Functional Ecology

British Ecological Society

Functional Ecology 2013, **27**, 1273–1274 doi: 10.1111/1365-2435.12157

TECHNICAL COMMENT

A revised estimate of daily ration in the tiger shark with implication for assessing ecosystem impacts of apex predators

Neil Hammerschlag*[1,2,3], Austin J. Gallagher[2,3] and John K. Carlson[4]

[1]*Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA;* [2]*Leonard and Jayne Abess Center for Ecosystem Science and Policy, University of Miami, PO Box 248203, Coral Gables, Florida 33124, USA;* [3]*RJ Dunlap Marine Conservation Program, University of Miami, 4600 Rickenbacker Cswy, Miami, Florida 33149, USA; and* [4]*NOAA, National Marine Fisheries Service, Southeast Fisheries Science Center, 3500 Delwood Beach Road, Panama City, Florida 32408, USA*

Apex predators may impact ecosystem structure and function through trophic cascades (Estes, Tinker & Williams 1998). Studies of diets, feeding patterns and food web dynamics can contribute to an understanding of community structure and ecological interactions (Winemiller 1989; Krebs 1998). Thus, understanding trophodynamics is important for developing ecosystem models for predicting community responses to anthropogenic changes (Walters, Christensen & Pauly 1997). Studies of this kind are especially critical in the case of large sharks, given that several species are experiencing varying levels of population declines on a global scale (Dulvy *et al.* 2008; Camhi *et al.* 2009). Accordingly, there is mounting concern – and increasing effort – to predict the consequences of large shark declines for food web dynamics (Estes *et al.* 2011).

In a recent study, Hammerschlag *et al.* (2012) investigated the movement patterns of an apex marine predator, the tiger shark (*Galeocerdo cuvier*), in relation to an ecotourism provisioning site. The authors rejected the null hypothesis that sharks displayed restricted long-term habitat use at the site. However, they speculated that the observed long-term and large-scale shark movements may be related to cryptic, lesser-understood aspects of Atlantic tiger shark life history (i.e. reproduction, mating, foraging forays).

As part of their discussion, Hammerschlag *et al.* (2012) considered the daily ration of 210-kg adult female tiger sharks. However, no published studies exist that have quantified this aspect of tiger shark food-consumptive needs. To get a broad approximation of daily ration, the authors averaged values derived from two other species of sharks found in the subtropical Atlantic: the lemon shark (*Negaprion brevirostris*), daily ration estimate of 2·1% body weight (Cortes & Gruber 1990); and shortfin mako shark (*Isurus oxyrinchus*), daily ration estimate of 4·6% body weight (Wood *et al.* 2009). The species used in the calculation here were chosen in part because of their behavioural and geospatial overlap with the tiger shark movements found in Hammerschlag *et al.* (2012). However, the resulting approximation of the daily ration value for an adult tiger shark (3·7%) is likely inflated for two primary reasons: (i) using values derived from juvenile species, although daily ration in sharks is known to decrease with size (Wetherbee & Cortés 2004) and (ii) averaging values from two species, one of which, the shortfin mako, is regionally endothermic, while tiger sharks are ectothermic (Carlson, Goldman & Lowe 2004).

Here we present a different, more traditional approach to estimate the daily ration for tiger sharks following Winberg (1956). Accordingly, daily ration (kcal day^{-1}) was calculated as: DR = C/F/W, where C = food consumption (kcal day^{-1}); F = energy value of the food source (kcal g^{-1} wet weight); and W = mass of the shark (g). Daily ration was then expressed as per cent body weight per day (C/F/W · 100 = %BW day^{-1}). C was calculated as: C = 1·37 (M+G), where G is the energy for growth and reproduction, M is the total energy of metabolism and 1·37 represents the 27% of food energy lost through egestion and excretion (Brett & Groves 1979). Given that no species-specific information on routine metabolism for tiger sharks exists, for inputs of the model, we used a weight-oxygen consumption rate for 1 to 10-kg sandbar shark derived by Dowd *et al.* (2006). Oxygen consumption rate was converted to calories using the oxycalorific coefficient for fish of 3·25 cal mg O_2 (Brafield & Solomon 1972). Species-specific growth rates (converted to mass) were obtained from von Bertalanffy growth functions following Kneebone *et al.* (2008). Litter size for mature females was taken from Clark & Von Schmidt (1965) and Branstetter, Musick & Colvocoresses (1987). Mass for both growth and reproduction was converted to kilocalories by using the energy density of shark tissue of 1·294 kcal g^{-1} (wet weight) based on estimates for lemon shark by Cortés and Gruber (1990). Proportions of food were taken from diet studies by Lowe *et al.* (1996). The caloric values were taken from studies by Thayer *et al.*

*Correspondence author. E-mail: nhammerschlag@rsmas.miami.edu

(1973) and Steimle & Terranova (1985). Using this approach, a resultant value for the DR of a 210-kg female tiger sharks is estimated at 0·561%. This value is likely more reflective of tiger shark daily ration as it falls within the values calculated for other large carcharhinid sharks (Wetherbee & Cortés 2004).

Although this new estimate of daily ration does not impact the results or conclusions of Hammerschlag *et al.* (2012), the estimated value presented here is lower than their estimate which can have implications for anyone using daily ration for generating ecosystem models. In particular, an inflated value may overestimate the consumptive predation effects on their prey. In such a situation, overfishing of tiger sharks would be predicted to result in a significant predation release on their prey.

References

Brafield, A.E. & Solomon, D.J. (1972) Oxy-calorific coefficients for animals respiring nitrogenous substrates. *Comparative Biochemical Physiology*, **43A**, 837–841.

Branstetter, S., Musick, J.A. & Colvocoresses, J.A. (1987) A comparison of the age and growth of the tiger shark, *Galeocerdo cuvier*, from off Virginia and from the northwestern Gulf of Mexico. *Fisheries Bulletin*, **85**, 269–279.

Brett, J.R. & Groves, T.D.D. (1979) Physiological energetics. *Fish Physiology*, Vol **VII** (eds W.S. Hoar & D.J. Randall), pp. 279–352. Academic Press, New York.

Camhi, M.D., Valenti, S.V., Fordham, S.V., Fowler, S.I. & Gibson, C. (2009) *The Conservation Status of Pelagic Sharks and Rays: Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop*. IUCN Species Survival Commission Shark Specialist Group, Newbury.

Carlson, J.K., Goldman, K.J., Lowe, C.G. (2004). Metabolism, energetic demand, and endothermy. *The Biology of Sharks and Their Relatives* (eds J.C. Carrier, J.A. Musick & M.R. Heithaus), pp. 203–224. CRC, Boca Raton, Florida.

Clark, E. & Von Schmidt, K. (1965) Sharks of the central Gulf coast of Florida. *Bulletin of Marine Science*, **15**, 13–83.

Cortés, E. & Gruber, S.H. (1990) Diet, feeding habits and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). *Copeia*, **1**, 204–218.

Dowd, W.W., Brill, R.W., Bushnell, P.G. & Musick, J.A. (2006) Standard and routine metabolic rates of juvenile sandbar sharks (*Carcharhinus plumbeus*) including the effects of body mass and acute temperature change. *Fisheries Bulletin*, **104**, 323–331.

Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L., Cortes, E., Domingo, A. *et al.* (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **18**, 459–482.

Estes, J., Tinker, M. & Williams, T. (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, **282**, 473–476.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.

Hammerschlag, N., Gallagher, A.J., Wester, J., Luo, J. & Ault, J.S. (2012) Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Functional Ecology*, **26**, 567–576.

Kneebone, J., Natanson, L.J., Andrews, A.H. & Howell, W.H. (2008) Using bomb radiocarbon analyses to validate age and growth estimates for the tiger shark, *Galeocerdo cuvier*, in the western North Atlantic. *Marine Biology*, **154**, 423–434.

Krebs, C.J. (1998) *Ecological Methodology*. Addison-Wesley Educational Publishers, Menlo Park, CA.

Lowe, C.G., Wetherbee, B.M., Crow, G.L. & Tester, A.L. (1996) Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environmental Biology of Fishes*, **47**, 203–211.

Steimle, F.W. & Terranova, R.J. (1985) Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. *Journal of Northwest Atlantic Fisheries Science*, **6**, 117–124.

Thayer, G.W., Schaff, W.E., Angelovic, J.W. & LaCroix, M.W. (1973) Caloric measurements of some estuarine organisms. *Fisheries Bulletin*, **71**, 289–296.

Walters, C., Christensen, V. & Pauly, D. (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Review in Fish Biology and Fisheries*, **7**, 139–172.

Wetherbee, B.M., Cortés, E. (2004) Food consumption and feeding habits. *The Biology of Sharks and Their Relatives* (eds J.C. Carrier, J.A. Musick & M.R. Heithaus), pp. 225–246. CRC, Boca Raton, Florida.

Winberg, G.G. (1956) *Rate of Metabolism and Food Requirements of Fishes*. Belorussian State University, Minsk. 251 pp.

Winemiller, K.O. (1989) Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan Llanos. *Environmental Biology of Fishes*, **26**, 177–199.

Wood, A.D., Wetherbee, B.M., Juanes, F., Kohler, N.E. & Wilga, C. (2009) Recalculated diet and daily ration of the shortfin mako (*Isurus oxyrinchus*), with a focus on quantifying predation on bluefish (*Pomatomus saltatrix*) in the northwest Atlantic Ocean. *Fishery Bulletin*, **107**, 76–88.

Received 25 February 2013; accepted 5 March 2013
Handling Editor: Duncan Irschick