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Bioenergetics of captive yellowfin tuna (*Thunnus albacares*)

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ABSTRACT

We utilized a unique opportunity to study the growth and bioenergetics of a highly migratory and commercially valuable marine fish under controlled environmental conditions. We maintained yellowfin tuna (*Thunnus albacares)* in holding tanks throughout a twenty-year period, routinely collecting data on mass and length of individual fish over time. The water temperature of the holding tanks was maintained at 19.9 ± 0.9 °C (mean ± s.d.) and the yellowfin tuna were fed a diet amounting to 176 ± 36 kJ·kg^{-1} of tuna biomass·day^{-1} across the study period. We integrated length records (n = 249) with a prior model of yellowfin tuna age to generate a von Bertalanffy growth function for this captive scenario with the parameters 224.26 cm straight fork length (SFL), 0.099, and −1.721 years for L_∞, k, and t_o, respectively. We combined our growth model and analyses of tuna tissue energy with metabolic data from various sources to estimate a bioenergetic budget for this difficult-to-study species. We found that the captive tunas in this experiment grew significantly slower than yellowfin tuna studied in the wild and in other captive scenarios. Our energetic budget indicates that only 7.8% of an ingested meal's energetic content was utilized for growth. Furthermore, we calculated an average food conversion ratio of 37.2:1 for an 8.4 kg yellowfin tuna when fed a mixed-diet of squid, sardine, and vitamin gelatin. We conclude with a discussion of the various factors influencing tuna bioenergetics including the role of water temperature, diet, and inter-species competition on growth and energy assimilation. These findings are uniquely suited to the relatively cool temperatures and low energy diet maintained in this captive scenario, an important consideration for others hoping to draw on these results for comparative research.

1. Introduction

The yellowfin tuna (*Thunnus albacares)* is an ecologically and commercially important fish species that is widely distributed throughout the tropical seas (Collette and Nauen, 1983). Yellowfin tuna are top predators that feed on forage fish, squid, and pelagic crustaceans, among other organisms (Alverson, 1963; Essington et al., 2002). Yellowfin tuna possess many unique specializations including internalized red muscle and vascular counter-current head exchangers, and they have slightly elevated metabolic rates relative to most fishes (Graham, 1975; Dizon and Brill, 1979; Korsmeyer and Dewar, 2001; Blank et al., 2007a; Klinger et al., 2016).

There is a strong international demand for yellowfin tuna for human consumption, and there are concerns about the effects of fishing pressure on some populations (Minte-Vera et al., 2014). In the eastern Pacific Ocean where the yellowfin tuna in this study were collected, purse seining is the most common type of fishing gear, though longline and pole-and-line techniques are also used (Hoyle and Maunder, 2005). The majority of purse-seining operations rely on fish aggregating devices (FADs) to capture yellowfin tuna, an activity that has been shown to have high bycatch rates of non-target species (Fonteneau et al. 2000). Due to concerns about overfishing, bycatch, and an increasing international demand for tuna, some groups have experimented with raising yellowfin tuna in aquaculture scenarios. Proponents of tuna aquaculture cite the potential for reduced fishing pressure on wild tuna populations, elimination of bycatch, and a more efficient economic system relative to capture-based fisheries (Zertuche-González et al., 2008). However, tuna aquaculture has been criticized for effluent contamination of coastal waters, a large carbon footprint, and

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overconsumption of feed species (i.e. clupeids) resulting from high food conversion ratios (FCRs) (Volpe, 2005; Zertuche-González et al., 2008).

Commercial scale tuna aquaculture began in the 1960s with Atlantic bluefin tuna (*Thunnus thynnus*), and currently large-scale developments exist for all three bluefin tuna species (including *Thunnus orientalis* and *Thunnus maccoyii*) in Australia, Mexico, Japan, and throughout the Mediterranean Sea (Metian et al., 2014). Aquaculture of bluefin tuna has been dominated by capture-based systems in which juvenile and adult tuna are collected in the wild, maintained in ocean pens where they are fattened with a diet of wild forage fish, and later harvested for market (Lioka et al., 2000; Ottolenghi, 2008; Klinger et al., 2013). Scientists at Kindai University in Japan, however, were the first to develop a closed-lifecycle approach, collecting fertilized eggs from broodstock tuna and growing them into market size bluefin tuna (Sawada et al., 2005). Despite these advances in understanding the spawning cycle and life history of tunas, capture-based operations continue to dominate bluefin tuna aquaculture production.

In contrast, yellowfin tuna aquaculture has primarily remained at a research level, with few attempts to commercially produce this species via capture-based or closed-lifecycle techniques. Several efforts to rear yellowfin eggs from land-based recirculating seawater systems have been successful, though there are few examples of operations that have grown these hatchlings past the juvenile stage (Harada et al., 1971; Mori et al., 1971; Harada et al., 1980; Kaji et al., 1999; Wexler et al., 2003; Margulies et al., 2016). Early studies conducted by researchers from the Japan Sea Farming Association (JASFA) grew yellowfin tuna in ocean pens from 1986 to 1997 in Yaeyama, Japan (Masuma, 2013). The Achotines Laboratory in Panama is owned and operated by the Inter-American Tropical Tuna Commission (IATTC) and has maintained captive yellowfin tuna broodstock in land-based tanks since 1996 for the purpose of studying their reproductive biology and early life history (Wexler et al., 2003; Margulies et al., 2007; Margulies et al., 2016). The Gondol Research Institute for Mariculture in Indonesia, in collaboration with the Overseas Fisheries Cooperation Foundation (OFCF) of Japan, has conducted aquaculture-focused research on captive yellowfin tuna since 2003. Despite the history of investment in yellowfin tuna aquaculture and the many indicators of feasibility, there have been no successful commercial-scale efforts to raise this species through its life cycle to date. This is largely attributable to the low market price of yellowfin tuna relative to bluefin tuna, however, it is possible that future yellowfin tuna prices will climb or production costs will decrease to a level at which potential profit margins will incentivize commercial-scale enterprises.

A sound understanding of the benefits and costs of yellowfin tuna aquaculture can only begin with a strong biological understanding of this species. Due to their highly migratory nature in the wild and sensitivity in captive scenarios, several biological parameters have proven difficult to accurately quantify for tuna species including growth, metabolism, energy conversion, egestion, excretion, and food conversion ratios (Korsmeyer and Dewar, 2001). With the advent of improved tuna husbandry and life support techniques and major investment by the research community, however, many of these basic data have become available for yellowfin tuna and other tuna species. Metabolic rates have been measured for yellowfin tuna using swim tunnel respirometers, where oxygen consumption over time is used as a proxy for metabolic rate under controlled temperatures and swimming speeds, with variation in published values for this species (Brill, 1987; Dewar and Graham, 1994; Blank et al., 2007a, 2007b; Klinger et al., 2016). Age and growth estimates for wild yellowfin tuna have been estimated by tag-recapture studies and the analysis of incremental growth rings in otoliths, vertebrae, and scales (Wild, 1986; Eveson et al., 2012; Shih et al., 2014). The first long-term estimates of food conversion, growth, and survival of tropical yellowfin tuna in a land-based system were accomplished by the IATTC at the Achotines Laboratory in Panama (Wexler et al., 2003; Margulies et al., 2016). Past studies have measured excretion and egestion rates of captive carnivorous fish species, however, no direct study on captive yellowfin tuna has been completed to date (Beamish et al., 1975; Kitchell et al., 1978; Brett and Groves, 1979; Halver and Hardy, 2002).

Further advances in understanding yellowfin tuna energetics would be of significant value should commercial scale aquaculture develop for this species. Drawing from observations of the bluefin tuna aquaculture industry, historically many tuna farms have not integrated bioenergetic information into their operational structures (Ottolenghi, 2008; Zertuche-González et al., 2008). This partly arises from the challenges of monitoring the growth of individuals over time and the difficulty of accurately assessing biomass levels in densely populated net pens. Furthermore, farmers are not likely to repeatedly risk the well-being of valuable fish to obtain measurements of length and weight (Zertuche-González et al., 2008). Feed represents a large portion of a farm's total operating costs, and as such, a better understanding of tuna energetics could facilitate more efficient feeding regimes that optimize tuna growth and minimize feed costs (Engle, 2010).

At the Tuna Research and Conservation Center (TRCC) in Pacific Grove, California, techniques have been developed that can contribute to academic and industry understanding of tuna energetics. The facility has maintained ~20 °C water temperatures and a fixed diet regime throughout its 20 years of operation. Furthermore, the TRCC team has collected morphometric measurements of all tuna mortalities throughout this period. This information has been archived in an extensive database and provides a unique opportunity to study tuna bioenergetics under controlled conditions. Our intention with this study, therefore, is to contribute to the understanding of tuna bioenergetics to inform future aquaculture and research efforts.

2. Materials and methods

2.1. Collection of tuna

The TRCC facility, transportation protocols, and life support system are described in greater detail by Farwell (2001). Tuna collection and research was performed under a protocol approved by the Institutional Animal Care and Use Committee (IACUC) for Stanford University. The yellowfin tuna used in this study were captured with rod and reel using barbless circle hooks and live Pacific sardines (*Sardinops sagax*) in the Eastern Pacific Ocean off of Baja California, Mexico. After capture they were kept alive in seawater holding wells aboard the fishing vessel for up to 4 days post-capture. Upon return of the vessel to the port of San Diego, California, the tuna were transferred using vinyl slings filled with seawater to a specialized transport vehicle and driven north to the Tuna Research and Conservation Center (TRCC) in Pacific Grove, California. Upon arrival to the TRCC facility, curved fork lengths (CFL) were measured from the tip of the rostrum across the body to the fork of the caudal fin using a flexible fiberglass measuring tape, and each individual had a passive integrated transponder (PIT) tag (Avid Identification Systems, Inc., Norco, CA) with a unique serial number implanted in its dorsal musculature. Tuna were maintained in the fiberglass holding tanks at the TRCC (one 340,000 L and two 110,000 L tanks). Some of the animals used in this study were subsequently transferred to the Outer Sea Exhibit (3,800,000 L) for display at the Monterey Bay Aquarium. The first yellowfin tuna was transported to the TRCC holding tanks in September of 1993 and more were collected annually for the next 20 years. Water temperatures were maintained at 19.9 ± 0.9 °C (mean ± s.d.) throughout the duration of the study period.

2.2. Diet

The diet regime for the captive tuna did not change throughout the course of the study. Yellowfin tuna were fed three times weekly with a mixed diet of Pacific sardine, market squid (*Loligo opalecens*) and vitamin gelatin mix (Mazuri Aquatic Gel Diet, Progress Drive, Richmond, IN) in quantities calculated to provide a target energetic input of 176 ± 36

$kJ \cdot kg^{-1}$ of fish biomass·day^{-1}. By weight, this target feeding level represents approximately 7% of the tuna biomass fed per day. The target feeding level was selected based on early experiences rearing juvenile yellowfin tuna at the TRCC and is designed to provide sufficient sustenance while maintaining water quality and fish health for physiological research. A regression of CFL and mass (described below) was used to estimate the weight of individual tuna and these values were summed to estimate the total biomass within a tank each month. Energy content of feed items was determined through proximate analysis of protein and fat composition using the Kjeldahl method (protein factor = 6.25) to measure total nitrogen content and the Mojonnier fat acid hydrolysis technique to measure crude fat content. Percent protein and fat values were converted to kilojoules using the energetic equivalents of 23.87 $kJ \cdot g^{-1}$ and 36.43 $kJ \cdot g^{-1}$ for protein and fat, respectively (Brett and Groves, 1979; Halver and Hardy, 2002; Dale et al., 2013). Representative samples of feed items were sent quarterly for analysis by a third party (N-P Analytical Laboratories, Checkerboard Square, St. Louis, MO) to account for any natural variability in feed energy content. The standard deviation in feed energy content across our proximate analysis dataset was used to quantify this natural variance. Unless specified otherwise, any variation around a reported mean in this study is a standard deviation.

2.3. Length and mass measurements

Morphometric data, including straight fork length (SFL), curved fork length (CFL), and mass (weight), were measured post-mortem for the captive yellowfin tuna. Typical causes of death were impact with the tank wall or euthanasia for physiological experiments. Only fish that were considered to be healthy (were not emaciated and observed to feed regularly) were included in the morphometric dataset. SFL was measured from the tip of the rostrum to the fork of the caudal fin using calipers. We analyzed the morphometric records to calculate regressions of CFL-to-SFL for different year classes of yellowfin tuna (n = 341, Table 1). Age at time of collection was calculated by converting initial CFL measurements to estimates of SFL, and assigning age to these SFL estimates using Equation 6 (Table 5) from Wild (1986) for otolith-aged yellowfin tuna from the Eastern Pacific Ocean. Age at mortality was calculated by adding the duration in captivity to the estimated age at the time of collection. Finally, we used the post-mortem length and weight records (n = 349) to calculate a regression of mass with SFL (Fig. 1).

2.4. Growth rates

Straight fork length data measured at capture and post-mortem were combined with age estimates and a von Bertalanffy growth function (VBGF) was fit to these data using a non-linear least squares regression (Fig. 2). In some instances where post-mortem straight fork length (SFL) data were not available, CFL values were converted to SFL using the conversion equation best suited to the size class of the fish (Table 1). Daily increases in SFL were estimated from our VBGF by dividing the growth curve into one-day increments, and daily weight increases were calculated from these SFL values using our SFL-mass regression for the captive tuna.

Table 1
Regression values for calculating straight fork length (SFL) from curved fork lengths (CFL) measured from yellowfin tuna (*Thunnus albacares*) (n = 341) maintained in captivity at the Tuna Research and Conservation Center.

Size ranges, CFL (cm)	Regression formula	R^2	Slope error	Intercept error	n
40–90	y = 0.9042× + 2.7504	0.98	0.01	0.56	254
91–128	y = 0.9759× − 4.2499	0.95	0.03	2.79	79
128–180	y = 0.9317× − 0.7775	0.93	0.11	15.32	8

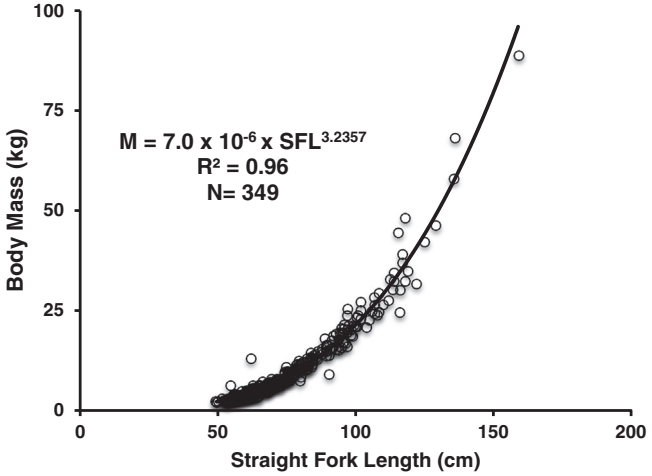

Fig. 1. Relationship between straight fork length (SFL) and the whole body mass (M) of yellowfin tuna (*Thunnus albacares*) maintained in captivity at the Tuna Research and Conservation Center.

2.5. Whole body caloric values

In order to construct a bioenergetic budget for the captive yellowfin tuna, we conducted proximate analyses of tuna tissues. We euthanized six healthy tuna and dissected each specimen, weighing each organ and component of the body and sending the samples to a third party for proximate analysis (N-P Analytical Laboratories, Checkerboard Square, St. Louis, MO). The methods of analysis of protein and fat concentrations are identical to those described above in the diet analysis section, and the same conversion factors were used to convert percentage fat and protein to kilojoules. We averaged the caloric values of individual organs across the different tuna sampled, and estimated an average energy content of the whole tuna body. The total weight of the individual organs and components was slightly less than the mass of each whole tuna, likely due to blood loss during the dissection process. To compensate for this unaccounted mass, a correction factor was applied that assumed that the missing mass contained the same average energy content as the rest of the tuna.

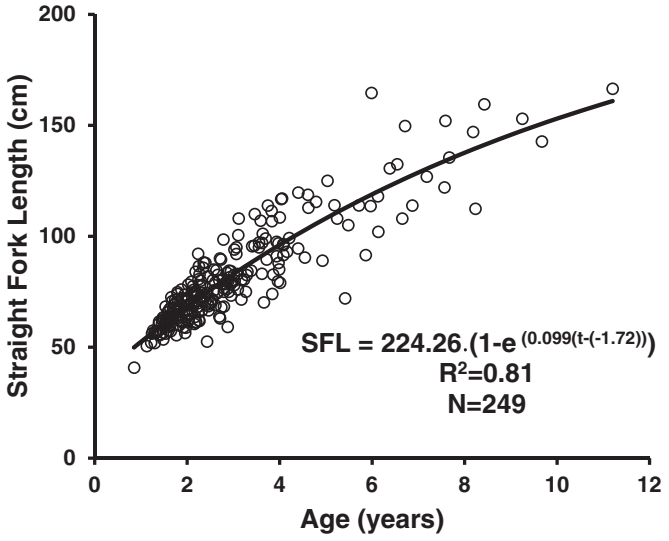

Fig. 2. Straight fork length (SFL) at age (t) and the fitted von Bertalanffy growth curve for yellowfin tuna (*Thunnus albacares*) maintained in captivity at the Tuna Research and Conservation Center.

2.6. Energetic budget

In this model of tuna bioenergetics, the energy available for growth is equal to the energy content of an ingested meal minus all metabolic costs. More specifically: retained energy = ingested energy − [specific dynamic action + routine metabolic rate + active metabolic rate + excretion and egestion] (Table 2). Ingested energy was defined as the target feeding level (176 ± 36 kJ·kg^{-1} of biomass·day^{-1}) multiplied by the mass of the model tuna (8.4 kg). Retained energy is considered to be the energy available to the tuna for growth after accounting for all quantifiable metabolic processes. Routine metabolic rates were sourced from Blank et al. (2007a), who studied the same tuna used in this study in a large swim tunnel respirometer at the TRCC. Klinger et al. (2016) proceeded to use the TRCC facility and respirometer to quantify Specific Dynamic Action (SDA), or the energy needed to digest and assimilate a meal, in yellowfin tuna (Secor, 2009). Data are not currently available on the egestion and excretion rates for yellowfin tuna specifically, and as such we relied on a study of other carnivorous teleosts (Brett and Groves, 1979).

There are few data available on the active metabolic rates of yellowfin tuna when they are stimulated to swim at relatively high speeds (Korsmeyer and Dewar, 2001). As such, we estimated active metabolic rates by combining the respirometry work of Blank et al. (2007a) with accelerometery studies of similar-sized yellowfin tuna in the tanks at the TRCC. Using dorsally mounted accelerometers Gleiss and Block (personal communication) found that TRCC yellowfin tuna typically swim with a tailbeat frequency translating to an average speed of 0.6 body lengths per second (BL·s^{-1}). Their analysis revealed that the captive tuna are stimulated to swim faster (0.9 BL s^{-1}) for periods of activity occurring for approximately 10% of a 24-h day. We relied on the Blank et al. (2007a) respirometry study to estimate the metabolic cost associated with this elevated swimming speed, and we relied on a scaling coefficient of 0.698 to account for the different masses of the tuna between studies (Killen et al., 2010).

2.7. Energy and food conversion ratios

Food conversion ratios (FCRs) were estimated for a model yellowfin tuna by estimating the daily weight gain and comparing this to the target feed amount. As described above, the daily weight gain rate was estimated by dividing the VBGF into one-day increments and converting the daily length changes into daily weight changes using our length-weight regression. We calculated FCRs for two diet regimes, one where the model tuna ingested a mixed-diet of squid, sardines, and gelatin and another with sardines as the sole feed type. We examined the influence of feed item energy content on the calculated FCR values by predicting FCRs under a high scenario (where the feed items have lower energy content) and a low scenario (where the feed items have higher energy content). This range in feed item caloric content was based on the standard deviation of measured values in our proximate analysis dataset.

The daily energy gain rate was calculated by multiplying the average tuna tissue energy value (determined through proximate analysis) by the rate of daily weight gain (estimated from the SFL-to-mass equation and VBGF). The gross energy conversion of the captive yellowfin tuna in this study was calculated as the ratio between the daily energy gain to the total energy ingested daily.

2.8. Comparison to other studies

We compared the growth rates, FCRs, tissue energy levels, longevity, and calculated energetic parameters of the captive yellowfin tuna in this study to related studies of both wild and captive yellowfin tuna. We calculated daily rates of length and weight gain from the length-age and length-weight regressions for the present study and for wild yellowfin tuna sampled in the Eastern Pacific Ocean using Equation 1 (L_∞ = 188.2 cm, k = 0.724, t_o = 1.825 years, and m = 1.434) and Equation 11 (a = −11.186 and b = 3.086) from Wild (1986), comparing the resulting growth curves with unpaired Student's t-tests. Furthermore, we examined the differences in the growth rates of the yellowfin tuna in this study to those of the bluefin tuna raised simultaneously in the TRCC tanks to elucidate inter-species patterns in growth (Estess et al., 2014).

3. Results

3.1. Diet analysis

Proximate analysis revealed that the sardines fed throughout this study contained 18 ± 1% protein and 11 ± 5% fat (n = 50, sample mass = 87 ± 43 g (mean ± s.d.)), and the average caloric content was 8.0 ± 2.1 kJ·g^{-1}. The squid were found to contain 16 ± 2% protein and 2 ± 0% fat (n = 37, sample mass = 45 ± 16 g), and the average caloric content was 4.5 ± 0.6 kJ·g^{-1}. The vitamin gel contained 28 ± 1%

Table 2
Processes involved in estimating energetic budget parameters, including references for each process. Model calculations are based on an 8.4 kg yellowfin tuna (*Thunnus albacares*) maintained in captivity at the Tuna Research and Conservation Center at 20 °C.

	Process	Estimated value (±S.D)	Units	References
Ingested energy				
Target feeding level	176 ± 36 kJ·kg^{-1} of biomass·day^{-1}	1478 ± 303	kJ·day^{-1}	Brett and Groves, 1979
Energetic costs				
Routine metabolism	26.3 ± 3.1 mgO_2·h^{-1} 1 mgO_2 = 13.59 J	606 ± 71	kJ·day^{-1}	Blank et al., 2007a; Killen et al., 2010; Jobling, 1994
Digestion	5.9 ± 0.2% of ingested energy	87 ± 3	kJ·day^{-1}	Klinger et al., 2016
Active metabolism	Routine metabolism at 0.9 body lengths·s^{-1} = 28.8 ± 4.0 mgO_2·h^{-1} for ~10% of day	66 ± 9	kJ·day^{-1}	Blank et al., 2007a; Gleiss and Block (Personal Comm.)
Excretion and egestion	27% of ingested energy	399	kJ·day^{-1}	Kitchell et al., 1978; Brett & Groves, 1979; Dale et al., 2013
Results				
Energy available for growth	Ingested energy − energetic costs	320 ± 386	kJ·day^{-1}	–
Daily growth rate	Calculated from growth curve	14.6	g·day^{-1}	–
Average tissue energy content	Via proximate analysis of whole tuna	7.9 ± 3.8	kJ·g^{-1}	–
Daily energy increase	Daily growth rate × average tissue energy content	116 ± 55	kJ·day^{-1}	–
Gross energy conversion	Daily energy increase/ingested energy	7.8% (high: 14.6%, low: 3.4%)		–

Table 3
Daily and yearly changes in straight fork length and mass for yellowfin tuna (*Thunnus albacares*) maintained in captivity at the Tuna Research and Conservation Center. Values calculated from the von Bertalanffy growth function where straight fork length, SFL = $224.26 \cdot (1\text{-}e^{(-0.099(t-(-1.72)))})$ at age, t, and from the regression of SFL and mass, M = $7.00 \times 10^{-6} \times SFL^{3.2357}$.

Age	Straight fork length	Daily length change	Mass at age	Yearly mass increase	Daily mass change	Yearly percent change in mass
Years	cm	mm·day^{-1}	kg	kg·year^{-1}	g·day^{-1}	%
1	53.41	0.47	2.7	2.0	7.7	73.4
2	69.67	0.42	6.4	3.7	12.7	57.6
3	84.38	0.38	12.0	5.5	17.6	46.1
4	97.69	0.35	19.2	7.3	22.1	37.7
5	109.73	0.31	28.0	8.8	25.9	31.3
6	120.63	0.28	38.0	10.0	29.0	26.3
7	130.49	0.26	49.0	11.0	31.2	22.4
8	139.42	0.23	60.7	11.7	32.8	19.2
9	147.49	0.21	72.9	12.1	33.6	16.6
10	154.80	0.19	85.2	12.3	33.9	14.4
11	161.41	0.17	97.6	12.3	33.7	12.6

Table 4
Comparative growth rates of captive yellowfin tuna (*Thunnus albacares*) maintained in captivity at the Tuna Research and Conservation Center (Table 3) and wild yellowfin tuna collected in the Eastern Pacific Ocean (Wild, 1986). A Student's *t*-test for unpaired means returns a significant difference at the 95% confidence level between the rate of length change (P = 0.03) and mass change (P = 0.01) between captive and wild yellowfin.

	Captive	Wild	Captive	Wild
Age	mm·day^{-1}	mm·day^{-1}	g·day^{-1}	g·day^{-1}
1	0.47	0.99	7.7	14.4
2	0.42	1.13	12.7	56.5
3	0.38	0.91	17.6	95.4
4	0.35	0.58	22.1	91.5
5	0.31	0.33	25.9	63.1

protein and 4 ± 0% fat (n = 8, sample mass = 71 ± 7 g), and the average caloric content was 8.1 ± 0.2 kJ·g^{-1}. To meet the target feeding level, the diet consisted of approximately 48% squid and sardine, respectively, and 4% gelatin by mass.

3.2. Age and growth

The relationship between the straight fork length (SFL) and the body weight (M) of the captive yellowfin tuna is described by the regression equation $M = 7.0 \times 10^{-6} \times SFL^{3.2357}$ ($R^2 = 0.96$, n = 349) (Fig. 1). The parameters (±S.E.) of the VBGF that provided the best fit to the length-age data were $L_\infty = 224.26 \pm 33.52$, $k = 0.099 \pm 0.026$, and $t_o = -1.721 \pm 0.356$ years ($R^2 = 0.81$, n = 249)(Fig. 2). Daily growth rates for weight and length were 14.6 g·day^{-1} and 0.4 mm·day^{-1}, respectively, for yellowfin tuna of average age 2.4 years and weight 8.4 kg (Tables 3 and 4). The average age at time of collection of the tuna was 1.2 ± 0.1 years and the average duration in captivity was 1.7 ± 1.7 years. The oldest fish sampled in this study was estimated to be 11.2 years old and had been in captivity for 10.1 years.

The rates of length and mass change were significantly lower (unpaired Student's *t*-test, P = 0.03 and 0.01, respectively) across all ages for the captive yellowfin tuna relative to those measured in the Eastern Pacific Ocean (Wild, 1986) (Fig. 3a and b). The TRCC yellowfin tuna also grew more slowly relative to yellowfin tunas held in captive facilities in Panama, Japan, and Indonesia under different water temperatures and feeding regimes (Fig. 4). Last, we found that the bluefin tuna held simultaneously in the tanks at the TRCC grew faster than the captive yellowfin tuna (Fig. 4).

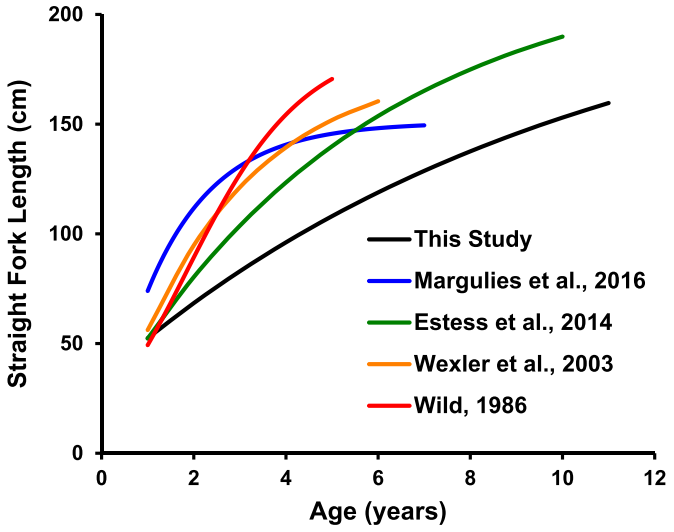

Fig. 4. A comparison of von Bertalanffy growth curves for yellowfin tuna (*Thunnus albacares*) from this study, Margulies et al. (2016), Wexler et al. (2003), and Wild (1986), and for captive Pacific bluefin (*Thunnus orientalis*) tuna held simultaneously at the Tuna Research and Conservation Center (Estess et al., 2014).

3.3. Whole body caloric analyses

Proximate analysis of tissues from six yellowfin tuna (average mass = 8.4 ± 2.6 kg, average length = 75.2 ± 7.3 cm, average age = 2.4 ± 0.5 years) measured an average energy content of 7.9 ± 3.8 kJ·g^{-1} (Table 5). The muscle, head, and skeleton accounted for a majority of the tuna's body mass at 60%, 12%, and 11%, respectively, and

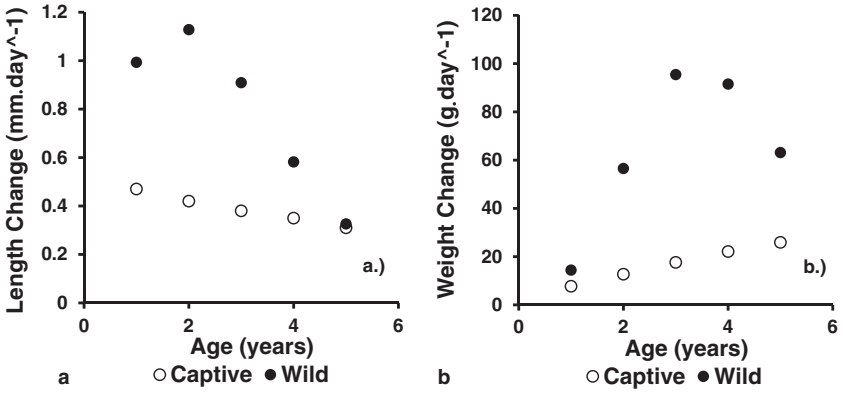

Fig. 3. a & b. Comparison of captive and wild growth rates of yellowfin tuna (*Thunnus albacares*) maintained in captivity at the Tuna Research and Conservation Center and wild yellowfin collected from the Eastern Pacific Ocean (Wild, 1986). Growth data from captive and wild fish are represented in Table 4.

Table 5
Results of proximate analysis of body parts from captive yellowfin tuna (*Thunnus albacares*) maintained in captivity at the Tuna Research and Conservation Center. Total kilojoules per gram and average percentage protein and fat values are shown for the whole tuna. Values represent the mean and standard deviation for six yellowfin tuna with a mean mass of 8.4 ± 2.6 kg and calculated age of 2.4 years. Skeletal Section 1 is comprised of the collar and pectoral fins. Skeletal Section 2 covers the skeletal system running posterior of the head to the end of the first dorsal fin, including the pelvic fins. Skeletal Section 3 consists of the area from the second dorsal fin down to the anal fin. *Atrium, ventricle, bulbous arteriosis, and gall bladder values were not available for all tuna sampled.

Sample	Mass (g)	S.D. (±)	Weight (% of total mass)	Protein (%)	Protein (kJ)	Fat (%)	Fat (kJ)	Total (kJ)	S.D. (±)
Liver	63	16	0.8	17.6	266	11.1	276	542	271
Atrium*	2	1	0.0	16.0	6	2.0	2	9	3
Ventricle*	12	5	0.1	16.6	46	2.6	10	56	22
Bulbous Arteriosis*	3	1	0.0	18.4	15	2.1	3	18	7
Caecum	108	47	1.3	14.6	372	5.3	243	614	363
Spleen	27	11	0.3	24.4	164	1.7	16	180	87
Stomach	94	27	1.1	18.7	419	3.0	114	534	197
Intestine	27	10	0.3	15.4	96	4.8	50	146	64
Gonad	11	12	0.1	18.0	46	2.4	10	56	60
Gallbladder*	7	3	0.1	10.4	17	8.7	14	31	9
Gills	385	114	4.6	14.9	1399	2.7	395	1794	852
Skin	368	158	4.4	21.4	1903	11.5	1349	3252	1585
Red Muscle	1089	501	12.6	21.5	5528	6.8	2825	8353	5012
White Muscle (Dorsal)	2063	658	24.6	23.8	11,581	4.9	4240	15,821	8006
White Muscle (Ventral)	1715	655	20.0	23.6	9622	4.8	3680	13,301	7828
Head	1008	381	11.9	15.0	3622	16.8	5742	9364	4003
Skeletal Section 1	393	132	4.7	18.4	1748	12.2	1792	3540	1909
Skeletal Section 2	291	57	3.6	18.1	1240	9.9	1022	2263	586
Skeletal Section 3	169	83	2.0	20.2	809	9.5	552	1361	639
Tail	220	66	2.8	20.7	1064	5.4	453	1517	585
Total	8053		95		39,963		22,788	62,752	

contained over 86% of the total energy content. On average, a whole yellowfin tuna consisted of 21% protein and 8% fat.

3.4. Energetic budget and food conversion efficiency

The food conversion ratio (FCR) estimated for the mixed diet of squid, sardines, and gel fed throughout the study period was 37.2:1 (high scenario = 46.9:1, low scenario = 30.9:1), where the high and low scenarios incorporate the standard deviation in food energy content measured across our proximate analysis dataset. If the tuna were fed a diet consisting solely of sardines amounting to the total caloric content of the target feeding level, this would return a food conversion ratio of 29.3:1 (high scenario = 39.5:1, low scenario = 23.2:1) to achieve the same growth rates measured in this study (Table 6).

After integrating the literature-derived values into our bioenergetic model, we estimated that a majority of the energy ingested by the tunas is devoted to routine metabolism and is possibly excreted as waste. Roughly 22% of an ingested meal's energy should be available to the tuna for growth, however, we observed that only 7.8% of this food energy is actually utilized for daily growth (Table 2). We estimate that this gross energy conversion level could be as high as 14.6% and as low as 3.4% due to variation in the daily energy gain rate and in the caloric content of ingested feed (Table 2).

4. Discussion

The Tuna Research and Conservation Center facility provided the unique, long-term opportunity to examine the growth of a highly-migratory fish species under controlled environmental and feeding conditions. Our bioenergetics model for the captive yellowfin tuna was consistent with previous observations for yellowfin tuna and other tuna species, while providing new insights into the mechanisms controlling tuna growth and energetics at lower water temperatures. These results, though unique to this captive scenario, can provide an important benchmark for understanding tuna energetics across species and environments.

The diet fed throughout the course of this study was chosen to optimize fish health, water quality, and research needs in a captive environment. We analyzed the energy content of feed items quarterly each year to improve the accuracy with which we met our target diet. Dietary intake for wild yellowfin tuna has been estimated at 4–7% of the body mass per day and 175–441 $kJ \cdot kg^{-1} \cdot day^{-1}$ for 87–97 cm tuna (Olson and Boggs, 1986). At the Achotines lab, yellowfin tuna were fed 1–2 times daily with feeding levels ranging from 39 to 436 $kJ \cdot kg^{-1} \cdot day^{-1}$, amounting to 1–10% body mass fed per day. In terms of the mass of food fed, the TRCC diet regime is at the high end of the range reported in comparable studies with a calculated ration of 6.5% body mass fed per day. However, in terms of absolute energy ingested, the TRCC target diet of 176 ± 36 $kJ \cdot kg^{-1} \cdot day^{-1}$ is at the low end of the range of values calculated for yellowfin tuna in captive and wild growth studies. This low energy diet is likely an important driver of the overall low growth rates and high food conversion ratios reported in this captive scenario.

We weighed and quantified the mass and tissue energy values of the main organs and structures of six captive yellowfin tuna, and the observed values are consistent with previous studies for this species. The combined mass of the red and white muscle comprised 60% of the overall mass of the yellowfin tuna sampled, similar to the values reported by Graham et al. (1983). Boggs and Kitchell (1990) reported an energy density of 6.0 $kJ \cdot g^{-1}$ for captive yellowfin tuna of 30–50 cm SFL, which is slightly lower than the value calculated here. Additionally, Peng et al. (2013) calculated average protein and fat levels at 24% and 2%, respectively, for dorsal white muscle samples from 36 ± 13 kg yellowfin tuna captured in the Western Pacific (n = 3), and Masuma (2013) recorded ventral white muscle fat levels ranging from 20 to

Table 6
Food conversion ratios (FCRs) estimated for an 8.4 kg yellowfin tuna (*Thunnus albacares*) maintained in captivity at the Tuna Research and Conservation Center. Calculated as the total food mass ingested daily ($g \cdot day^{-1}$) divided by the estimated daily growth rate ($g \cdot day^{-1}$).

Food types and amounts	Squid (g)	Sardine (g)	Gelatin (g)	Total Fed (g)	Growth ($g \cdot day^{-1}$)	Food conversion ratio
Mixed diet	262	262	20	544	14.6	37.2:1 FCR
All-sardine diet	0	428	0	428	14.6	29.3:1 FCR

36% for captive yellowfin tuna greater than 10 kg. Wexler et al. (2003) reported mean protein and fat levels of 23% and 10%, respectively, for captive yellowfin tuna in the Achotines facility. The protein levels of the yellowfin tuna measured in this study are consistent with other published values, and our estimated fat concentrations fall in the middle of the range found in related studies. The wide range of fat concentrations reported likely stem from different water temperatures and dietary intake levels found between study scenarios, though maturation status and body size are likely important factors as well.

The data underlying our growth equation represents an extensive morphometric dataset, however it does have some inherent biases. For example, 80% of the tuna sampled in the length-age data set are below 100 cm SFL, meaning that the resulting VBGF is less robust for larger yellowfin tuna. Furthermore, it is possible that the method used to assign age at the time of arrival to the TRCC facility could have introduced error. We relied on a robust study of yellowfin tuna growth from the Eastern Pacific Ocean to assign age at arrival to the facility. Polacheck et al. (2004) noted that age-length relationships in wild tuna populations can shift over time due to fishing pressure and environmental changes, potentially reducing the accuracy with which we assigned age to our captive animals. Regardless of these potential limitations, we feel that our growth dataset remains a valuable benchmark for comparative studies of tuna growth.

Our results are consistent with previous findings that hypothesize that yellowfin tuna have high energetic inputs to fuel active lifestyles, leaving a small margin of energy available for growth. In the present study, we calculated that 7.8% of an ingested meal's energy content was utilized for daily growth, the same gross energy conversion value calculated by Olson and Boggs (1986). Furthermore, we documented high food conversion ratios for the captive yellowfin tuna, with a ratio of 37.2:1 for the mixed diet of sardine, squid, and gelatin and 29.3:1 for a sardine-only diet. These estimates are higher than those documented by Wexler et al. (2003), who calculated FCRs ranging from 10.9–34.6:1 for captive yellowfin tuna at the Achotines facility in Panama. These FCRs represent the relationship between the daily weight gain of the tuna and the amount of food fed per day, and therefore, a relatively low daily weight gain or an overestimate of food intake levels would yield high FCR estimates. We proceed to examine both of these hypotheses in detail below.

Comparison of yellowfin tuna growth curves between studies indicates that some aspect of the conditions in captivity, whether it be the effect of water temperature, diet, interspecies competition, or other unknown factors, resulted in a reduced growth rate for the TRCC yellowfin tuna population. Additionally, our bioenergetic model either overestimates the amount of food consumed by the yellowfin tuna, underestimates the metabolic costs, or the tuna did not efficiently absorb ingested energy due to some aspect of captivity (i.e. water temperature). In any case, we have documented a captive scenario that can promote tuna longevity but is non-optimal for growth, and as such we may be able to derive useful lessons for aquaculture operations seeking to maximize growth in captivity.

Differences in diet regimes, competitive feeding, water temperature, stocking densities, and stressors from the captive environment could have contributed to the relatively low growth rates observed between this experiment and other studies of yellowfin tuna growth. As described above, the TRCC's target feed energy level is relatively low compared to those calculated for other studies. Feed has always been distributed in a broadcast style from above the tanks at the TRCC, rendering it nearly impossible to visually identify which species or individuals are getting more food items. Anecdotally, bluefin tuna are the more aggressive feeders, and as such the yellowfin tuna may not be receiving their allotted ration at each feeding. Another possibility is that the stocking densities of tuna in the TRCC tanks were excessively high and induced stress in the population, conditions that have been shown to reduce growth rates in other fish species (Jørgensen et al., 1993; Wedemeyer, 1996; Iwama et al., 2011). The TRCC tanks typically contain between 0.5 and 2 kg of tuna biomass$\cdot m^{-3}$, whereas the Achotines facility maintained lower stocking densities with a maximum of 0.75 kg of tuna biomass$\cdot m^{-3}$ (Wexler et al., 2003). The TRCC staff closely monitors fish condition, behavior, and tank water quality to maintain a healthy population of tuna, and it is unlikely that high stress rates resulted in the slow growth observed in this study. Furthermore, it is doubtful that overstocking of the tanks would disproportionately impact the yellowfin tuna growth relative to the bluefin tuna, which exhibited growth rates similar to wild bluefin tuna (Estess et al., 2014).

The tank water temperature maintained throughout this study is an important contributing factor to the low yellowfin tuna growth rates observed. Schaefer et al. (2007) reported on the thermal preferences of yellowfin tuna outfitted with archival electronic tags in the waters off Southern California and Mexico, finding that they routinely experience 20 °C water temperatures. However, these tagged fish made seasonal excursions to warmer, southerly waters (up to 30 °C). Indeed, an examination of the broader yellowfin tuna distribution in the Eastern Pacific reveals a warmer preference (Collette and Nauen, 1983; Block et al., 2011). Thus, while yellowfin tuna can clearly expand their niche into the cooler waters of the California Current, they consistently utilize warmer southerly waters. It is important to note that the Achotines facility maintained warmer water temperatures (average 28 °C) for their captive tuna (Wexler et al., 2003), and that Wild (1986) sampled yellowfin tunas captured in warmer, equatorial waters for his ageing study. Thus, water temperature must be kept in consideration when comparing the results of this study to others.

The cooler water temperatures maintained in this study could have affected the growth of the TRCC yellowfin tuna through two mechanisms. First, lower than optimal temperatures are associated with increased metabolic demands in some tuna species, leaving less energy available for growth (Blank et al., 2007b). Respiration experiments have shown that Pacific bluefin tuna experience a minimum routine metabolic demand between 15 and 20 °C, and this optimal temperature is likely higher for yellowfin tuna (Blank et al., 2007b). It is noteworthy that Pacific bluefin and yellowfin tuna exhibit niche separation in their Eastern Pacific range, the bluefin tuna venturing into colder northern waters than the more tropical yellowfin tuna (Block et al., 2011). Recent research has suggested that cardiac function may be the major factor limiting yellowfin tuna from utilizing cooler waters (Blank et al., 2004). Second, Russell et al. (1996) described how low water temperatures can reduce energy absorption rates in fish. Enzymatic activity can slow and as a result, overall digestive efficiencies can decline. In this scenario, the TRCC yellowfin tuna may have actually ingested the expected mass of feed, but they were at a functional disadvantage in absorbing the feed energy due to the cool water temperatures. Our comparisons between different studies suggest that water temperature plays an important, yet difficult-to-distinguish role in influencing yellowfin tuna growth rates.

Though we are confident that our bioenergetic model is built on the most representative values available for this species, we may have underestimated the energetic costs, explaining the gap between the calculated amount of energy available to the tuna for growth and the observed daily growth rates. The routine metabolism and specific dynamic action values utilized in our energetic model were sourced from peer-reviewed respiration experiments on the TRCC population of captive yellowfin tuna, however, there is considerable variation in the metabolic rate values reported from other study scenarios. Furthermore, our technique to estimate active metabolic rates from accelerometer-tagged yellowfin tuna relied on a short-term (7-day) dataset recorded in the TRCC facility, and direct comparison between observed tailbeat frequencies in the tank and the swim-tunnel respirometry experiments of Blank et al. (2007a) may be prone to error. Finally, species-specific data on yellowfin tuna excretion and egestion rates were not available and as such we relied on values from a study of other carnivorous fish species. Future research is needed to quantify the active metabolism and waste energy levels of tuna species.

At this time, we are unable to disentangle the relative contributions of water temperature, competitive feeding, stress, and other effects of the captive environment on the observed growth rates of yellowfin tuna at the TRCC. Comparison of these findings to other studies of wild and captive yellowfin tuna reveals the plasticity of tuna physiology, and highlights the need to better understand how subtle changes in environmental parameters may have significant consequences for the growth, energetics, and reproduction of these marine predators. Indeed, other studies have utilized basic bioenergetic data, such as those provided here, to forecast the effects of rapid climate change on species ecology and distribution (Pörtner and Peck, 2010). These results confirm that yellowfin tuna have high energetic demands and food conversion ratios, making them a relatively expensive species to culture, particularly in the low water temperatures and mixed-species scenario described here. Shifts in feed costs and technologies, in conjunction with changes in market prices for yellowfin tuna, will determine the economic feasibility of aquaculture operations moving forward. In conclusion, it is our hope that the academic and commercial sectors will draw on this unique study to enhance the efficiency of tuna aquaculture operations and promote the conservation of tunas internationally.

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