ORIGINAL PAPER

Stingray life history trade-offs associated with nursery habitat use inferred from a bioenergetics model

Jonathan J. Dale · Jeffrey C. Drazen · Kim N. Holland

Abstract Consumption rates of marine predators are vital to assessing their trophic impacts and potential consequences of fisheries removal and habitat alteration, yet are rarely estimated. Standard metabolic rates were estimated for juvenile brown stingrays, *Dasyatis lata*, and used as input parameters for a bioenergetics model to predict consumption rates. Temperature and mass had significant effects on metabolic rates. The energy budget of juvenile brown stingrays was heavily weighted toward metabolism, accounting for 66 % of consumed energy. Growth accounted for 7 % of the energy budget indicating very slow growth potentially due to limited food resources. Population consumption rates suggest potential for strong top-down effects on prey populations due to stingray predation. This study suggests the use of Kāneʻohe Bay as a nursery habitat for juvenile brown stingrays is a trade-off between increased juvenile survival through predator avoidance and a late age at first maturity due to slow growth rates resulting from low prey availability.

Communicated by M. A. Peck.

J. J. Dale (✉)
Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, USA
e-mail: jjdale@stanford.edu

J. C. Drazen
Department of Oceanography, University of Hawaiʻi, Honolulu, HI 96822, USA

K. N. Holland
Hawaiʻi Institute of Marine Biology, University of Hawaiʻi, Kāneʻohe, HI 96744, USA

Introduction

Dietary studies of elasmobranchs suggest they are high trophic position predators in marine ecosystems (Cortés 1999; Ebert and Bizzarro 2007) with the potential for significant impacts on prey populations and food web dynamics (Heithaus 2004). However, food habit studies only provide information on the relative contribution of prey items to the predator's diet. In order to evaluate the ecosystem impacts of elasmobranch predation, consumption rates must also be quantified. Understanding the trophic impacts of elasmobranchs has become increasingly important due to the effects of fisheries removal and habitat alteration on elasmobranch populations (Cortés 2004; Jennings et al. 2008; Pierce and Bennett 2010). Because biological systems conform to the laws of thermodynamics, information on energy used in growth and metabolism and energy lost through wastes can be incorporated into bioenergetics models to estimate consumption rates (Brett and Groves 1979). Yet despite the growing need for estimates of elasmobranch consumption rates, only a handful of studies have utilized this technique (e.g., Lowe 2002; Schindler et al. 2002; Dowd et al. 2006a; Bethea et al. 2007).

Metabolic rates are typically the largest and most variable components of an organism's daily energy budget (Boisclair and Sirois 1993; Lowe 2001), having the greatest effect on consumption rates estimated from bioenergetics models (e.g., Bartell et al. 1986). Due to the difficulties of measuring metabolic rates for elasmobranchs, bioenergetics models often lack species-specific data for metabolism (Stillwell and Kohler 1982, 1993; Medved et al. 1988; Schindler et al. 2002), limiting the accuracy of consumption rate estimates. For example, estimates of daily ration for juvenile sandbar sharks, *Carcharhinus plumbeus*, which incorporated species-specific metabolic rates (Dowd et al.

2006a), were 60–70 % higher than previous estimates, which used metabolic rates of spiny dogfish (*Squalus acanthias*, Stillwell and Kohler 1993; Medved et al. 1988). Such inconsistencies could create significant bias when evaluating the trophic impacts of elasmobranchs on marine ecosystems. Clearly, obtaining species-specific estimates of metabolic rates should be of high priority when estimating daily ration from bioenergetics models.

Another application of bioenergetics models is the evaluation of impacts from habitat alteration. Several demographic studies have shown that survivorship of juvenile age classes contributes significantly to elasticity analyses, and minimizing negative impacts on juveniles is one of the most effective ways of stabilizing populations (Heppell et al. 1999; Cortés 2002; Pierce and Bennett 2010). Juveniles of many elasmobranch species use coastal estuaries as nursery habitats (Heupel et al. 2007) where the potential for anthropogenic impacts is high (Lotze et al. 2006; Jennings et al. 2008). Estimates of consumption rates could provide a means of evaluating the effects of anthropogenic impacts on juvenile populations within these nursery habitats. For example, an individual-based bioenergetics model predicted a 12 % increase in consumption rates for cownose rays (*Rhinoptera bonasus*) due to an increase in water temperature (Neer et al. 2007). Kāneʻohe Bay (Oahu, Hawaiʻi) is one such nursery habitat, used by juvenile brown stingrays (JBS), *Dasyatis lata*, and juvenile scalloped hammerhead sharks, *Sphyrna lewini*. Juvenile brown stingrays forage within Kāneʻohe Bay for the majority of their juvenile lives before shifting to offshore habitats with the onset of sexual maturity (~8 and 15 years for males and females, respectively; Dale et al. 2011a; Dale and Holland 2012). With a lack of fisheries exploitation for this species in Hawaiʻi, habitat alteration may have the greatest impacts on juvenile populations (e.g., Jennings et al. 2008). This bay is relatively small (46 km²) and provides an excellent system to evaluate the trophic role of an abundant benthic predator. The objectives of this study were to estimate the standard metabolic rates of JBS through respirometry and incorporate previous estimates of food habits and growth (Dale et al. 2011a; Dale and Holland 2012) to develop an energy budget and estimate their age-specific daily ration with a bioenergetics model. Results from the model are then used to evaluate the potential influences of nursery habitat use on the life history of this species.

Materials and methods

Sample collection

Juvenile brown stingrays were captured within Kāneʻohe Bay (21°26.1′N, 157°46.6′W) using standard demersal longlines. Upon capture, stingrays were transported back to the Hawaiʻi Institute of Marine Biology (HIMB, located within Kāneʻohe Bay) where they were maintained in a 7-m-diameter tank with flow-through seawater. Stingrays were fed ad libitum (squid and sardines) and maintained for a minimum of 7 days. Prior to experimental trials, stingrays were starved for 96 h to ensure that they were in a post-absorptive state (Lowe 2001).

Respirometry

Measurements of oxygen consumption were made on individual JBS in a rectangular 650-L closed-system, recirculating respirometer (107 × 107 × 57 cm, acrylic) (Fig. S1). Seawater for the respirometer was taken from Kāneʻohe Bay adjacent to HIMB at ambient temperature and salinity, and no manipulation of water temperature was conducted (i.e., experiments were run on seasonally acclimated rays). The respirometer could also be operated in flow-through mode allowing stingrays to acclimate to the respirometer for 24 h prior to experimental trials. During acclimation, fresh seawater was continuously pumped into the respirometer to maintain ambient oxygen concentrations. The respirometer was isolated with shade cloth to minimize visual disturbance.

Immediately prior to experimental trials, the inflow water was shut off and the respirometer switched to closed circuit. Oxygen concentration and water temperature were measured once per minute with a fiber optic oxygen sensor (Aanderaa Data Instruments, oxygen optode 3830) interfaced with a notebook computer through HyperTerminal, and salinity was measured at the end of each trial. All equipment was calibrated to the manufacturer's specifications. Trials lasted a minimum of 2 h and were terminated after a maximum of 3.5 h or when oxygen concentration in the respirometer dropped to 70 % saturation. On average, water temperature during experimental trials increased by 0.32 ± 0.15 °C. Activity of the ray was monitored with an infrared video camera mounted above the respirometer. However, activity in the respirometer was not representative of natural swimming activity (i.e., rays resisted straight-line swimming and would move in small circles around the respirometer) preventing measurements of routine metabolic rates. Therefore, only trials where the ray remained quiescent were used for calculation of oxygen consumption. At the conclusion of each experimental trial, the respirometer was run without animals to measure background respiration, which was accounted for in final MO_2 calculations. Additionally, the disk width of each ray was measured to the nearest 0.1 cm, weight measured to the nearest 0.1 kg, and the animal was subsequently released back into Kāneʻohe Bay following resumption of feeding in the holding tank.

Data analysis

Oxygen consumption rate was calculated using the slope of the change in O_2 concentration over the course of the experimental trial (Lowe 2001) and normalized by mass for mass-specific metabolic rates (mgO_2 kg^{-1} h^{-1}). The decrease in water volume due to stingray displacement was measured and accounted for in final calculations. Multiple linear regression analysis was used to estimate the effects of stingray mass and water temperature on mass-independent metabolic rates (mgO_2 h^{-1}). In order to meet the assumptions of parametric testing, data were log transformed prior to analysis.

Proximate chemical analysis

Proximate chemical analysis was conducted on five JBS to determine their energy density. For each stingray, disk width, total mass and liver mass were measured and a sample of white muscle and liver tissue was analyzed for percent dry matter, ash, crude protein and crude fat (Ag Diagnostic Services, University of Hawai'i, Honolulu). Energy densities of muscle and liver samples were estimated using a conversion factor of 5.7 kcal g^{-1} for protein and 8.7 kcal g^{-1} for lipid. Values were converted from kcal to kJ using the conversion factor 4.19 kJ $kcal^{-1}$ (McNeill and Lawton 1970; Drazen 2007). Total energy density of the stingrays was estimated by multiplying the tissue-specific energy density by the relative contribution of that tissue to total mass assuming the energy density of all nonliver tissue was approximated by the energy density of white muscle. Energy densities of three whole crabs, *Podophthalmus vigil*, an important component of the stingray diet and commonly found in Kāne'ohe Bay, were also estimated from proximate chemical analysis using the same conversion factors.

Bioenergetics model

A bioenergetics model was used to develop an energy budget and estimate age-specific daily energy consumption (kJ day^{-1}) of individual JBS in Kāne'ohe Bay, expressed as follows:

$$C = RMR(T,M) + G(M) + SDA + W \qquad (1)$$

where RMR (T, M) = energy used in daily routine metabolic rate as a function of temperature and individual mass, $G(M)$ = energy used for daily growth as a function of individual mass, SDA = daily metabolic costs of specific dynamic action, W = daily energy lost as waste and is the sum of energy lost through feces and urine (Brett and Groves 1979). The model used a daily time step and ran for 1 year beginning July 1. Because SDA and W were represented as fractions of consumption (see below), Eq. (1) was rearranged and solved for C as follows:

$$C = \frac{RMR + G}{(1 - SDA - W)} \qquad (2)$$

Model parameters

Daily standard metabolic rates were calculated for each individual in the model using a regression equation relating mass-independent standard metabolic rates (SMR) to mass and temperature for JBS (see Results);

$$SMR = aM^bT^c \qquad (3)$$

where a = intercept, b = mass scaling coefficient, c = temperature scaling coefficient, M = mass and T = temperature. There are currently no quantitative estimates relating routine metabolic rates to standard metabolic rates for batoids. The relationship between MO_2 and swimming speed for blacknose sharks was used (*Carcharhinus arconotus*, Carlson et al. 1999);

$$\log MO_2 = 0.007U + 2.38 \qquad (4)$$

where U = swimming speed (cm s^{-1}), with the average rate of movement for JBS actively tracked in Kāne'ohe Bay (6.78 cm s^{-1}, Cartamil et al. 2003) as an approximation of the increase in standard metabolic rate due to activity. Based on this relationship, the mean ratio of RMR/SMR was 1.11, which was the initial estimate of the activity multiplier (ACT) to generate field metabolic rates (Schindler et al. 2002). In comparison, this ACT value is lower than those estimated for juvenile sandbar sharks, *Carcharhinus plumbeus* (1.6, Dowd et al. 2006b), and juvenile scalloped hammerhead sharks (1.4, Lowe 2002), both obligate ram ventilators, and subadult lemon sharks, *Negaprion brevirostris* (1.3, Sundström and Gruber 1998), but similar to that of a dorsoventrally flattened teleost, *Platichthys flesus* (1.1, Stevens et al. 2006). Daily metabolic rates (mgO_2 day^{-1}) were converted to daily metabolic energy consumption (kJ day^{-1}) using the oxycalorific coefficient 13.59 J mgO_2^{-1} (Elliott and Davison 1975).

The growth component of the bioenergetics model is composed of somatic and reproductive growth. Reproductive growth was assumed negligible as the model only included juvenile stingrays. Somatic growth was based on growth rates obtained from a logistic growth function fit to observed weight-at-age data (Dale and Holland 2012), which were used to calculate daily growth increments (kg day^{-1});

$$M_t = M_{t-1} + \frac{kM_{t-1}(W_\infty - M_{t-1})}{W_\infty} \qquad (5)$$

where M = mass, k = growth coefficient, W_∞ = asymptotic size. Growth in mass was then converted to growth in energy (kJ day^{-1}) using the energy density of JBS determined from proximate chemical analysis.

Specific dynamic action represents energy expended on pre- and post-absorptive activities, including gastrointestinal muscle contraction, production of digestive acids and enzymes, nutrient absorption and the synthesis of compounds from absorbed nutrients (Jobling 1981; Secor et al. 2007), and has only been estimated for a few elasmobranchs (range 0.6–0.17C; Du Preez et al. 1988; Sims and Davies 1994; Duffy 1999; Ferry-Graham and Gibb 2001). A nominal value of 0.1 C was used to estimate the fraction of consumed energy attributed to SDA in the model (sensu Schindler et al. 2002; Dowd et al. 2006a).

Absorption efficiency has only been estimated for a single elasmobranch species, *N. brevirostris*, and ranged from 61.9 to 83.1 %, with the greatest absorption efficiencies occurring at the highest ration levels which approached feeding rates in the field (Wetherbee and Gruber 1993). Based on these values and mean waste values ($F + U$) for carnivorous teleosts, a total waste component of 27 % of consumed energy is generally accepted (Brett and Groves 1979; Lowe 2002; Schindler et al. 2002; Dowd et al. 2006a; Bethea et al. 2007; Neer et al. 2007). Energy lost as feces and urine accounts for 20 and 7 %, respectively (Brett and Groves 1979; Wetherbee and Gruber 1993).

To calculate consumption rates for individuals of each age class (males 0–8 year, females 0–14 year), starting weights were estimated by a logistic growth function based on observed weight-at-age data (Dale and Holland 2012);

$$M_t = \frac{W_\infty}{\left(1 + e^{-k(t-t_0)}\right)}, \tag{6}$$

where t_0 is the inflection point of the curve and the other parameters are as previously defined. Water temperature data from 2009 and 2010 were taken from a NOAA weather station located in Kāne'ohe Bay, and daily water temperatures for the model were averaged between years and ranged from 22.2 to 28.3 °C. Diet composition data were taken from a recent diet study of JBS in Kāne'ohe Bay (Dale et al. 2011a). Dietary data were represented as the gravimetric contribution (%Weight) of individual prey items, and observed ontogenetic shifts were incorporated into calculations of consumption rates (Table 1). Estimated daily energy rations (kJ day^{-1}) were converted to daily ration (%Body Weight (BW) day^{-1}) using the relative gravimetric contribution of prey items to the stingray diet and the energy density of prey items (Table 1). Energy densities of prey items which could not be sampled were obtained from the literature (Table 1). Portunid crabs were approximated by the energy density of *P. vigil*. The relative abundance (Catch Per Unit Effort, CPUE) and sex ratio of JBS age classes in Kāne'ohe Bay were taken from longline surveys conducted from 2006 to 2010 (J. Dale unpubl data). Sex ratios were not significantly different from 1:1 (chi-square test, $X_2^2 = 2.9$, $P = 0.09$) for stingrays < 9 years old (all stingrays > 8 years old were female).

Error analysis

A Monte Carlo simulation was used to evaluate the sensitivity of consumption rate estimates to variation in input parameters (Bartell et al. 1986; Dowd et al. 2006a; Bethea et al. 2007). Probability density functions were used to generate variation within model parameters (Table 2). Multivariate normal distributions were used for metabolic scaling exponents based on their covariance and estimated from the relationship between mass, temperature and SMR (SMR$_a$ = intercept, SMR$_b$ = mass coefficient, SMR$_c$ = temperature coefficient). Normal distributions were used for daily water temperature, age-specific starting mass, waste and stingray energy density. The ACT and SDA were represented by triangular distributions due to the limited amount of data for these variables. Asymptotic size (W_∞) and the growth coefficient (k) were estimated from

Table 1 Gravimetric contribution of individual prey items to the diets of juvenile brown stingray age classes

Age class divisions are based on observed ontogenetic diet shifts from Dale et al. (2011a). Energy density of Stomatopoda based on the average energy density of benthic decapods from Thayer et al. (1973). Energy density of unidentified prey estimated as the average energy density of all prey types

Prey	% Gravimetric contribution by age class			Energy Density (kJ g^{-1})	Source
	0–3	4–7	7–14		
Alpheidae	55.58	20.4	2.64	3.6	Bush (2002), Lowe (2002)
Gobiidae	1.25	8.82	13.88	4.64	Bush (2002), Lowe (2002)
Portunidae	31.93	53.28	70.71	2.67	This study
Podophthalmus vigil	9.50	20.83	47.11	2.67	This study
Stomatopoda	0.22	4.89	8.2	5.2	Thayer et al. (1973)
Polychaeta	6.69	6.01	1.44	3.55	Thayer et al. (1973)
Unidentified	4.46	6.6	3.13	3.93	

Table 2 Parameters, probability distributions, nominal values and variability used in the bioenergetics model

Parameters	Distribution	Nominal value	SE or range	IPP	RPSS	Source
SMRa	Multivariate normal	−0.05	−0.002, −0.071	65.0, −37.6	18.5	This study
SMRb	Multivariate normal	0.78	−0.002, 0.002	92.4, −45.2	0.6	This study
SMRc	Multivariate normal	1.48	−0.071, 0.050	55.4, −34.1	9.7	This study
ACT	Triangular	1.11	1.06–1.16	8.9	6.7	Carlson et al. (1999), Cartamil et al. (2003)
SDA	Triangular	0.1	0.06–0.17	4.6	1.6	Du Preez et al. (1988), Sims and Davies (1994), Duffy (1999), Ferry-Graham and Gibb (2001)
Wi and k				0.3, 1.1	19.3, 17.1	Dale and Holland (2012)
Female	Bivariate normal	63.7, 0.23	−0.008			
Male	Bivariate normal	35.6, 0.25	−0.008			
Waste	Normal	0.27	3	1.1	0.6	Brett and Groves (1979), Wetherbee and Gruber (1993)
Energy density	Normal	6.03	0.4	1.8	1.5	This study

Results of sensitivity analyses are represented as the mean value for all age classes. IPP, individual parameter perturbation (±10 %). Values represent the percent change in consumption rate estimates due to a 10 % change in nominal parameter values. Single values represent linear sensitivities. RPSS, relative residual sum of squares. Values represent the contribution of each parameter to the variance of consumption rate estimates. Energy density parameter represents the energy density of brown stingrays. See text for remaining parameter definitions

a bivariate normal distribution based on the covariance between W_∞ and k (Dale and Holland 2012). Parameters SMR_a, SMR_b, SMR_c, W_∞ and k were considered individual traits and were assigned to each individual at the start of a simulation run and then held constant. The remaining parameters were considered environmental traits and were allowed to vary on a daily basis. For each run of the simulation, parameter values were randomly chosen from the assigned probability density functions. An average daily value over the 1-year simulation was calculated for each parameter in each age class. This process was repeated 2,000 times, providing frequency distributions, medians and confidence intervals (2.5th and 97.5th percentiles) for parameter estimates. Monte Carlo simulations were run in R (R Development Core Team 2010). Individual parameters where ranked in importance by their relative contribution to the variance of daily consumption rates using relative partial sum of squares (RPSS, Bartell et al. 1986). This method estimates the sensitivity of consumption rate estimates to modeled variation in individual parameters. A sensitivity analysis using individual parameter perturbations (IPP) was also conducted (Bartell et al. 1986). Age-specific consumption rates were estimated from a deterministic model using nominal input parameter values. Each parameter was then increased or decreased by 10 % with the remaining parameters fixed at their nominal values.

The percent change in consumption rate estimates due to a ±10 % change in parameter values was then calculated to assess the sensitivity to variation in individual parameters due to model structure.

Results

Metabolic rates

Standard metabolic rates were calculated for 22 JBS ranging in mass from 1.03 to 9.85 kg at temperatures ranging from 22.5 to 27.3 °C and salinities ranging from 34 to 37 ‰ (Table S1). Estimates of mass-specific MO_2 ranged from 53.06 mgO_2 kg^{-1} h^{-1} for a 9.85-kg individual at 23 °C to 115.99 mgO_2 kg^{-1} h^{-1} for a 1.16-kg animal at 27 °C (mean ± SD = 76.98 ± 15.31 mgO_2 kg^{-1} h^{-1} at 25 °C) (Fig. 1). Both log-transformed mass and temperature had significant effects on mass-independent MO_2 ($P < 0.001$), explained 98 % of the variance in MO_2 values and was represented by the equation (SE): log MO_2 (mgO_2 h^{-1}) = −0.05 (0.32) + log Mass*0.78 (0.02) + log Temp*1.48 (0.22) (Fig. 1). This equation was used to standardize the mass of all animals to 5.0 kg in order to calculate a Q_{10} value, which was 1.8 (22–27 °C). Similarly, temperature was standardized to 25 °C in order to estimate
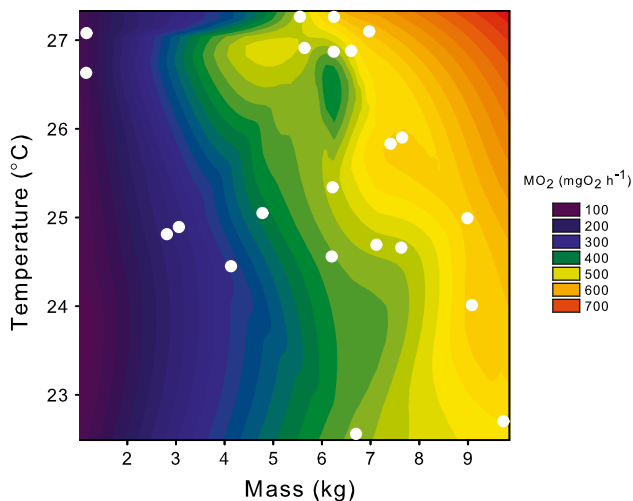
Fig. 1 Contour plot of standard mass-independent metabolic rates (mgO_2 h^{-1}) as a function of mass (kg) and temperature (°C) determined for juvenile brown stingrays. *Circles* represent measured values for each stingray ($n = 22$)

the allometric relationship between mass and MO_2, which was best represented by the equation: MO_2 (mgO_2 h^{-1}) = $105*Mass^{0.78}$.

Bioenergetics

Average energy density of JBS (mass range 2.8–9.9 kg) determined from proximate chemical analysis was 6.03 ± 0.40 kJ g^{-1} and ranged from 5.58 kJ g^{-1} for a 2.8-kg individual to 6.55 kJ g^{-1} for a 7.3-kg individual. Average water, crude protein and crude fat content were 76.9 ± 1.8, 21.8 ± 1.1 and 2.3 ± 1.0 % respectively. There was a slight increase in energy density with increasing size; however, this relationship was insignificant (linear regression, $F_{(1,4)} = 7.0$, $P = 0.08$), likely due to the small sample size. Average water, crude protein, crude fat and energy density of the three *P. vigil* individuals were 65.9 ± 6.4, 10.7 ± 1.9, 0.3 ± 0.2 % and 2.67 ± 0.56 kJ g^{-1}, respectively.

The energy budget of JBS was heavily weighted toward metabolism (RMR + SDA), which represented 66 ± 0.4 % of total consumed energy. Routine metabolic rate alone represented 55 ± 0.4 % of total consumed energy. Growth on the other hand was a relatively small fraction of the energy budget representing 7 ± 0.4 % of total consumed energy (Fig. 2). The percentage of total energy expenditure devoted to growth relative to metabolism remained stable at ~9 %.

Variation in consumption rate estimates from the use of stochastic input parameters ranged from 48 kJ day^{-1} for age-1 individuals to 345 kJ day^{-1} for age-10 individuals (Table 3). Median daily energy rations increased from
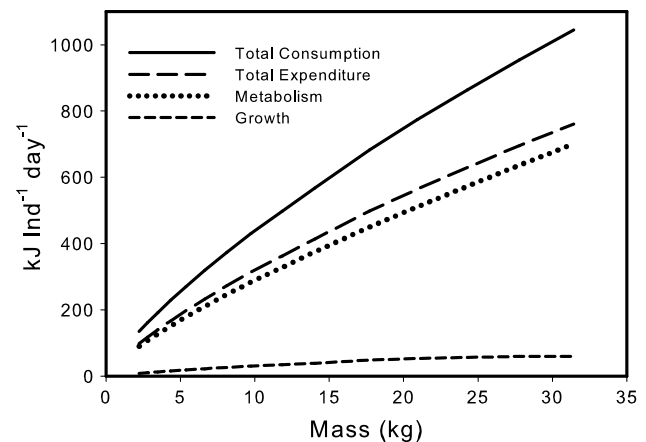

Fig. 2 Daily energy budget (kJ Ind^{-1} day^{-1}) for individual juvenile brown stingrays as a function of mass (kg). Total expenditure is the sum of metabolism and growth. Total consumption is the sum of metabolism, growth and waste

135 kJ day^{-1} for age-0 (mean BW = 2.2 kg) individuals to 1,045 kJ day^{-1} for age-14 (mean BW = 31.4 kg) individuals. Relative to BW, daily ration decreased from a high of 1.81 %BW day^{-1} for age-0 individuals to 1.03 %BW day^{-1} for age-14 individuals (Table 3). Gross conversion efficiency, the fraction of consumed energy incorporated into growth, was ~7 % for all age classes. Maintenance ration, the consumption rate at zero growth, was ~93 % of total energy consumption.

Total yearly consumption ranged from 15 (661 % mean BW) to 118 kg $year^{-1}$ (375 % mean BW) (Table 3), and total yearly energy consumption ranged from 49,200 (365 % total stingray energy content) to 381,320 kJ $year^{-1}$ (201 % total stingray energy content) for age-0 and age-14 individuals, respectively. Based on the relative abundance of juvenile age classes, population consumption rates were highest for the 4- and 5-year age classes and decline with increasing age (Fig. 3). This trend is due to individual consumption increasing with size, coupled with a corresponding decrease in the relative abundance of older age classes.

Individual parameter perturbations indicated that the model was highly sensitive to variation in the scaling coefficients related to metabolism (SMR_a, SMR_b, SMR_c) (Table 2). The response of consumption rate estimates to variation in these parameters was nonlinear, with a 10 % increase resulting in an average increase in consumption rate estimates of 65, 92 and 52 % for SMR_a, SMR_b and SMR_c, respectively. A 10 % decrease in these parameters resulted in an average decrease in consumption rate estimates of 37, 45 and 34 % for SMR_a, SMR_b and SMR_c, respectively. Consumption rate estimates were linearly sensitive to the remaining parameters, and a 10 % change resulted in a change in consumption rate estimates < 10 %.

Table 3 Median daily energy ration (DER), daily consumption relative to mass and total prey consumption over the course of 1 year for an average juvenile brown stingray individual of each age class estimated from Monte Carlo simulations of the bioenergetics model

Confidence intervals (CI) are represented as the 2.5 and 97.5 percentiles

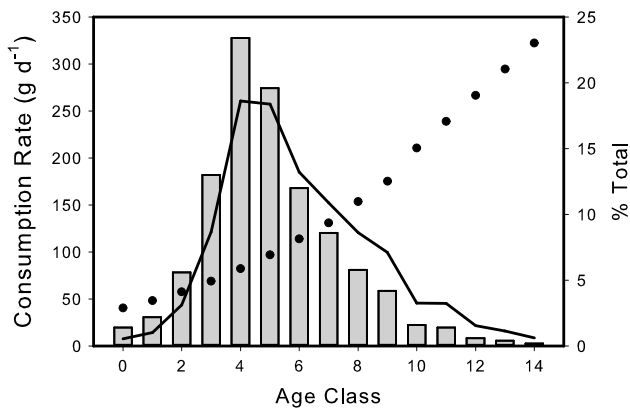| Age class (year)	DER (KJ day^{-1})	CI	Consumption rate (%BW day^{-1})	CI	Consumption rate (kg year^{-1})	CI
0	135	101–168	1.81	1.36–2.23	15	11–61
1	161	136–184	1.73	1.46–1.98	18	15–67
2	192	161–223	1.65	1.39–1.92	21	18–81
3	230	183–269	1.58	1.26–1.85	25	20–98
4	271	227–316	1.53	1.28–1.78	30	25–115
5	319	265–366	1.46	1.21–1.68	35	29–134
6	375	309–434	1.40	1.15–1.62	42	34–158
7	431	334–519	1.34	1.04–1.62	48	37–189
8	498	392–595	1.30	1.02–1.55	56	44–217
9	568	478–659	1.25	1.05–1.45	64	54–241
10	683	511–856	1.19	0.89–1.49	77	58–312
11	775	609–940	1.14	0.90–1.39	87	69–343
12	864	707–1017	1.10	0.90–1.29	97	80–371
13	954	843–1085	1.06	0.94–1.21	108	95–396
14	1045	938–1159	1.03	0.92–1.14	118	106–423

Fig. 3 Relative abundance of each age class (%, *vertical bars*), age-specific consumption rate (g day^{-1}, *black circles*) and percent of total population consumption by age class (%, *solid line*) calculated from the relative abundance of each age class. Relative abundance is based on longline surveys conducted from 2006 to 2010 within Kāneʻohe Bay (J. Dale unpubl data)

Table 4 Comparison of mass-specific metabolic rates among myliobatiform stingrays

Species	N	MO$_2$ (mgO$_2$ kg^{-1} h^{-1})	Source
Myliobatis aquila	5	47.5	Du Preez et al. (1988)
Myliobatis californica	6	158.1[b]	Hopkins and Cech (1994)
Dasyatis americana	6	93.6[a,b]	Fournier (1996)
Dasyatis violacea	8	63.3	Ezcurra (2001)
Rhinoptera bonasus	19	73.0	Neer et al. (2006)
Dasyatis lata	22	52.8	This study

When necessary, metabolic rates have been corrected to 20 °C and 5 kg using species-specific scaling coefficients. A mass coefficient of 0.8 was used (McNab 2002) when unavailable from the literature

[a] Routine metabolic rate

[b] Mass scaling coefficient of 0.8 used

Discussion

Metabolic rates

Mass-specific metabolic rates for JBS in this study were similar to those reported for other myliobatiform stingrays when standardized to 5 kg and 20 °C (Table 4). The metabolic rate of a 5-kg JBS at 20 °C was most similar to those of the bull ray (*Myliobatis Aquila*, Du Preez et al. 1988), pelagic stingray (*Pteroplatytrygon violacea*, Ezcurra 2001) and cownose ray (*Rhinoptera bonasus*, Neer et al. 2006) despite significant differences in their autecology. The pelagic stingray, cownose and bull ray are specialized for active swimming (McEachran 1990), whereas brown stingrays are primarily benthic and relatively sedentary

Of these remaining parameters, consumption rate estimates were most sensitive to variation in the ACT parameter with a 10 % change resulting in a 9 % change in consumption rate estimates. Error analysis with RPSS indicated the metabolic coefficient SMR$_a$, and growth coefficients W_i and k contributed most to the variance of estimated consumption rates (Table 2). The percentage of variance due to these parameters was 18, 19 and 17 % for SMR$_a$, W_i and k, respectively. Parameters SMR$_c$ and ACT had marginal contributions to model variance of 10 and 7 %, respectively. The relative contributions of the remaining parameters to the variance of estimated consumption rates were all negligible.

(Cartamil et al. 2003). Metabolic rates of the pelagic stingray and cownose ray were notably higher than those of the bull ray, which has the lowest metabolic rate of any previously studied myliobatiform stingray. Adaptations for active swimming could include large gill surface area and greater cardiac and swimming muscle capacity, which would increase SMR (Brill 1996). Due to the potential morphological and physiological adaptations, metabolic rates of these active stingrays might be expected to be closer to that of the bat ray (*Myliobatis californica*, Hopkins and Cech 1994), whose metabolic rates are more similar to active sharks (Carlson et al. 2004). Alternatively, the metabolic rates of the pelagic stingray, cownose and bull rays may be representative of stingrays specialized for active swimming, and the metabolic rates of brown stingrays and bat rays are unusually high. However, due to the low number of myliobatiform species for which metabolic rates have been experimentally determined, the effects of active swimming specialization can not yet be evaluated.

Mass and temperature explained the majority of variance in mass-independent metabolic rates. The mass scaling exponent was 0.78 and falls within range of scaling exponents estimated for other elasmobranchs (e.g., 0.68–0.85; Du Preez et al. 1988; Sims 1996; Dowd et al. 2006b). The Q_{10} of 1.8 in this study is among the lowest value yet reported for a batoid species. However, comparisons of Q_{10} between studies may be misleading due to differences in experimental procedures. For example, experimental temperatures for the bat ray were increased by 0.5 °C h^{-1} until desired temperatures were reached (Hopkins and Cech 1994), resulting in a mean Q_{10} of 3.0. Such rapid changes in temperature could increase the effects of temperature on metabolic rates, resulting in inflated Q_{10} values (McNab 2002). In contrast, temperatures for the bull ray were increased by 1 °C 24 h^{-1}, and animals were allowed to acclimate to experimental temperatures for 8 days prior to trials resulting in a Q_{10} of 1.87 (Du Preez et al. 1988). Acclimation to warmer temperatures is generally quicker compared to cooler temperatures (McNab 2002), and 8 days may have been sufficient for complete acclimation to occur. Q_{10} values may also vary between temperature ranges (Gillooly et al. 2001). A pattern of decreasing Q_{10} values with increasing temperature was found for the bull ray and was lowest at the highest temperature range ($Q_{10} = 1.61$, 20–25 °C, Du Preez et al. 1988). The bat ray had a Q_{10} value of 6.81 at a temperature range of 14–20 °C, but Q_{10} was notably lower at higher and lower temperature ranges (Hopkins and Cech 1994). The bat ray Q_{10} at a temperature range of 20–26 °C was 1.85, similar to the value for JBS in this study at a temperature range of 22–27 °C. The Q_{10} of juvenile scalloped hammerhead sharks in Kāne'ohe Bay was also relatively low (1.34) at a

temperature range of 21–29 °C (Lowe 2001). Because Q_{10} is also temperature dependent, metabolic rates will depart from a purely exponential relationship with temperature at high temperatures (Gillooly et al. 2001). The low Q_{10} values for JBS, bull rays, bat rays and juvenile scalloped hammerhead sharks are likely due to the relatively high temperatures at which they were estimated.

Bioenergetics

Metabolism was the largest component of the energy budget, accounting for 66 % of total energy consumed. This value is relatively high in comparison with estimates for other elasmobranch species and carnivorous teleosts, which range from 44 (Brett and Groves 1979, various teleosts) to 60 % (Gruber 1984, lemon shark *Negaprion brevirostris*; Dowd et al. 2006a, sandbar shark *Carcharhinus plumbeus*; Chen et al. 2008, whitespotted bamboo shark *Chiloscyllium plagiosum*). Growth was a much smaller component of the energy budget accounting for 7 % of total consumed energy, which is substantially lower than those estimated for other elasmobranchs and carnivorous teleosts (20–30 %, Brett and Groves 1979; Gruber 1984; Dowd et al. 2006a; Chen et al. 2008). However, these estimates are remarkably similar to estimates for juvenile scalloped hammerhead sharks in Kāne'ohe Bay which exhibited positive growth ($M = 69$ %, $G = 5$ %, Lowe 2002). For both of these species, 93–95 % of their total energy consumption was allocated to maintenance and routine activity.

Daily ration estimates (as %BW) decreased with increasing age primarily due to associated decreases in mass-specific metabolic rates. Consumption rates for age-0 to age-5 brown stingrays (1.8–1.5 %BW day^{-1}) were comparable to those estimated for similarly aged sandbar sharks (2.2–1.3 %BW day^{-1}) in Chesapeake Bay (Dowd et al. 2006a). Although sandbar sharks are a relatively active species with higher mass-specific metabolic rates (Dowd et al. 2006b), modeled water temperatures in Chesapeake Bay were on average 2–3 °C cooler than those used in this bioenergetics model. Daily ration was markedly lower than estimates for juvenile scalloped hammerhead sharks in Kāne'ohe Bay which showed positive growth (3.9 %BW day^{-1}, Lowe 2002). These differences can be attributed to the significantly higher metabolic rates required to sustain activity rates of juvenile scalloped hammerhead sharks (Lowe 2001, 2002). However, gross conversion efficiency was similar between the two species (~4 %, Lowe 2002; Duncan 2006), but lower than juvenile sandbar sharks (10–16 %, Dowd et al. 2006a).

Gross conversion efficiency generally increases with decreasing temperature due to the effects of temperature on metabolic rates (Mateo 2007), which may partially explain differences between studies. Conversion efficiencies are

also linked to prey density and quality (Stewart and Ibarra 1991). Low conversion efficiencies may be an adaptation to an abundant prey base, maximizing foraging at the expense of efficiency (Mateo 2007). However, Kāne'ohe Bay is an oligotrophic system represented by a low diversity of benthic fauna (Laws and Allen 1996; Smith and Kukert 1996), and the very low growth rates of JBS suggests food is limiting as has been suggested for sympatric juvenile scalloped hammerhead sharks (Bush and Holland 2002; Lowe 2002). Conversion efficiency has also been shown to decrease with decreasing protein content of consumed energy (e.g., Pérez-Casanova et al. 2009). The diet of JBS is dominated by crustaceans, which are generally of low protein and energy content relative to teleosts (Bush 2002; Lowe 2002; Goodman-Lowe et al. 1999). For example, crude protein content of *P. vigil* and *Alpheus malabaricus*, two common prey items of JBS in Kāne'ohe Bay, were 31 and 50 % (dry weight), respectively (Bush 2002; Lowe 2002), significantly lower than the crude protein content of Hawaiian teleosts (mean = 63 % dry weight, Goodman-Lowe et al. 1999). The combination of low gross conversion efficiency, relatively high metabolic requirements, low prey quality and warm subtropical waters of Kāne'ohe Bay likely explains the very low growth rates of JBS.

Individual parameter perturbations indicated that several input parameters had minimal impacts on predicted consumption rates. Fortunately, these low-impact parameters included those parameters for which the least amount of empirical data were available (e.g., waste, SDA). This analysis also indicated that uncertainty in input parameters associated with metabolism (SMR_a, SMR_b, SMR_c and to a lesser extent ACT) can have important impacts on consumption rate estimates, consistent with sensitivity analyses in other bioenergetics studies (Bartell et al. 1986; Dowd et al. 2006a; Bethea et al. 2007). The input parameters identified by RPSS analysis as contributing most significantly to the variance in consumption rate estimates were associated with metabolism (SMR_a) and growth (Wi and k). Values used for these parameters were experimentally determined for JBS in this study and a concurrent age and growth study (Dale and Holland 2012), and these results likely represent the contribution of natural variation to the variability in consumption rate estimates. However, the relationships between SMR and mass and temperature were only calibrated for stingrays up to 10 kg, whereas juveniles up to 30 kg were modeled. Extrapolation of these relationships to larger stingrays may have introduced additional error to the model. Although the ACT parameter used to estimate RMR had a minimal contribution to the variance of consumption rates, it may have introduced additional variance through its multiplicative effects on the error associated with RMR. The relationship between metabolic rate and swimming speed was based on data for blacknose sharks (Carlson et al. 1999). However, this assumes that these two species have similar body shapes and swimming kinematics and may overestimate the effects of activity on standard metabolic rates. Additionally, estimates of rate of movement for juvenile brown stingrays were point-to-point estimates (Cartamil et al. 2003), which tend to underestimate actual rates of movement (Gruber et al. 1988) and would therefore underestimate RMR. These results highlight the need for quantitative data on energy expenditures in the field for stingrays (e.g., Lowe 2002).

Population consumption rates were highest for the 4- and 5-year age classes due to their high abundance relative to other age classes. A number of factors can affect the relative catchability of different age classes such as hook and bait size, variation in foraging behavior and competition with conspecifics (e.g., Godø et al. 1997; Dale et al. 2011b). To minimize gear effects, multiple gear configurations were concurrently used during longline surveys (see Dale and Holland 2012 for additional information on gear configurations). However, the influence of foraging behavior and competitors on stingray catchability could not be accounted for and may have led to underestimates of relative abundance for the smallest age classes.

In order to evaluate the ecosystem impacts of JBS within Kāne'ohe Bay, an estimate of 3,000 individuals was modeled as their population size. This value is based on the population estimates for juvenile scalloped hammerhead sharks in Kāne'ohe Bay (Duncan and Holland 2006) and the ratio of JBS to juvenile scalloped hammerhead CPUE from longline survey data. The use of CPUE data to estimate population size assumes this metric accurately reflects the actual abundance of these two species and the catchability of these two species is equivalent. Although there are currently no empirical estimates of population size for JBS to compare with CPUE data, juvenile scalloped hammerhead CPUE based on longline data closely follows the relative seasonal trends in actual juvenile scalloped hammerhead population size (Duncan and Holland 2006). Several lines of evidence also support this value: (1) 500 animals were captured during longline surveys. The majority of these animals were tagged with external ID tags and released. Very low numbers of recaptures (<1 %) suggests either a transient population or a population size larger than the number of tagged animals, (2) a stable isotope study revealed that JBS forage within Kāne'ohe Bay for the majority of their juvenile lives, indicating long-term use of this habitat (Dale et al. 2011a) and a population size greater than 500 stingrays, and (3) the density of JBS in Kāne'ohe Bay based on a population size of 3,000 individuals (0.0002 stingrays m^{-2}) is similar to that of similarly sized giant shovelnose rays (*Glaucostegus typus*, 0.00014 rays m^{-2}) in Sharks Bay, Australia (Vaudo and Heithaus 2009).
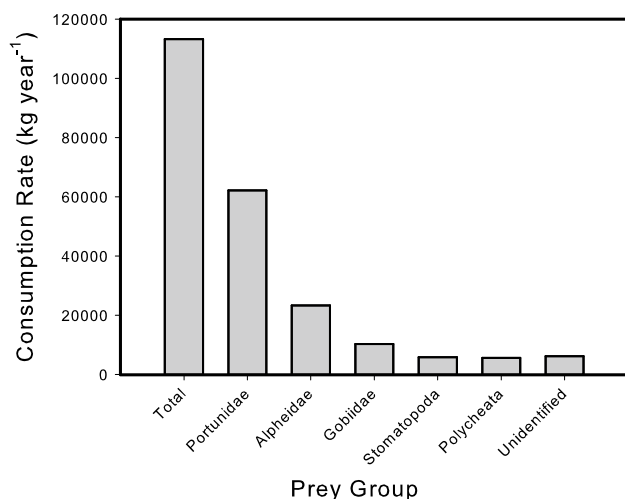
Fig. 4 Prey-specific population consumption rates by juvenile brown stingrays in Kāneʻohe Bay based on a population size of 3,000 individuals. Estimates based on the relative abundance of each age class, the yearly consumption of an average individual of each age class and the gravimetric contribution of prey items to the diet of each age class

A population of 3,000 stingrays within Kāneʻohe Bay would consume ~113,000 kg of benthic prey year^{-1} (Fig. 4) based on the relative abundance of JBS age classes (Fig. 3) and the estimated yearly consumption of an average individual of each age class (Table 3). Consumption rates were highest on portunid crabs (~62,000 kg year^{-1}) followed by alpheid shrimps (~23,000 kg year^{-1}) based on the gravimetric contribution of prey types to the diet of each age class (Table 1). *Podophthalmus vigil* is the most common portunid crab consumed, with consumption rates of ~29,500 kg year^{-1}. The average *P. vigil* consumed by juvenile brown stingrays weighs ~9 g and an average alpheid shrimp weighs ~0.4 g (Bush 2002). These weights would translate to ~3.2 × 10^6 *P. vigil* and ~5.8 × 10^7 alpheid shrimps consumed per year. The most recent estimates of population density for *P. vigil* and *A. malabaricus* are 1.27 and 3.62 m^{-2}, respectively (Bush 2003), and the mud floor of Kāneʻohe Bay covers 14.9 × 10^6 m^{-2} (Smith et al. 1981). Assuming these prey are uniformly distributed, total population sizes for these species may be 1.9 × 10^7 crabs and 5.4 × 10^7 shrimps. Therefore, the stingray population would consume ~17 and 108 % of the crab and shrimp population by number, respectively, without replacement, over the course of 1 year. However, the productivity of *A. malabaricus* was estimated to be 0.669 g m^{-2} year^{-1} ash-free dry weight (Bush and Holland 2002), which amounts to 47,636 kg year^{-1} wet weight (13.3 % ash, 25 % water, Bush 2002), and the stingray population would consume ~49 % of the estimated productivity. Based on the estimates of daily ration, population size and mortality rates for juvenile scalloped hammerhead sharks in Kāneʻohe

Bay, which are sympatric with JBS, their population consumption rate would be 4,658 kg year^{-1} (Bush and Holland 2002; Lowe 2002; Duncan and Holland 2006). They would consume 658 kg of alpheids year^{-1} (Bush 2003) or 1.4 % of alpheid productivity, and the combined consumption by these two elasmobranchs would be 50.4 % of alpheid productivity. Assuming the true stingray population size in Kāneʻohe Bay is in the low thousands as suggested by low recapture rates and CPUE data, the population would have a moderate to strong impact on these two species, and their impacts on the shrimp population are significantly greater than those of juvenile hammerhead sharks. These results suggest that slow growth rates for JBS may be due to insufficient prey resources to support higher consumption rates and therefore higher growth rates. Food limitation is supported by growth rates of two juvenile stingrays held in captivity at HIMB (J. Dale unpubl data). These stingrays were fed ad libitum daily and gained 14 and 11 kg in mass over the course of 1 year. These growth rates are substantially higher than field-based rates, which peak at 3.7 and 2.3 kg year^{-1} for females and males, respectively (Dale and Holland 2012), and demonstrate the capacity for faster growth with sufficient dietary intake. Additionally, other factors such as habitat complexity, anti-predator behavior or interspecific competition with carnivorous teleosts such as jacks may decrease encounter rates or capture efficiency, further limiting growth in the field (Laprise and Blaber 1992; Meyer et al. 2001; Bush and Holland 2002).

Conclusions

An increased forage base and/or refuge from predation are generally the two main factors proposed to explain the advantages of nursery habitat use. The high energetic requirements of JBS and low energetic quality of their prey suggest that their slow growth rates in Kāneʻohe Bay are a trade-off between increased juvenile survival and a late age at first maturity resulting in delayed recruitment to adult populations (Dale et al. 2011a; Dale and Holland 2012). Survival would be enhanced through decreased predation from larger predators such as tiger sharks, which are less abundant in Kāneʻohe Bay compared to surrounding waters (Crowe et al. 1996). Stomach content analysis indicated the youngest age classes of JBS had the highest proportion of empty stomachs relative to older age classes (Dale et al. 2011a). Slow development of foraging skills may explain the especially low relative growth rates of the youngest age classes as has been suggested for juvenile scalloped hammerhead sharks (Bush and Holland 2002; Lowe 2002; Duncan and Holland 2006). Estimated consumption rates suggest that JBS can have a strong impact on their prey populations. These results are in agreement with previous

studies, which suggest that some elasmobranchs may have a substantial top-down ecosystem role (e.g., Stevens et al. 2000; Bascompte et al. 2005). Estimates of prey population densities have decreased in recent years due to the diversion of treated waste water, which was dumped into the bay between 1951 and 1978 (Smith et al. 1981). These changes in habitat quality due to anthropogenic impacts, although generally beneficial for a coral reef ecosystem, may have decreased stingray consumption rates resulting in the current slow growth rates. Although no data exist concerning growth rates for JBS concurrent with elevated prey densities in the field, accelerated growth rates in captivity suggest that bottom-up effects could have important implications on the life history of brown stingrays (e.g., Jennings et al. 2008).

References

Bartell SM, Breck JE, Gardner RH, Brenkert AL (1986) Individual parameter perturbation and error analysis of fish bioenergetics models. Can J Fish Aquat Sci 43:160–168

Bascompte J, Melian CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. PNAS 102:5443–5447

Bethea DM, Hale LF, Carlson JK, Cortés E, Manire CA, Gelsleichter J (2007) Geographic and ontogenetic variation in the diet and daily ration of the bonnethead shark, *Sphyrna tiburo*, from the eastern Gulf of Mexico. Mar Biol 152:1009–1020

Boisclair D, Sirois P (1993) Testing assumptions of fish bioenergetics models by direct estimation of growth, consumption, and activity rates. Trans Am Fish Soc 122:784–796

Brett JR, Groves TD (1979) Physiological energetics. In: Hoar WS, Randall DJ, Brett JR (eds) Fish physiology, vol VIII. Academic Press, New York, pp 279–352

Brill RW (1996) Selective advantages conferred by the high performance physiology of tunas, billfishes, and dolphin fish. Comp Biochem Phys A 113:3–15

Bush A (2002) Feeding ecology of juvenile scalloped hammerheads in Kaneohe Bay, Oahu, Hawaii. Dissertation, University of Hawaii

Bush A (2003) Diet and diel feeding periodicity of juvenile scalloped hammerhead sharks, *Sphyrna lewini*, in Kaneohe Bay, Oahu, Hawaii. Env Biol Fish 67:1–11

Bush A, Holland K (2002) Food limitation in a nursery area: estimates of daily ration in juvenile scalloped hammerheads, *Sphyrna lewini* (Griffith and Smith, 1834) in Kane'ohe Bay, O'ahu, Hawai'i. J Exp Mar Biol Ecol 278:157–178

Carlson JK, Goldman KJ, Lowe CG (2004) Metabolism, energetic demand, and endothermy. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 203–224

Carlson JK, Palmer CL, Parsons GR (1999) Oxygen consumption rate and swimming efficiency of the blacknose shark, Carcharhinus arconotus. Copeia 1:34–39

Cartamil DP, Vaudo JJ, Lowe CG, Weherbee BM, Holland KN (2003) Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. Mar Biol 142:841–847

Chen W-K, Liu KM, Liao YY (2008) Bioenergetics of juvenile whitespotted bamboo shark *Chiloscyllium plagiosum* [Anonymous (Bennett)]. Fish Biol 72:1245–1258

Cortés E (1999) Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717

Cortés E (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Cons Biol 16:1048–1062

Cortés E (2004) Life history patterns, demography, and population dynamics. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, FL, pp 449–469

Crowe GL, Lowe CG, Weherbee BM (1996) Shark records from longline fishing programs in Hawaii with comments on Pacific Ocean distributions. Pac Sci 50:382–392

Dale JJ, Holland KN (2012) Age, growth and maturity of the brown stingray (*Dasyatis lata*) around Oahu, Hawaii. Mar Fresh Res 63:475–484

Dale JJ, Stankus AM, Burns MS, Meyer CG (2011a) The shark assemblage at French Frigate Shoals Atoll, Hawaii: species composition, abundance and habitat use. PLoS ONE 6:e16962. doi:16910.11371/journal.pone.0016962

Dale JJ, Wallsgrove NJ, Popp BN, Holland KN (2011b) Nursery habitat use and foraging ecology of the brown stingray *Dasyatis lata* determined from stomach contents, bulk and amino acid stable isotopes. Mar Ecol Prog Ser 433:221–236

Dowd WW, Brill RW, Bushnell PG, Musick JA (2006a) Estimating consumption rates of juvenile sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay, Virginia, using a bioenergetics model. Fish Bull 104:332–342

Dowd WW, Brill RW, Bushnell PG, Musick JA (2006b) Standard and routine metabolic rates of juvenile sandbar sharks (*Carcharhinus plumbeus*), including the effects of body mass and acute temperature change. Fish Bull 104:323–331

Drazen JC (2007) Depth related trends in proximate composition of demersal fishes in the eastern North Pacific. Deep-Sea Res I 54:203–219

Du Preez HH, McLachlan A, Marias JFK (1988) Oxygen consumption of two nearshore marine elasmobranchs, *Rhinobatos annulatus* (Muller and Henle, 1841) and *Myliobatus aquila* (Linnaeus, 1758). Comp Biochem Phys A 89:283–294

Duffy KA (1999) Feeding, growth and bioenergetics of the chain dogfish, *Scyliorhinus retifer*. Dissertation, University of Rhode Island

Duncan KM (2006) Estimation of daily energetic requirements in young scalloped hammerhead sharks, *Sphyrna lewini*. Environ Biol Fish 76:139–149

Duncan KM, Holland KN (2006) Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. Mar Ecol Prog Ser 312:211–221

Ebert DA, Bizzarro JJ (2007) Standardized diet compositions and trophic levels of skates (Chondrichthyes : rajiformes : Rajoidei). Environ Biol Fish 80:221–237

Elliott JM, Davison W (1975) Energy equivalents of oxygen consumption in animal energetics. Oecolog 19:195–201

Ezcurra JM (2001) The mass-specific routine metabolic rate of captive pelagic stingrays, *Dasyatis violacea*, with comments on energetics. Masters Thesis, California State University, Stanislaus

Ferry-Graham LA, Gibb AC (2001) Comparison of fasting and post-feeding metabolic rates in a sedentary shark, Cephaloscyllium ventriosum. Copeia 4:1108–1112

Fournier RW (1996) The metabolic rates of two species of benthic elasmobranchs, nurse sharks and southern stingrays. M.S. thesis, Hofstra University, Hempstead, NY 29 pp

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. Science 293:2248–2251

Godø OR, Huse I, Michalsen K (1997) Bait defence behavior of wolffish and its impact on long-line catch rates. ICES J Mar Sci 54:273–275

Goodman-Lowe GD, Carpenter JR, Atkinson S, Ako H (1999) Nutrient, fatty acid, amino acid and mineral analysis of natural prey of the Hawaiian monk seal, *Monachus schauinslandi*. Comp Biochem Phys A 123:137–146

Gruber SH (1984) Bioenergetics of captive and free-ranging lemon sharks. AAZPA Annual Conference Proceedings, pp 340–373

Gruber SH, Nelson DR, Morrissey JF (1988) Patterns of activity and space utilization of lemon sharks, *Negaprion brevirostris*, in a shallow Bahamian lagoon. Bull Mar Sci 43:61–76

Heithaus MR (2004) Predator-prey interactions. In: Carrier JC, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 487–522

Heppell SS, Crowder LB, Menzel TR (1999) Life table analysis of long-lived marine species with implications for conservation and management. In: Musick JA (ed) Life in the slow lane: ecology and conservation of long-lived marine animals, American Fisheries Society Symposium 23. Bethesda, Maryland, pp 137–148

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297

Hopkins TE, Cech JJ (1994) Effect of temperature on oxygen consumption of bat rays, *Myliobatis californica* (Chondrichthyes, Myliobatididae). Copeia 2:529–532

Jennings D, Gruber S, Franks B, Kessel S, Robertson A (2008) Effects of large-scale anthropogenic development on juvenile lemon shark (*Negaprion brevirostris*) populations of Bimini, Bahamas. Environ Biol Fish 83:369–377

Jobling M (1981) The influence of feeding on the metabolic rate of fishes: a short review. J Fish Biol 18:385–400

Laprise R, Blaber SJM (1992) Predation by moses perch, *Lutjanus russelli*, and blue-spotted trevally, *Caranx bucculentus*, on juvenile brown tiger prawn, *Penaeus esculentus*: effects of habitat structure and time of day. J Fish Biol 40:627–635

Laws EA, Allen CB (1996) Water quality in a subtropical embayment more than a decade after diversion of sewage discharges. Pac Sci 50:194–210

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809

Lowe C (2001) Metabolic rates of juvenile scalloped hammerhead sharks (*Sphyrna lewini*). Mar Biol 139:447–453

Lowe CG (2002) Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kane'ohe Bay, O'ahu, HI. J Exp Mar Biol Ecol 278:141–156

Mateo I (2007) A bioenergetics based comparison of growth conversion efficiency of Atlantic cod on Georges Bank and in the Gulf of Main. J North Atl Fish Sci 38:23–35

McEachran JD (1990) Diversity of rays: why are there so many species? Chondros 2:1–6

McNab BK (2002) The physiological ecology of vertebrates: a view from energetics. Cornell University Press, New York

McNeill S, Lawton JH (1970) Annual production and respiration in animal populations. Nature 225:472–474

Medved RJ, Stillwell CE, Casey JG (1988) The rate of food consumption of young sandbar sharks (*Carcharhinus plumbeus*) in Chincoteague Bay, Virginia. Fish Bull 83:395–402

Meyer CG, Holland KN, Wetherbee BM, Lowe CG (2001) Diet, resource partitioning and gear vulnerability of Hawaiian jacks captured in fishing tournaments. Fish Res 53:105–113

Neer J, Carlson J, Thompson B (2006) Standard oxygen consumption of seasonally acclimatized cownose rays, *Rhinoptera bonasus* (Mitchill 1815), in the northern Gulf of Mexico. Fish Phys Biochem 32:67–71

Neer JA, Rose KA, Cortés E (2007) Simulating the effects of temperature on individual and population growth of *Rhinoptera bonasus*: a coupled bioenergetics and matrix modeling approach. Mar Ecol Prog Ser 329:211–223

Pérez-Casanova JC, Lall SP, Gamperl AK (2009) Effect of feed composition and temperature on food consumption, growth and gastric evacuation of juvenile Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.). Aquaculture 294:228–235

Pierce SJ, Bennett MB (2010) Destined to decline? Intrinsic susceptibility of the threatened estuary stingray to anthropogenic impacts. Mar Fresh Res 61:1468–1481

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Schindler DE, Essington TE, Kitchell JF, Boggs C, Hilborn R (2002) Sharks and tunas: fisheries impacts on predators with contrasting life histories. Ecol App 12:735–748

Secor SM, Wooten JA, Cox CL (2007) Effects of meal size, meal type, and body temperature on the specific dynamic action of anurans. J Comp Phys B 177:165–182

Sims DW (1996) The effect of body size on the standard metabolic rate of the lesser spotted dogfish. J Fish Biol 48:542–544

Sims DW, Davies SJ (1994) Does specific dynamic action (SDA) regulate return of appetite in the lesser spotted dogfish, *Scyliorhinus canicula*? J Fish Biol 45:341–348

Smith CR, Kukert H (1996) Macrobenthic community structure, secondary production, and rates of bioturbation and sedimentation at the Kaneohe Bay lagoon floor. Pac Sci 50:211–229

Smith SV, Kimmerer WJ, Laws EA, Brock RW, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. Pac Sci 35:279–395

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476–494

Stevens M, Maes J, Ollevier F (2006) A bioenergetics model for juvenile flounder *Platichthys flesus*. J App Ichthy 22:79–84

Stewart DJ, Ibarra M (1991) Predation and production by salmonine fishes in Lake Michigan, 1978–88. Can J Fish Aqua Sci 48:909–922

Stillwell CE, Kohler NE (1982) Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. Can J Fish Aquat Sci 39:407–414

Stillwell CE, Kohler NE (1993) Food habits of the sandbar shark *Carcharhinus plumbeus* off the U.S. northeast coast, with estimates of daily ration. Fish Bull 91:138–150

Sundström LF, Gruber SH (1998) Using speed-sensing transmitters to construct a bioenergetics model for subadult lemon sharks, *Negaprion brevirostris* (Poey), in the field. Hydrobiologia 371(372):241–247

Thayer GW, Schaaf JW, Angelovic JW, LaCroix MW (1973) Caloric measurements of some estuarine organisms. Fish Bull 71:289–296

Vaudo JJ, Heithaus MR (2009) Spatiotemporal variability in a sandflat elasmobranch fauna in Shark Bay, Australia. Mar Biol 165:2579–2590

Wetherbee BM, Gruber SH (1993) Absorption efficiency of the lemon shark *Negaprion brevirostris* at varying rates of energy intake. Copeia 2:416–425