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# A REVIEW OF METHODS TO DETERMINE PREY CONSUMPTION RATES, GASTRIC EVACUATION AND DAILY RATION OF PELAGIC FISHES: A PRECURSOR TO ESTIMATING Q/B FOR KEY PREDATORS IN THE TUNA FISHERIES OF THE EASTERN PACIFIC OCEAN

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### 1. INTRODUCTION

1.1. Ecosystem dynamics approach to fisheries management

The traditional paradigm of fisheries management has been one of a single-species focus balancing the interchange between exploitation and biological sustainability of target species, but has generally not considered the ecology of the species, interactions among other species, or the impact of fisheries interactions on the assemblage as a whole (Link 2002a; Link 2002b; Latour *et al.* 2003). Many fisheries interact with species and habitats other than the target species. Species caught incidentally during fishing operations are collectively regarded as "bycatch", which can be subdivided into species that are discarded at sea ("discards" or "non-retained catch") and those retained for sale or consumption ("byproduct"). Fishing effort in most of the world's oceans is increasing to maintain the increasing global demand for seafood products (Kobayashi *et al.* 2015; FAO 2021). World capture production of the main commercial tuna species surpassed 5 million tons in 2014 (FAO 2021) and increased to nearly 6 million tons by 2019 (Figure 1). With this increase in fishing catch and effort, there is also great potential for fishing activities to concomitantly increase their direct and indirect impacts on non-target species, and thus the structure and function of the broader ecosystems that support commercial fisheries.

Consequently, over the past two decades there has been a widespread shift in fisheries worldwide towards ecosystem approaches to fisheries (EAF)—also commonly referred to as ecosystem-based fisheries management (EBFM)—as a tool for fisheries to show greater initiative and transparency in demonstrating that they are operating in an ecologically responsible manner (Link 2002a; Link 2002b; Hall and Mainprize 2004; Pikitch *et al.* 2004; Scandol *et al.* 2005). This has become especially important for some fisheries that can be subjected to aggressive public scrutiny for impacting large numbers of taxa of marine flora and fauna (*e.g.*, shrimp trawling; Aslin and Byron 2003), or species of conservation concern,

such as sea turtles and marine mammals that incur mortality in industrial tuna fisheries (Joseph 1994; Jacquet and Pauly 2007). Addressing ecological sustainability helps to conserve the integrity and optimize the productivity of marine ecosystems but fisheries have also benefited by using their demonstration of ecologically sustainable practices as a marketing tool for fisheries through eco-labelling, after being certified by accreditation organizations such as the Marine Stewardship Council (MSC) (Kirby *et al.* 2014).

The Inter-American Tropical Tuna Commission (IATTC) is one of the only tuna Regional Management Fisheries Organizations (t-RFMOs) that has explicitly adopted an ecosystem approach to managing tuna fisheries in the eastern Pacific Ocean (EPO) through the Antigua Convention, which was ratified in 2003 and entered into force in 2010. Several conservation and management measures (CMMs) have been implemented for non-target species such as the prohibition of retention of silky sharks (*Carcharhinus falciformis*) (C-16-06), oceanic whitetip sharks (*C. longimanus*) (C-11-10), whale sharks (*Rhincodon typus*) (C-13-04), and mobulids (C-15-04). The IATTC is therefore committed to ensuring the long-term sustainability of tuna and tuna-like species, associated non-target species and the supporting ecosystems in the EPO by meeting the objectives of various Antigua Convention Articles such as "to adopt, as necessary, conservation and management measures and recommendations for species belonging to the same ecosystem and that are affected by fishing for, or dependent on or associated with, the fish stocks covered by this Convention...".

EAF can be a significant and expensive proposition for most fisheries, especially for t-RFMOs that cover large spatial scales, include vessels that operate with several gear types each of which has different levels of impacts on individual species (*e.g.*, longline, purse seine, pole and line), and incorporate multiple political jurisdictions from provinces within a country's Exclusive Economic Zone (EEZ) to areas beyond national jurisdictions (ABNJ) (*i.e.*, the high seas). Therefore, fisheries have used a range of methods to undertake ecological assessments, but they mainly fall into two broad categories as either: i) single species stock assessment for data-rich species, or ecological risk assessment (ERA) often for a suite of data-poor species or ii) whole-of-ecosystem models.

In most fisheries, especially tuna fisheries where the suite of impacted species is diverse, quantitative single species stock assessment models are the most desirable approach but are generally not feasible since a time series of reliable catch data is not available for species of little or no economic or conservation importance. As a result, ERA methods have been used as an alternative as they are generally designed to be applied in data-limited settings, being based on qualitative expert opinion (Fletcher 2005), semi-quantitative data (*e.g.*, Productivity-Susceptibility Analysis (PSA); Stobutzki *et al.* 2001) or quantitative data describing key aspects of the species and fisheries in question (*e.g.*, SAFE, EASI-Fish; Zhou and Griffiths 2008; Griffiths *et al.* 2019a). However, both ERAs and single species stock assessments generally fail to accommodate and quantify the complexities in the spatial and temporal dynamics of predator/prey relationships that essentially control the integrity and dynamics of the ecosystem.

### 1.2. Ecosystem models and trophic dynamics

Ecosystem models are often the only means by which the complex interactions between constituent species, the environment, and fisheries can be quantified, and scenarios be posed to forecast the potential outcomes of specific perturbations, such as changes in fishing effort or climate. There are several ecosystem models that have been developed to characterize marine ecosystems with the capability of exploring the potential impacts by fisheries in moving towards EAF. Such models include Ecopath with Ecosim, (Polovina 1984; Christensen and Pauly 1992; Walters *et al.* 1997), Atlantis (Fulton *et al.* 2011), SEAPODYM (Lehodey *et al.* 2008), individual-based growth and multispecies bioenergetics models (MSBE) (Latour *et al.* 2003), multiple species virtual population analysis (MSVPA) (Helgason and Gislason 1979; Pope 1979), and multispecies production models (*i.e.*, extensions to traditional single species assessment models to incorporate ecological interactions) (see Latour *et al.* 2003).

A criticism of ecosystem models has been their requirement of estimating a large number of parameters that describe the biology and ecology of a species or "functional group" (*i.e.*, a group of species having biological and ecological similarities), dietary data to establish and quantify trophic linkages and energy flows between species, and reliable data on the fishery impact on each species or group—both in terms of retained catch and discards (Plaganyi and Butterworth 2004). One of the most widely used ecosystem models to characterize marine ecosystems—applied in over 433 settings (Colléter *et al.* 2015)—is Ecopath, which is a mass-balance trophic model that balances the static state of energy flows of the net production of a species, with all sources of mortality and migration. The Ecopath master equation has been expressed by Christensen and Pauly (1992) as:

$$B_{i} \cdot (P/B)_{i} = \sum_{j=1}^{n} B_{j} \cdot (Q/B)_{j} \cdot (DC_{ji} + Y_{i} + E_{i} + BA_{i} + B_{i}) \cdot (P/B)_{i} \cdot (1 - EE_{i})$$

where,  $B_i$  and  $B_j$  is the standing biomass of prey (*i*) and predators (*j*), respectively, in the modelled region,  $P/B_i$  is the production/biomass ratio (year<sup>-1</sup>)—equivalent to total mortality (*Z*)—*EE<sub>i</sub>* is the ecotrophic efficiency,  $Q/B_j$  is the consumption/biomass ratio quantifying the annual food consumption rate per unit biomass of *j* (*i.e.*, the annual ration, or daily ration multiplied by 365),  $DC_{ji}$  is the proportion of prey *i* in the average diet of predator *j*,  $Y_i$  is the total annual fisheries catch,  $E_i$  is the annual net migration of *i*, and  $BA_i$ is the annual biomass accumulation rate of *i*.

Although many of the parameters in the Ecopath model can be measured or estimated with some reliability, *Q/B* is one of the most difficult parameters to measure experimentally, especially for large oceanic pelagic fishes such as tunas that require large, specialized facilities for experiments to be conducted. However, it is imperative to have reliable estimates of *Q/B* since it determines the prey biomass that is required to be available for the predator to exist. Having reliable estimates of *Q/B* also facilitates the determination of the type of trophic mechanisms that are controlling the internal dynamics of an ecosystem, such as determining whether a predator exerts "top-down" regulation of the ecosystem through high predation pressure, or relies on "bottom-up" processes by being dependent on the biomass of prey at low trophic levels, especially phytoplankton and zooplankton (Essington *et al.* 2002). Understanding what and which of these processes is occurring can only be attained by quantifying diet composition, daily ration, gastric evacuation, and the consumption rate of consumers within an ecosystem (*e.g.*, Olson and Boggs 1986; Olson and Galván-Magaña 2002; Griffiths *et al.* 2009; Abitia-Cárdenas *et al.* 2011; Griffiths *et al.* 2019b).

Other ecosystem models that are individual-based growth and bioenergetics models (Latour *et al.* 2003) may be as useful as Ecopath models, but they require the experimental estimation of other parameters, such as weight-specific-maximum consumption and -metabolic rates, and specific dynamic action (SDA), to estimate net growth and the energetic costs associated with sustained swimming (Sharp and Francis 1976; Olson and Boggs 1986; Dewar and Graham 1994) and meal consumption (Fitzgibbon *et al.* 2007; Klinger *et al.* 2016; Stieglitz *et al.* 2018). Such experiments—that would be required to characterize *Q/B* for a species or functional group for diverse tropical ecosystems—generally provide limited, reliable estimates under natural conditions and over a wide range of sizes of tropical, pelagic fishes.

The objective of this paper is to provide a comprehensive review of the methods available to estimate prey consumption and gastric evacuation rates thus, daily ration and Q/B of tropical tunas and tuna-like fishes. The review concludes with recommendations as to which method(s) is most feasible, practical, cost-effective, and likely to produce the most reliable estimates of Q/B for key species within the EPO ecosystem that will be included in future ecosystem models of the EPO that are currently planned under the IATTC's proposed Strategic Science Plan (SSP) (IATTC-93-06a) and outlined in SAC-10-01, Project 0.1.c.

#### 2. METHODS FOR ESTIMATING Q/B

#### 2.1. Direct methods to estimate daily ration with stomach content data and gastric evacuation rates

#### 2.1.1. Feeding and gastric evacuation rate models

The most widely used methods to estimate prey consumption and daily ration by wild fishes quantify the amount of food in the stomachs of a species of fish over a known sampling time interval (usually a 24 hour period) and adjust that amount of food by the rate of stomach evacuation (Héroux and Magnan 1996). Gastric evacuation rates have been obtained from laboratory tank experiments (*e.g.*, Magnuson 1969; Daan 1973; Elliott and Persson 1978; Diana 1979; Olson and Boggs 1986; Boisclair and Leggett 1988; Ruggerone 1989a; Bush and Holland 2002; Beaudreau and Essington 2009), from field experiments under natural conditions (*e.g.*, Bajkov 1935; Mehl and Westgård 1983), and from feeding models applied to sequential field sampling of stomachs and variations in gut fullness over 24-hour cycles of feeding (*e.g.*, Boisclair and Leggett 1985; Sainsbury 1986; Young et al. 1997; Butler et al. 2010).

Prior to 1969, stomach evacuation data were not fitted with regression functions and model parameters were not used to estimate gastric evacuation rates (Windell 1967; Elliott and Persson 1978). Gastric evacuation (earlier termed "gastric digestion") was described and calculated as the average percentage decrease in stomach contents following a meal (*e.g.*, Kitchell and Windell 1968) or as the time until total stomach evacuation (*e.g.*, Bajkov 1935).

The earliest consumption (*i.e.*, feeding) model by Bajkov (1935) was based on the mean weight of field sampled stomach contents and a gastric evacuation rate assumed to be constant (linear), viz,

$$D = A \cdot (24/n)$$

where, *D* is the daily "consumption" (g prey consumed  $d^{-1}$ ), *A* is the average amount of food in the stomach during the 24-hour interval, and *n* is the number of hours for total stomach evacuation. Since then, several other food consumption models have been developed over the years (see reviews in Eggers 1977; Elliott and Persson 1978; Richter et al. 2004; Berens 2005). The most commonly used models assume a continuous and constant rate of feeding and are based on the assumption that the amount of food evacuated from the stomach should increase exponentially over time (*e.g.*, Eggers 1977; Elliott and Persson 1978). The Elliott and Persson 1978) model (based on the model approach by Eggers 1977) is described as

$$C = \sum C_t$$

where, C = daily ration (%BW d<sup>-1</sup>) and  $C_t =$  the amount of food consumed between two sampling periods described by the following equation:

$$C_t = \frac{(S_t - S_0 e^{-GER \cdot t})GER \cdot t}{1 - e^{-GER \cdot t}}$$

where,  $S_0$  = amount of food present at the beginning of the sampling interval,  $S_t$  = amount of food present at the end of the sampling interval, t = time interval length of the sampling period, and *GER* = the instantaneous rate of gastric evacuation =  $\log_e (\frac{S_0}{S_t})t^{-1}$ . The simplified form of this equation becomes

$$DR = 24 \cdot \overline{S} \cdot GER$$

where, daily ration (*DR*) is a function of the mean stomach fullness of the hourly means (*S*) and the *GER* over a 24-hour period.

Despite the popular usage of this model to estimate daily ration, gastric evacuation rates are not always exponential functions, and have been modelled using binomial (*e.g.*, Magnuson 1969), linear (*e.g.*, Swenson and Smith Jr 1973; Jones 1974; Olson and Boggs 1986; Olson and Mullen 1986), exponential (*e.g.*, Eggers 1977; Elliott and Persson 1978; Macdonald *et al.* 1982), square root (*e.g.*, Jobling 1981; Gillum *et al.* 2012), logistic (*e.g.*, Hopkins and Larson 1990) and power exponential (*e.g.*, Elashoff *et al.* 1982; Hopkins and Larson 1990; Santos and Jobling 1992; Berens 2005; Berens and Murie 2008) functions (Table 1.). Temming and Andersen (1994) developed a general gastric evacuation model that determines the shape parameter of the curve by integrating time after ingestion, the predator weight, water temperature, and meal size as predicting variables.

In general, the instantaneous rate of evacuation has been expressed by the slope of the regression, following integration and linearization of the curvilinear models, as an average rate of decline in the proportion of food in the stomach relative to the time it takes for a fish to evacuate food during a complete evacuation cycle (Bromley 1994). The rate parameter k in the power exponential functions fitted to evacuation data is related to the time at which one-half the meal present at time zero has emptied (Elashoff et al. 1982; Santos and Jobling 1992), and the shape parameter in the power exponential and logistic functions is used to describe changes in the increase or slowing of food evacuation (Elashoff et al. 1982; Hopkins and Larson 1990).

Prior to fitting an appropriate model to the evacuation data with increasing postprandial time, Olson and Mullen (1986) recommended truncating the data (Figure 2) at the time when empty stomachs first begin to appear. This is because the exact time when they became empty is not known and so the data distributions before truncation can result in a substantial downward bias of evacuation rate estimates, and thus lower calculated daily rations (Olson and Mullen 1986). The coefficients of the models providing the best fit to the adjusted data after truncation, are then incorporated into a consumption model.

Factors that may affect rates of stomach evacuation include temperature, size of predator, and the prey type, size, and proximate composition (for a review and summary, see Bromley 1994 and Berens 2005). In general, the absolute rate of gastric evacuation (i.e., grams of food leaving the stomach per hour) will increase with increasing predator size, but the relative rate (grams per unit body weight) will decrease or stay the same (Flowerdew and Grove 1979; Jobling 1980; Bromley 1994). Results from evacuation experiments of skipjack (*Katsuwonus pelamis*) (Magnuson 1969) and yellowfin (Olson and Boggs 1986) tunas showed that a constant proportion of the meal of most prey types is evacuated per unit time, regardless of the size of the meal (Olson and Mullen 1986). However, Olson and Boggs (1986) found that large meal sizes of prey with high lipid content (*i.e.*, mackerel, *Scomber japonicus*) were evacuated more slowly by yellowfin tuna than prey with a lower percentage of lipids (Figure 2). Consequently, they found it necessary to develop separate equations for calculating daily ration for each prey type.

Experimental designs to estimate gastric evacuation rates typically work with a group of fish of the same species captured from the wild that are acclimated to a land-based tank facility and fed meals of frozen-thawed prey items (*e.g.*, Olson and Boggs 1986; Wexler *et al.* 2003). Fish are sorted by size and either tagged to identify individuals during group feedings (Olson and Boggs 1986), placed into separate tanks (Berens and Murie 2008; Gillum *et al.* 2012), or fed known quantities and types of prey containing individually labeled beads (Hughes et al. 2014). Prior to the experiment, food is withheld from the fish for at least 24 hours to facilitate clearing of the entire stomach and intestines. Meal items are selected based on natural diet preferences and each prey species is thawed, blotted dry and weighed prior to feeding. Depending on the experiment objectives, mixed or singular prey meals are offered, usually one food item at a time, until satiation. Serial sampling (*i.e.*, sacrificing) of fish (Olson and Boggs 1986) or gastric lavage (Bush and Holland 2002; Gillum *et al.* 2012) are usually performed at short time intervals (*e.g.*, 1, 2, 4, 8

hours) following satiation, and the time is recorded from the time of food particle ingestion by an individual fish until the time the fish is sacrificed or lavaged. Each sacrificed fish is measured and weighed, and all prey items in the stomach are removed, sorted, blotted dry, and weighed. Although wet-mass prey data are preferable to use in the daily ration calculations, the stomach contents can also be further analyzed after oven drying to obtain dry weights for estimation of calorific intake (*e.g.*, Eggleton and Schramm Jr 2002).

Most gastric evacuation experiments have been designed to test single meals rather than sequential multiple meals (Bromley 1994). Multiple meals could result in an increased evacuation rate of the initial meal and a decreased rate of the subsequent meal (Persson 1984; Ruggerone 1989b), or in an overall increase in the rate compared to that of a single fed meal (Jones 1974). Species specific differences of evacuation rates in response to single or multiple sequential meals should be considered when designing experiments for estimates of feeding rates.

The measurement unit (volume, wet weight, dry weight) of prey type amounts used to describe the evacuation process should be the same as that of the mean stomach contents analyzed prior to fitting models to the evacuation data and estimating feeding rates (Hopkins and Larson 1990; Bromley 1994). Because most field studies measure the wet weight of stomach contents (but see Griffiths et al. 2007), it is more appropriate to measure evacuation in terms of wet weight (Bromley 1994), unless calorific measurements are of interest.

One consumption model commonly used to estimate daily ration in sub-tropical and tropical pelagic predator species of fish such as tunas (Olson and Boggs 1986; Olson and Mullen 1986; Maldeniya 1996; Ménard *et al.* 2000; Griffiths *et al.* 2007; Griffiths *et al.* 2009; Young *et al.* 2010; Olson *et al.* 2016), billfish (*Tetrapturus audax* and *Xiphias gladius*, Young et al. 2010), dolphinfish (*Coryphaena hippurus*) (Olson and Galván-Magaña 2002), and sharks (*Sphyrna lewini*, Bush and Holland 2002) (*Prionace glauca* and *Isurus oxyrinchus*, Young *et al.* 2010) that consume a variety of prey that are evacuated at different rates, has been described by Olson and Mullen (1986), using the following equation:

$$\hat{r} = \sum_{i=0}^{I} \frac{\overline{W}i}{Ai}$$

where feeding rate ( $\hat{r}$ , grams per hour) is calculated by dividing the mean weight of the stomach contents per predator ( $\overline{W}$ , grams) by the integral (A, proportion × hours = hours, *i.e.*, the regression parameters aand b are used to calculate the area under the evacuation model) of the function that best fits the adjusted experimental gastric evacuation data after truncation (see above). Parameter A was defined as "the average amount of time required to evacuate the average proportion of all meals present in the stomach at any instant in time". The subscripts *i* refer to each of *I* prey types and the daily meal ( $\hat{r}$ ) is multiplied by 24 for fish that feed both day and night. Daily ration is the daily meal expressed as a weight-specific daily rate of consumption—as either percent body weight per day (BW d<sup>-1</sup>), or as grams body weight per day (g BW d<sup>-1</sup>)—of specific prey types and quantities for different size predators (Olson *et al.* 2016).

The consumption model accounts for fishes that feed multiple times during a day, is flexible, can be used for a variety of stomach evacuation functions (Olson *et al.* 2016), and does not require back-calculated estimates of prey size. The model, however, does not address the possibility of one meal affecting the evacuation rate of another meal that had already been consumed but not completely evacuated prior to sampling the stomach (*e.g.*, Persson 1984).

Some of the other consumption models require back-calculated estimates of the original prey mass based on prey size—at the time of ingestion (Elliott and Persson 1978), which is difficult to estimate for field-sampled stomachs, especially for soft-bodied prey that can be digested and evacuated more rapidly than other prey. Some prey types leave residual hard parts (*e.g.*, otoliths, backbones, beaks) that accumulate over several meals. If these issues are not carefully considered, they can lead to significant overestimates in consumption as back-calculated prey biomass may predict a total meal biomass that is higher than the stomach can physically contain. Furthermore, reliable length-weight relationships are required for each prey taxon ingested, thus requiring extensive ancillary studies on each prey taxon. Models for digestion rates derived from laboratory experiments using indices of prey digestive states are, therefore, also necessary to estimate species-specific prey consumption (Bush and Holland 2002; Berens and Murie 2008; Beaudreau and Essington 2009).

2.1.2. Sequential field sampling of stomachs and variations in gut fullness

Other feeding models have been used to estimate daily ration without independent laboratory estimates of gastric evacuation rates (as described in Héroux and Magnan 1996) based on sequential field sampling of stomachs and variations in gut fullness (*e.g.*, Stillwell and Kohler 1982; Boisclair and Leggett 1985; Sainsbury 1986; Jarre-Teichmann et al. 1991). Young et al. (1997) estimated the instantaneous rate of evacuation of southern bluefin tuna (*Thunnus maccoyii*) from the greatest decline in gut fullness (*i.e.*, the maximum evacuation rate) over one-hour intervals of field sampling within a 24-hr period using a model by Boisclair and Marchand (1993) that assumes no feeding occurs during the period of maximum food evacuation. The estimated evacuation rate was then assumed to be exponential and incorporated into a feeding model after Elliott and Persson (1978) to estimate daily ration. Butler et al. (2010) used high and low periods of stomach fullness from Atlantic bluefin tuna (*Thunnus thynnus*) that were sampled hourly from sunrise to sunset over a 24-hour period to estimate the gastric evacuation rate using the exponential decay model of Elliott and Persson (1978). The gastric evacuation rate and the mean stomach fullness of the hourly means were then incorporated into the feeding model of Eggers (1977) to estimate the daily ration.

Daily ration has also been estimated from model parameters of stomach content data in relation to the time trajectory to attain stomach fullness over one (Sainsbury 1986) (Figures 3A, 3B) and two feeding cycles (Jarre-Teichmann et al. 1991) (Figures 3C, 3D) without laboratory estimates of gastric evacuation rates. Both methods assumed exponential rates of decline in gastric evacuation after methods by Eggers (1977) and Elliott and Persson (1978). Computation of the daily rations ( $R_d$ ) for the two methods—based on initial equations by Sainsbury (1986) and slightly modified and described in Appendices 1-4 of Jarre-Teichmann *et al.* (1991)—are described below:

Model IA (assumes constant ingestion over time for one feeding period) (Figure 3A):

$$R_{d} = \int_{Fb}^{Fs} J1 \cdot dt = J1 \cdot (F_{s} - F_{b})$$

Model IIB (assumes that ingestion declines with increasing stomach fullness over a single feeding period) (Figure 3B):

$$\begin{aligned} \mathsf{R}_{d} &= \int_{\mathsf{F}b1}^{\mathsf{F}s1} [\mathsf{S}_{\infty} \cdot (\mathsf{E} + \mathsf{J}2) - \mathsf{J}2 \cdot \mathsf{S}_{t}] \mathsf{d}t \\ &= \mathsf{E} \cdot \mathsf{S}_{\infty} \cdot (\mathsf{F}_{s} - \mathsf{F}_{b}) + (\mathsf{S}_{\infty} - \mathsf{S}_{r}) / (1 + \mathsf{E}/\mathsf{J}2) \cdot (1 - \exp(-(\mathsf{E}+\mathsf{J}2) \cdot (\mathsf{F}_{s} - \mathsf{F}_{b}))) \end{aligned}$$

Model IC (similar to Model IA but adjusts for two feeding periods) (Figure 3C)

$$R_{d} = \int_{Fb1}^{Fs1} J1 \cdot dt + \int_{Fb2}^{Fs2} J1 \cdot dt = J1 \cdot (F_{s1} - F_{b1} + F_{s2} - F_{b2})$$

Model IID (similar to Model IIB but adjusts for two feeding periods) (Figure 3D):

$$R_{d} = \int_{Fb1}^{Fs1} [S_{\infty} \cdot (E + J2) - J2 \cdot S_{t}] dt + \int_{Fb2}^{Fs2} [S_{\infty} \cdot (E + J2) - J2 \cdot S_{t}] dt$$
  
=  $E \cdot S_{\infty} \cdot (F_{s1} - F_{b1} + F_{s2} - F_{b2}) + (S_{\infty} - S_{r1}) / (1 + E/J2) \cdot (1 - \exp(-(E+J2) \cdot (F_{s1} - F_{b1})))$   
+ $(S_{\infty} - S_{r2}) / (1 + E/J2) \cdot (1 - \exp(-(E+J2) \cdot (F_{s2} - F_{b2})))$ 

where,  $F_s$  is the end of a single feeding,  $F_b$  is the beginning of a single feeding,  $F_{s1}$  is the end of the first feeding,  $F_{s2}$  is the beginning of the first feeding,  $F_{s2}$  is the end of the second feeding,  $F_{b2}$  is the beginning of the second feeding, J1 is ingestion rate (g h<sup>-1</sup>), J2 is instantaneous rate of ingestion (h<sup>-1</sup>), E is instantaneous rate of gastric evacuation (h<sup>-1</sup>), S is stomach contents (g), *t* is time (h), S<sub>t</sub> is stomach contents at time *t*, S<sub>r</sub> is residual stomach contents, and S<sub>∞</sub> is the asymptotic stomach contents. Time trajectories of stomach contents for feeding period (Appendix 2 in Jarre-Teichmann *et al.* 1991) and residual stomach contents are parameters for each feeding period (Appendix 3 in Jarre-Teichmann *et al.* 1991).

The trajectories of stomach fullness for brown trout (*Salmo trutta*) (Elliott 1975; Elliott and Persson 1978) and skipjack tuna (Magnuson 1969) were compared with stomach content trajectories of the two different models of feeding cycles to test the model's performance with previous experimentally determined estimated consumption rates from laboratory studies (Figure 4). In comparison to estimates of a continuous feeding model by Elliott and Persson (1978), the ration estimates determined by either one or two of the models were reasonably comparable (Sainsbury 1986). However, the assumption of an exponential rate of decline in stomach evacuation by all feeding models used, prior to truncation of the evacuation data (Olson and Mullen 1986), was not appropriate in the case of skipjack consumption rates (Magnuson 1969) (Figure 4, top panel). This is because Magnuson (1969) found that a binomial regression fit the evacuation data better than other models. Subsequent studies (Olson and Boggs 1986; Olson and Mullen 1986; Berens and Murie 2008) recommended that prior to fitting a model to the gastric evacuation data with increasing postprandial time, data should be omitted after empty stomachs begin to occur to avoid biases associated with the rate of evacuation (section 2.1.1.).

Parameterizing the feeding times of fish in nature and their feeding rates using stomach content data may provide fairly reliable estimates of food consumption without having to conduct labor-intensive experiments that may be logistically difficult or cost-prohibitive (Jarre-Teichmann *et al.* 1991). However, this approach assumes that feeding only occurs during arbitrary feeding periods and assumes a simple exponential rate of evacuation which is probably inappropriate and does not take into account the effect of meal types and different temperatures on the rate of decline, thus, these types of assumptions of predator-specific feeding periodicity and prey-specific rates of evacuation have the potential to result in under- or over-estimation of daily ration (Mullen 1986; Olson and Mullen 1986; Hansson *et al.* 1996).

#### 2.1.3. Empirical relationships of stomach content data

Others have used stomach content data and a generalized relationship between the maximum gastric evacuation rate (*R*) and temperature (*T*) (i.e.  $R = ae^{bT}$ ) (Elliott 1972) developed from a literature review of several marine and freshwater fishes (Durbin and Durbin 1980; Durbin et al. 1983). This relationship

was used to estimate the instantaneous rate of gastric evacuation for species of fish such as the eastern Pacific bonito, *Sarda chiliensis lineolata*, (Pauly et al. 1987), skipjack tuna (Durbin et al. 1983 using data by Magnuson 1969), Atlantic and Pacific whiting, *Merluccius* spp., (Durbin et al. 1983; Livingston 1983; Livingston and Bailey 1985), and Atlantic cod, *Gadus morhua*, (Durbin et al. 1983). However, this type of inference has the potential for underestimating the daily ration for predatory pelagic species of fish.

## 2.1.4. Daily ration estimates for pelagic predators

The most reliable estimates of daily ration appear to be those estimates that incorporate feeding models associated with species-specific stomach content data collected in nature and gastric evacuation rates conducted in controlled, laboratory settings. Daily ration has been estimated for a number of pelagic predators but very few studies (Magnuson 1969; Olson and Boggs 1986; Bush and Holland 2002) have conducted gastric evacuation rate experiments on tropical or subtropical species of pelagic fish (Table 1) due to lack of suitable holding facilities for maintaining these fish in captivity, and the logistics and cost of collecting and transporting live specimens. As a result, most diet studies have assumed rates of evacuation for pelagic predators (*e.g.*, Maldeniya 1996; Ménard et al. 2000; Olson and Galván-Magaña 2002; Griffiths et al. 2009; Young et al. 2010; Abitia-Cárdenas et al. 2011) based on experimental results of a single species and limited size range of yellowfin tuna (*Thunnus albacares*) in captivity (Olson and Boggs 1986), or based on feeding model parameters of changes in gut fullness from fish sampled at short time intervals in the field (section 2.1.2) such as that applied to southern bluefin tuna, *Thunnus maccoyii*, (Young et al. 1997) and Atlantic bluefin tuna, *Thunnus thynnus*, (Butler et al. 2010).

It is interesting to compare daily ration estimates between some known predators that co-occur within similar ecosystems of tropical and sub-tropical waters of the Pacific Ocean (Table 1.). For example, mean daily ration for yellowfin ranged from 2.8–4.6% BW day<sup>-1</sup> for age classes of 1–4+ years with the highest rations being for the 2-year age class (55–86 cm FL) (Olson and Boggs 1986). The estimated daily rations of 3.6% BW day<sup>-1</sup> for adult striped marlin (*Kajikia audax*) (Abitia-Cárdenas *et al.* 2011) and 2.2-4.3% BW day<sup>-1</sup> for scalloped hammerhead sharks (Bush and Holland 2002), were comparable to that of yellowfin tuna (Olson and Boggs 1986). In contrast, the daily ration estimates for dolphinfish of comparable sizes to yellowfin were considerably higher in the EPO (9.6–19.8% BW day<sup>-1</sup>) (Olson and Galván-Magaña 2002) but much lower off eastern Australia (ca 2-3% BW day<sup>-1</sup> if estimated over a 24-hr period) (Young et al. 2010). Compared with other pelagic predators of comparable sizes sampled off eastern Australia, prey consumption and daily ration was the highest for blue sharks (*Prionace glauca*) at 8.88% BW day<sup>-1</sup> (Young et al. 2010). For most of the aforementioned species, daily ration estimates were based on stomach content analysis of wild-caught specimens that were assumed to have a gastric evacuation rate similar to yellowfin tuna (Table 1.).

The average daily ration for yellowfin tuna in the EPO (Olson and Boggs 1986) is similar to yellowfin and other tunas of comparable sizes (*i.e.*, < 122 cm FL) from other tropical oceans (Maldeniya 1996; Ménard *et al.* 2000; Griffiths *et al.* 2009), but much higher than those reported for longtail tuna (*Thunnus tonggol*) (Griffiths *et al.* 2007), bigeye tuna (*Thunnus obesus*) (Young et al. 2010), and southern bluefin tuna (*Thunnus maccoyii*) (Young *et al.* 1997; Young et al. 2010) in subtropical and temperate waters (Table 1.). These differences are likely due to differences in metabolic rates and the cooler water temperatures from which these species were sampled, which can influence prey evacuation rates (Brett and Higgs 1970; Jobling 1980; Bromley 1994), or from different methodology of calculating evacuation rates and thus, daily ration (*e.g.*, Young et al. 1997).

The daily ration method used by Olson and Mullen (1986) has shown that it can provide reliable estimates of prey-specific consumption rates for some key predators despite some limitations of the stomach and evacuation rate analyses (Olson and Boggs 1986; Olson and Mullen 1986), labor intensive procedures, and

concerns that laboratory experiments may not produce results that are directly applicable to fish in nature (Bromley 1994). However, contrary to the assertions of Bromley (1994), *in situ* and laboratory comparisons of evacuation rates have shown remarkably similar results (Hopkins and Larson 1990), providing some confidence in laboratory-derived evacuation estimates. In addition to providing corroboration of field-estimated consumption and gastric evacuation rates, controlled laboratory experiments can directly evaluate the effect of water temperature, prey type, meal size, and ontogenetic predator stage on these rates.

#### 2.2. Indirect methods to estimate consumption rates

#### 2.2.1. Bioenergetics modeling

Bioenergetic expenditures for routine metabolism, somatic growth, reproduction, SDA (specific dynamic action), egestion, and excretion are used in mass-balanced models to estimate food consumption, daily ration, and thus Q/B in many fish species at the individual and population level (Olson et al. 2016; Deslauriers et al. 2017). A generic energy balance model (Winberg 1956) has been represented by:

$$C = R + SDA + F + U + \Delta B$$

where *C* is consumption rate (joules (J) g<sup>-1</sup> d<sup>-1</sup>; total energy intake required), *R* is the energetic cost of total metabolic rate (*i.e.*, standard and active metabolic rates that are usually determined from respirometry experiments of oxygen consumption rates), SDA (*i.e.*, the energetic cost of digestion and protein synthesis determined from respirometry and feeding experiments), *F* is egestion (*i.e.*, energy lost to undigested food (faeces) and other substances), *U* is energy lost to nitrogenous excretion, and  $\Delta B$  is energy accumulated and allocated toward growth and reproductive output. Kitchell et al. (1977) rewrote this equation as:

where,

$$C = R + \Delta B + A$$
$$A = F + U + SDA$$

and *A* is the proportion of energy lost to *U*, *F*, and *SDA* which are constant proportions of consumption. Thus, in order to solve for *C*, the equation is differentiated as explained in the Supplementary information of Lawson et al. (2018) using parameters *FA* as the proportion of ingested energy lost to *F*, *UA* as the proportion of assimilated energy lost to *U*, and *S* as the proportion of assimilated energy lost to *SDA*. The equation for consumption then becomes:

$$C = \frac{(\Delta B + R)}{1 - (FA + UA(1 - FA) + S(1 - FA))}$$

The consumption rate (*C*) is converted to daily ration (% BW  $d^{-1}$ ) by dividing by the weighted mean prey energy (J  $g^{-1}$ ) consumed by an age- and weight-specific predator (obtained from diet data).

Individual age- or length-structured bioenergetics models can be expanded to the population level if reliable information of mortality and recruitment of the population is known (Essington 2003). This, in turn, can provide a means to estimate predator demand on available prey and evaluate predation responses to fishing intensity and size- and age-selective fishing methods (Essington et al. 2002; Schindler et al. 2002).Olson *et al.* (2016) provided a thorough review of bioenergetics modelling for tunas. Bioenergetic models (*e.g.*, Kitchell *et al.* 1977; Olson and Boggs 1986; Hansen *et al.* 1993) offer the advantage of requiring fewer fish compared to the large sampling field efforts required for direct

estimation of daily ration. However, bioenergetics models also require reliable data on size- and temperature-specific and meal-dependent metabolic rates, which are generally acquired from experiments of fish in captivity (*e.g.*, Korsmeyer and Dewar 2001; Stieglitz *et al.* 2018). Many pelagic fish species (*e.g.*, billfishes, bigeye tuna, and sharks) cannot be maintained easily in captivity, so several of these bioenergetic parameters cannot be obtained experimentally or reliably using other proxies, but have been inferred or extrapolated from other species of fish (*e.g.*, Kirby 2005; Bethea *et al.* 2007; Chapman *et al.* 2011).

The allometric function of mass-specific standard metabolic rate (*i.e.*, SMR, the "resting" rate) is obtained from measurements of oxygen consumption from immobilized fish that swim continuously (*i.e.*, tunas and dolphin fish) using neuromuscular blocking agents (Brill 1979; 1987; Benetti et al., 1995) and from extrapolation of oxygen consumption and swimming velocity relationships back to zero speed (Dewar and Graham 1994). SMR (in gO<sub>2</sub> g<sup>-1</sup> d<sup>-1</sup>) is converted to an energy equivalent value compatible with bioenergetics modeling using an oxy-calorific coefficient (based on species-specific proximate composition and caloric values) to convert O<sub>2</sub> consumption into Joules. This value can be further adjusted by a temperature-dependent function (Deslauriers et al. 2017) before combining with the active metabolic rate for the total respiration costs. Metabolic rates of free-swimming captive tunas have also been estimated from weight loss and changes in energy caloric densities during starvation (Boggs, 1984; Boggs and Kitchell, 1991). Equations for allometric scaling of SMR have been limited to smaller sample sizes and narrow size ranges of pelagic fish in captivity (*e.g.*, Brill 1979; Brill 1987; Dewar and Graham 1994; Benetti et al. 1995). As a result, the allometric relationship has been frequently used in bioenergetics models for sizes beyond the experimental range of tunas (*e.g.*, Essington 2003).

The energetic costs of locomotion (*i.e.*, swimming metabolism as a function of fish length and swimming speed) (Olson and Boggs 1986) are combined with the mass-specific SMR to obtain total respiration expenditures. Sustained speeds for tunas have been estimated from acoustic telemetry tracking (Carey and Olson 1982; Holland et al. 1990), from tank experiments (Magnuson 1973), and from an empirically derived model to predict the minimum sustained swim speed required to achieve sufficient hydrodynamic lift for species-specific tuna sizes and densities (Magnuson 1973; Magnuson and Weininger 1978). The ratio of observed tuna swim speeds (from tracking and tank studies) to estimated minimum swim speeds varies between 1.1 and 1.75 (depending on species) and are used as multipliers of the calculated minimum swim speed (Essington et al. 2002; Ferriss and Essington 2014) to estimate the average swimming speed of locomotory costs.

Oxygen consumption rates measured in the laboratory to estimate metabolic rates and SDA require adequate holding facilities and sound handling practices for pelagic fishes. Reliable measurements may be affected by the stress of large pelagic fish associated with confinement and training in respirometer/swimming tunnels unless they are acclimated and "trained" properly prior to measurements (Klinger et al. 2016). Due to the potential difficulties associated with experimentation, SDA has only recently been measured for the first time in captive tunas (Fitzgibbon *et al.* 2007; Clark *et al.* 2010; Klinger *et al.* 2016) and dolphinfish (Stieglitz *et al.* 2018). SDA is a critical component of bioenergetics models of pelagic fishes, with mean SDA coefficient values of 6–35% for captive tunas and dolphinfish, which varied with diet composition (Fitzgibbon *et al.* 2007; Clark *et al.* 2010; Klinger *et al.* 2018). SDA was also found to be temperature-dependent in yellowfin tuna in which digestion rates and metabolic expenditure increased with increasing temperature (Klinger *et al.* 2016).

Reliable estimates of the parameters for the allometric function of maximum consumption rate (g g<sup>-1</sup> d<sup>-1</sup>) are essential as inputs for some bioenergetics models in order to place an upper limit on the growth potential of a fish (*e.g.*, Kitchell et al. 1977, 1978; Deslauriers et al. 2017), given that some species of fish,

especially tunas, have the capacity to consume more food than is needed to fulfil average daily energy expenditures (Olson et al. 2016). However, maximum consumption rates have only been determined for skipjack tuna fed limited types of prey in captivity and ranged from 12–35% BW day<sup>-1</sup> (Magnuson 1969; Kitchell et al. 1978). Direct determination has not been made for yellowfin tuna (Olson 1990) but was estimated at about 30% BW day<sup>-1</sup> based on stomach content and laboratory experiments (Olson and Boggs 1986; Olson et al. 2016).

Ontogenetic diet variation can also have a profound effect on consumption rates estimated from bioenergetics models if changes in prey energy consumed over the lifetime of a predator, such as yellowfin tuna (Graham *et al.* 2007), are not considered (Lawson *et al.* 2018). Unfortunately, the majority of models incorporate only the most common prey of adults (Lawson *et al.* 2018), and therefore underestimate consumption rates of other prey types consumed during younger life stages.

Some of the largest concerns of using bioenergetics models to characterize the trophic and energy dynamics of predator and prey populations has been the use of empirical and laboratory data to estimate physiological parameters, which may not be representative of conditions in the wild (Hansen et al. 1993). Frequently there is poor agreement between direct methods of daily ration (*i.e.*, trophic studies and laboratory estimates of gastric evacuation rates) and those obtained from bioenergetics models (Ney 1993). Estimates of energy consumption/daily ration from bioenergetic models are only as good as the quality and reliability of the input values. Some of the more important errors in the output of the models described by Ney (1993) are associated with unknown species-specific activity expenditures and extrapolation of power functions to describe maximum consumption and standard metabolism relative to weight of one life stage of fish and applied to other life stages. For example, the same power function relationship estimated for juvenile yellow perch (Perca flavescens) (Post 1990) and largemouth bass (Micropterus salmoides) (Rice et al. 1983) in captivity was extrapolated to younger and older fish. Another source of error is associated with using physiological values from another species. For example, bioenergetic model parameters of Atlantic cod (Gadus morhua) were used for a lake fish, burbot (Lota lota) (Rudstam et al. 1995). Errors are also associated with the inappropriate use of field data—habitat temperatures and energy densities of predators and prey are seasonally and spatially variable—in assuming that the species is exposed to only those habitat conditions measured at the time of sampling (e.g., as described by Olson and Boggs (1986). Therefore, it has been recommended that estimates of consumption rates obtained through bioenergetic models should be verified with estimates obtained from controlled laboratory experiments of stomach evacuation (Ney 1993) and field consumption rates estimated from long-term diet analyses that consider spatial and temporal dynamics in foraging patterns, especially in pelagic species, such as tunas (Olson and Boggs 1986).

Typically, daily rations estimated from bioenergetic models are higher than those estimated from the direct method when compared and estimated for the same species of fish (*e.g.*, Olson and Boggs 1986; Hansson et al. 1996; Overholtz 2006; Beaudreau and Essington 2009) (Tables 1. and 2.). A positive bias could be due to unrealistic measurements in tuna metabolic rates during handling, captivity, or stress (Olson and Boggs 1986). Activity costs associated with metabolic processes (Ney 1993; Beaudreau and Essington 2009) and variable prey and consumer energy density values (Lawson et al. 2018) continue to be a major source of uncertainty in many bioenergetic models. However, stomach fullness may also be underrepresented in field sampling of forage biomass for direct estimates of feeding rates, and sampling should be more repetitive and sufficient to provide more than just point estimates in time and scale (as discussed in Olson and Boggs 1986) and to account for sex-specific differences in foraging rates (Beaudreau and Essington 2009).

### 2.2.2. Contaminant dynamics to estimate consumption

Dietary uptake models have been used to model the bioaccumulation of organic contaminants in fishes

(Barber 2008). Therefore, it has been possible to estimate fish consumption rates based on mass balance models of contaminant concentrations in predators and their prey (*e.g.*, Rowan and Rasmussen 1996; Trudel *et al.* 2000).

Several studies have modeled consumption rates based on radioactive cesium (<sup>137</sup>Cs) concentrations in fish and their prey (Olson and Boggs 1986; Forseth et al. 1992; Rowan and Rasmussen 1996; Rowan et al. 1997; Tucker and Rasmussen 1999) According to Trudel et al. (2000), the models require knowledge of the concentration of the chemical both in the predator and their prey, the chemical absorption efficiency from the prey, and the elimination rate of the chemical by the predator. Some advantages in using the cesium concentration analysis and the applied models to estimate consumption rates for fish are that low or high levels of ambient cesium contamination can be used (Rowan and Rasmussen 1996; Rowan et al. 1997; Tucker and Rasmussen 1999), and that they provide food consumption rates similar to those derived using stomach evacuation and content analyses (see Forseth et al. 1992 and Forseth et al. 1994) but require fewer numbers of fish and a lower frequency of sampling for the analyses once the weight- and temperature-specific turnover rates of the contaminant in the fish are known. Forseth et al. (1992) have demonstrated that the radioisotope method (*i.e.*, radiocesium) can be used to detect variations in ration size due to temperature, fish weight, and food availability in brown trout and provides sensitive shortterm and robust long-term estimates of food consumption. In an earlier study, Olson and Boggs (1986) examined cesium concentration in yellowfin tuna and their prey to estimate prey consumption. However, their model was based on several assumptions including the inference of cesium concentrations in prey from different prey species, a similar elimination rate of cesium concentration to that of albacore, and an assumed absorption efficiency of cesium from the prey.

One of the more promising contaminants used to estimate consumption rates with a mass balance model has been mercury (Hg) (Trudel et al., 2000). This is because, similar to <sup>137</sup>Cs, Hg is mainly absorbed by fish through their food, and Hg is globally occurring in the environment due to natural and anthropogenic processes. Furthermore, reasonably accurate Hg concentrations can easily be measured with small tissue samples by atomic absorption spectroscopy even at low levels of Hg concentrations, and the elimination rate of Hg by fish can be accurately determined using only fish weight and water temperature (Trudel and Rasmussen 1997). Trudel and Rasmussen (1997) were able to examine the influence of fish body size, water temperature, Hg burden (*i.e.*, total quantity of Hg) and concentration on elimination rates, and duration of experiments for 16 species of fishes from the literature using correlation and regression analyses and found that Hg excretion rate was negatively correlated to body size and positively correlated to water temperature. Because Hg is routinely measured by various agencies to test concentration levels in fish (Trudel *et al.* 2000), a large tissue database exists that can potentially be used to examine long-term, spatial, and temporal patterns of consumption rates of predators.

Integration of the differential equation for the mass balance model of Hg concentration results in the following equation to solve for the food consumption rate. [Here, consumption rate is determined by solving for the amount of prey Hg ( $C_{d:}$ ) that must have been consumed to match the observed changes in predator Hg ( $C: \mu g g^{-1}$ ) and body size over discrete age intervals (G: g fish weight g food  $d^{-1}$ ) assuming levels of assimilation efficiency of Hg from prey ( $\alpha$ ), elimination rates ( $E: d^{-1}$ ), and Hg lost to reproduction ( $K: \mu g d^{-1}$ ). If prey Hg concentrations ( $C_d: \mu g g^{-1}$ ) are known, then the model can estimate total consumption. The basic model relates instantaneous consumption rate (I: g food g fish weight  $d^{-1}$ ) to these model inputs.]

$$I = \frac{C_{t+\Delta t} - C_t \cdot e^{-(E+G+K)\Delta T}}{\alpha \cdot C_d [1 - e^{-(E+G+K)\Delta t}]} (E+G+K)$$

where,  $C_t$  and  $C_t + \Delta t$  are the concentration of Hg in fish at time t and  $t + \Delta t$ , and  $\Delta t$  is the time interval (days).

Mercury contaminant analysis may be a useful tool in combination with (*e.g.*, Ferriss and Essington 2014) or in place of other direct and indirect methods for estimating prey consumption rates. Contaminant sampling and analyses are less labor intensive since the method works well with small sample sizes of piscivorous fish because mean fish weight and Hg concentration of fish in each age-class can be determined using a regression model. Furthermore, because this method requires less effort compared with stomach sampling analyses, sampling efforts can be expanded over greater temporal and spatial ranges to estimate prey consumption rates. Compared with bioenergetics models that require accurate estimates of standard metabolic rates and activity costs (Kitchell *et al.* 1977) (see section 2.21), the Hg mass balance model does not require measurements for fish ingestion rates since the elimination rate of Hg is independent of activity rates (Östlund 1969). Although it is possible to accurately measure <sup>137</sup>Cs in muscle tissue samples of fish (Rowan and Rasmussen 1996), these analyses require larger sample sizes and quantity of prey tissue than for the Hg mass balance model analysis (Trudel *et al.* 2000). Thus, the Hg mass balance model (Trudel *et al.* 2000) may provide a better tool than traditional approaches in quantifying the complexities of the predator/prey dynamics in marine ecosystems.

However, a major shortcoming of the Hg mass balance model is its sensitivity to Hg concentrations in fish prey tissue. High variance estimates in the Hg-at-size data for albacore (*Thunnus alalunga*) and the uncertainty in their prey Hg concentrations failed to generate biologically plausible daily consumption estimates in this species using an integrated model that linked growth and metabolism with changes in Hg concentrations (Ferriss and Essington 2014). Therefore, this method requires accurate predator-specific diet information or increased frequency of fish sampling to analyze the concentration of Hg directly from stomach contents if prey contamination varies seasonally (Trudel *et al.* 2000).

### 2.2.3. Energy intake estimates (consumption) from visceral temperature increases

Archival tag information from temperate and subtropical tuna species (*e.g., T. maccoyii* and *T. orientalis*) (Table 2.) has improved our understanding of temporal feeding patterns and daily intake rations over extended periods of time (Bestley et al. 2008; Gunn et al. 2001; Whitlock et al. 2013; Whitlock et al. 2015). Tags implanted within the body cavity of bluefin tunas have recorded visceral warming patterns in relation to feeding events (*i.e.*, postprandial increases in metabolism or heat increment feeding (HIF)) that can be quantified by the time to maximum visceral temperature, the height of the heat increment above the basal visceral temperature, the duration of the heating event, and the area calculated under the curve of the thermal response. Strong increases in visceral temperatures primarily occur in association with metabolic heat production of digestion (*i.e.*, SDA; Carey et al. 1984). The HIF unit (the extent and increase in the amount of visceral warming) is related to the amount and composition of the prey type (meal energy in kcal) consumed at various ambient water temperatures (Whitlock et al. 2013) but requires validation in a captive setting for inference to field applications. The uncertainty in the estimated daily caloric intake of wild tuna was associated with the effects of meal size and ambient temperature on HIF magnitude and the measurement uncertainty due to differences in tag placement of individuals (Whitlock et al. 2013).

The information collected from archival tagged fish appears useful for estimating long-term consumption rates but is limited to species that prefer more temperate habitats, and by the numbers of individuals tagged and recaptured, the cost and retrieval of the tags, and the amount of uncertainty in the caloric intake estimates.

## 2.2.4. Growth-based estimates of consumption

Growth models, such as the von Bertalanffy growth function (VBGF) (von Bertalanffy 1938), are commonly

fit to size-at-age data for economically important fish species. This model of size-at-age data is similar to a fish growth rate model based on a mass-balance equation of bioenergetic models (von Bertalanffy 1938; Ursin 1967), and theoretically, can be used to estimate consumption rates (Pauly 1986). Pauly (1986), Temming (1994a) and He and Stewart (1998) have used this method to estimate consumption rates, but they did not determine the accuracy or precision of the consumption rates calculated (Essington *et al.* 2001).

Pauly (1981), Temming (1994a), Temming (1994b), Essington *et al.* (2001), Temming and Herrmann (2009), and Wiff *et al.* (2015) described the derivation of the VBGF to show how it relates to an energy balance equation similar to that used in bioenergetic models and to show the underlying assumptions associated with these equations and how they can be used to estimate consumption rate.

Following is the general growth model described by Paloheimo and Dickie (1965) where weight time<sup>-1</sup>  $(dW_t/dt)$  is equal to the difference between the total rate of energy assimilation  $(HW^d_t)$  and the energy expenditures (energy losses)  $(kW^n_t)$ ;

$$\frac{\mathrm{d}W_t}{\mathrm{d}t} = HW_t^d - kW_t^n$$

where, *d* = allometric scaling of consumption, *n* = allometric scaling of energy costs, and *k* is an energy loss constant.

With the assumption that n = 1 (von Bertalanffy 1938), the above growth equation can be simplified, and fish will approach an asymptotic weight that can be solved by setting the growth rate to 0; the simplified equation can be integrated to form the "generalized VBGF" (gVBGF) (Pauly 1981; Temming 1994a) as,

$$W_t = W_{\infty}(1 - \exp(-k(1 - d)(t - t_0)))^{\frac{1}{1 - d}}$$

where,  $t_0$  is the age at which weight (*W*) equals 0 and *d* is the exponent of the relationship between gill surface area to body mass, generally ranging between 0.5 to 0.95 in marine fishes (Pauly 1981).

The original von Bertalanffy growth models were in fact developed for pigs and then applied to a range of other animals, including fishes. In its original application to fishes, von Bertalanffy (1938) used the guppy that had been estimated to have d=0.667. In developing population models for fisheries, Beverton and Holt (1957) used the VBGF, and largely out of mathematical convenience assumed d=0.667 for all species, and thus were able to simplify the equation to what is known as the "special VBGF" (sVBGF). Given the widespread adoption of the work of Beverton and Holt (1957) the sVBGF has become one of the most commonly used growth models applied to fishes. The sVBGF is represented as:

$$W_t = W_{\infty}(1 - \exp(-k/3(t - t_0)))^3$$

In terms of fish length, the sVBGF is expressed through the length-weight relationship,  $W = aL_b$  and assumes that b = 3 (b is the slope of the length-weight regression) and d = 2/3 (Beverton and Holt 1957; Ursin 1967; Pauly 1981) and is described by the simplified form of the equation (through integration of the general growth model above):

$$L_t = L_{\infty}(1 - \exp(-K(t - t_0)))$$

where, K = k/b.

The daily mass-specific consumption rate of an individual (*i.e.*,  $C_{ind}$ : kg·kg<sup>-1</sup>·day<sup>-1</sup>) is therefore related to the general growth model above and is represented by:

$$C_{\rm ind} = (H/A) \bullet W_t^{d-1}/365$$

where A is assimilation efficiency and H is an assimilation constant.

Essington *et al.* (2001) applied a sensitivity analysis to the assumptions (*i.e.*, those regarding allometry of energy expenditures in the gVBGF (n = 1) and those regarding allometry of consumption in the sVBGF (d = 2/3)) to assess the accuracy and precision of VBGF-derived estimates of consumption rates from bioenergetic and contaminant studies (see Appendix in Essington *et al.* 2001). They found that the estimates were variable among fish and dependent on the form of VBGF used (*i.e.*, "special" or "generalized") and on the size-at-age data used to parameterize the model. However, they found that the gVBGF was robust to reasonable violations in its assumption of allometric scaling of energy expenditures (n) and provided unbiased estimates of consumption rates, thus, potentially the size-at-age data may be used to refine estimates of consumption. However, the sensitivity analysis indicated that for values of d, consumption rates estimated from the sVBGF were considerably biased and generally underestimated the true consumption rates. This indicates that size-at-age based parameter estimates of the sVBGF used in the majority of published growth studies (Wiff *et al.* 2015) are unreliable for estimating consumption rates.

In order to quantify the uncertainty in consumption rates, Essington et al. (2001) further evaluated the precision of the gVBGF-derived estimates of consumption rates using the size at age data for western Atlantic bluefin tuna (Thunnus thynnus thynnus) (Mather III and Schuck 1960; Butler et al. 1977) and yellowfin tuna (Thunnus albacares) (Wild 1986) (Figure 5). They used Bayesian statistics to assess the precision of the estimates for the two species of tunas—using the posterior distribution of consumption rate for a 50-kg individual—by providing the probability of each parameter value and calculating the "uncertainty in probabilistic terms" (i.e., the parameter value has multiple possible outcomes with each having varying degrees of certainty or uncertainty of its occurrence). The length-at-age data (Mather III and Schuck 1960; Butler et al. 1977) converted to weight-at-age data from a length-weight relationship (Clay 1991) for bluefin showed a slowing of growth at the larger body sizes but this was not apparent from the weight at age data of yellowfin (Wild 1986). There was a high probability that consumption rates of bluefin were within a well-defined and narrow interval, whereas there was more uncertainty with the yellowfin estimates (Figure 5). Thus, consumption rates were poorly estimated from the VBGF parameters of the size at age data for yellowfin tuna and were estimated with relatively high precision in bluefin. The precision of these estimates appear to be dependent on the species-specific size-at-age data used to estimate the growth parameters of the VBGF, therefore, VBGF-based consumption estimates may not be as useful for faster growing fish, such as yellowfin (Essington et al. 2001). The precision and biases of consumption rates estimated from the VBGF need to be evaluated for species-specific size-at-age data before it can be used with confidence.

### 2.2.5. Empirical relationships

Given the difficulty and expense of estimating Q/B with field sampling and laboratory experiments, yet its importance in a wide variety of applications in the study of fishes, Palomares and Pauly (1989) developed a predictive model for Q/B based on empirical regressions of asymptotic weight, habitat temperature, a morphological parameter describing tail shape, and food type as independent variables for 108 populations from 38 species of marine and freshwater fishes where Q/B had been experimentally determined. Some years later, Palomares and Pauly (1998) developed an empirical relationship for species of fish where the Q/B values were unavailable expressed as:

$$\log(Q/B) = 7.964 - 0.204 \log W_{\infty} - 1.965T' + 0.083A + 0.532h + 0.398d$$

where  $W_{\infty}$  (asymptotic weight in grams) is the mean weight of a fish in a population if it were to grow indefinitely, T' is the mean water temperature inhabited by the species expressed as 1000/ (°C+273.15), A is the aspect ratio of the caudal fin (a proxy of metabolic activity) and expressed as the ratio of the square of the height of the caudal fin and its surface area, while h and d are dummy variables indicating

herbivores (h=1, d=0), detritivores (h=0, d=1) and carnivores (h=0, d=0). The default value for  $W_{\infty}$  is taken either from  $L_{\infty}$  (the mean asymptotic length) in a length-weight relationship or from  $W_{max}$  (the maximum weight ever recorded for the species). The predicted values of Q/B from the empirical relationship were correlated with observed values (Figure 6) and the residuals of the fit were found to be normally distributed suggesting that the key assumptions of linear regression were met and the model fit the data well ( $r^2=0.516$ ). The effect of asymptotic weight on Q/B was about three times stronger than the effect of A; salinity and morphometric variables were not significant, while the remaining variables had a moderate influence on the predictive power of the model.

Palomares and Pauly (1998) modified their equation to examine the effect of the instantaneous natural mortality rate (M)—estimated from the empirical relationship of Pauly (1980)—on Q/B and to derive predictive models of Q/B across a range of M values corresponding to a multiplicative factor (f) of either 0.5, 1, 2, or 4, and expressed as:

 $\log(Q/B) = 8.056 - 0.300 \log f - 0.201 \log W_{\infty} - 1.989T' + 0.081A + 0.522h + 0.393d$ 

and, for cases where an estimate of the total instantaneous mortality rate (Z) is available, Palomares and Pauly (1998) recommend the following predictive model be used:

$$\log(Q/B) = 5.847 + 0.280\log Z - 0.152\log W_{\infty} - 1.360T' + 0.062A + 0.510h + 0.390d$$

The value of Z showed a strong, positive correlation with Q/B and the gross food-conversion efficiency (GE), defined as GE = Z / (Q/B), due to size related changes in consumption and mortality rates (Pauly 1986) (*i.e.*, smaller fish consume relatively more food and are often more abundant than larger fish). It should be noted that these models represent an update of the predictive models given by Palomares and Pauly (1989), including a typographical correction in the sign of the temperature factor from negative to positive (see Christensen *et al.* 2009).

The empirical model of Palomares and Pauly (1998) was thought to be useful for the parameterization of trophic models of ecosystems without further requirements of data collection and laboratory analyses to estimate consumption rates (Jarre *et al.* 1991). However, a major shortcoming of this method is its reliance on assumptions of constant coefficients for a species, regardless of the environment it inhabits (*i.e.*, marine versus freshwater), and it does not account for changes in population size structure (Wiff *et al.* 2015) and how these changes affect predation rates (Essington *et al.* 2001). The biological premise for predicting Q/B from life history and temperature parameters has been considered reasonable, but for many species, the models do not result in precise estimates of food consumption (Jarre *et al.* 1991), especially if the values of  $L_{\infty}$  and Z used—that can be difficult to estimate even for data-rich species—are imprecise.

## 3. SUMMARY AND CONCLUSIONS

One of most widely used ecosystem models that characterizes marine ecosystems is Ecopath with Ecosim software (Christensen and Pauly 1992), a mass-balance trophic model, that describes and quantifies the complexities in the spatial and temporal dynamics of predator/prey relationships and the influence of fisheries impacts on these dynamics. An important parameter of the model is Q/B, the consumption biomass ratio. This parameter facilitates the quantification of the trophic impact of each predator on each of its prey within an ecosystem (Essington *et al.* 2002) and determines the prey biomass that is required to be available to each predator, after taking into account the standing biomass, total mortality (P/B) and ecotrophic efficiency of both the predator and prey. Quantifying diet composition, daily ration, gastric evacuation, and the consumption rate of top consumers within an ecosystem (*e.g.*, Olson and Boggs 1986; Olson and Galván-Magaña 2002; Griffiths *et al.* 2009; Abitia-Cárdenas *et al.* 2011; Griffiths *et al.* 2019) are all essential requirements for estimating Q/B.

Although there are several direct and indirect methods to estimate consumption of key predators within

the EPO ecosystem, all are subject to error and not without their limitations and assumptions in producing reliable estimates of consumption rates. Direct methods (*i.e.*, trophic studies and gastric evacuation experiments) continue to be valuable for estimating fine-scale variations in food consumption (*i.e.*, daily) and are useful in calibrating and refining bioenergetics models that can provide more long-term information from fewer individuals. General agreement alone does not provide validation of consumption rates estimated from different methods, but the observed consistency of the estimates between methods will provide more confidence in their application of prey consumption rates (Cochran and Rice 1982). In addition to comparing estimates from the different approaches (*e.g.*, Olson and Boggs 1986) it may also be useful to integrate and link different consumption models (*e.g.*, Table 2.) to account for the amount of uncertainty in parameter estimates (Essington et al. 2001; Walters and Essington 2010; Ferriss and Essington 2014).

Most of the methods used to estimate consumption rates still require information from species-specific trophic studies and gastric evacuation rates that will be used either directly into a model or to meet a model's assumptions. Feeding studies and experiments will continue to be critical for providing data for estimating *Q/B* to quantify the trophic impact of a consumer on ecosystems. Given that data-poor situations are common in open ocean ecosystems, including the EPO, a combination and corroboration of methods and analyses may contribute to more refined estimates of consumption rates (Ney 1990; Ney 1993; Essington *et al.* 2001; Ferriss and Essington 2014). However, because most methods will require laboratory tested rates of stomach evacuation, (*i.e.*, serial sampling of fish after feeding known amounts and types of prey at known water temperatures) and field sampling of forage biomass, direct methods are highly recommended to estimate consumption rates for key pelagic predators of the EPO ecosystem.

This review has shown that determination of daily ration and feeding rates using stomach content analyses from field sampled fish and gastric evacuation rates from fish in captivity can produce reliable estimates of prey consumption in pelagic species of fish, such as tunas, especially when used to calibrate or refine estimates from bioenergetics models (*e.g.*, Olson and Boggs 1986; Beaudreau and Essington 2009). Experimental determination of species-, prey-, and temperature-specific evacuation rates and some bioenergetics parameters is possible at laboratory facilities where nearshore accessibility to pelagic species is feasible (*e.g.*, yellowfin tuna, black skipjack, *Euthynnus lineatus*, and dolphinfish at the IATTC's Achotines Laboratory in Panama (Wexler et al. 2003; Margulies *et al.* 2007; IATTC 2013)), dolphinfish at the University of Miami Experimental Hatchery (Stieglitz et al. 2017), and scalloped hammerhead sharks and yellowfin tuna at the Hawaii Institute of Marine Biology (Bush and Holland 2002; Graham et al. 2007; Gleiss et al. 2010)). Daily ration parameters estimated from experiments and long-term diet analyses of species representing a range of trophic levels in the Pacific Ocean would significantly improve the realism of ecosystem models developed to characterize open ocean ecosystems and their fisheries.

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Table 1. Daily rations estimated for pelagic apex predators using direct methods.

Species (Reference)	Length (cm) Weight (kg) (Age class)	Ocean	Feeding Model	Gastric evacuation rate (GER) model	Daily ration estimate (% BW d <sup>-1</sup> )	Comments
Coryphaena hippurus Dolphinfish (Olson and Galván- Magaña 2002)	41.7-177 cm FL c.a. 1.7-79.9 kg	Eastern Pacific	Olson and Mullen (1986) (24-hr feeding)	Linear <sup>c</sup>	Range 0.4-9.6% Mean ± 1SE = 5.6 ± 0.56%	Purse seine caught as bycatch from associated and non- associated sets. Mean rations increased with size in most size classes Q/B = 20.44 times the population biomass yr <sup>1</sup>
Coryphaena hippurus Dolphinfish Young et al. 2010)	<100 cm FL 5.53 ± 0.57 kg Mean wt ± SE >100 cm FL 14.3 ± 0.39 kg Mean wt ± SE	South Pacific (Eastern Australia) (Coral Sea and Tasman Sea) (>18°C and <18°C)	Olson and Mullen (1986) (12-hr feeding)	Linear <sup>c</sup>	1.12% (<100 cm) 1.56% (>100 cm)	Longline sets
Euthynnus affinis Kawakawa (Griffiths e al. 2009)	28.4 – 80.9 cm FL Mean wt ± 1SD 0.946 ± 0.720 kg – 5.36 ± 1.254 kg	South Pacific (Tasman Sea) (16°-25°C)	Bootstrap estimate (Efron and Tishirani 1993) of Olson and Mullen (1986) model	Linear <sup>c</sup>	Mean ± 1SD 2.18 ± 0.26% (Range 4.1-1.95%)	Daily ration decreased with increasing fish size
Isurus oxyrinchus Shortfin Mako shark (Stillwell and Kohler 1982)	67-328 cm FL Mean weight = 63 kg	NW Atlantic Mean SST 18.8°C	Elliot and Persson (1978) (24-hr feeding)	Exponential	2.2%	Pelagic longlines and sport fishing tournaments
Isurus oxyrinchus Shortfin Mako shark (Wood et al. 2009)	146-335 cm FL 63.5 kg (median weight)	NW Atlantic Mean SST 18.8°C	Elliot and Persson (1978) (24-hr feeding)	Exponential	Range 4.44-4.93%	

Species (Reference)	Length (cm) Weight (kg) (Age class)	Ocean	Feeding Model	Gastric evacuation rate (GER) model	Daily ration estimate (% BW d <sup>-1</sup> )	Comments
Isurus oxyrinchus Shortfin Mako shark (Young et al. 2010)	66-257 cm FL 47.52 ± 8.24 kg Mean wt ± SE	South Pacific (Eastern Australia) (Coral Sea and Tasman Sea) (>18°C and <18°C)	Olson and Mullen (1986) (12-hr feeding)	Linear <sup>c</sup>	9.28%	Longline sets
Kajikia (Tetrapturus) audax Striped marlin (Young et al. 2010)	107.7-253.8 cm FL 83.7 ± 3.38 kg Mean wt ± SE	South Pacific (Eastern Australia) (Coral Sea and Tasman Sea) (>18°C and <18°C)	Olson and Mullen (1986) (12-hr feeding)	Linear <sup>c</sup>	1.30%	Longline sets
Kajikia audax Striped marlin (Abitia-Cárdenas et al. 2011)	Mean ±1 SD 176.81 ± 11.47 cm FL 56.14 ± 10.95 kg	Eastern Pacific Temperature preference 20°-25°C	Stillwell and Kohler (1982) (24-hr feeding)	Linear <sup>c</sup>	3.6%	
Katsuwonus pelamis Skipjack (Magnuson 1969)	39-50 cm FL 0.9-2.4 kg	Central Pacific (23.3°-25.7°C)	N/A	Binomial	15.0%ª 3.25% <sup>b</sup>	Laboratory estimates of consumption and GER
<i>Katsuwonus pelamis</i> Skipjack (Ménard et al. 2000)	<90 cm FL 0.8-15.2 kg	Eastern tropical Atlantic (26°-29°C)	Olson and Mullen (1986) (12-hr feeding)	Linear <sup>c</sup>	1.16% 5.51%	FAD associated Unassociated tuna school
Katsuwonus pelamis Skipjack (Olson et al. 2016)	65.1 ± 9.2 cm FL Mean length ± SD	Western Indian	Olson and Mullen (1986) (12-hr feeding)	Linear <sup>c</sup>	3.5% 4.2%	Purse-seine surface Long line at depth
Prionace glauca Blue shark (Kohler 1988)	53-285 cm FL	Atlantic	Elliott and Persson (1978) (24-hr feeding)	Exponential	0.6%	
Prionace glauca Blue shark (Young et al. 2010)	<100 cm FL 4.78 ± 0.22 kg Mean wt ± SE	South Pacific (Eastern Australia)	Olson and Mullen (1986) (24-hr feeding)	Linear <sup>c</sup>	8.88% (<100 cm)	Longline sets

Species (Reference)	Length (cm) Weight (kg) (Age class)	Ocean	Feeding Model	Gastric evacuation rate (GER) model	Daily ration estimate (% BW d <sup>-1</sup> )	Comments
	>100 cm FL 35.51 ± 2.88 kg Mean wt ± SE	(Coral Sea and Tasman Sea) (>18°C and <18°C)			2.32% (>100 cm)	
Sarda chiliensis Eastern Pacific bonito (Pauly et al. 1987)	50-75 cm FL 1.6-5.5 kg (2-12 yrs age)	Eastern Pacific (14°-24°C)	Elliot and Persson (1978)	Generalized model of GER, predator weight, and temperature for skipjack	2.23% (14°C) 2.80% (16°C) 3.53% (18°C) 4.44% (20°C) 5.59% (22°C) 7.04% (24°C)	Age-structured population model used to estimate Q/B from estimates of daily ration
Sphyrna lewini Scalloped hammerhead shark (Bush and Holland 2002)	50-60 cm TL 0.5 kg	Central Pacific (19.5°-27.5°C) GER expt 21.2°-26.6°C 26.2°-29.2°C	Diana (1979) Olson and Mullen (1986)	Surface area, Gompertz, and Logistic models	3.5%* (Diana method) 2.7% (Olson and Mullen method)	*larger amounts of food in stomachs during winter may be due to slower GER at lower temperatures
Thunnus alalunga Albacore (Young et al. 2010)	<100 cm FL 14.91 ± 0.55 kg Mean wt ± SE >100 cm FL 23.4 ± 0.88 kg	South Pacific (Coral Sea and Tasman Sea) (>18°C and <18°C)	Olson and Mullen (1986) (12-hr feeding)	Linear <sup>c</sup>	0.48% (<100 cm) 0.45% (>100 cm)	Longline sets
<i>Thunnus alalunga</i> Albacore (Olson et al. 2016)	102.1 ± 6.9 cm FL Mean length ± SD	Western Indian	Olson and Mullen (1986) (12-hr feeding)	Linear <sup>c</sup>	1.5% 0.9%	Purse-seine surface Long line at depth
<i>Thunnus albacares</i> Yellowfin tuna (Olson and Boggs 1986)	<u>Field stomach samples</u> (age classes 1-4+) ≤ 55 - >122 cm FL 0.97-95.4 kg <u>GER experiment</u> :	Eastern Pacific	Olson and Mullen (1986) (24-hr feeding)	Linear	Range of means 2.8-4.5% Mean = 3.9%	Purse-seine caught P/B = 1.2 yr <sup>-1</sup>

Species (Reference)	Length (cm) Weight (kg) (Age class)	Ocean	Feeding Model	Gastric evacuation rate (GER) model	Daily ration estimate (% BW d <sup>-1</sup> )	Comments
	24-45 cm FL	(23.5°-25.5°C)				Q/B = 14.24x
	0.22-1.76 kg	Central Pacific				population biomass yr <sup>-</sup>
Thunnus albacares		Western and Central	(Olson 1982)	Unknown	Adjusted to 3 7% (see	Yellowfin caught by
Yellowfin tuna	116-155 cm FL	Pacific	Olson and		Olson et al. 2016)	handline at the
(Yesaki 1983)	(3-5+ yrs)		Mullen 1986)		,	surface under payaos
(Barut 1988)			(24-hr feeding)			by chumming
(Olson et al. 2016)			(			
Thunnus albacares	22-69 cm FL	Western Indian	Olson and	Linear <sup>c</sup>	2.1-5.5%	Yellowfin caught by
Yellowfin tuna		c.a. 28°C	Mullen (1986)			gillnet
(Maldeniya 1996)			(12-hr feeding)			Daily rations
	70->130 cm FL				5.2-1%	decreased with
						increasing size after
						70 cm FL
Thunnus albacares		Eastern Atlantic	Olson and	Linear <sup>c</sup>		FAD associated
Yellowfin tuna	<90 cm FL; 0.8-12.7 kg	(26°-29°C)	Mullen (1986)		0.89%	<90 cm
(Ménard et al. 2000)	>90 cm FL; 15-81 kg		(12-hr feeding)		3.04%	>90 cm
						Unassociated tuna
						school
	<90 cm FL; 1.6-2.75 kg				16.0%	<90 cm
	>90 cm FL; 30.4-90.3 kg				2.59%	>90 cm
Thunnus albacares	<100 cm FL	South Pacific	Olson and	Linear <sup>c</sup>	1.65% (<100 cm)	
Yellowfin tuna	14.07 ± 0.36 kg	(Coral Sea and	Mullen (1986)			
(Young et al. 2010)	Mean wt ± SE	Tasman Sea)	(12-hr feeding)			Longline sets
	>100 cm FL	(>18°C and <18°C)			1.04% (>100 cm)	
	41.04 ± 0.68 kg					
Thunnus albacares	108 ± 30.3 cm FL	Western Indian	Olson and	Linear <sup>c</sup>	2.0%	Purse-seine surface
Yellowfin tuna	Mean length ± SD		Mullen (1986)			
(Olson et al. 2016)			(12-hr feeding)		1.1%	Long line at depth
Thunnus maccoyii	40-130 cm FL	South Pacific	Elliot and	Boisclair and	2.69 %	Inshore troll fishery
Southern bluefin tuna	2.5-60 kg	(Tasman Sea)	Persson (1978)	Marchand		
(Young et al. 1997)			and Boisclair	(1993)		

Species (Reference)	Length (cm) Weight (kg) (Age class)	Ocean	Feeding Model	Gastric evacuation rate (GER) model	Daily ration estimate (% BW d <sup>-1</sup> )	Comments
	74-192 cm 15-145 kg	(14°-16°C)	and Marchand (1993) (24-hr feeding)		0.81%	Offshore longline
<i>Thunnus maccoyii</i> Southern bluefin tuna (Young et al. 2010)	<100 cm FL 16.02 ± 0.13 kg Mean wt ± SE	South Pacific (Coral Sea and Tasman Sea)	Olson and Mullen (1986)	Linear <sup>c</sup>	1.70% (<100 cm)	Longline sets
	>100 cm FL 54.76 ± 1.21 kg	(>18°C and <18°C)	(12-hr feeding)		0.72% (>100 cm)	
<i>Thunnus obesus</i> Bigeye tuna (Ménard et al. 2000)	<90 cm FL 0.8-11.5 kg	Eastern tropical Atlantic	Olson and Mullen (1986)	Linear <sup>c</sup>	1.27%	FAD associated <90 cm
	<90 cm FL 1.1-8.12 kg	(26°-29°C)	(12-hr feeding)		4.82%	Unassociated tuna school <90 cm
<i>Thunnus obesus</i> Bigeye tuna (Young et al. 2010)	<100 cm FL 15.3 ± 1.08 kg Mean wt ± SE >100 cm FL	South Pacific (Coral Sea and Tasman Sea) (>18°C and <18°C)	Olson and Mullen (1986) (24-hr feeding)	Linear <sup>c</sup>	1.71% (<100 cm)	Longline sets
	51.97 ± 1.77 kg	,			0.89% (>100 cm)	
Thunnus obesus Bigeye tuna	100.6 ± 26.8 cm FL Mean length ± SD	Western Indian	Olson and Mullen (1986)	Linear <sup>c</sup>	3.6%	Purse-seine surface
(Olson et al. 2016)			(12-hr feeding)		0.6%	Long line at depth
Thunnus thynnus Atlantic bluefin tuna	Mean ± SD = 194.59 ± 0.62 – 225.92 ±	Western Atlantic (N. Carolina continental	Eggers (1977) (12-hr feeding)	Exponential Elliot and		Commercial trolling from baitboats
(Butler et al. 2010)	1.12 cm FL 110.89 ± 1.40 kg – 179.17 ± 3.37 kg	shelf) c.a. 8°-14° C (fall and winter)		Persson (1978)	Mean ± SE = 2.03± 0.59%	

Thunnus thynnus	Mean ± SD =	Eastern Atlantic	Olson and	Linear <sup>c</sup>		Baitboat capture
Atlantic bluefin tuna	130.45 ± 24.74 cm FL	2012	Mullen (1986)		(mean ± SD)	
(Sorell et al. 2017)	(77-212 cm FL)	(19.65° ± 1.76°C)	(24-hr feeding)		2.52 ± 1.24% (2012)	
	119.92 ± 8.86 cm FL	2013				
	(105-152 cm FL)	(22.28° ± 0.22°C)			5.84 ± 1.06% (2013)	
Thunnus tonggol	60-80 cm FL	South Pacific	Olson and	Linear <sup>c</sup>	(mean ± SE)	Gillnets and trolling
Longtail tuna	5.7 ± 0.101 kg	(Gulf of Carpentaria)	Mullen (1986)*		2.17 ± 0.08%	*Monte Carlo
(Griffiths et al. 2007)	(Mean wt ± SE)	(21°-28°C)	(12-hr feeding)			simulations used to
						obtain mean biomass
	80-100 cm FL				2.26 ± 0.13%	of prey consumed
	9.4 ± 0.156 kg					
	100-125 cm FL				$1.30 \pm 0.07\%$	
	17.66 ± 0.589 kg					
Xiphias gladius	Mean length and weight	Western north	Reduced	Used GERs of		Q/B = 3.4-5.8 x
Swordfish	153 cm and 58 kg	Atlantic	version of Elliot	blue and	0.94-1.6%	average BW yr <sup>-1</sup>
(Stillwell and Kohler 1985)	(5-204 kg)		and Persson	shortfin		Commercial longline
			(1978)	mako sharks		and sport fishing
			(24-hr feeding)	from		tournament
				previous		
				publications		
Xiphias gladius	<100 cm FL	South Pacific	Olson and			
Swordfish	12.51 ± 1.13 kg	(Coral Sea and	Mullen (1986)	Linear <sup>c</sup>	2.40% (<100 cm)	Longline sets
(Young et al. 2010)	Mean wt ± SE	Tasman Sea)	(12-hr feeding)			
	>100 cm FL	(>18°C and <18°C)			1.88% (>100 cm)	
	76.48 ± 2.13 kg					
	Mean wt ± SE					

<sup>a</sup> Skipjack consumed 15% BW d<sup>-1</sup> during laboratory feedings every 15 minutes for 12-hr periods over 3 days at 23.3-25.7°C. The ration estimate does not incorporate the GER.

<sup>b</sup>Daily ration for a 24-hr period estimated using the Olson and Mullen (1986) feeding model that incorporates the integral of the binomial GER function with the daily mean meal size over 3 days of feeding estimated by Magnuson (1969) from the laboratory feeding trials<sup>a</sup>.

<sup>c</sup>Assumed a gastric evacuation rate and A<sub>i</sub> values for similar prey in digestibility to that of yellowfin tuna in Olson and Boggs (1986)

Table 2. Indirect estimates of daily rations for pelagic apex predators using bioenergetics and other models.

Species (Reference)	Length (cm) Weight (kg) (Age class)	Ocean	Feeding Model	Energy budget components and expenditures <sup>a</sup> /or other parameters	Daily ration estimate (% BW d <sup>-1</sup> )	Comments
<i>lsurus oxyrinchus</i> Shortfin mako shark (Wood et al. 2009)	146-335 cm FL 63.5 kg (median weight)	NW Atlantic Mean SST 18.8°C	Bioenergetics model	AMR, SDA, GRW, REP, F and U PED = 4.909 kJ g <sup>-1</sup> PRED ED = 5.562 kJ g <sup>-1</sup>	4.42-4.66%	2001-2002 sampled from shark fishing tournaments
<i>Isurus oxyrinchus</i> Shortfin mako shark (Stillwell and Kohler 1982)	67-328 cm FL Mean weight = 63 kg	NW Atlantic Mean SST 18.8°C	Bioenergetics model	Same as above without GRW, and AMR estimated from other shark species	3.49-4.28%	1972-1979 samples (inshore tournaments and offshore longline vessels)
Katsuwonus pelamis Skipjack (Kitchell et al. 1978)	1 kg immature skipjack	Central Pacific (24°C)	Bioenergetics model	AMR, SMR, SDA, GRW, REP, F, U PED = 4.6 kJ g <sup>-1</sup> PRED ED = 6.1 kJ g <sup>-1</sup>	5.9% 7.3% 13.1% 19%	Maintenance Minimally active 2x activity level 3x activity level
Katsuwonus pelamis Skipjack (Essington 2003)	25.4-91 cm FL 0.26-19.07 kg (0.5-4 yrs) <sup>b</sup> Estimates at weekly age intervals Age at recruitment = 0.2 yrs	Pacific (23-25°C)	Bioenergetics and age- and size- structured population models Models linked by calculating age- specific predation and survival rates	AMR, SMR, GRW, REP, A (includes SDA, F and U losses) PED = 5 kJ g <sup>-1</sup> PRED ED = 6.2 kJ g <sup>-1</sup>	9.9%	Q/B = 32.4 (based on growth rates, metabolic costs, and population size structure) Biomass dominated by SKJ <0.5 kg
Katsuwonus pelamis Skipjack (Kirby 2005)	(0.2-4 yrs) Quarterly age classes estimated from a length-based age-structured model	Western and central Pacific	Bioenergetics model and MFCL <sup>c</sup> (Fournier et al. 1998; Hampton and Fournier 2001)	AMR, SMR, GRW, REP, SDA, PED, A (includes F and U losses) PED = 6 kJ g <sup>-1</sup> PRED ED = 6 kJ g <sup>-1</sup>	4-14.5% <sup>d</sup> (at 1yr) 3.5-10% <sup>d</sup> (at 4 yrs)	Q/B = 20-57 (at 1 yr age) Q/B = 15-40 (at 4 yrs age)

Species (Reference)	Length (cm)	Ocean	Feeding Model	Energy budget components and	Daily ration	Comments
	Weight (kg)			expenditures <sup>a</sup> /or other parameters	estimate	
	(Age class)			to estimate consumption (C)	(% BW d⁻¹)	
Katsuwonus pelamis	10 kg	Pacific	Statistical estimation	AMR, SMR, GRW, REP, A (includes	4.5-6.7%	
Skipjack		(25°C)	procedures based on	SDA, F and U losses)		
(Ferriss and Essington			coupled	PED =5.5 kJ g <sup>-1</sup>		
2014)			bioenergetics and Hg	PRED ED = 6.8 kJ g <sup>-1</sup>		
			models.	Hg loss to REP, F, U,		
			Models coupled by	SDA, GRW		
			size-specific	Hg gain from prey consumption		
			consumption rate.			
Prionace glauca	(0-20 yrs)	Central Pacific	Coupled	AMR, SMR, SDA, GRW, REP, F and U	1%	Blue shark
Blue shark	Growth calculated		bioenergetics and			populations
(Schindler et al. 2002)	at 1-year intervals		population models	PED = 4.4 kJ g <sup>-1</sup> (squid) and		sensitive to low
			incorporating age-	5.02 kJ g⁻¹ (fish)		exploitation rates
			and size-selective	PRED ED = 5.4 kJ g <sup>-1</sup>		by longline
			mortality and			fisheries and will
			recruitment to			have a large
			estimate predation			impact on shark
			responses to changes			predation
			in fishing intensities			response
			fishing intensities			
Thunnus alalunga	38-100 cm FL	North Pacific	<b>Bioenergetics and</b>	AMR, SMR, GRW, REP, A (includes	3.8%	<i>Q/B</i> = 13.9
Albacore	2.5-45.5 kg		age- and size-	SDA, F and U losses)		(based on growth
(Essington 2003)	(1-6 yrs) <sup>e</sup>	15-19.4°C	structured			rates, metabolic
	Estimates calculated		population models.	PED = 5 kJ g <sup>-1</sup>		costs, and
	at 0.1-yr intervals		Models linked by	PRED ED = 6.8 kJ g <sup>-1</sup>		population size
	Age at recruitment		calculating age-			structure)
	= 0.5 yrs		specific predation			
			and survival rates			
Thunnus alalunga	(1-20 yrs)	Western and	<b>Bioenergetics model</b>	AMR, SMR, GRW, REP, SDA, PED,	2.5-7.5% <sup>d</sup>	<i>Q/B</i> = 11-30
Albacore	Annual age classes	central Pacific	and MFCL <sup>c</sup>	A (includes F and U losses)	(at 1yr)	(at 1 yr age)
(Kirby 2005)	estimated from a		(Fournier et al. 1998;			
	length-based age-		Hampton and	PED = 6 kJ g <sup>-1</sup>	2-6% <sup>d</sup>	<i>Q/B</i> = 5.5-22
	structured model		Fournier 2001)	PRED ED = 6 kJ g <sup>-1</sup>	(at 20 yrs)	(at 20 yrs age)

Species (Reference)	Length (cm) Weight (kg)	Ocean	Feeding Model	Energy budget components and expenditures <sup>a</sup> /or other parameters	Daily ration estimate	Comments
	(Age class)			to estimate consumption (C)	(% BW d⁻¹)	
Thunnus alalunga Albacore (Ferriss and Essington 2014)	10 kg	Pacific (25°C)	Statistical estimation procedures based on coupled bioenergetics and Hg models. Models coupled by size-specific	AMR, SMR, GRW, REP, A (includes SDA, F and U losses) PED = 5.5 kJ g <sup>-1</sup> PRED ED = 6.8 kJ g <sup>-1</sup> Hg loss to REP, F, U, SDA, GRW Hg gain from prey consumption	Reliable estin obtained (unre Hg concentrati their prey an bioenerge est	nates could not be eliable estimates of ons in albacore and d uncertainties of tics parameter imates)
Thunnus albacares Yellowfin tuna (Olson and Boggs 1986)	87-98 cm FL 13.4-19.3 kg (n=4; age class 3)	Eastern Pacific	Bioenergetics model	AMR, SMR, GRW, REP Assumed losses due to A, SDA, F and U = 35% of the energy consumed in food PED = $4.6 \text{ kJ g}^{-1}$ PRED ED = $6.03 \text{ kJ g}^{-1}$ Total mean energy expended = $241 \text{ J g}^{-1} \text{ d}^{-1}$	Mean daily ration =5.2% (3.8-9.6%)	Q/B = c.a. 11-17x mean population biomass yr <sup>-1</sup>
Thunnus albacares Yellowfin tuna (Essington et al. 2002)	30-168 cm FL 0.5-102.4 kg (0.5-5(6) yrs) <sup>f</sup> Predation and survival rates estimated at 0.1-yr intervals	Eastern Pacific	Bioenergetics model coupled with a population model based on natural mortality estimates and age-specific vulnerabilities for each fishery type	AMR, SMR, GRW, REP, A (includes SDA, F and U losses) PED = 4.6 kJ g <sup>-1</sup> PRED ED = 6.03 kJ g <sup>-1</sup>	3.5-6%	Age- and size-at- capture differences among fishery types in EPO affects yellowfin predation rates and distribution of predation pressure on prey

Species (Reference)	Length (cm)	Ocean	Feeding Model	Energy budget components and	Daily ration	Comments
	Weight (kg)			expenditures <sup>a</sup> /or other parameters	estimate	
	(Age class)			to estimate consumption (C)	(% BW d⁻¹)	
Thunnus albacares	30-168 cm FL	Central Pacific	Coupled	AMR, SMR, GRW, REP, A (includes F	4-5%	Yellowfin
Yellowfin tuna	0.5-102.4 kg		bioenergetics and	and U losses)		populations
(Schindler et al. 2002)	(0.5-5 yrs) <sup>f</sup>		population models			robust across a
			incorporating age-	PED = 4.6 kJ g <sup>-1</sup>		wide range of
	Growth calculated		and size-selective	PRED ED = 6.03 kJ g <sup>-1</sup>		exploitation rates
	at 0.1-yr intervals		mortality and			by longline
			recruitment to			fisheries so
			estimate predation			changes of
			responses to changes			yellowfin
			in fishing intensities			predation
						response minimal
Thunnus albacares	30-168 cm FL	Eastern Pacific	<b>Bioenergetics and</b>	AMR, SMR, GRW, REP, A (includes	5.4%	<i>Q/B</i> = 19.8
Yellowfin tuna	0.5-102.4 kg		age- and size-	SDA, F and U losses)		(based on growth
(Essington 2003)	(0.5-5 yrs) <sup>f</sup>		structured			rates, metabolic
	Predation and		population models	PED = 4.6 kJ g <sup>-1</sup>		costs, and
	survival rates			PRED ED = 6.03 kJ $g^{-1}$		population size
	estimated at 0.1-yr		Models linked by			structure)
	intervals		calculating age-			
	Age at recruitment		specific predation			
	= 0.5 yrs		and survival rates			
Thunnus albacares	(0.2-7 yrs)	Western and	Bioenergetics model	AMR, SMR, GRW, REP, SDA, PED,	1.9-7% <sup>d</sup>	<i>Q/B</i> = 8-26
Yellowfin tuna	Quarterly age	central Pacific	and MFCL <sup>c</sup>	A (includes F and U losses)	(at 1yr)	(at 1 yr age)
(Kirby 2005)	classes estimated		(Fournier et al. 1998;			
	from a length-based		Hampton and	PED = 6 kJ g <sup>-1</sup>	1.8-7.4% <sup>d</sup>	<i>Q/B</i> = 6-29
	age-structured		Fournier 2001)	PRED ED = 6 kJ g <sup>-1</sup>	(at 7 yrs)	(at 7 yrs age)
	model					
Thunnus albacares	10 kg	Pacific	Statistical estimation	AMR, SMR, GRW, REP, A (includes	5.8-9%	
Yellowfin tuna		(25°C)	procedures based on	SDA, F and U losses)		
(Ferriss and Essington			coupled	PED =5.5 kJ g <sup>-1</sup>		
2014)			bioenergetics and Hg	PRED ED = 6.03 kJ g <sup>-1</sup>		
			models	Hg loss to REP, F, U,		
			Models coupled by	SDA, GRW		
			size-specific	Hg gain from prey consumption		
			consumption rate			

Species (Reference)	Length (cm)	Ocean	Feeding Model	Energy budget components and	Daily ration	Comments
	Weight (kg)		-	expenditures <sup>a</sup> /or other parameters	estimate	
	(Age class)			to estimate consumption (C)	(% BW d⁻¹)	
Thunnus maccoyii	94-118 cm FL	Southern	Thermodynamics	Ambient, depth, and visceral	1-11% BW d <sup>-1</sup>	Sea cage
Southern bluefin tuna	15.2-36.9 kg	Indian	model relating total	temperatures measured over time		experiments of
(Gunn et al. 2001)	(3 yrs)		intake amount of	and duration		archival-tagged
		c.a. 21-23°C	prey and time to			fish fed known
		(summer)	maximum visceral	HIF (heat increment of feeding)		rations of 1-11%
			temperature ( <i>T<sub>max</sub></i> ),	magnitude measured by HIF area		BW d <sup>-1</sup> over 18
		c.a. 14-17°C	height of the heat			days
		(winter)	increment above	Prey energy density and composition		
			basal visceral	based on wet weight proximate		
			temperature,	analyses of a single prey type		
			duration of heating			
			event, and the area			
			calculated under the			
			curve of the thermal			
			response			
Thunnus maccoyii	(3 yrs)	Southern	Thermodynamics	Ambient, depth, and visceral	2.9-4.9%	Archival tag data
Southern bluefin tuna		Indian	model relating total	temperatures over time and	Mean ± SD =	used to measure
(Bestley et al. 2008)	93-111 cm FL		intake amount of	duration	3.8 ± 0.5%	HIF which is
	16.4-27.5 kg	(4.9°-22.9°C)	prev and time to			strongly
			reach the maximum	HIF magnitude measured by HIF area	Relative food	correlated with
					intake based	the energetic
				Prey energy density and composition	on a single	value of a meal
			reach gastric	(from Gunn et al. 2001)	prey type	and provides a
			evacuation) above		used in prior	measure of
			the basal		experiments	feeding frequency
			temperature			and prey intake
Thunnus obesus	10 kg	Pacific	Statistical estimation	AMR, SMR, GRW, REP, A (includes	9.4-13%	
Bigeye tuna		(25°C)	procedures based on	SDA, F and U losses)		
(Ferriss and Essington		. ,	coupled	PED = 5.5 kJ g <sup>-1</sup>		
2014)			bioenergetics and Hg	PRED ED = 6.03 kJ g <sup>-1</sup>		
			models.	Hg loss to REP, F, U,		
			Models coupled by	SDA, GRW		
			size-specific	Hg gain from prey consumption		
			consumption rate.			

Species (Reference)	Length (cm) Weight (kg)	Ocean	Feeding Model	Energy budget components and expenditures <sup>a</sup> /or other parameters	Daily ration estimate	Comments
	(Age class)			to estimate consumption (C)	(% BW d⁻¹)	
Thunnus orientalis	All age/size classes	Pacific	Dynamic energy	Simulations of food availability and	No estimates	
Pacific bluefin tuna	within the entire life		budget to describe	temperature to predict growth,		
(Jusup et al. 2011)	cycle		the rates at which an	respiration, reproduction,		
			organism assimilates	maintenance, and development		
			and utilizes energy			
			from food			
<i>Thunnus orientalis</i> Pacific bluefin tuna (Whitlock et al. 2013)	13.8, 14.4, 16.7 kg (at recapture) 84, 84, 85 cm CFL (at tagging)	Eastern Pacific (15°-22°C)	Thermodynamic and	Magnitude and duration of HIF positively correlated with the caloric value of the ingested meal and used to estimate energy intake	Archival-	Visceral warming
			heirarchial Bayesian		tagged fish	higher for squid
			regression models		fed known rations of 1-	vs sardine meals
			applied to visceral			and at lower
			temperature		12% DW U	temperature
			increases as a		at 15° 20°	temperature
			function of meal		and 22°C	
			energy intake and		0.10 22 0	
			ambient water			
			temperature			
Thunnus orientalis	59-148 cm FL	Eastern Pacific	Thermodynamic and	Magnitude and duration of HIF	Mean dailv	Mean dailv
Pacific bluefin tuna	4.35-62.11 kg <sup>g</sup>	(11°-26.7°C)	, heirarchial Bayesian	5	, energy intake	energy intake
(Whitlock et al. 2015)	(1-5 yrs)		regression models		± SD =	decreased with
			applied to visceral		1034 ± 669	increasing BW
			temperature		kcal	and a decrease in
			increases as a		(summer	ambient water
			function of meal		months)	temperatures
			energy intake and		944 ± 579	
			ambient water		kcal	
			temperature		(winter	
					months)	

Species (Reference)	Length (cm)	Ocean	Feeding Model	Energy budget components and	Daily ration	Comments
	Weight (kg)			expenditures <sup>a</sup> /or other parameters	estimate	
	(Age class)			to estimate consumption (C)	(% BW d⁻¹)	
Thunnus thynnus	Mean length ± SD	Western north	Empirical data on	N/A	0.15-1.1%	Hook and line and
Atlantic bluefin tuna	124 ± 30 cm to	Atlantic	stomach contents			purse seine
(Chase 2002)	251 ± 19 cm FL	c.a. 15°-20°C	and predator			
	Mean weight ± SD		biomass in relation to			% food to
	36 ± 38 kg to		predator size			biomass declined
	273 ± 58 kg					with increasing
	(2-10+ yrs)					predator size (FL)
Thunnus thynnus	Age 3+ years	Northwest	Probability based	Meta-analysis of observational and	Mean ± SD =	Analyses based
Atlantic bluefin tuna		Atlantic	estimation approach	empirical data over 32 years to	3.2 ± 1.4%	on stomach
(Overholtz 2006)				estimate consumption	(1.0-4.7%)	content data and
						VPA

<sup>a</sup>*A* is assimilation efficiency (%) (*i.e.* includes *F*, *U*, and *SDA* as constant proportions of consumed food available for bioenergetic expenditures), *F* is egestion (*i.e.* energy lost to undigested food (faeces) and other substances), *U* is energy lost to nitrogenous excretion, *SDA* is specific dynamic action (*i.e.* refers to the elevation in metabolic activity associated with ingestion, digestion, absorption and assimilation of a meal or the energetic cost of digestion and protein synthesis), *AMR* is the increase in metabolic energy due to swimming (length-based scaling), *SMR* is standard metabolic activity (based on measured respiration rates; weight-based scaling), *GRW* is energy allocated to somatic tissue growth (mean length/weight-at-age parameters), *REP* is energy allocated to reproductive output, and *PED* is the prey energy density (kJ g<sup>-1</sup>) used to calculate daily ration. PRED ED is the caloric value for predator biomass used to estimate energy allocated to somatic growth and reproductive output (kJ g<sup>-1</sup>)

<sup>b</sup>Growth curve from Uchiyama and Struhsaker (1981) and length-weight relationship from Nakamura and Uchiyama (1966) used to estimate age-specific lengths and weights

<sup>c</sup>MFCL (MULTIFAN-CL) is a length-based, age-structured model using length frequencies

<sup>d</sup>Daily rations and *Q/B* estimates are approximate ranges presented in Figure 7 of Kirby 2005

<sup>e</sup> von Bertalanffy growth curve reported by Bartoo and Foreman (1994) and converted to mass using the length-weight relationship from Clemens (1961) to estimate age-specific lengths and weights

<sup>f</sup>Growth curves described by Wild (1986) and length-weight conversion provided by Wild (1994)

<sup>g</sup>Weight-length relationship of Shimose et al. (2009) used to estimate weight range



**FIGURE 1.** Total global tuna catches in tons by species between 1950 and 2019. FAO. 2021. Fishery and Aquaculture Statistics. Global capture production 1950-2019 (FishstatJ). In: *FAO Fisheries and Aquaculture Department* [online], Rome, updated 2021, (www.fao.org/fishery/statistics/software/fishstatj/en).



**FIGURE 2.** The proportion of the initial meal (in wet mass) of four experimental prey types recovered from stomachs of yellowfin tuna in captivity with increasing postprandial time. T<sub>B</sub> is the point beyond which data were omitted prior to fitting the linear models. Figure and caption are from Olson and Boggs (1986).





**FIGURE 3.** Schematic representation (interpreted by Jarre *et al.* 1991) of a single feeding cycle showing two models of stomach content dynamics by Sainsbury (1986). Model I (A) assumes a constant ingestion over time. Model II (B) assumes that the ingestion declines with increasing stomach contents over a single feeding period. Panels C and D are extensions made to the models by Sainsbury (1986) to incorporate two feeding cycles. Figures have been recreated from Jarre *et al.* (1991).



**FIGURE 4.** Stomach evacuation data of skipjack tuna (after Magnuson 1969) (top panel) with a least squares fit of an exponential decline model (solid line) and a superimposed exponential model (dashed line) estimated by fitting model 2 (Figure 3B) of Sainsbury (1986) to the trajectory of stomach content fullness (solid line; bottom panel). The stomach contents of skipjack during the feeding period are shown (bottom panel) with the trajectories estimated by fitting model 1 (Figure 3A) (dashed line) and model 2 (Figure 3B) (dotted line) to the data. Model 2 (Figure 3B) assumes that feeding does not occur at a constant rate and decreases during the feeding period, as a result of satiation (Sainsbury 1986). Figures are from Sainsbury (1986).



**FIGURE 5.** Posterior probability distribution of individual daily consumption rate for 50-kg Atlantic bluefin (*Thunnus thynnus thynnus*) (white bars) and yellowfin (*Thunnus albacares*) tunas (blue bars) based on weight-at-age data. Each bar represents the probability that the consumption rate falls within that interval of individual mass-specific consumption. (figure and descriptions from Essington *et al.* 2001).



**FIGURE 6.** The observed Q/B values of 108 populations and 38 species of fishes correlated against the predicted values of the relationship developed by Palomares and Pauly (1998) to empirically estimate Q/B. Figure is from Palomares and Pauly (1998).