Feeding Habits of *Mobula japanica* (Chondrichthyes, Mobulidae) in Butuan Bay, Mindanao Island, Philippines

Shirlamaine Irina G. Masangcay
Caraga State University

Ephrime B. Metillo*
Mindanao State University-Iligan Institute of Technology

Ken-Ichi Hayashizaki
Kitasato University

Satoru Tamada
Kitasato University

Shuhei Nishida
University of Tokyo

ABSTRACT

The diet of the Spinetail Devil Ray *Mobula japanica* Müller and Henle 1841 from Butuan Bay, Philippines was investigated from January to May 2016 using data on its stomach contents, and C and N stable isotope analyses, in order to contribute to the scarce information on the feeding biology of the threatened tropical populations of the *Mobula* species. Examination of 16 *M. japanica* stomachs revealed ingestion of the euphausiid *Pseudeuphausia latifrons*, sergestid shrimps *Acetes intermedius* and *Lucifer* spp., copepods, and other rare prey items. The tropical krill *P. latifrons* was the most common, often the sole food, that increases body length of individuals towards the warmer months of April and May, which coincide with the peak season of *M. japanica* fisheries. Results from δ^{13}C and δ^{15}N stable isotope analysis are consistent with the assimilation of large zooplankton and micronektonic crustaceans. This study is the first report on the feeding of *M. japanica* in tropical waters and the identification of euphausiid *P. latifrons* as its dominant prey.

Keywords: Stomach content, *Mobula, Pseudeuphausia latifrons*, population structure, tropical

Corresponding Author

INTRODUCTION

The Spinetail Devil Ray *Mobula japanica* from the family Mobulidae is a large marine fish with cartilaginous skeleton (Couturier et al. 2012). Locally known as Pantihan, mobulids or devil rays are pelagic fishes found in shallow and deep waters in the tropical and temperate regions (Cortes and Blum 2008; Bizzarro et al. 2009; Scacco et al. 2009; Canese et al. 2011; Metillo and Masangcay 2015; Croll et al. 2016; Francis and Jones 2016). In New Zealand, the species is a common bycatch in skipjack tuna purse seine fisheries (Francis and Jones 2016). Most *Mobula*, particularly *M. japanica,* vary in size with disk width ranging 1–3 meters (Paulin et al. 1982; Notarbartolo di Sciara 1987; White et al. 2006b), and are commonly known to be very fast swimmers that feed on zooplankton (Couturier et al. 2012). They have low natural rate of mortality, slow-growth with long life span, late sexual maturation, and have few but large offspring (Dulvy et al. 2003; Musick and Ellis 2005; Garcia et al. 2008; Croll et al. 2016). *Mobula japanica* is currently listed as near-threatened by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (White et al. 2006a), yet they are still being actively fished in Bohol Sea, central Philippines via the traditional harpoon and purse seine methods for sale and local consumption in the coastal area (Alava et al. 2002; Rayos et al. 2012; Acebes 2013; Freeman 2014; Croll et al. 2016). Fishermen (Galdo and Sanchez, personal communication) confirmed that *M. japanica* are seasonally observed in Butuan Bay, Mindanao Island during the Northeast monsoon when coastal enrichment is highest in eastern Bohol Sea (Cabrera et al. 2011).

Mobula species are pelagic megafauna yet they subsist on a primary diet of zooplankton and ichthyoplankton (Couturier et al. 2012). They grow very large due to the direct feeding on abundant zooplankton and ichthyoplankton in the second trophic level much closer to abundant primary producers (Shwenk 2000). Zooplanktivorous devil rays are indispensable in the marine ecosystem since they tap the lower trophic levels (Couturier et al. 2012; Jaine et al. 2012), and become important indicator species of climate change, as their planktonic food source is highly susceptible to environmental changes (e.g., ocean acidification and warming waters) (Hays et al. 2005; Richardson 2008; Weeks et al. 2015).

Studies on the biology and ecology of Mobulidae started since the 17th century, but information on its feeding habits is limited (Willoughby 1686; Stewart et al. 2016). Aggregations of devil rays are generally linked with local productivity and food availability (Celona 2004; Sleeman et al. 2007; Dewar et al. 2008; Marshall et al. 2009; Anderson et al. 2011; Couturier et al. 2011; Marshall et al. 2011*)*. Zooplanktivory is their generic feeding habit (Weeks et al. 2015), but species-

specific differences occur. For instance, *M. thurstoni* is known to feed on mysid shrimps and euphausiids, and dwells in non-overlapping microhabitats with other species (Notarbartolo di Sciara 1988). Examination of the stomach contents, and C and N stable isotope techniques have shown varying feeding habits among subtropical and temperate sub-populations under the genus *Mobula*, such as *M. mobular, M. hypostoma, M. rochebrunei, M. tarapacana, M. birostris, M. alfredi, M. japanica*, and *M. munkiana*, which generally feed on small fishes and crustaceans like krill (*Meganyctiphanes norvegica, Nyctiphanes simplex*), the mysid *Mysidium* sp., and other planktonic organisms (Notarbartolo di Sciara 1988; Sampson et al. 2010; Couturier et al. 2012). The diets of the near threatened species *M. kuhlii* and *M. eregoodootenkee* are unknown thus far (Pierce and Bennett 2003; Bizzarro et al. 2009).

Current knowledge of the prey preference of the tropical *Mobula japanica* based on its stomach contents is limited to the studies of Notarbatolo di Sciara (1988) and Sampson et al. (2010) conducted off the coast of California, USA. Analyzing feeding habits of tropical populations will determine diet preference and allow inference on habitat use and feeding behavior, which are both very important to the conservation and management of the ray (Stewart et al. 2016). Hence, this work investigated the feeding habits of *M. japanica* in Butuan Bay, northeastern part of Mindanao Island, Philippines with specific aims of analyzing the composition of its stomach contents, and indirectly inferring its feeding habits using C and N stable isotope analysis.

MATERIALS AND METHODS

Study area

Butuan Bay is located in the northeastern area of Mindanao (Figure 1). Its coastline is connected to the north with Bohol Sea or Mindanao Sea, which is known to have extreme southwest movement of surface currents coming from the Pacific Ocean (Cabrera et al. 2011). The entire bay has an average depth of 100 meters and a maximum depth of 800 meters (NGA Nautical Chart 1996). Numerous river tributaries flow directly into the bay, including the Agusan River, the third longest river in the Philippines, carrying water discharges from interconnecting rivers, channels, and lakes (Primavera and Tumanda 2008). A biologically enriched estuarine frontal plume usually occurs near the mouth of the large Agusan River in the bay (Cabrera et al. 2011). Climatic condition in Butuan Bay includes significant amount of rainfall throughout the year even in the driest month. The bay is exposed to strong trade winds and storms during the northeast monsoon (December-April).

Buenavista is a fishing coastal municipality located at the Southern portion of the bay (Figure 1) (Indab and Suarez-Aspilla 2004). The area is considered as a major fishing ground with rich fishery resources (BFAR 2015). Personal interviews in the locality validated the regular landing of *Mobula* in Buenavista, but fisherfolks report catching of rays at other locations in the bay, particularly off the coast of Carmen, Nasipit, Cabadbaran, and Tubay (Figure 1) (Metillo and Masangcay 2015).
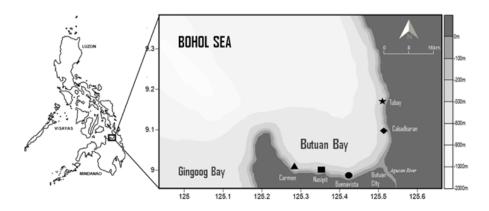

Figure 1. Geographical location of Butuan Bay in Northeastern Mindanao, and collection sites of landed *Mobula japanica* and plankton samples off the municipality of Carmen (triangle), Nasipit (square), Buenavista (dot), Cabadbaran (diamond), and Tubay (star) in the Province of Agusan del Norte. Inset is the map of the Philippines with the study site enclosed in a square.

Field sampling of ray stomach, muscle tissue, and prey items

Field collection of ray stomach samples, potential prey, and tissues for C and N stable isotopes was conducted from 18 January to 13 May 2016 to coincide with the fishing season in Butuan Bay. Sixteen specimens of *M. japanica* (Table 1) were purchased from local fishermen who caught the fish as bycatch from sardine and skipjack tuna gill net fishing during the day in five locations in Butuan Bay (Figure 1). Fishermen from Buenavista and other locations in Butuan Bay consistently stressed that their devil ray collection sites are just within the Bay (Metillo and Masangcay 2015). During specimen collections of this study, a standard procedure of asking fishermen where they captured the rays revealed that they can be found in the deep portions of Butuan Bay. The digestive tract of the 16 individuals was removed by cutting the most anterior end of the esophagus and the most posterior end of the intestine. The length and outer diameter of the stomach were measured to estimate the stomach volume that will be used in the stomach content analysis.

Afterwards, the stomach and intestine (Figure 2) were longitudinally dissected, spread apart, and the stomach contents were thoroughly flushed into clean plastic containers and preserved in 10% buffered formalin in filtered seawater. Muscle tissue samples from five *Mobula japanica* individuals were obtained near the ventro-posterior area of the pectoral fins using a sharp scalpel, and were immediately placed in a clean vial and labeled properly. Tissue samples were brought to the laboratory in an ice chest, and immediately dried in an oven at a temperature of 60°C for 48 hours.

Table 1. Body measurements (cm) of the 16 *Mobula japanica* individuals collected in Butuan Bay, Northeastern Mindanao, Philippines

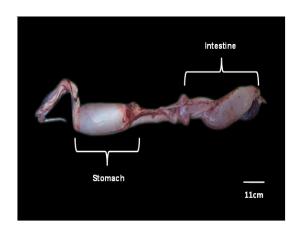| #	Sex	Disk width (D_w)	Disk length (C_F)	Cephalic fin length (C_F)	Tail length (T_L)	Date collected	Site collected
a	Female	148	72	19	166	18-Jan-16	-
b	Male	130	68	23	160	25-Jan-16	-
c	Male	120	55	5	148	12-Feb-16	-
d	Male	137	67	16.4	146	27-Feb-16	Buenavista Area
e	-	-	-	-	-	11-Mar-16	Buenavista Area
f	Male	134	60	8	143	18-Mar-16	Buenavista Area
g	Male	-	-	-	-	18-Mar-16	Cabadbaran Area
h	-	-	-	-	-	30-Mar-16	Cabadbaran Area
i	Male	129	59	17	150	31-Mar-16	Buenavista Area
j	Male	146	69	22	142	31-Mar-16	Tubay Area
k	-	-	-	-	-	02-Apr-16	Buenavista Area
l	Female	135	60	18	154	09-Apr-16	Carmen Area
m	-	-	-	-	-	10-Apr-16	Carmen Area
n	Male	130	66	12	140	09-May-16	Buenavista Area
o	Male	134	63	17	148	11-May-16	Buenavista Area
p	Male	157	73	22	178	13-May-16	Buenavista Area

Note: "-", undetermined

Figure 2.The digestive tract of *Mobula japanica* from Butuan Bay, Philippines.

Plankton samples were collected on 25 January 2016 at the location where *M. japanica* were caught (Table 2), particularly off Buenavista. Conical nets with mesh sizes of 100 μm and 20 μm were towed horizontally at sub-surface depths to collect zooplankton and particulate organic matter (POM), respectively (Metillo et al. 2015). Night sampling involving several 3-minute tows was performed until the desired amounts of plankton and POM triplicate samples were collected. Zooplankton samples were size-fractionated using a series of sieves with nylon gauzes of different mesh sizes (<100 μm, 100–200 μm, 200–335 μm, 335–1000 μm, >1000 μm), and were viewed under a dissecting stereo microscope to remove any debris in the sample. Zooplankton taxa (e.g. crab megalopa, decapod shrimp, hydrozoa) were sorted from the bulk samples to represent extra-large zooplankton (ZXL). Samples from the 20-μm mesh plankton net were filtered, and particles trapped in the 20-μm sieve were regarded as POM (Table 3). Large zooplankton samples (ZXL, ZL, ZM) were carefully handpicked using fine forceps, placed in foil, and dried in an oven at a temperature of 60°C for 48 hours. Smaller size fractions (ZS) of zooplankton and POM samples were separately filtered onto pre-combusted glass fiber filters (GF/F), dried in the same manner as large zooplankton, and placed inside Eppendorf tubes until stable isotope analysis.

Table 2. Tabulated coordinates of each plankton tow for stable isotopes analysis collected on 2016 January 25 in Butuan Bay, Northeastern Mindanao, Philippines

Tow No.	Net mesh size μm	Coordinates Longitude	Latitude
1	100	125.401405°	8.987764°
2	100	125.399261°	8.988452°
3	100	125.397559°	8.988784°
4	100	125.396298°	8.988920°
5	20	125.394506°	8.989511°
6	20	125.393166°	8.989122°
7	20	125.391468°	8.988398°
8	20	125.389072°	8.988368°
9	20	125.386612°	8.988413°
10	20	125.384991°	8.988234°
11	20	125.383185°	8.988025°

Table 3. List of specimens used for C and N stable isotope analysis.

Sampling dates	Taxa/size group	Code	Period of collection	No. of specimen*	Source
18-Jan-16	*Mobula japanica* (female)	MJ	Day	1	Fish landing
18-Jan-16	*Pseudeuphausia latifrons*	KA	N/A	30	Net towing
25-Jan-16	*M. japanica* (male)	MJ	Day	1	Fish landing
12-Feb-16	*M. japanica* (male)	MJ	Day	1	Fish landing
27-Feb-16	*M. japanica* (male)	MJ	Day	1	Fish landing
18-Mar-16	*M. japanica* (male)	MJ	Day	1	Fish landing
25-Jan-16	*Lucifer* spp.	LU	Night	6	Net towing
25-Jan-16	*Acetes intermedius*	AC	Night	15	Net towing
25-Jan-16	Clupeidae	FJ	Night	4	Net towing
25-Jan-16	Exocoetidae	FJ	Night	1	Net towing
25-Jan-16	Blennidae	FL	Night	4	Net towing
25-Jan-16	Carangidae	FL	Night	6	Net towing
25-Jan-16	Gobidae	FL	Night	4	Net towing
25-Jan-16	Crab megalopa	ZXL	Night	2	Net towing
25-Jan-16	Decapod shrimp	ZXL	Night	2	Net towing
25-Jan-16	Hydrozoa	ZXL	Night	1	Net towing
25-Jan-16	*Macrosetella* sp.	ZXL	Night	2	Net towing
25-Jan-16	*Acartia* sp.	ZL	Night	18	Net towing
25-Jan-16	*Labidocera* sp.	ZL	Night	7	Net towing
25-Jan-16	Calanid copepods	ZL	Night	22	Net towing
25-Jan-16	*Parthenope* sp. (zoea)	ZL	Night	3	Net towing
25-Jan-16	*Paracalanus* sp.	ZM	Night	18	Net towing
25-Jan-16	Copepods (200-335 µm)	ZM	Night	1 g	Net towing
25-Jan-16	mesozooplankton (100-200 µm)	ZS	Night	1 g	Net towing
25-Jan-16	particulate matter (20-100 µm)	POM	Night	1 g	Net towing

Legend: *specimen means individual organism, except the bottom three rows where specimen is expressed in gram (g)

Stomach content analysis

The stomach content of each individual ray was removed and placed in a beaker for subsampling. The entire sample was divided into 10 parts with each tenth regarded as a subsample. Three sub-samples were then thoroughly identified using a stereomicroscope for large particles and a compound microscope for smaller ones. The contents of the intestine were also inspected, but the materials were already heavily digested and unidentifiable; hence, they were not included in the analysis. The index of relative importance (IRI) of each food item category was computed using the formula of Pinkas et al. (1971): IRI = $(Cn + Cv)$ x F , where Cn is the percentage numerical count of each food item relative to the total count of all food items; C_v is the percentage volume (assuming cylindrical shape of the ray cardiac stomach) of each food item (estimated from the product of the proportion

of space occupied by each food item and the volume of the cylindrical cardiac stomach) relative to the volume of all food item combined; and F is the percentage occurrence of each food item in the stomachs of all fish individuals analyzed. The use of the IRI (Pinkas et al. 1971) reduces biased description of animal dietary data. This method has been widely used in studying diet composition of large marine animals and proved efficient in determining a snapshot view of prey items in the stomach (Notarbatolo di Sciara 1988; Alonso et al. 2001; Moura et al. 2008; Schluessel et al. 2010).

Analysis of C and N stable isotopes

Dried samples were pulverized using acid-washed mortar and pestle. Powdered samples were aseptically placed in Eppendorf tubes and properly labelled. All samples were analyzed through dual C and N stable isotopes technique using the Thermo Stable Isotopes Analyzer coupled with the Thermo Finnigan DELTA plus XP isotope ratio mass spectrometer via a ConFlo-III continuous flow interface (Metillo et al. 2015). Samples with elemental C and N ratio > 4 were corrected for effects of lipids (Post 2002).

Data treatment

Isotopic values between the two *M. japanica* individuals were compared using Student homoscedastic t-test (SPSS 2002). Results of the stable isotope analysis (SIA) were plotted and interpreted using OmniGraphSketcher version 1.1.4. Relationships between prey and predator were calculated using the trophic enrichment factor values 3.2±0.43‰ for $\delta^{15}N$ and 1.8±0.29‰ for $\delta^{13}C$ (McCutchan et al 2003). Trophic levels (TL) of all samples were determined based on nitrogen isotopic values using the equation (Vander Zanden and Rasmussen 2001): $TL_{consumer}= [(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4 + 2]$, where $\delta^{15}N_{consumer}$ is the mean value of the predator, $\delta^{15}N_{baseline}$ is the isotopic $\delta^{15}N$ values from the microplankton (Z1,100– 200 µm) samples, and a trophic efficiency factor value of 3.4.

RESULTS

Stomach content

The state of the 16 *M. japanica* individuals only allowed sexing 12 which comprised ten males and two females (Table I). Body size as disk width (D_w) ranged from 120– 157 cm, while disk length (D_L) ranged from 55–73 cm. The stomach of all 16

individuals examined contained ingested food composed of intact identifiable prey items mixed with few digested food items. Prey organisms identified were mostly planktonic euphausiids, sergestid shrimps, copepods, and other categories as minor food items (Table 4). Stomach contents from all rays consisted almost exclusively of adult and eggs of the krill *Pseudeuphausia latifrons* G.O. Sars 1883, which exhibited IRI values of 15,180.28 and 4,537.11, respectively. The other prey items in decreasing order of IRI values were the sergestoid shrimp *Lucifer* > sergestid shrimp *Acetes intermedius* > copepods > flatworm > plant fragments > polychaete larvae = mollusc veligers. Although *A. intermedius* was found to have a low IRI value of 10.65, it dominated the stomach content of one *M. japanica.*

**Table 4. Diet analysis of *Mobula japanica* based on 9 prey types
collected from the stomachs of 16 individuals.
N, Number; V, Volume; FO, Frequency of occurrence;
IRI, Index of relative importance**

Prey	Number	% N	% V	% FO	IRI	% IRI
Pseudeuphausia latifrons	588,413	76.594	75.209	100.00	15,180.28	76.66
Krill egg	175,866	22.893	22.479	100.00	4,537.11	22.91
Lucifer sp.	3,348	0.436	0.638	68.75	73.85	0.37
Acetes intermedius	540	0.070	1.634	6.25	10.65	0.05
Copepods	47	0.006	0.017	31.25	0.72	0.00
Flatworm	5	0.001	0.018	6.25	0.12	0.00
Mollusc veligers	1	0.000	0.001	6.25	0.01	0.00
Polychaete larvae	1	0.000	0.001	6.25	0.01	0.00
Plant fragments	1	0.000	0.003	6.25	0.02	0.00

C and N stable isotope values

We obtained muscle tissues from five *M. japanica* individuals with sizes ranging from 130–147 cm (D_w) (Table 5). Individual values of C and N stable isotopes for these individuals were not significantly different (t = 1.56, df = 3, p = 0.22). Mean isotopic values for the five *M. japanica* were -16.07±0.52‰ for δ^{13}C and 10.69±0.34‰ for δ^{15}N. The δ^{15}N isotopic values were accordingly used to calculate and determine the trophic positions of *M. japanica* and its potential prey types. The 3.27 (female) and 3.16 (male) TL for the five *M. japanica* fall within those of secondary consumers. The stable isotope biplot displays the TL and carbon source of each taxon (Figure 3). On the other hand, isotopic signals of *M. japanica* show an enriched ^{13}C compared to potential preys which have mean values ranging from -19.46‰ (medium size zooplankton) to -17.15‰ (juvenile fish), with the exception of fish larvae (-13.83‰). Mean δ^{13}C values for ichthyoplankton (juvenile and larvae) differed with more depleted values for juveniles than those of larvae. Sergestid

shrimps *A. intermedius* had more enriched mean values (-18.47‰ for δ^{13}C and 7.89‰ for δ^{15}N) than those of *Lucifer* spp (-19.03‰ for δ^{13}C and 6.29‰ for δ^{15}N). The mean δ^{13}C values of both large zooplankton (ZL 335-1000 µm, and ZXL >1000µm) are more enriched at -18.65‰ to -18.40‰ in comparison to the value of smaller zooplankton (Z1 100–200 µm: -19.27‰). The krill *P. latifrons* exhibited a mean δ^{13}C value (-17.96‰) which is roughly similar to those of large zooplankton.

**Table 5. δ^{13}C and δ^{15}N isotopic values (mean±standard deviation)
and trophic position of *M. japanica* and its potential prey.
Numbers in the species codes represent the replicate used for analysis.**

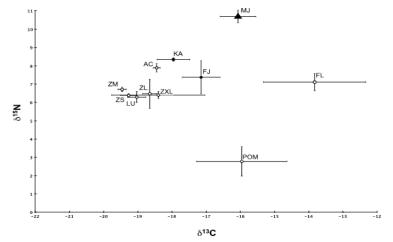| Taxa	Code	Mean δ^{13}C	Mean δ^{15}C	n	Trophic position (TP)
M. japanica (female)	MJ1	-16.20±0.16	10.69± 0.04	1	3.27
M. japanica (male)	MJ2	-15.68±0.35	10.44±0.25	4	3.16
Acetes intermedius	AC	-18.45±0.10	7.89±0.23	3	2.44
Lucifer spp.	LU	-19.03±0.27	6.29±0.30	3	2.44
P. latifrons	KA	-17.96±0.48	8.34±0.08	3	2.34
Fish juvenile	FJ	-17.15±0.55	7.37±1.00	2	2.29
Fish larvae	FL	-13.83±4.67	7.11±0.47	2	2.22
Macrozooplankton (>1000µm)	ZXL	-18.40±1.36	6.40±0.19	3	2.01
Mesozooplankton (100-200µm)	ZS	-19.27±0.24	6.38±0.10	3	2.00
Mesozooplankton (200-335µm)	ZM	-19.46±0.12	6.71±0.12	3	2.10
Mesozooplankton (335-1000µm)	ZL	-18.65±0.21	6.47±0.80	3	2.03
Microzooplankton (20-100µm)	POM	-15.96±1.32	2.78±0.80	3	1.82

Figure 3. Isotopic values of ^{13}C and ^{15}N for *Mobula japanica* (MJ) and potential prey from Butuan Bay, Northeastern Mindanao, Philippines. ZS, zooplankton (100–200 µm); ZM, zooplankton (200–335 µm); ZL, zooplankton (335–1000 µm); ZXL, zooplankton (> 1000 µm); FJ, fish juvenile; FL, fish larva; POM, particulate organic matter; AC, *Acetes intermedius*; KA, adult *Pseudeuphausia latifrons*; LU, *Lucifer* spp.

DISCUSSION

Diet of *M. japanica*

All collected *M. japanica* (D_w = 120–157 cm) in this study were immature (Notarbatolo Sciara 1988; White et al. 2006b) and dominated by males. According to Sampson et al. (2010), *M. japanica* individuals that are <205 cm (D_w) are considered immature. The sizes of the *M. japanica* of the present study were definitely smaller compared to those of the New Zealand population with individuals showing an average of 200 cm (D_w) and 100 cm (D_L) (Francis and Jones 2016). The predominance of immature individuals may reflect the movement of larger rays to other areas (White et al. 2006b). These rays were caught by fishermen during the day, which validates the findings of Croll et al. (2012) that *M. japanica* is commonly observed at the surface waters (<5 m) during daytime and goes to deeper waters (>50 m) at night in search for food. Devil rays in general are surface water dwellers that spend long periods in the surface during the day (Gadig et al. 2003). It is suggested that surface aggregation of this species may be attributed to the daytime swarming of the krill prey *P. latifrons* (Wilson et al. 2001) and *Nyctiphanes simplex* (Gendron 1992).

Generally, stomach content analysis (SCA) provides information on prey items in limited time scales (e.g. hours to days). In this study, SCA results confirmed *M. japanica* to have a strong feeding affinity with planktonic organisms, which may be associated with its gill morphology (Paig-Tran et al. 2011). Rays are efficient in capturing zooplanktonic prey by funnelling microscopic plankton into their mouth and trapping them onto the gills which are made up of filter-like mesh of small bones (Paig-Tran et al. 2013). All 16 *M. japanica* actively fed since their stomachs contained quantifiable prey. By contrast, Notarbatolo di Sciara (1988) reported only 19 (24%) out of 78 *M. japanica* individuals had food in their stomach.

In this study, the predominance of the tropical krill *P. latifrons* in almost all of the stomach contents of *M. japanica* was observed (Masangcay et al. 2018). By comparison, the subtropical populations of *M. japanica* and *M. thurstoni* exclusively feed on the subtropical krill *N. simplex*, while *M. munkiana* feed on the mysid *Mysidium* sp. (Notarbatolo di Sciara 1988; Sampson et al. 2010). *Mobula thurstoni* primarily feeds on euphausiids (Gadig et al. 2003), but it was also observed to intensively feed on mysid shrimps (Notarbartolo di Sciara, 1988). *Manta birostris* (Wilson et al. 2001) and *Rhincodon typus* (Wilson and Newbound 2001; Jarman and Wilson 2004) are also reported to prey on *P. latifrons* at daytime. These findings are in close agreement with our study, which identifies the krill species *P. latifrons*

as the most important prey of *M. japanica* from Butuan Bay. In addition, our local plankton net tows did yield a few *P. latifrons* at the locations off Buenavista where fishermen capture devil rays. The few *P. latifrons* collected is attributable to the inefficiency of the conical plankton net in catching micronektonic krill (Nemoto 1983; Wiebe et al. 2005).

Aside from adult krill, other prey items include krill eggs, whose abundance is due to the large number of egg-carrying female *P. latifrons* that can bear up to 164 eggs or more per individual (Wilson et al. 2003a). Although it is possible that the eggs would have been ingested as freely suspended eggs in the water column, we believe these were most likely dislodged from the mother krill's brood pouch as a result of the peristalsis of the ray stomach. Interestingly, the shallow water sergestid shrimp *A. intermedius* dominated one stomach of *M. japanica*, indicating ingestion of other shallow water/estuarine micronektonic crustaceans (Jarman and Wilson 2004) and a possible switch to alternative prey (Notarbatolo di Sciara 1988; Wetherbee and Cortés 2004). Past studies on ray stomach content report the importance of pelagic micronektonic crustaceans like euphausiids (true krill), sergestid shrimps like *Acetes* spp., and other planktonic species (Couturier et al. 2012). Micronektonic crustaceans form dense swarms and filter-feeding devil rays might have evolved to track large aggregations of micronektonic crustaceans whose sizes ensure energy to support the activities of these pelagic megafauna (Sampson et al. 2010; Couturier et al. 2013).

Population structure analysis of *P. latifrons* showed changes in the size-structure, reflecting individual growth from January to May (Masangcay et al. 2018). Breeding season of this species appears to be during the warm and dry months of March to May, which coincides with the decrease in number of juvenile individuals and the increase in abundance of large egg-carrying females during these months. Incidentally, the fishing season of *M. japanica* in Bohol Sea (Alava et al. 2002; Acebes 2013; Freeman 2014) and Butuan Bay (Metillo and Masangcay 2015) is from September to May with the peak season lasting from February to April. However, sightings and fishing of devil rays could extend up to June in Butuan Bay (Metillo and Masangcay 2015) and Bohol Sea (Freeman 2014). We are convinced that the preponderance of *M. japanica* individuals during these months could be linked with the availability of swarms of *P. latifrons*.

High primary production in Butuan Bay drives the abundance of *P. latifrons*, which prefer habitats with high abundance of zooplankton depending on dense phytoplankton (Wilson et al. 2003b). However, *P. latifrons* are reported to also feed on detritus (Hirota and Nemoto 1989). The peak of surface chlorophyll α is often observed in Butuan Bay at around 20–30 m depth (Villanoy, personal

communication). The primary production in Butuan Bay is at maximum during December to February when heavy rainfall causes highest river discharge (as indicated by highest chromophoric dissolved organic matter or CDOM) (Figure 4 in Cabrera et al. 2011) and a pronounced plume from Agusan River, the second largest river in the Philippines (Villanoy et al. 2011). Another primary production enhancement mechanism in Butuan Bay is the "double estuarine type circulation", which is mostly driven by the large inflow of waters from the Pacific Ocean passing through Surigao Strait and entrains large amounts of deep, nutrient-rich waters to the surface (Cabrera et al. 2011). This mechanism is strongest during the months of December to March when the northeast monsoon winds generate the westbound surface current Bohol Jet in the Bohol Sea (Cabrera et al. 2011). This regular circulation pattern, together with the highest freshwater discharge from the large Agusan River, eventually leads to nutrient enrichment and phytoplankton bloom, which in turn fuel high zooplankton abundance that feed the *P. latifrons* population.

C and N stable isotope values

Stable isotope analysis allowed the determination of a consumer-food relationship between *M. japanica* and its potential prey in Butuan Bay. The isotopic signature of $\delta^{15}N$ reflects an organism's trophic position, while isotopic differences among $\delta^{13}C$ values can trace the original dietary carbon source of the consumer, whether it originated from a marine, freshwater, or terrestrial environment (Shiffman et al. 2012). Furthermore, $\delta^{13}C$ gradients may also reflect the food web relationship between coastal or benthic, and offshore or pelagic regions (Dahl et al. 2003; Hussey et al 2011). Depleted $\delta^{13}C$ values (-22‰ to -17‰) denote pelagic feeding, whereas enriched $\delta^{13}C$ values (> -17‰) imply coastal and/or benthic foraging (France 1995).

Here, we report the C and N stable isotopes values of one female and four male *M. japanica* individuals from Butuan Bay. Values among *M. japanica* individuals did not differ, which agrees with the study of Sampson et al. (2010) who reported no difference in $\delta^{13}C$ and $\delta^{15}N$ values between stage of maturity, between sex, among monthly values, and between species (*M. thurstoni* and *M. japanica*). Similarly, Couturier et al. (2013) found similar $\delta^{13}C$ and $\delta^{15}N$ stable isotopes in *Manta alfredi* from both Lady Elliot Island and North Stradbroke Island in Queensland, Australia. Less stable isotope variation in these large organisms may be explained by the long-term (months) turnover rates of C and N stable isotopes in muscle tissues of mobulids (Sampson et al. 2010). The low variability in stable isotope values (0.16—

0.35 for δ^{13}C and 0.04−0.25 for δ^{15}N in this study) is also indicative of a highly specialized diet (Sweeting et al. 2005).

Mean δ^{13}C isotopic value (-16.07‰) of *M. japanica* falls within the enriched category which implies that its diet would most likely be composed of prey from offshore marine and planktonic habitat (France 1995). The present study reports comparable δ^{13}C values reported in other Mobulidae studies: *M. thurstoni* (-16.74‰) and *M. japanica* (-16.78‰) (Sampson et al. 2010); *M. diabolus* (-16.02‰) (Borell et al. 2011); and *M. alfredi* (-17.4‰) (Couturier et al. 2013). ^{13}C values of potential prey are enriched. The difference in values for juvenile and larval fishes may be related with migration, wherein larvae are spawned in deep spawning ground (more enriched ^{13}C signature) but juveniles move to shallow nursery habitats (more depleted ^{13}C signature) (Tanaka et al. 2008). Therefore, the ^{13}C values of the juvenile fish *Acetes* spp., *P. latifrons*, and zooplankton are reflective of shallow neritic and estuarine organisms.

The stomach content analysis in this study reveals that *M. japanica* preys on zooplankton, particularly micronektonic shrimps euphausiid (*P. latifrons*) and sergestid (*A. intermedius*) in Butuan Bay. The calculated trophic position based on mean values of *M. japanica* suggests the species is a low trophic level secondary consumer that assimilates nitrogen of primary consumers, concurring with the findings of the stomach analysis. However, following the mean trophic enrichment factors (3.2‰ for δ^{15}N and 1.8±0.29‰ for δ^{13}C) of McCutchan et al. (2003), *M. japanica* would primarily eat not only the krill *P. latifrons* and the sergestid *Acetes intermedius*, but also juvenile fish. This is not surprising as other mobulids are reported to ingest ichthyoplankton, proving plasticity in its feeding habits (Stewart et al. 2016).

CONCLUSION

Stomach contents of 16 *M. japanica* individuals were dominated by adults and eggs of *Pseudeuphausia latifrons* euphausiid, followed by a much lesser amount of sergestid shrimps (*Lucifer* sp. and *Acetes intermedius*), copepods, and planktonic remains. Larger female *P. latifrons* was observed to be the most dominant in the diet of *M. japanica*, which coincided during the peak of the reproductive cycle of the krill. Stable isotopes of C and N in muscle tissues of five *M. japanica* individuals and potential preys confirm the strong feeding affinity of *M. japanica* with micronektonic crustaceans. This study is the first formal report on the feeding of *M. japanica* in tropical Philippine waters. Although the current findings are useful

input to local conservation and management of *M. japanica*, we recommend that longer period of study should be made to include other ray species in the Philippines.

ACKNOWLEDGEMENTS

REFERENCES

Acebes JMV. 2013. Hunting "Big Fish": A marine environmental history of a contested fishery in the Bohol Sea [doctoral dissertation]. Perth, Western Australia: Murdoch University.

Alava MNR, Dolumbalo ERZ, Yaptinchay AA, Trono RB. 2002. Fishery and trade of whale sharks and manta rays in the Bohol Sea, Philippines. In: Fowler SL, Reed TM, Dipper FA, editors. Elasmobranch biodiversity, conservation and management: Proceedings of the international seminar and workshop; July 1997; Sabah, Malaysia. Gland, Switzerland: IUCN Species Survival Commission no. 25. p 132-148.

Alonso MK, Crespo EA, García NA, Pedraza SN, Mariotti PA, Vera BB, Mora NJ. 2001. Food habits of *Dipturus chilensis* (Pisces: Rajidae) off Patagonia, Argentina. ICES Journal of Marine Science. 58:288-297.

Anderson RC, Adam MS, Goes JI. 2011. From monsoons to mantas: seasonal distribution of *Manta Alfredi* in the Maldives. Fisheries Oceanography. 20:104-113.

Bizzaro J, Smith W, White WT, Valenti SV [Internet]. 2009. *Mobula kuhlii*. The IUCN Red List of Threatened Species 2009: e.T161439A5424139; [cited 2015 November 10]. Available from http://www.iucnredlist.org.

Borrell A, Cardona L, Kumarran RP, Aguilar A. 2011. Trophic ecology of elasmobranchs caught off Gujarat, India, as inferred from stable isotopes. ICES Journal of Marine Science. 69:357-1371.

Brinton E. 1975. Euphausiids of the Southeast Asian waters. Scientific results of marine investigations of the South China Sea and the Gulf of Thailand 1959-1961. Naga Report. 4:1-287.

[BFAR] Bureau of Fisheries and Aquatic Resources [Internet]. 2015. Comprehensive National Fisheries Industry Development Plan (CNFIDP); [cited 2015 December 2]. Available from http://www.bfar.da.gov.ph/files/img/photos/CNFIDP.

Cabrera OC, Villanoy CL, David LT, Gordon AL. 2011. Barrier layer control of entrainment and upwelling in the Bohol Sea, Philippines. Oceanography. 24:130-141.

Canese S, Cardinali A, Romeo T, Giusti M, Salvati E, Angiolillo M, Greco S. 2011. Diving behavior of the giant devil ray in the Mediterranean Sea. Endangered Species Research. 14:171-176.

Celona A. 2004. Caught and observed giant devil rays *Mobula mobular* (Bonnaterre, 1788) in the Strait of Messina. Annales Series Historia Naturalis. 14:11-18.

Cortes J, Blum S. 2008. Life at 450 m depth to Isla del Coco, Costa Rica. International Journal of Tropical Biology. 56:189-206.

Couturier LIE, Jaine FRA, Townsend KA, Weeks SJ, Richardson AJ, Bennett MB. 2011. Distribution, site affinity and regional movements of the manta ray, *Manta alfredi* (Krefft, 1868), along the east coast of Australia. Marine and Freshwater Research. 62:628-637.

Couturier LIE, Marshall AD, Jaine FRA, Kashiwagi T, Pierce SJ, Townsend KA, Weeks SJ, Bennet MB, Richardson AJ. 2012. Biology, ecology and conservation of the Mobulidae. Journal of Fish Biology. 80:1075-1119.

Couturier LIE, Rohner CA, Richardson AJ, Marshall AD, Jaine FRA, Bennet MB, Townsend KA, Weeks SJ, Nichols PD. 2013. Stable isotope and signature fatty acid analyses suggest reef manta rays feed on demersal zooplankton. PLoS ONE. 8:e77152.

Croll DA, Newton KM, Weng K, Galván-Magaña F, Sullivan JO, Dewar H. 2012. Movement and habitat use by the spine-tail devil ray in the Eastern Pacific Ocean. Marine Ecology Progress Series. 465:193-200.

Croll DA, Dewar H, Dulvy NK, Fernando D, Francis MP, Galvan-Magana F, Hall M, Heinrichs S, Marshall A, McCauley D, Newton K, Notarbartolo-di-Sciara G, O'Malley M, O'Sullivan J, Poortvleit M, Roman M, Stevens G, Tershy B, White WT. 2016. Vulnerabilities and fisheries impacts: the uncertain future of manta and devil rays. Aquatic Conservation: Marine and Freshwater Ecosystems. 26:562–575.

Dahl TM, Falk-Petersen S, Gabrielsen GW, Sargent JR, Hop H, Millar RM. 2003. Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar: A trophic study from an Arctic fjord. Marine Ecology Progress Series. 256:257-269.

DeNiro MJ, Epstein S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta. 42:495-506.

Dewar H, Mous P, Domeier M, Muljadi A, Pet J, Whitty J. 2008. Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. Marine Biology. 155:121-133.

Dulvy NK, Sadovy Y, Reynolds JD. 2003. Extinction vulnerability in marine populations. Fish and Fisheries. 4:25-64.

France RL. 1995. Carbon-13 enrichment in benthic compared to planktonic algae: Food web implications. Marine Ecology Progress Series. 124:307-312.

Francis MP, Jones EG. 2016. Movement, depth distribution and survival of spinetail devil rays (*Mobula japanica*) tagged and released from purse-seine catches in New Zealand. Aquatic Conservation: Marine and Freshwater Ecosystems. 27(1):219-236.

Freeman AL. 2014. Mobulidae fishery in Bohol, Philippines: An assessment of its sustainability [MRes thesis]. UK: Swansea University.

Gadig OBF, Namora RC, dos Santos Motta F. 2003. Occurrence of the bentfin devil ray, *Mobula thurstoni* (Chondrichthyes: Mobulidae), in the western Atlantic. Journal of the Marine Biological Association of the UK. 83:869-870.

Garcia VB, Lucifora LO, Myers RA. 2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. Proceedings of the Royal Society B: Biological Sciences. 275:83-89.

Gendron D. 1992. Population structure of daytime surface swarms of *Nyctiphanes simplex* (Crustacea: Euphausiacea). Marine Ecology Progress Series. 87:1-6.

Hanamura Y, Saito N, Hayashi KI. 2003. Shore stranding of the neritic euphausiid *Pseudeuphausia latifrons* (GO Sars, 1883) in western Japan. Crustaceana. 76:1147-1152.

Hays GC, Richardson AJ, Robinson C. 2005. Climate change and marine plankton. Trends in Ecology and Evolution. 20:337-344.

Hirota Y. 1987. Vertical distribution of euphausiids in the western Pacific Ocean and the eastern Indian Ocean. Bulletin of Japan Sea Regional Fisheries Research Laboratory. 37:175-224.

Hirota Y, Nemoto T. 1989. Relationship between feeding and vertical distribution of euphausiids in the western Pacific Ocean. Bulletin of the Plankton Society of Japan. 36:127-135.

Hussey NE, Dudley SFJ, McCarthy ID, Cliff G, Fisk AT. 2011. Stable isotope profiles of large marine predators: Viable indicators of trophic position, diet, and movement in sharks? Canadian Journal of Fisheries and Aquatic Sciences. 68:2029-2045.

Indab JD, Suarez-Aspilla PB. 2004. Community-based marine protected areas in the Bohol (Mindanao) Sea, Philippines. NAGA, WorldFish Center Quarterly. 27:4-8.

Jaine FRA, Couturier LIE, Weeks SJ, Townsend KA, Bennett MB, Fiora K, Richardson A.J. 2012. When giants turn up: Sighting trends, environmental influences and habitat use of the manta ray *Manta alfredi* at a Coral Reef. PLoS ONE. 7:e46170.

Jarman SN, Wilson SG. 2004. DNAbased species identification of krill consumed by whale sharks. Journal of Fish Biology. 65:586-591.

Marshall AD, Compagno LJV, Bennett MB. 2009. Redescription of the genus *Manta* with resurrection of *Manta alfredi* (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). Zootaxa. 2301:1-28.

Marshall AD, Dudgeon CL, Bennett MB. 2011. Size and structure of a photographically identified population of manta rays *Manta alfredi* in southern Mozambique. Marine Biology. 158:1111-1124.

Masangcay SIG. 2016. Feeding biology of devil rays (Mobulidae, Chondrichthyes) in Butuan Bay, Northeastern Mindanao, Philippines [MSc Thesis]. Iligan City, Philippines: Mindanao State University-Iligan Institute of Technology.

Masangcay SIG, Metillo EB, Nishida S. 2018. Population structure of the krill prey of the Spinetail Devil Ray *Mobula japanica* (Chondrichthyes, Mobulidae) from Southeastern Bohol Sea, Philippines. Science Diliman. 30(1):74-81.

McCutchan JH, Lewis WM, Kendall C, McGrath CC. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos. 102:378-390.

Metillo EB, Cadelinia E, Hayashizaki K, Tsunoda T, Nishida S. 2015. Feeding ecology of two sympatric species of *Acetes* (Decapoda: Sergestidae) in Panguil Bay, the Philippines. Marine and Freshwater Research. 67:1420-1433.

Metillo EB, Masangcay SIG. 2015. Rapid assessment of rays (Mantas and Mobulids) in Sulu Sea and Bohol Sea. Technical Report submitted to the Manta Trust Fund, UK; Save Our Seas and Mindanao State University-Iligan Institute of Technology.

Mintenbeck K, Brey T, Jacob U, Knust R, Struck U. 2008. How to account for the lipid effect on carbon stable-isotope ratio ($\delta13C$): sample treatment effects and model bias. Journal of Fish Biology. 72(4):815-830.

Moura T, Figueiredo I, Farias I, Serra-Pereira B, Neves A, Borges MDF, Serrano Gordo L. 2008. Ontogenetic dietary shift and feeding strategy of *Raja undulata* Lacepède, 1802 (Chondrichthyes: Rajidae) on the Portuguese continental shelf. Scientia Marina. 72(2): 311-318.

Musick JA, Ellis JK. 2005. Reproductive evolution of chondrichthyans. In: Hamlett WC, editor. Reproductive Biology and Phylogeny of Chondrichthyes: Sharks, Batoids and Chimeras. Enfield, NH: Science Publishers. p.45-79.

Nemoto T. 1983. Net sampling and abundance assessment of euphausiids. Biological Oceanography. 2(2,3,4):211-226.

NGA Nautical Chart. 1996. Asia Philippines central part bathymetric chart (6th Ed.); [cited 2016 August 16]. Available from http://www.oceangrafix.com/chart/zoom?chart=91005.

Notarbartolo di Sciara G. 1987. A revisionary study of the genus *Mobula rafinesque*, 1810 (Chondrichthyes: Mobulidae) with the description of a new species. Zoological Journal of the Linnean Society. 91(1):1-91.

Notarbartolo di Sciara G. 1988. Natural history of the rays of the genus *Mobula* in the Gulf of California. Fishery Bulletin. 86(1):45-66.

O'Reilly CM, Hecky RE, Cohen AS, Plisnier PD. 2002. Interpreting stable isotopes in food webs: recognizing the role of time averaging at different trophic levels. Limnology and Oceanography. 47(1):306-309.

Paig-Tran EM, Bizzarro JJ, Strother JA, Summers AP. 2011. Bottles as models: predicting the effects of varying swimming speed and morphology on size selectivity and filtering efficiency in fishes. Journal of Experimental Biology. 214:1643-1654.

Paig-Tran EWM, Kleinteich T, Summers AP. 2013. The filter pads and filtration mechanisms of the devil rays: variation at macro and microscopic scales. Journal of Morphology. 274:1026-1043.

Paulin CD, Habib G, Carey CL, Swanson PM, Voss GJ. 1982. New records of *Mobula japanica* and *Masturus lanceolatus*, and further records of *Luvaris imperialis* (Pisces: Mobulidae, Molidae, Louvaridae) from New Zealand. New Zealand Journal of Marine and Freshwater Research. 16:11-17.

Pierce SJ, Bennett MB. 2003. *Mobula eregoodootenkee*. The IUCN Red List of Threatened Species 2003: e.T41832A10575938; [cited 2016 June 26]. Available from http://www.iucnredlist.org.

Pinkas LM, Oliphant S, Iverson ILK. 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. California Fish and Game. 152:1-105.

Post DM. 2002. Using stable isotope to estimate trophic position: models, methods and assumptions. Ecology. 83:703-718.

Primavera J, Tumanda Jr MI. 2008. The Agusan marsh: a situationer with focus on scientific aspects. Proceedings of the First Scientific Conference on the Agusan Marsh; 2007 May 21-23; Butuan City, Agusan del Norte, Philippines. UNESCO Jakarta Office: Philippine Council for Aquatic and Marine Research and Development. p. 5-14.

Rayos JCC, Santos MD, Barit NC. 2012. Devil ray resources in Bohol Sea, Philippines. In: Fish for the People, editors. Fish for the People, 44. Bangkok: SEAFDEC; [cited 2017 August 27]. Available from http://www.seafdec.org/download/fish-for-the-people-vol-10-no-1/.

Richardson AJ. 2008. In hot water: zooplankton and climate change. ICES Journal of Marine Sciences. 65:279-295.

Sampson L, Galván-Magaña F, De Silva-Dávila R, Aguíñiga-García S, O'Sullivan JB. 2010. Diet and trophic position of the devil rays *Mobula thurstoni* and *Mobula japanica* as inferred from stable isotope analysis. Journal of the Marine Biological Association of the United Kingdom. 90:969-976.

Scacco U, Consalvo, Mostarda E. 2009. First documented catch of the giant devil ray *Mobula mobular* (Chondrichthyes: Mobulidae) in the Adriatic Sea. Marine Biodiversity Records. 2:e93.

Schluessel V, Bennett MB, Collin SP. 2010. Diet and reproduction in the white-spotted eagle ray *Aetobatus narinari* from Queensland, Australia, and the Penghu Islands, Taiwan. Marine and Freshwater Research. 61:1278-1289.

Shiffman DS, Gallagher AJ, Boyle MD, Hammerschlag-Peyer CM, Hammerschlag N. 2012. Stable isotope analysis as a tool for elasmobranch conservation research: a primer for non-specialists. Marine and Freshwater Research. 63:635-643.

Shwenk K. 2000. Feeding. Form, function and evolution in tetrapod vertebrates. California: Academic Press. p 493-494.

Sleeman JC, Meekan MG, Wilson SG, Jenner CKS, Jenner MN, Boggs GS, Steinberg CC, Bradshaw CJA. 2007. Biophysical correlates of relative abundances of marine megafauna at Ningaloo Reef, Western Australia. Marine and Freshwater Research. 58:608-623.

SPSS. 2002. SPSS for Windows version 11. Chicago, IL: SPSS Inc.

Stewart JD, Hoyos-Padilla EM, Kumli KR, Rubin RD. 2016. Deep-water feeding and behavioral plasticity in *Manta birostris* revealed by archival tags and submersible observations. Zoology. 119(5):406-413.

Sweeting CJ, Jennings S, Polunin NVC. 2005. Variance in isotopic signatures as a descriptor of tissue turnover and degree of omnivory. Functional Ecology. 19:777–784.

Tanaka H, Takasuka A, Aoki I, Ohshimo S. 2008. Geographical variations in the trophic ecology of Japanese anchovy, *Engraulis japonicus*, inferred from carbon and nitrogen stable isotope ratios. Marine Biology. 154:557-568.

Vander Zanden M, Rasmussen JB. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography. 46:2061-2066.

Villanoy C, Cabrera O, Yniguez A, Camoying M, de Guzman A, David L, Flament P. 2011. Monsoon-driven coastal upwelling off Zamboanga Peninsula, Philippines. Oceanography. 24:156-165.

Weeks SJ, Magno-Canto MM, Jaine FRA, Brodie J, Richardson AJ. 2015. Unique sequence of events triggers manta ray feeding frenzy in the Southern Great Barrier Reef, Australia. Remote Sensing. 7:3138-3152.

Wetherbee BM, Cortés E. 2004. Food consumption and feeding habits. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of Sharks and their Relatives. Florida: CRC Press. p. 225-246.

White WT, Clark TB, Smith WD, Bizzarro JJ. 2006a. *Mobula japanica*. The IUCN Red List of Threatened Species 2006: e.T41833A10576180; [cited 2016 June 15]. Available from http://www.iucnredlist.org.

White WT, Giles J, Potter IC. 2006b. Data on the bycatch fishery and reproductive biology of mobulid rays (Myliobatiformes) in Indonesia. Fisheries Research. 82:65-73.

Wiebe PH, Ashian CJ, Gallager SM, Davis CS, Laweson GL, Copley NJ. 2004. Using a high powered strobe light to increase the catch of *Antarctic krill*. Marine Biology. 144:493-502.

Willoughby F. De historia piscium Ray J, editor. Oxonii: Royal Society; 1686.

Wilson SG, Newbound DR. 2001. Two whale shark faecal samples from Ningaloo Reef, Western Australia. Bulletin of Marine Science. 68:361-362.

Wilson SG, Pauly T, Meekan MG. 2001. Daytime surface swarming by *Pseudeuphausia latifrons* (Crustacea, Euphausiacea) off Ningaloo Reef, Western Australia. Bulletin of Marine Science. 68(1):157-162.

Wilson SG, Carleton JH, Meekan MG. 2003a. Spatial and temporal patterns in the distribution and abundance of macrozooplankton on the southern North West Shelf, Western Australia. Estuarine, Coastal and Shelf Science. 56:897-908.

Wilson SG, Meekan M, Carleton J, Stewart T, Knott B. 2003b. Distribution, abundance and reproductive biology of *Pseudeuphausia latifrons* and other euphausiids on the southern North West Shelf, Western Australia. Marine Biology. 142:369-379.

_____

Shirlamaine Irina G. Masangcay is a graduate of B.S. Marine Biology from Mindanao State University-Iligan Institute of Technology. She graduated M.S. Marine Biology from Mindanao State University-Iligan Institute of Technology on time as a DOST-ASTHRDP scholarship in 2016, and was hired immediately after graduation as Instructor at the Caraga State University, Butuan City, Philippines.

Ephrime B. Metillo <ephrime.metillo@g.msuiit.edu.ph> is B.S. Zoology graduate at the Mindanao State University Marawi City. He was University Research Assistant at the Marine Science Institute of the University of the Philippines Diliman before doing a straight Ph.D. Program at the University of Tasmania at Hobart, Australia under the Australian International Development Assistance Bureau (AIDAB) Equity and Merit Scholarship Scheme. He is now Professor at the Mindanao State University-Iligan Institute of Technology, Iligan City, Philippines.

Ken-Ichi Hayashizaki is a marine scientist, an expert on stable isotope analysis and currently Associate Professor at Kitasato University, Sagamihara, Japan.

Satoru Tamada is a recent graduate of Master of Science Marine Bioscience at Kitasato University, Japan with focus on the use of stable isotope analysis in the ecology of the Japanese flounder.

Shuhei Nishida is a recently retired Professor at the Atmosphere and Ocean Research Institute of the University of Tokyo, Japan. He has published more than 110 papers in the field of marine biology and became Editor of the Springer journal Marine Biology. His main field of interest is marine zooplankton biology and ecology.