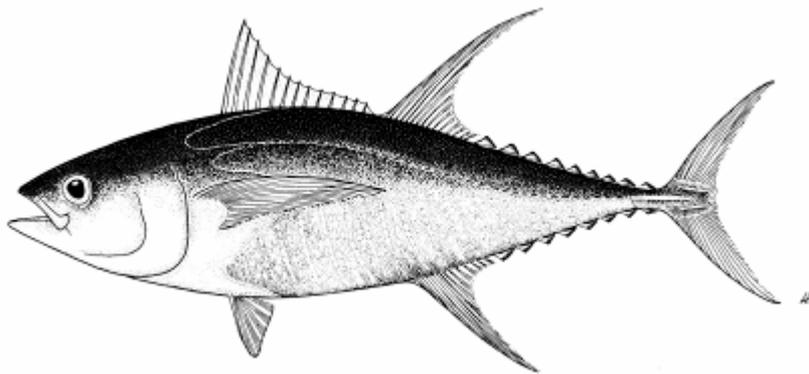




Prey consumption estimates for tunas in the WCPO



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August 2005

PREY CONSUMPTION ESTIMATES FOR TUNAS IN THE WESTERN AND CENTRAL PACIFIC OCEAN

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ABSTRACT

Using biomass estimates from the most recent stock assessments for skipjack, yellowfin and albacore tuna in the Western and Central Pacific Ocean (WCPO) coupled with bioenergetics models based on field and laboratory observation, estimates of total prey consumption by age class, consumption to biomass ratio and daily ration are derived. The results demonstrate the extent to which top-down control is exerted by these oceanic top predators, enable the parameterisation of ecosystem models and highlight areas of biological uncertainty that must be addressed in future studies of tunas and their prey.

INTRODUCTION

The development of an ecosystem approach to fisheries requires the extraction of new information from existing analyses as well as the development of new methods exploring new ideas. In this context, it is worth considering the results of traditional single-species stock assessments in terms of their implications for the ecosystem as a whole. Recent work has demonstrated how the results of single-species stock assessments may be pooled and analysed together, considering long-term variability in size structure of a tuna 'meta-population' (Hampton 2004) and coherence in recruitment time series among species and with climate indicators (Kirby et al. 2004). These studies provide a means to infer how the pelagic ecosystem of the WCPO has changed over the ca. 50 yr time period for which stock assessments are carried out and are complementary to more mechanistic approaches to modelling the ecological interactions and spatial population dynamics of tunas (Bertignac et al. 1998, Lehodey 2001, 2004a,b, Kirby et al. 2000, 2003). The work detailed in this paper interprets the results of the most recent stock assessments for yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*) and albacore (*Thunnus alalunga*) in terms of the energy demands of the tuna stocks for metabolism, movement, growth and reproduction, and the consequent consumption of prey necessary to sustain the stocks. The basis for the work is the calculation of energy demand by the tuna stocks based on bioenergetics models for individual tuna. The results provide an idea of the role of the different tuna species in structuring marine ecosystems through predation. They also help to parameterise ecosystem models (e.g. Cox et al. 2002a,b, Godinot and Allain 2003, Lehodey 2004a,b, Allain 2005a), while sensitivity analysis serves to highlight areas where further biological research on both predator and prey species is required.

METHODS

WCPO stock assessments using MULTIFAN-CL

Stock assessments in the WCPO are routinely carried out for the principal market species of tuna (albacore, bigeye, skipjack, yellowfin) and have also been attempted for billfish (marlins, swordfish) and sharks (blue shark) using MULTIFAN-CL (MFCL; Fournier et al. 1998, Hampton and Fournier 2001). MFCL provides the best available estimates of population characteristics by implementing a size-based, age- and spatially-structured statistical model fitted to size-frequency, catch, effort and tagging data from the fisheries.

MFCL uses data on length-frequencies obtained from port sampling and at-sea observers to raise the log-sheet data and estimate the number of individuals in any age class of the population. Estimates of growth parameters are then used to estimate biomass. (See Fournier et al. 1998, Hampton and Fournier 2001 and the MFCL website and manual for further details: www.multifan-cl.org).

The MFCL Regions for which these assessments are carried out vary by species: see stock assessment papers¹ for maps. In this study, results are presented for the regions representing the western tropical Pacific (Region 3 for YFT; Region 5 for SKJ) and the central tropical Pacific (Region 4 for YFT; Region 6 for SKJ), with a single MFCL Region used for this year's assessment of albacore.

In this study the MFCL estimates for the number of individuals and the mean length/weight-at-age are used to calculate the energy required for metabolism, growth

¹ http://www.spc.int/OceanFish/Html/WCPFC/SC1/scientific_committee.htm

and reproduction for each age class, with a final conversion from energy demand to prey biomass consumed, as detailed in the next section.

Bioenergetics

The energy demand and biomass consumed for each individual in the population is calculated from the following bioenergetics equation, which conserves energy by specifying the most important components of the energy budget and including a combined faecal/excretory loss term, represented by the assimilation efficiency:

$$\text{Eq. 1. Prey biomass consumed} = (1/A) \times (\text{AMR} + \text{SMR} + \text{SDA} + \text{REP} + \text{GRW}) \times (1/\text{PED})$$

where:

- A = assimilation efficiency (%)
- AMR = increase in metabolic energy due to swimming (J)
- SMR = standard metabolic rate (J)
- SDA = specific dynamic action (J)
- REP = energy lost due to reproduction (J)
- GRW = energy allocated to somatic tissue growth (J)
- PED = prey energy density (kJ/g)

The prey consumption for each tuna population is calculated by multiplying individual consumption by the number of individuals in the population and the time period. The bioenergetics model used is essentially the same as that of Kirby et al. (2000, 2003), being based on the same body of experimental work cited therein; the length-based scaling of AMR is explicit, based on the equations given in Sharp and Francis (1976) and Gerritsen (1984) after Webb (1975), as is the weight-based scaling of SMR, based on Brill (1979, 1987) (see Table 1). The functional form of the relationships is as follows:

$$\text{Eq. 2. SMR} = a W^b$$

$$\text{Eq. 3. AMR} = a L^b v^c$$

In defining the equation above and carrying out the subsequent calculations it is necessary to make various assumptions concerning individual or population characteristics. MFCL is an age-structured model using quarterly age classes for yellowfin and skipjack and annual age classes for albacore. Growth parameters are estimated in the model but it is recognised that growth of the youngest age classes is accelerated by comparison with a von Bertalanffy growth function (Labelle et al. 1993, Lehodey and Leroy 1999). Mean length/weight-at-age parameters are therefore estimated separately for the first 6 and 8 quarters respectively, in the case of skipjack and yellowfin, and for the first annual age class in the case of albacore.

In order to calculate the effect of specific dynamic action (i.e. the increase in metabolic energy demand for digestion) an idealised feeding frequency of 2 full meals a day is assumed, with energy demand doubling after the first 2 hours and decreasing to normal over the next 8 hours. The additional energy cost of Specific Dynamic Action is equivalent therefore to 40% of the Standard Metabolic Rate.

The bioenergetic calculations rely on estimates of tuna and prey energy density obtained in the field and lab during earlier studies (Boggs 1991, Boggs and Kitchell 1991, Olson and Boggs 1991). For the purpose of this study a constant, healthy tuna energy density is assumed, while the prey energy density varies as detailed below. In calculating the energetic cost of reproduction a sex ratio of 1:1 is assumed, with the energy cost of reproduction for males being half that for females (Schaeffer 1998).

There are no comprehensive studies on assimilation efficiency for tunas but Andersen and Riis-Vestergaard (2004) recently provided estimates for saithe (*Pollachius virens*), finding that efficiency increased with age from ca. 50% to 80% in the lab, while in the wild it was uniform and less, ranging from ca. 40% to 50%. Essington (2003) assumes an assimilation efficiency of $90 \pm 10\%$ plus an excretory loss term of 10%, giving a net efficiency of 70–100%; this could be a significant overestimate if the results of Andersen and Riis-Vestergaard (2004) also apply to tuna. Here the calculations of maximum prey consumption use an efficiency of 40%, while for minimum consumption a value of 80% is used. Both extremes are plausible and the need for better estimates is obvious.

For model parameters where there is considerable uncertainty, plausible extreme values are used to calculate the additive effect of this uncertainty on the overall results. Maximum, minimum and average estimates of prey consumption are then presented, with no assumption as to the likely distribution in between. This gives a clear picture of the uncertainty at the population/ecosystem scale, which must be addressed by physiological and behavioural studies at the individual scale. The calculations of minimum prey consumption assume a relatively high prey energy density and a relatively high assimilation efficiency, along with the minimum average tuna swimming speed and a conservative estimate of the number of individuals in the tuna population; the calculations of maximum prey consumption assume a relatively low prey energy density, along with low assimilation efficiency, higher average swimming speed and a higher estimate of the number of individuals in the tuna population. The parameters that remain fixed in these calculations are given in Table 1; those that are varied to generate the maximum and minimum estimates are given in Table 2.

RESULTS

The energy budgets calculated for each species (Figs.1 to 3) allow the estimation of daily ration by age class. This is then scaled up to estimate prey consumption by the population and the annual $Q:B$ ratio, i.e. consumption Q over the MFCL tuna biomass estimate B .

Skipjack

Total annual prey consumption by all age classes of skipjack tuna in MFCL Regions 5 and 6 are given in Figs. 4 & 5 respectively; average annual prey consumption by each age class of skipjack for MFCL Regions 5 and 6 combined is given in Fig. 6; and the annual consumption:biomass ratio and daily ration are given in Fig. 7.

Yellowfin

Total annual prey consumption by all age classes of yellowfin tuna in MFCL Regions 3 and 4 are given in Figs. 8 & 9 respectively; average annual prey consumption by each age class of yellowfin for MFCL Regions 4 and 5 combined is given in Fig. 10; and the annual $Q:B$ ratio and daily ration are given in Fig. 11.

Yellowfin plus Skipjack

Total annual prey consumption by yellowfin and skipjack tuna in the tropical western Pacific Ocean (MFCL Regions 3 and 4 for yellowfin; MFCL Regions 5 and 6 for skipjack) is given in Fig. 12. Skipjack prey consumption pre-1972 is an average of the post-1972 estimates due to the absence of fisheries catch and effort data for this period, therefore interannual and decadal variability is not well captured.

Albacore

Total annual prey consumption by all age classes of southern albacore tuna in the single MFCL Region is given in Fig. 13; average annual prey consumption by age class is given in Fig. 14; and the annual $Q:B$ ratio and daily ration are given in Fig. 15.

DISCUSSION

The energy budgets and the estimates of daily ration and $Q:B$ ratio reflect the different life histories of the 3 species. Skipjack has the highest SMR as a percentage of its energy budget, with SDA as a fixed percentage of SMR being consequently higher. Being relatively small it expends proportionately less energy on swimming (as AMR scales to at least the 4th power of length: Eq. 3; Table 1) and with year-round spawning at the near-daily frequency it is no surprise that its energy budget becomes dominated by reproductive activity as growth slows. The annual $Q:B$ ratio is significantly higher than for yellowfin and more than twice that of albacore. For the first and second quarters the $Q:B$ ratio / daily ration is extremely high, which is a requirement to attain the accelerated growth observed in the length-frequency data. With such a high standing stock the overall consumption of prey by skipjack in the tropical WCPO of ca. 200 Mt per annum must be the greatest top-down control on forage biomass in the epipelagic zone in which it feeds.

The energy budget for yellowfin becomes progressively dominated by AMR as, like skipjack, it continues to grow throughout its life. The $Q:B$ ratios and daily ration are intermediate between skipjack and albacore, reflecting its intermediate energy costs. The resulting prey consumption estimates are several times less than for skipjack, although they also feed on mesopelagic forage that are not exploited by skipjack (Allain 2005b).

Albacore is the most energy-efficient species, with the lowest daily ration and $Q:B$ ratio, reflecting its slow growth over a long life span and its seasonal reproductive activity. However, although the results are given by quarter the seasonal spawning has been averaged over the year, hence it appears to be a minor component of the energy budget; in fact, the frequency of spawning during the season is 1.62 d, so not all that different from yellowfin (1.93 d) and skipjack (1.18 d), i.e. daily or every second day. We would expect changes in condition and therefore an increase in somatic energy density as a precursor to spawning, which is not reflected here. However, it is assumed that there is no difference in mean swimming speed (in bodylengths.s⁻¹) among species and in all cases the AMR resulting from the minimum estimate is shown here.

CONCLUSIONS

Sharp and Francis (1976) were the first to try and synthesise biological data with hydrodynamic and population dynamic theory in order to derive an energetics model for an exploited tuna population. Much of their thinking is reflected here, with some of the uncertainties flagged at the time still remaining. A great deal of progress on the physiological ecology of tunas has been made in the meantime (e.g. Brill 1979, 1987), along with some important work on reproductive biology (e.g. Ramon and Baily 1996), but work remains to be done in both these fields, as well as in tuna behaviour (e.g. swimming speeds), sensory biology, and feeding physiology, i.e. digestion and food assimilation. The prey consumption estimates, $Q:B$ ratios and estimates of daily ration that result from this analysis are broadly consistent with other studies (e.g. Essington 2003), while providing more detailed information on prey consumption over time and by age class, and highlighting the additive effect of parameter uncertainty.

This work is illustrative of the ongoing utility of single species stock assessment results in the development of an ecosystem approach to fisheries management. It also demonstrates the importance of physiological understanding of predator and prey species when trying to determine ecosystem structure and function, and highlights the uncertainty that prevails as we seek to develop quantitative models for exploited ecosystems.

Acknowledgements

I am grateful to Valerie Allain for comments on earlier drafts of this paper.

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Table 1. Fixed parameter estimates used for calculation of prey consumption

	Skipjack	Yellowfin	Albacore
Reproductive energy loss per spawning event	2% female; 1% male		
Spawning frequency (d ⁻¹)	1.18	1.93	19.44
Standard metabolic rate coefficients:	a = 412.0 b = 0.563	a = 286.8 b = 0.573	a = 293.0 b = 0.573
Active metabolic rate coefficients: (J hr ⁻¹)	a = 2.002 × 10 ⁻⁴	b = 1.5	c = 2.5
Somatic energy density (kJ g ⁻¹)	6.0		

Table 2. Variable parameter estimates used for calculation of prey consumption

	minimum	maximum	average
Average swimming speed (bodylengths s ⁻¹)	1	2	1.5
Prey energy density (kJ g ⁻¹)	7	5	6
Assimilation efficiency (%)	80	40	60
N(individuals) MFCL estimate ±x%	-10%	+10%	MFCL

FIGURE LEGEND

Fig. 1. Energy budget for skipjack tuna

Fig. 2. Energy budget for yellowfin tuna

Fig. 3. Energy budget for albacore tuna

Fig. 4. Total annual prey consumption by all age classes of skipjack in MFCL Region 5. Solid line is the average of the maximum/minimum (dotted lines)

Fig. 5. Total annual prey consumption by all age classes of skipjack in MFCL Region 6. Solid line is the average of the maximum/minimum (dotted lines)

Fig. 6. Average annual prey consumption by each age class of skipjack tuna in MFCL Regions 5 & 6 combined. Solid line is the average of the maximum/minimum (dotted lines)

Fig. 7. Annual consumption:biomass ratio and daily ration by age class for skipjack tuna. Solid line is the average of the maximum/minimum (dotted lines)

Fig. 8. Total annual prey consumption by all age classes of yellowfin in MFCL Region 3. Solid line is the average of the maximum/minimum (dotted lines)

Fig. 9. Total annual prey consumption by all age classes of yellowfin in MFCL Region 4. Solid line is the average of the maximum/minimum (dotted lines)

Fig. 10. Average annual prey consumption by each age class of yellowfin in MFCL Regions 3 & 4 combined. Solid line is the average of the maximum/minimum dotted lines

Fig. 11. Annual consumption:biomass ratio and daily ration by age class for yellowfin. Solid line is the average of the maximum/minimum dotted lines

Fig. 12. Total prey consumption by yellowfin and skipjack tuna in the tropical western Pacific Ocean (MFCL Regions 2 & 3 for yellowfin; MFCL Regions 5 & 6 for skipjack). Solid line is the average of the maximum/minimum (dotted lines). Skipjack prey consumption pre-1972 is set at the average consumption post-1972.

Fig. 13. Total annual prey consumption by all age classes of southern albacore tuna in the WCPO. Solid line is the average of the maximum/minimum (dotted lines)

Fig. 14. Average annual prey consumption by each age class of southern albacore tuna in the WCPO. Solid line is the average of the maximum/minimum (dotted lines)

Fig. 15. Annual consumption:biomass ratio and daily ration by age class for southern albacore tuna. Solid line is the average of the maximum/minimum (dotted lines)

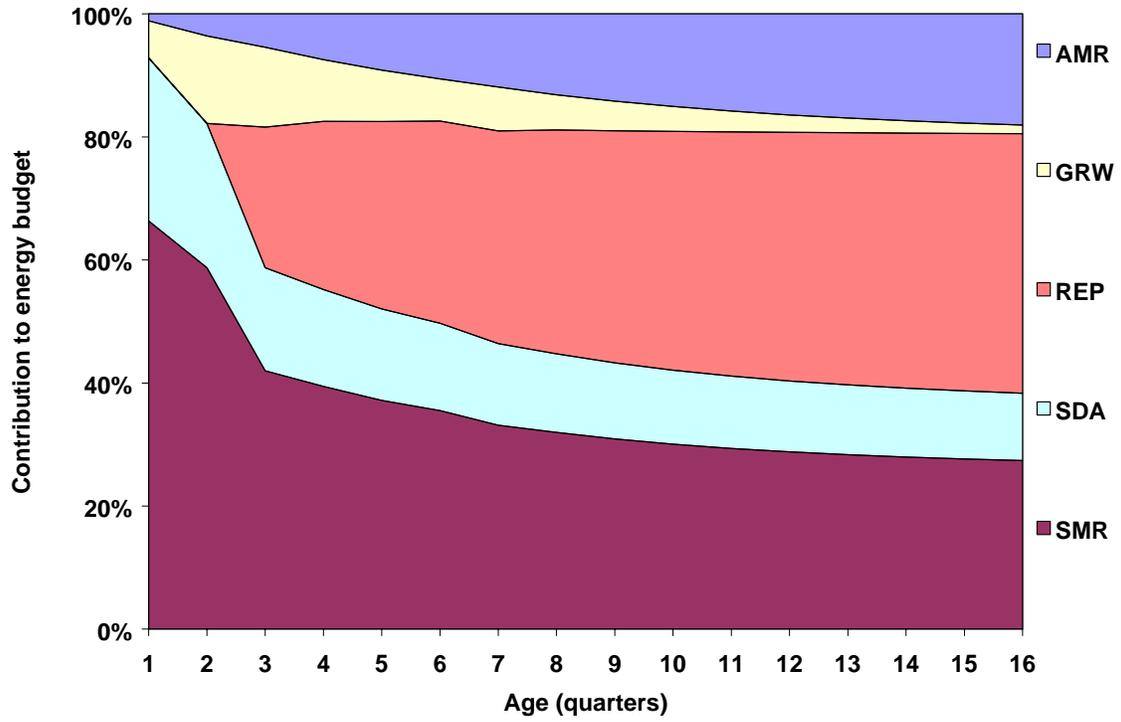


Fig. 1. Energy budget for skipjack tuna

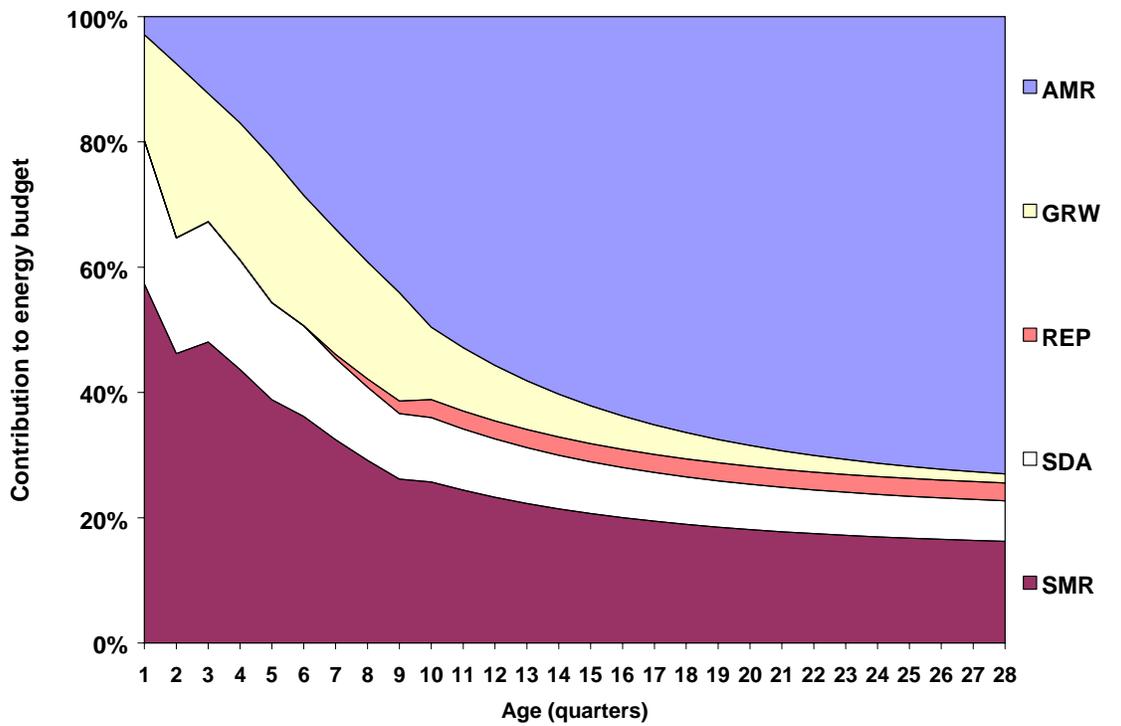


Fig. 2. Energy budget for yellowfin tuna

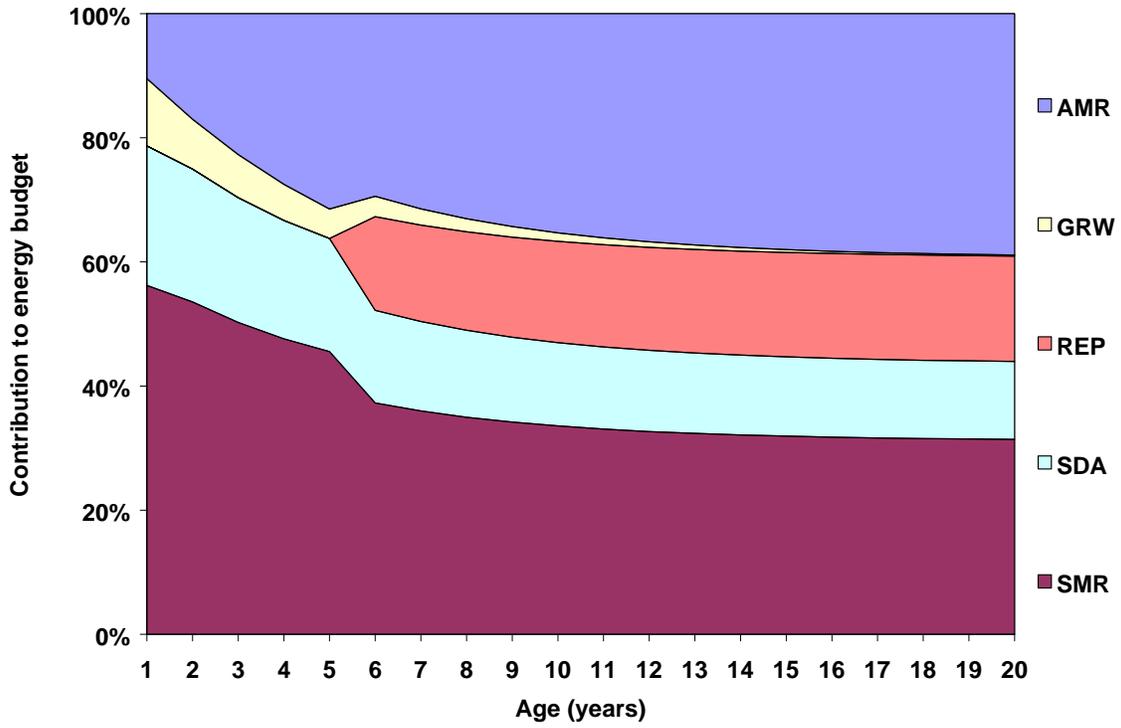


Fig. 3. Energy budget for albacore tuna

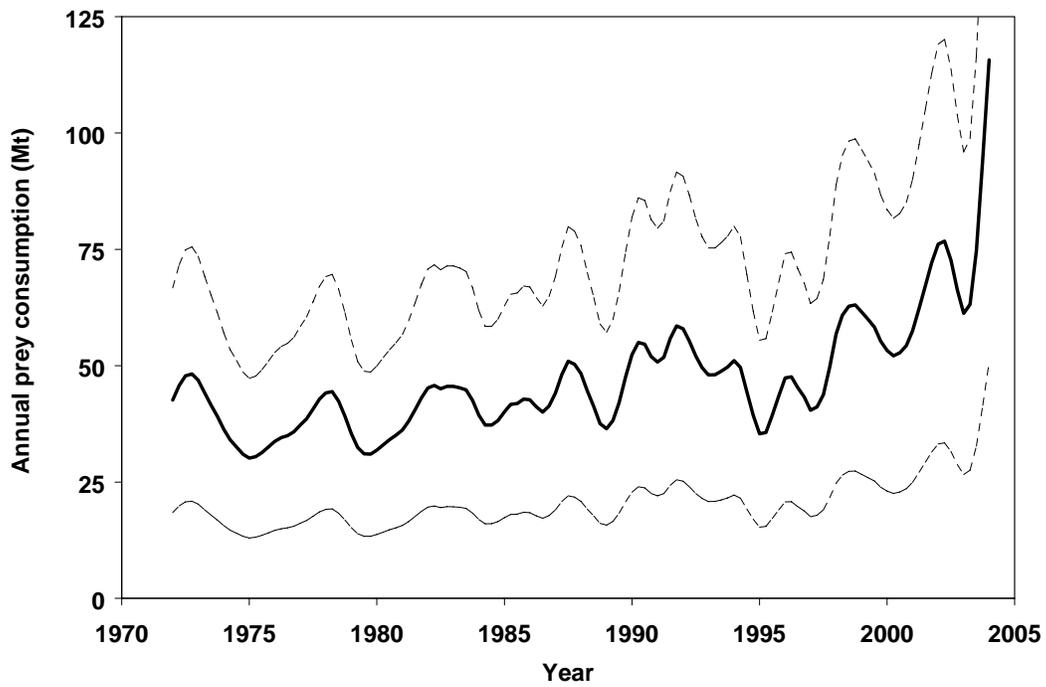


Fig. 4. Total annual prey consumption by all age classes of skipjack in MFCL Region 5. Solid line is the average of the maximum/minimum (dotted lines)

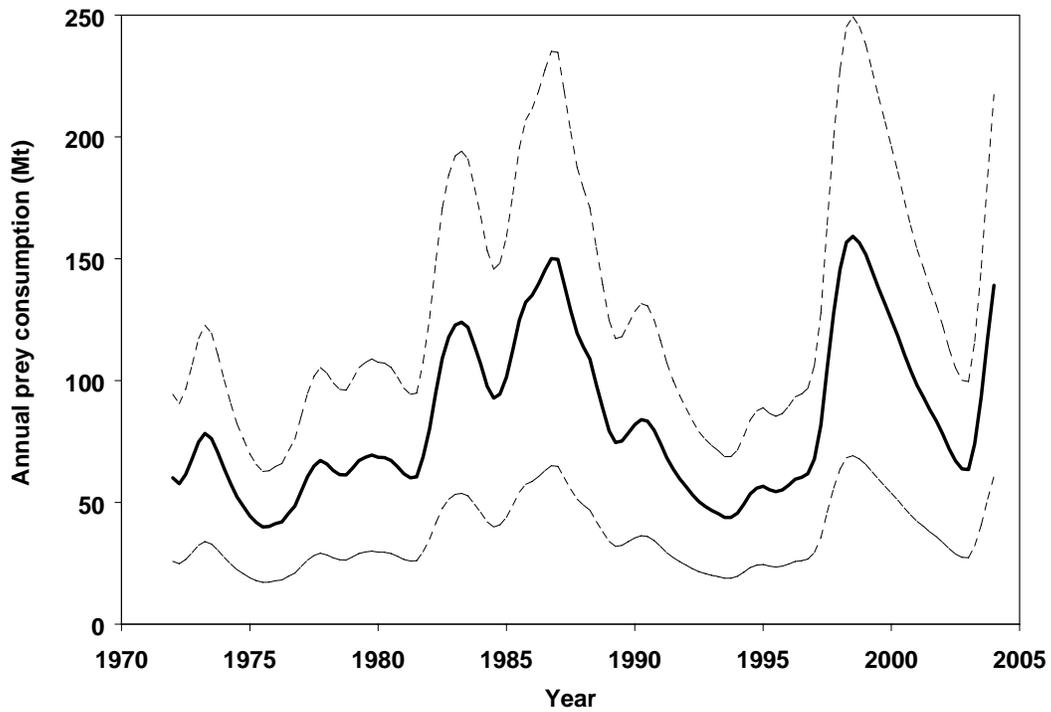


Fig. 5. Total annual prey consumption by all age classes of skipjack in MFCL Region 6. Solid line is the average of the maximum/minimum (dotted lines)

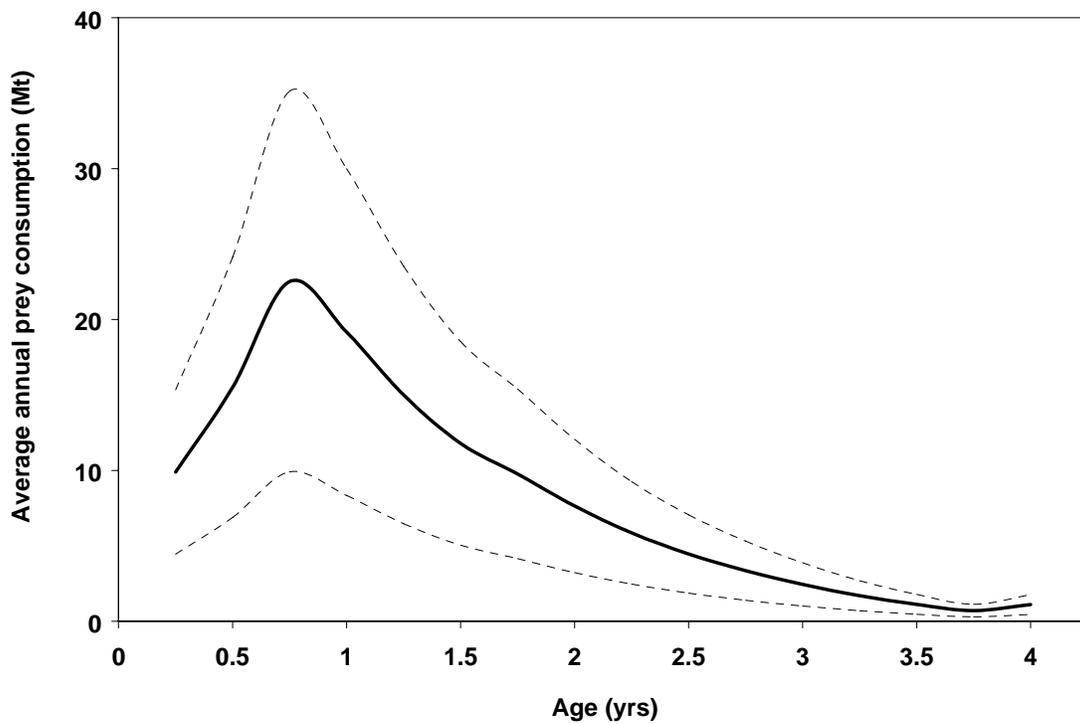


Fig. 6. Average annual prey consumption by each age class of skipjack in MFCL Regions 5 & 6 combined. Solid line is the average of the maximum/minimum (dotted lines)

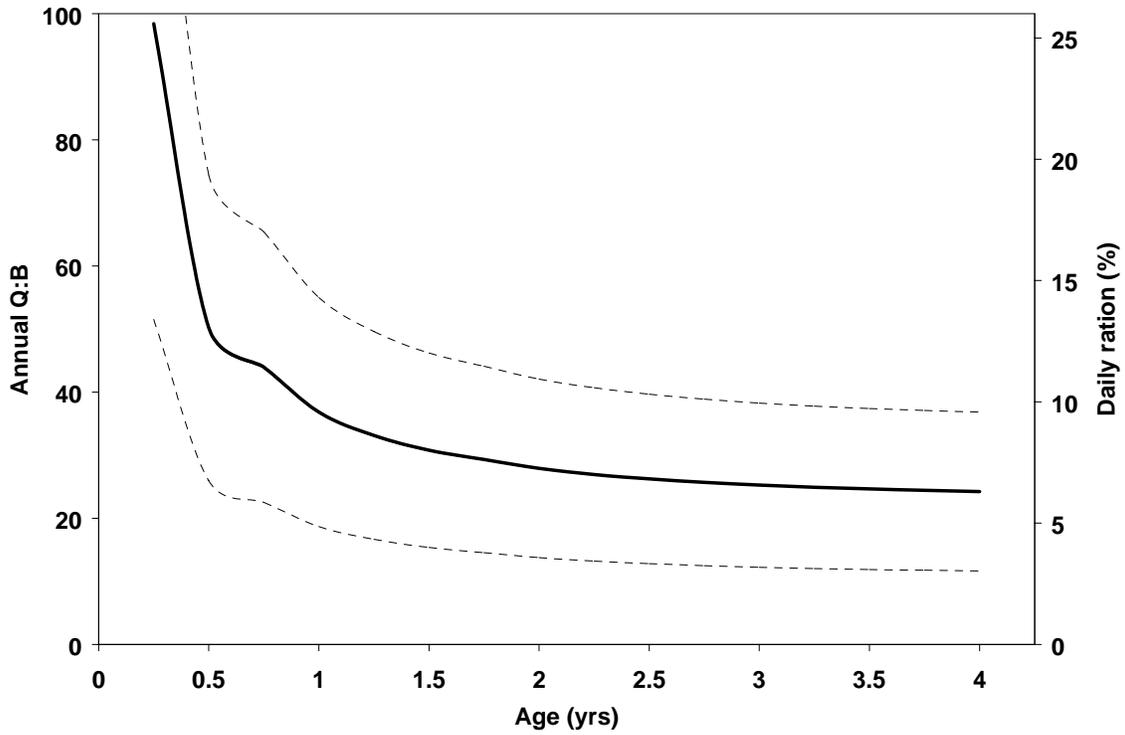


Fig. 7. Annual consumption:biomass ratio and daily ration by age class for skipjack tuna. Solid line is the average of the maximum/minimum (dotted lines)

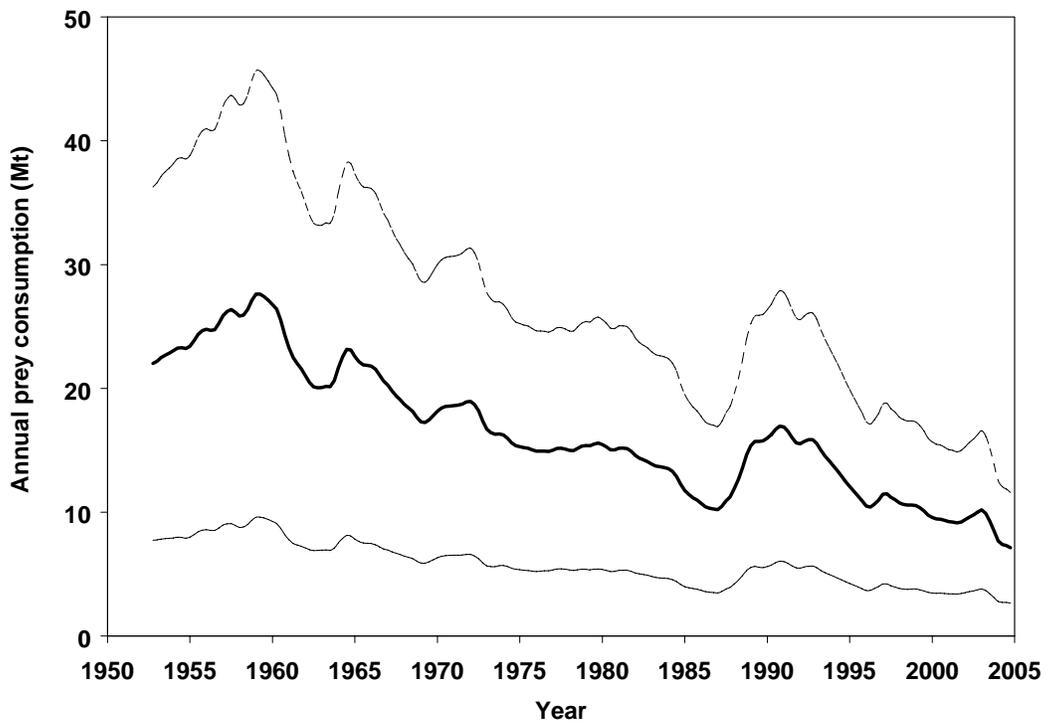


Fig. 8. Total annual prey consumption by all age classes of yellowfin in MFCL Region 3. Solid line is the average of the maximum/minimum (dotted lines)

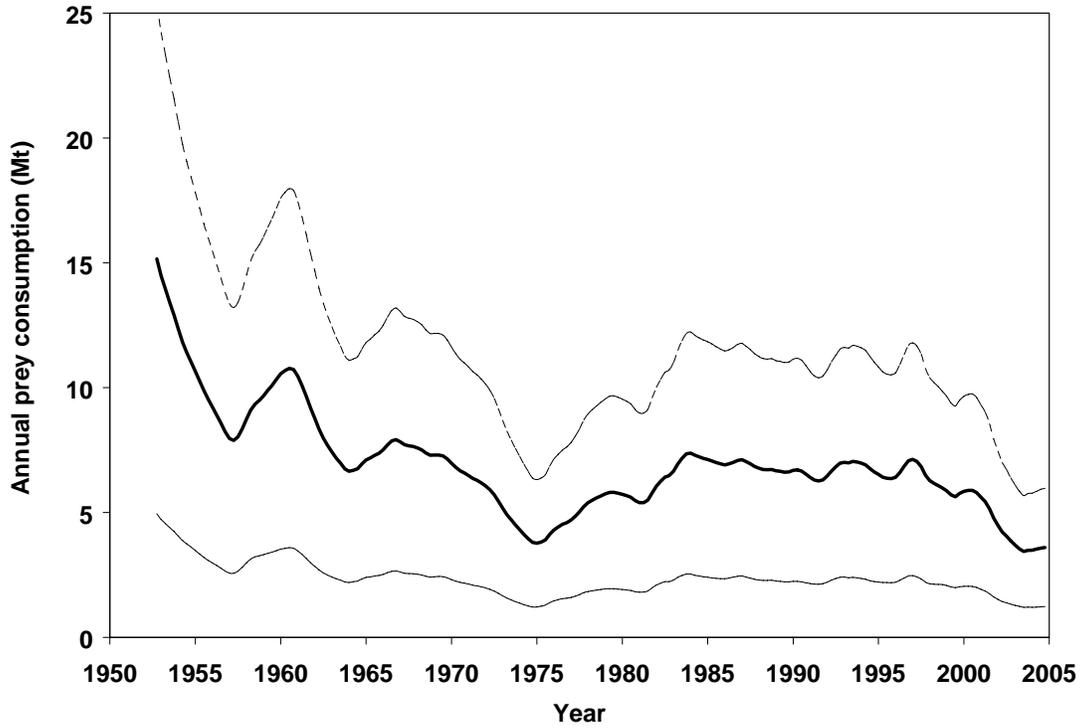


Fig. 9. Total annual prey consumption by all age classes of yellowfin in MFCL Region 4. Solid line is the average of the maximum/minimum (dotted lines)

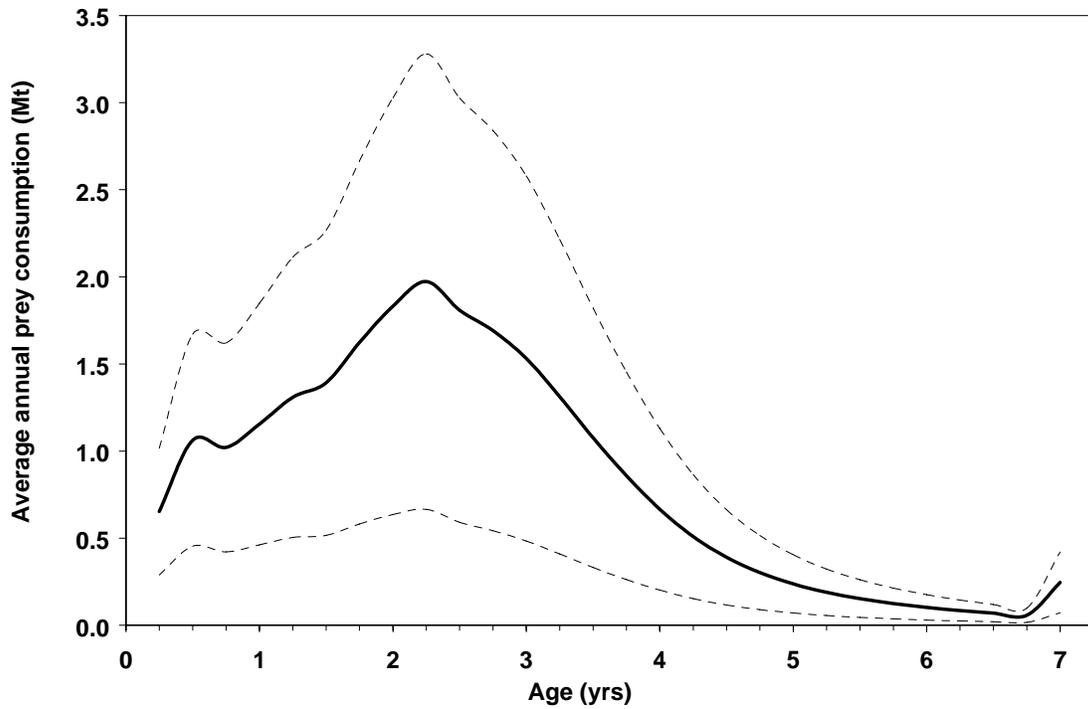


Fig.10. Average annual prey consumption by each age class of yellowfin in MFCL Regions 2 & 3 combined. Solid line is the average of the maximum/minimum (dotted lines)

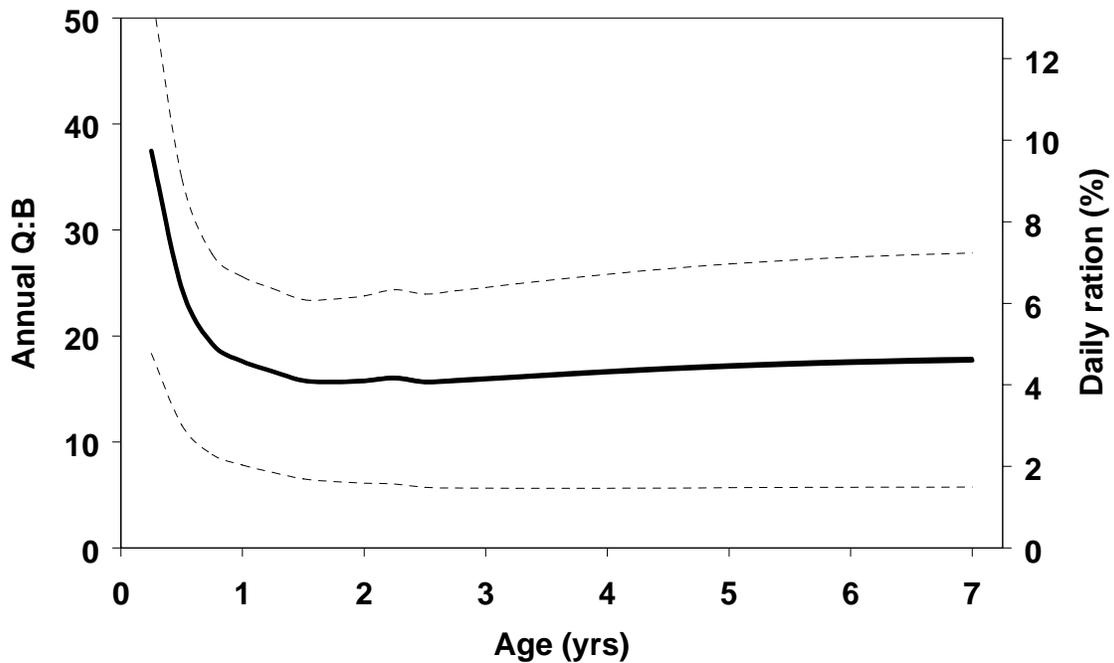


Fig. 11. Annual consumption:biomass ratio and daily ration by age class for yellowfin. Solid line is the average of the maximum/minimum (dotted lines)

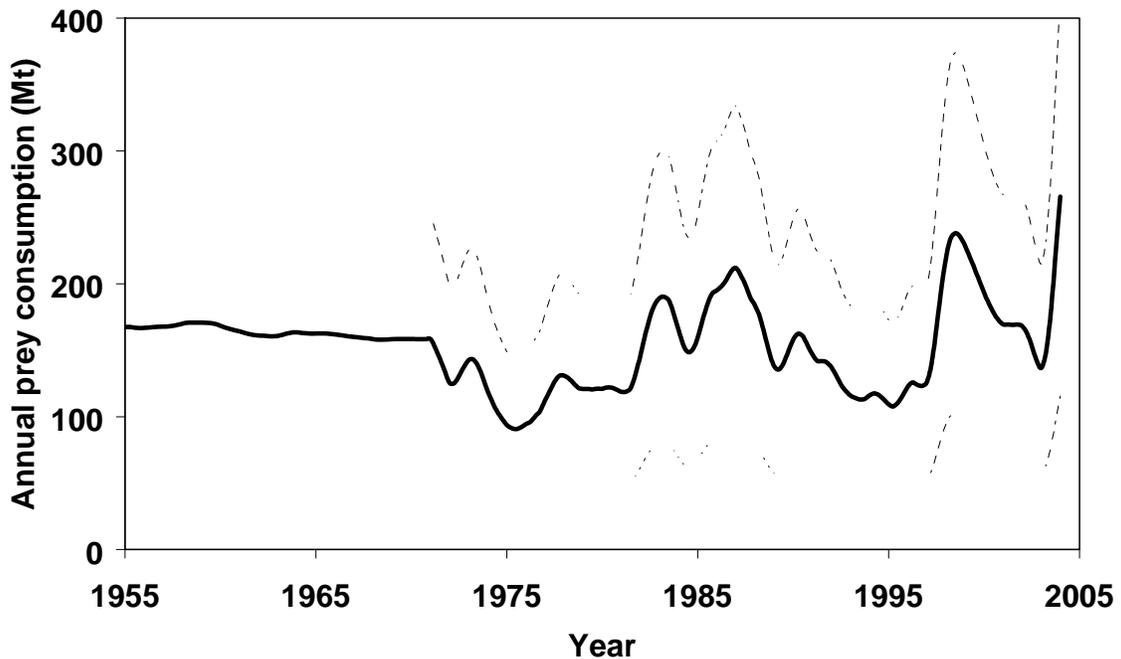


Fig. 12. Total prey consumption by yellowfin and skipjack tuna in the tropical western Pacific Ocean (MFCL Regions 5 & 6 for skipjack; MFCL Regions 3 & 4 for yellowfin). Solid line is the average of the maximum/minimum (dotted lines). Skipjack prey consumption pre-1972 is set at the average consumption post-1972.

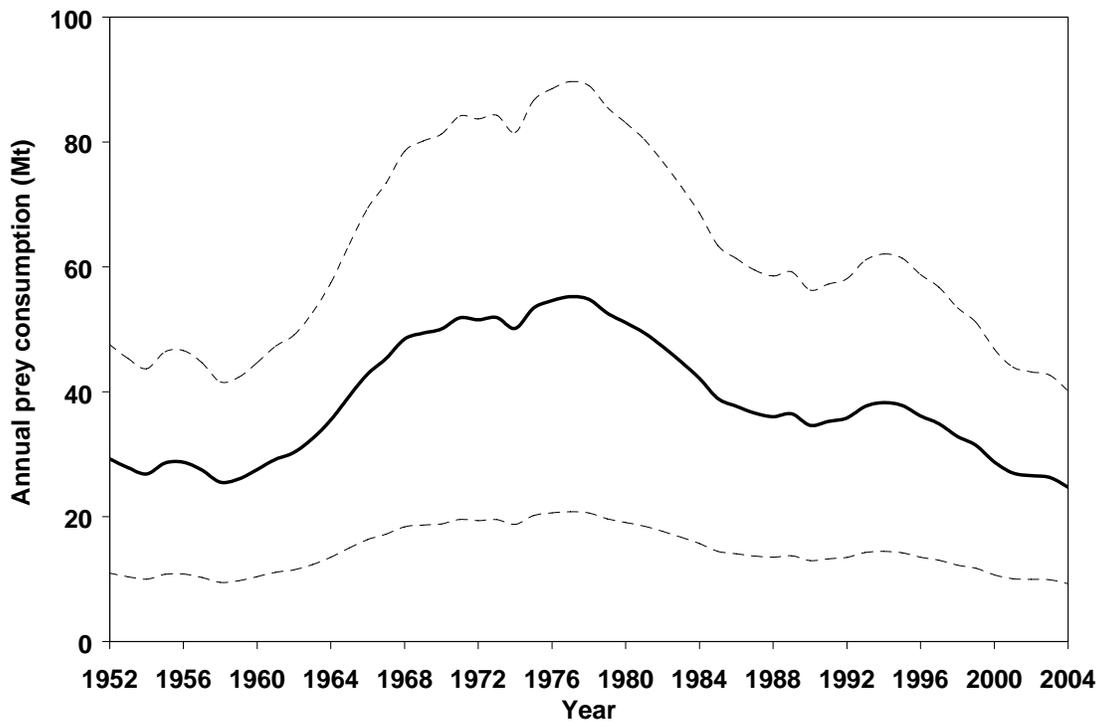


Fig. 13. Total annual prey consumption by all age classes of southern albacore tuna in the WCPO. Solid line is the average of the maximum/minimum (dotted lines)

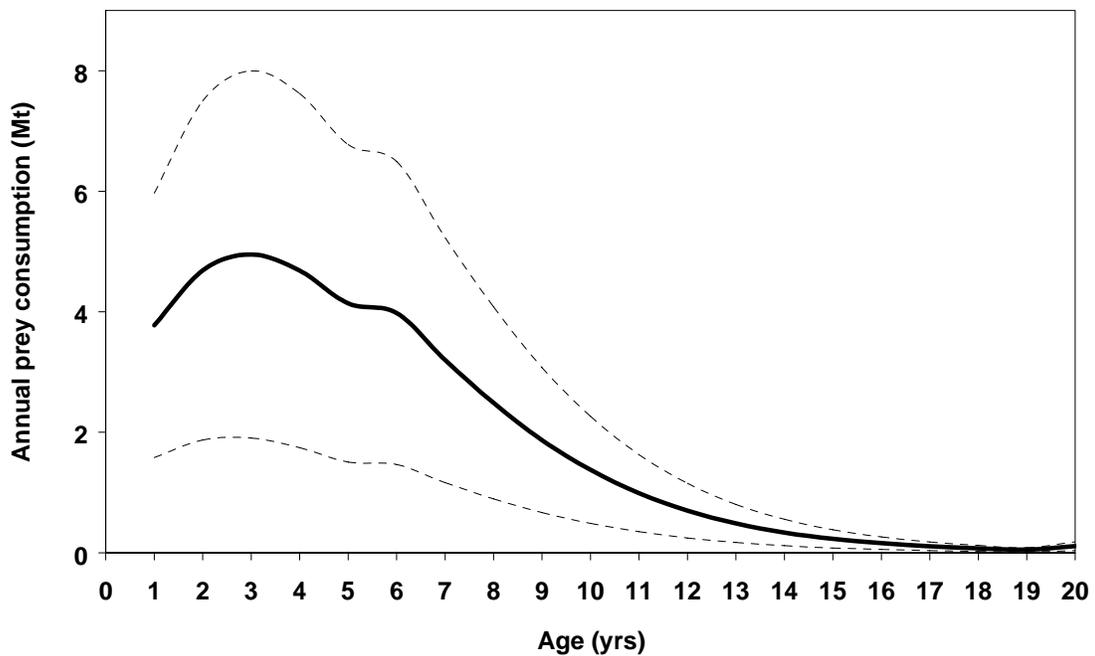


Fig. 14. Average annual prey consumption by each age class of southern albacore tuna in the WCPO. Solid line is the average of the maximum/minimum (dotted lines)

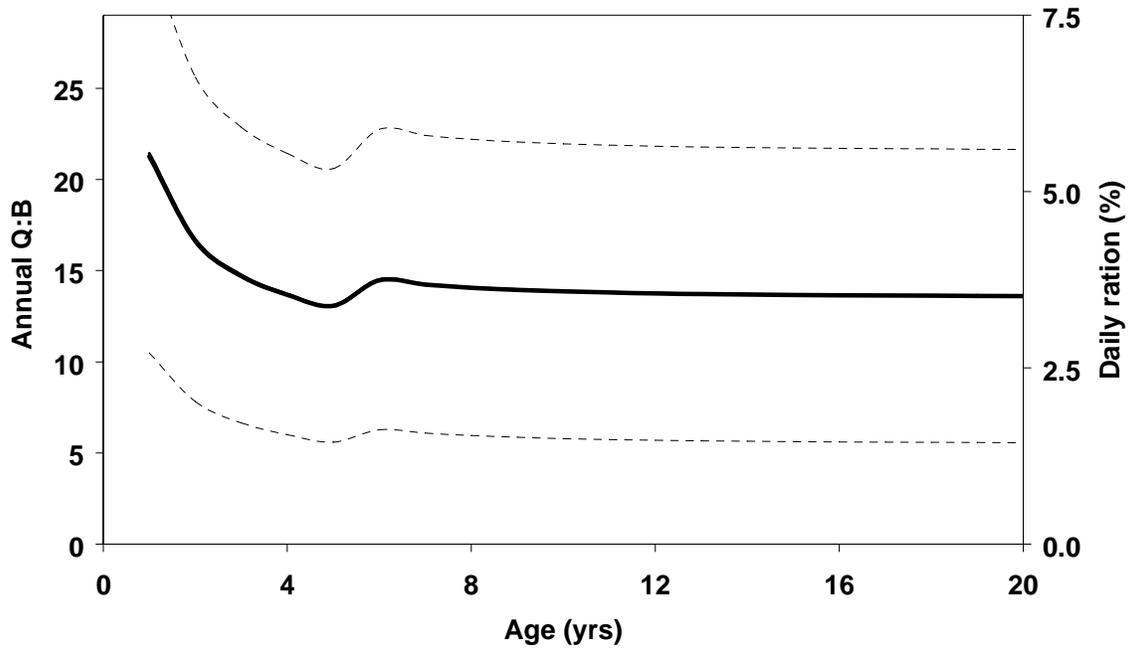


Fig. 15. Annual consumption:biomass ratio and daily ration by age class for southern albacore tuna. Solid line is the average of the maximum/minimum (dotted lines)