SHORT COMMUNICATION

Observations on the specific associations found between scyphomedusae and commensal fish and invertebrates in the Philippines

Sheldon Rey Boco^{1,2,*}, Ephrime B. Metillo¹

¹Department of Biological Sciences, Mindanao State University-Iligan Institute of Technology,
Andres Bonifacio Avenue, Tibanga, Iligan City 9200, Philippines

²Present address

Australian Rivers Institute – Coasts and Estuaries, Griffith School of Environment, Gold Coast
Campus, Griffith University, QLD 4222, Australia

*Corresponding author

Telephone: +61405606524

Email: sheldonrey.boco@griffithuni.edu.au

Abstract

Our observations on scyphomedusae from selected Philippine embayments identified specific animals commensal with five species of rhizostome scyphomedusae, *Acromitoides purpurus*, *Mastigias* sp., *Phyllorhiza punctata*, *Rhopilema hispidum* and *Versuriga anadyomene*. *Acromitoides purpurus* medusae harbor the crab *Charybdis feriata*, the carangid fish *Alepes djedaba* and the poecilostomatoid copepod *Paramacrochiron* sp. The carangid *A. djedaba* was an associate of the blue morph of *A. purpurus* and *Rhopilema hispidum* in Panguil Bay. A black-pigmented *Alepes* sp. was found associated with burgundy *A. purpurus* medusae in Carigara Bay. *Charybdis feriata* juveniles are common commensals of all morphs of *A. purpurus*, *R. hispidum* and *P. punctata* medusae. Only the zooxanthellate *Mastigias* sp. lacked animal symbionts. We invoke the “meeting-point hypothesis” and the general theory of fish aggregation to floating structures to explain fish symbiosis with their medusan hosts. The invertebrate-medusa associations are attributed to feeding behaviors and predator avoidance by resident commensals. This study provides record of the poorly studied scyphozoan species and their association with animals in Philippine waters. Finally, we discuss the potential reasons why the golden spotted jellyfish, *Mastigias* sp., appears to lack animal commensals.

Keywords: color morph, gelatinous zooplankton, jellyfish, Scyphozoa, symbiosis

1 Introduction

While jellyfishes seem synonymous to danger and injury, they provide societal and ecological benefits (Doyle et al. 2014). Some jellyfish species serve as food for humans (Brotz et al. 2016; Omori and Nakano 2001), sequester carbon which help regulate climate processes (Lebrato et al. 2012), and provide shelter for associated organisms (Doyle et al. 2014).

Associations between jellyfish and commensals have been reported for over 150 years (Peach 1855; Mortensen 1917; Ohtsuka et al. 2009). Thiel (1976), Purcell and Arai (2001) and Ohtsuka et al. (2009) thoroughly reviewed the worldwide interactions between medusae and animal commensals. Studies of jellyfish-commensal associations in Southeast Asian waters exist (Ohtsuka et al. 2009, 2010 and 2013) but similar studies in the Philippines are few (Kondo et al. 2014) despite the high species richness of Philippine jellyfish (Mayer, 1910; Light 1914; Gershwin 2003) and the status of the archipelago as the global center of marine biodiversity (Carpenter and Springer 2005; Nañola et al. 2011; Sanciangco et al. 2013).

Jellyfish-commensal associations have implications for marine biodiversity and commercially important fisheries (Purcell and Arai 2001). For instance, cnidarian medusae prey on ichthyoplankton, compete with their symbionts for food, and transmit parasites to fish (Purcell and Arai 2001; Ohtsuka et al. 2009). The association with medusae can enhance the population or diversity of these commensals since medusae can provide shelter, act as food (jellyfish tissue) of fish (Masuda et al. 2008), and protect the larval stages of commensals from predators (Masuda 2009; Ohtsuka et al. 2009; Sal Moyano et al. 2012).

The jellyfish symbiotic interactions in the marine environment and effects on ecological processes are still poorly understood (Ohtsuka et al. 2009). These animal associations are affected by natural and anthropogenic perturbations (Brotz et al. 2016; Nagelkerken et al. 2016). Ocean acidification as a mark of climate change threatens these animal associations by negatively affecting the behavior of commensals which take shelter with medusa hosts (Nagelkerken et al. 2016). Several species of edible jellyfish known to associate with animal commensals are harvested annually for large-scale commercial fisheries (Browne and Kingsford 2005; Ohtsuka et al. 2009; Ohtsuka et al.

2010; Brotz et al. 2016). Harvesting these medusae can alter the recruitment or population structure of these commensals caught with the host medusae (Brotz et al. 2016; Ohtsuka et al. 2010). In Southeast Asian jellyfish fisheries, the annual catch of rhizostomes based on export data attains approximately 321,000 tons in weight of semi-dried jellyfish product (Omori and Nakano 2001). In Vietnam, approximately 6,948 tons of this semi-dried product are being exported (Nishikawa et al. 2008). This potential fisheries pressure on commensals was one of the bases for the establishment of a policy of harvesting medusae in some parts of the Philippines (e.g. Palawan Is.) specifically requiring the return of oral arms of medusae to the sea to free the commensals (Pagliawan et al. 2015).

This paper reports observations on the specific associations between several medusae of several scyphozoan species with commensal fish and crustaceans during ecological surveys of various embayments in the Philippines. We also discuss possible reasons for the unusual absence of commensals that associated the golden spotted jellyfish, *Mastigias* sp.

2 Materials and Methods

Jellyfish sampling stations were located in Panguil Bay, Iligan Bay (both in Northern Mindanao province), Illana Bay (Zamboanga del Sur province), Carigara Bay (Leyte Is.), municipality of Marabut and Guiuan (Leyte Gulf; Samar Is., Eastern Visayas region) and Lipusan Bay (Samar Is.) (Fig. 1). The stations were selected based on anecdotal reports of sightings of jellyfish medusae, importance as fishing grounds and representativeness of the biogeographic zones of the archipelago with unique biophysical dynamics (Celebes Sea, Southern Philippine Sea and Visayan Region; see Nañola et al. 2011). Sampling at these stations was done per sampling time point (see Table 2). Three transect lines (200 m x 5 m) per station were covered during sampling. Prevalence and intensity of symbionts were calculated. Prevalence (P) is the proportion (in %) of medusae with commensals among all the medusae examined ($P = \text{number of host} \div \text{total number of medusa examined} \times 100$) while intensity is expressed as the mean ($\pm$ s.d.) number of commensals found in the associated hosts (Rózsa et al. 2000). Carapace width (cw) of crabs, and standard length of fish symbionts were obtained using a digital caliper (Ares 70018, ARES; 0.02 mm accuracy). Copepod

commensal body length was measured using a stereomicroscope (SteREO Discovery V8, Zeiss) with an eyepiece micrometer. Oceanographic variables from subsurface (about 0.5 m depth) water samples were determined from specific spots where the jellyfish were located. Salinity was measured using a refractometer (ATAGO Japan, S/Mill-E). Water temperature was measured using a mercury thermometer (FS 15142C, Fisher Scientific). Dissolved oxygen was determined following the Winkler titration method (Strickland and Parsons 1972). Sampling depth was measured using a weighted and calibrated rope and a meter stick. Only macroscopic jellyfish medusae with an umbrella size (diameter) between 5.0 cm and 54 cm were collected. The smallest size is based from a chirodropid medusa (Mayer 1910) while the largest is from a commercial medusa (Kondo et al. 2014). Locations of the collection were recorded using a GPS device (Etrex 10, Garmin). The medusae and their commensals found per station per sampling time point were located and collected using a scoop-net with 50 cm diameter and 2 cm mesh size on board an outrigger boat (as in Kondo et al. 2014). Each medusa with commensals was placed separately in a clean polyethylene bag and placed in a styrofoam container with ice. Commensals were picked from jellyfish individuals for counting and observations, and the jellyfish host was identified. Immediately after collection, oral arm tissues from voucher medusae were obtained and preserved in clean Eppendorf tubes with 99% ethanol. The tubes were covered with a dark plastic bag before putting into a container with ice. Soft-bodied invertebrate commensals were anesthetized with menthol crystals before preservation (Callaway et al. 2003). Voucher specimens of medusae and symbionts were preserved in 4% formalin in seawater (Nogueira and Haddad 2005) and stored for future reference.

Jellyfish were identified according to descriptions of the medusae by Mayer (1910), Light (1914, 1921), Stiasny (1924) and Stiasny (1926), Kramp (1961), Galil et al. (1990), Heeger (1998), Omori and Kitamura (2004), Dawson (2005a, b, c), Kitamura and Omori (2010), Bayha and Graham (2011), Gul and Morandini (2013). The canal system of each medusa was stained with methylene blue using a hypodermic needle to aid in the identification. We were able to identify medusae that belong to genus *Mastigias*. The taxonomic placement of *Mastigias* spp. is currently under scrutiny due to the discovery of cryptic species of *Mastigias* that form clades (China Seas, Pacific Islands, and Solomon Sea clade) which are regionally and genetically distinct (Swift et al. 2016). Although the morphology

of the medusae conforms to the descriptions of the nominal species of *M. papua* (see Kramp 1961), we believe in the possibility that the *Mastigias* observed from different stations belong to more than one cryptic species similar to cases with medusae reported as *M. papua* but were later found to belong to different cryptic species (Dawson 2005c). Thus, we refer the medusae here as *Mastigias* sp.

In the laboratory, the external parts of the medusae were carefully checked for commensals. Microscopic animal commensals were examined by direct observation of medusa tissues under a microscope and by washing the medusae with filtered seawater and examining the supernatant filtered using a 100- μ m mesh sieve. Invertebrate commensals were identified using the descriptions by Kaburaki (1923), Fielder et al. (1984), Poore (2004), Abelló and Hispano (2006), and Ohtsuka et al. (2012). Fish symbionts were identified using the descriptions by Iwatsuki and Kimura (1996), Miller and Tsukamoto (2004), Allen (2009), and Golani et al. (2011).

3 Results

Oceanographic variables (Table 1). Highest mean salinities were recorded in Station (Stn.) 3 during the intermonsoon month of May (32 ± 0.5 PSU) and the Southwest monsoon month of July (32 ± 1.0 PSU) while the lowest mean salinities were recorded during the Northeast monsoon month of February (22 ± 1.0 PSU) and May (22 ± 7.5 PSU) in Stn. 1. The highest mean temperatures were observed in the intermonsoon month of April at the stations in Leyte Gulf (33 ± 0.3 °C in Stn. 5; 33 ± 0.6 °C in Stn. 6) and in May 2014 in Stn. 3 (33 ± 0.8 °C). Jellyfish medusae sampling stations had mean dissolved oxygen concentration range of 5.6 ± 0.9 mg L⁻¹ to 14 ± 0.5 mg L⁻¹. A mean depth range of 0.9 ± 0.1 m to 8.1 ± 6.0 m was recorded for all the stations.

Acromitoides purpurus (Mayer 1910) Stiasny 1924. In the waters of the municipality of Kolambugan, Lanao del Norte (Stn. 1), blue *A. purpurus* medusae (Fig. 2a) are abundant and are locally called *bulbog*. Color morphs of the medusae are present in Stn. 1, the adjacent Stn. 2 and Stn. 4 in Eastern Visayas (Fig. 1 and 2, Table 2). In Stn. 1, color morphs of the medusae were observed during the following survey periods [blue morph: August 30, 2014 and November 16, 2014; orange

morph: November 2014 survey]. White and burgundy morphs were found in Stn. 4 in June 15, 2014 (Fig. 1 and 2) while the collection in August 2, 2014 in Stn. 2 (municipality of Linamon, Lanao del Norte) revealed an orange morph and blue morph medusae. Commensals of this jellyfish included the carangid fish *Alepes djedaba*, crab *Charybdis feriata*, and copepod *Paramacrochiron* sp. (Fig. 3, Table 2). In Carigara Bay, dark-pigmented carangids that closely resemble *A. djedaba* (Fig. 3f) associated with the burgundy *A. purpurus* hosts (Fig. 2c-d, Table 2). Because of its pigmentation, we thought the fish commensal to be a potentially different species of *Alepes*. Hence, we identified it here as *Alepes* sp.

Mastigias sp. Agassiz 1862. *Mastigias* sp. medusae were observed in Stns. 1, 3, 5, 6 and at the northernmost station (Stn. 7) in Lipusan Bay of Eastern Visayas (see Fig. 1, Fig. 2g and Table 2). In May 18, 2014 at the station located in the municipality of Dimataling, Zamboanga del Sur (Stn. 3) (Fig. 4a), the medusae were observed in the seagrass bed of a lagoon with their subumbrella resting upside-down (Fig. 4b). *Mastigias* sp. is the only medusoid examined that lacks animal commensals (Table 2).

Phyllorhiza punctata von Lendenfeld 1884. The medusae of this spotted jellyfish (Fig. 2h) were observed in May 30, 2014 near the mouth of Kolambugan River (Stn. 1). The medusae were observed again in August 8, 2014 at Stn. 1. Station 6 at Leyte Gulf also revealed the medusae of this species during April 12, 2015 survey (Fig. 2, Table 2). Commensals: *C. feriata* megalopa and copepod *Paramacrochiron* sp. (Table 2).

Rhopilema hispidum Vanhöffen 1888. The stinger rhizostome *Rhopilema hispidum* (Fig. 2j-l) was recorded in February 20, 2014 in Panguil Bay, near the coast of Mukas village, Kolambugan. Six medusae of the species were observed in August 8, 2014 and collected with the rhizostome species, *P. punctata* (Fig. 2, Table 2). Commensals: fishes (carangid *A. djedaba*, eel larvae of Order Anguilliformes, ponyfish *Equulites elongatus*), shrimp species of Family Hippolitidae, juvenile and megalopa of crab *C. feriata*, copepod *Paramacrochiron* sp. and a turbellarian flatworm. In total, seven species of commensals were collected from *R. hispidum* which could be the largest rhizostome in Panguil Bay (Fig. 3, Table 2).

Versuriga anadyomene Maas 1903. Large medusae of this jellyfish species (Fig. 2e) were found at Stn. 6 in Leyte Gulf in April 2015 (Fig. 1, Fig. 2, Table 2). Commensals: fish *A. djedaba* and two crustacean species: *C. feriata* and *Paramacrochiron* sp. (Fig. 3, Table 2).

4 Discussion

This paper presents new records of associations of rhizostome jellyfish medusae with fish and invertebrates in the Philippines. The rare association of eel larvae, ponyfish, shrimp and a flatworm with *Rhopilema hispidum* adds to the records of commensals of the jellyfish host. The majority of medusae and commensals occurred in shallow waters with salinity and warm temperatures that are typical in Philippine embayments (Gordon et al. 2011).

Alepes djedaba fish, *C. feriata* crab and *Paramacrochiron* sp. copepods associated with several species of rhizostome jellyfish, but these animals are known commensals of different species of jellyfish (Panikkar and Prasad 1952; Browne and Kingsford 2005; Towanda and Thuesen 2006; Cevik et al. 2011; Ohtsuka et al. 2009, 2010, 2012, 2013; Kondo et al. 2014; see also Table 3). We note, however, that some of them could be kleptobionts or kleptoparasites, symbionts that steal food from their hosts (see definitions in Vollrath 1984; Iyengar 2008), but proving this hypothesis requires further work.

The prevalence and intensity of copepod and fish commensals here are lower than the values in other reports of rhizostome-commensal associations (Browne and Kingsford 2005; Ohtsuka et al. 2010; Kondo et al. 2014). Browne and Kingsford (2005) found $1,034.0 \pm 282$ *Paramacrochiron* copepods per medusa (prevalence of 100 %) whereas the highest average value obtained in this study is only 27 ± 21 copepods per medusa (67 % prevalence in *R. hispidum*). Further, Ohtsuka et al. (2010) collected 43 *A. djedaba* carangid commensals from one *R. hispidum* medusa in Thailand. In Carigara Bay (Leyte Island, Philippines), Kondo et al. (2014) collected an average of 49.4 *A. djedaba* juveniles (100% prevalence) per medusa of large *Lobonemoides robustus*. These reports show relatively high prevalence and intensity of *A. djedaba* commensals compared to the values (3.0 ± 1.4 intensity, 67% prevalence in *R. hispidum*) obtained in this study. Although the exact cause of this discrepancy is unknown, factors such as size of the host (see

Rountree 1983; Lo et al. 1998; Reitzel et al. 2007; Browne et al. 2017), timing of the year (or seasonality), and abundance of both medusae and symbionts (Nogueira and Haddad 2005; Sal Moyano et al. 2012; Browne et al. 2017) could have affected the prevalence and intensity of the commensals.

The cause of the absence of animal commensals of *Mastigias* in this study is unknown. This finding leads to the hypothesis that *Mastigias* cannot effectively collect food for the commensals because this zooxanthellate species do not largely depend on zooplankton prey to survive (McCloskey et al. 1004); hence, the jellyfish is an inadequate host. However, reports of the association of *Mastigias* and zooxanthellate medusae of other scyphozoan species with commensals exist (Brandon and Cutress 1985; Bruce 1988; Spotte et al. 1991; Ohtsuka et al. 2009), refuting such hypothesis. Certainly, the absence of commensals of *Mastigias* is not purely stochastic because the medusae were sampled in different locations and time points with varied environmental conditions. A possible mechanism is that this species (or subspecies) releases deterrent substances upon physical contact with potential symbionts or predators (Shanks & Graham 1988; Pohnert 2004). Jellyfish hosts are known to regulate access even among commensals that are ‘immune’ to stings using deterrent chemicals (Shanks & Graham 1988). Additional observations of *Mastigias* in the field and experiments that allow potential commensals to choose this jellyfish as a host in controlled conditions are recommended to determine the cause of the absence of commensals.

Animal commensals may benefit from the protection against predators, shelter and dispersion of larvae and juveniles that jellyfish hosts provide (Tunberg and Reed 2004; Nogueira and Haddad 2005; Masuda et al. 2008; Ohtsuka et al. 2009; 2010). Medusa tissue can be a direct food source to commensal crabs and fish (Sal Moyano et al. 2012; D’Ambra et al. 2015), while mucus from medusa may nourish copepod commensals (Browne and Kingsford 2005). Commensals may use hosts as sites for feeding prey (Ohtsuka et al. 2009). Aside from protection (Masuda et al. 2008; Ohtsuka et al. 2009; 2010), zooplankton food concentrated in the oral arms of jellyfish elicited commensals to stay with their hosts (Colin et al. 2003; Gemmell et al. 2013). The jack mackerel *Trachurus japonicus*, for example, benefitted from this mechanism and showed ontogenetic patterns of association with its jellyfish host (Masuda 2009). Two hypotheses may explain the association of fish commensal and hosts: meeting point hypothesis (MPH; Fréon and Dagorn 2000; Soria et al. 2009) and the general

theory of fish aggregation on floating objects (Castro et al. 2002). The MPH suggests that fish commensals use floating structures such as jellyfish medusae as sites for encountering conspecifics to form schools and that school formation protects fish against predators (Soria et al. 2009). The latter explains that fish aggregate on floating structures, including presumably host medusae, not only for acquiring planktonic food and protection against predators but also for protecting delicate stages of the fish, i.e. larvae and small juveniles (Castro et al. 2002).

Commensals of stinging jellyfishes, in general, adapted protection from stinging nematocysts of most jellyfish hosts (Mebs 2009). They may have thick exoskeleton such as carapace of some crustaceans (Wirtz 1997), tight scales like in other pelagic fishes (Masuda 2009) and integumentary mucus that inhibits nematocyst activity by imitating the host's body chemistry, a mechanism known as chemical mimicry (Mebs 1994, 2009). Symbiotic fishes (perhaps excluding leptocephali), copepods, juvenile crabs and shrimps in this study may have body covering that protected them from nematocysts. The eel leptocephali of *R. hispidum* must have protective mucus that presumably enabled them to enter the subgenital ostia of their hosts since these delicate larvae of eels have thin and fragile integument (Miller 2009). Commensal shrimps and other species of commensal crustaceans are also known to secrete protective mucus from their integument (Wirtz 1997; Mebs 2009). Nevertheless, the mechanisms of protection of symbiotic fish (Karplus 2014) and invertebrate species (Nedosyko et al. 2014) against nematocysts is still unclear.

Acknowledgments

This work is supported by a MSc. Scholarship grant (NSC-ASTHRDP) of SRB provided by the Philippine Department of Science and Technology. We thank M.E. Malugao, S.A.U. Balt, J.B. Villaroya, B. Sebial, and Z.M. Agir for assistance in the field. We are very grateful for the help of the residents of Kolambugan, Lanao del Norte with Mayor Eyoy Maniegos during our Panguil Bay surveys. Agir Family is greatly acknowledged for logistical support during Zamboanga del Sur surveys. We thank Prof. F.R.M. Ladio of Leyte Normal University, Tacloban City, P.J. Mayo of Visayas State University, Baybay City and K. Salamida with the Salamida family of Guiuan, Eastern

Samar for logistical support during Eastern Visayas surveys. Dr. T. Heeger is acknowledged for relevant discussions about Philippine jellyfishes.

References

- Abelló P, Hispano C (2006) The capture of the Indo-Pacific crab *Charybdis feriata* (Linnaeus, 1758) (Brachyura: Portunidae) in the Mediterranean Sea. *Aquat Invasions* 1: 13-16
- Allen GR (2009) Field guide to marine fishes of tropical Australia. Western Australian Museum
- Arai MN (1997) A functional biology of Scyphozoa. Chapman and Hall, London
- Bayha KM, Graham WM (2011) First confirmed reports of the rhizostome jellyfish *Mastigias* (Cnidaria: Rhizostomeae) in the Atlantic basin. *Aquat Invasions* 6 (3): 361-366
- Boco SR, Metillo EB, Papa RD (2014) Abundance, size and symbionts of *Catostylus* sp. medusae (Scyphozoa, Rhizostomeae) in Panguil Bay, Northern Mindanao, Philippines. *Philippine Journal of Systematic Biology* 8: 63-81
- Brandon M, Cutress CE (1985) A new *Dondice* (opisthobranchia: Favorinidae), predator of *Cassiopea* in southwest Puerto Rico. *Bull Mar Sci* 36 (1): 139-144
- Brotz L, Schiariti A, López-Martínez J et al (2016) Jellyfish fisheries in the Americas: origin, state of the art, and perspectives on new fishing grounds. *Rev Fish Biol Fish* 27 (1): 1-29
- Browne JG, Kingsford MJ (2005) A commensal relationship between the scyphozoan medusae *Catostylus mosaicus* and the copepod *Paramacrochiron maximum*. *Mar Biol* 146: 1157-1168
- Browne JG, Pitt KA, Norman MD (2017) Temporal patterns of association between the jellyfish *Catostylus mosaicus* and a sphaeromatid isopod and parasitic anemone. *Mar Freshwater Res* A-G
- Bruce AJ (1988) *Periclimenes tonga* sp. nov., a commensal shrimp associated with a scyphozoan host from Tonga (Crustacea: Decapoda: Palaemonidae). *Micronesica* 21: 23-32
- Callaway R, Robinson L, Simon PR (2003) Methods Manual in Managing Fisheries to Conserve Groundfish and Benthic Invertebrate Species Diversity. MAFCONS Project

- Carpenter KE, Springer VG (2005) The center of the center of marine shore fish biodiversity: the Philippine Islands. *Environ Biol Fishes* 72: 467–480
- Castro J, Santiago J, Santana-Ortega A (2002) A general theory on fish aggregation to floating objects: an alternative to the meeting point hypothesis. *Rev Fish Biol Fish* 11 (3): 255–277
- Cevik, C, Derici OB, Cevik F (2011) First record of *Phyllorhiza punctata* von Lendenfeld, 1884 (Scyphozoa: Rhizostomeae: Mastigiidae) from Turkey. *Aquat Invasions* 5 (Supplement 1) S79–S84.
- Colin SP, Costello JH, Klos E (2003) In situ swimming and feeding behavior of eight co-occurring hydromedusae. *Mar Ecol Prog Ser* 253: 305–309
- D’Ambra, I, Graham WM, Carmichael RH, Hernandez FJ Jr. (2015) Fish rely on scyphozoan hosts as a primary food source: evidence from stable isotope analysis. *Mar Biol* 162: 247–252
- Dawson MN (2005a) Morphologic and molecular redescription of *Catostylus mosaicus conservativus* (Scyphozoa: Rhizostomeae: Catostylidae) from south-east Australia. *J Mar Biol Assoc UK* 85: 723–731
- Dawson MN (2005b) Morphological variation and systematics in the Scyphozoa: *Mastigias* (Rhizostomeae, Mastigiidae) – a golden unstandard? *Hydrobiologia* 537: 185–206
- Dawson MN (2005c) Five new subspecies of *Mastigias* (Scyphozoa: Rhizostomeae: Mastigiidae) from marine lakes, Palau, Micronesia. *J Mar Biol Assoc UK* 85: 679–694
- Doyle TK, Hays GC, Harrod C et al (2014) Ecological and Societal Benefits of Jellyfish. In *Jellyfish Blooms* (pp. 105–127). Springer Netherlands
- Fielder DR, Greenwood JG, Campbell G (1984) The megalopa of *Charybdis feriata* (Linnaeus) with additions to the zoeal larvae descriptions (Decapoda, Portunidae). *Crustaceana* 46 (2): 160–165
- Fréon P, Dagorn L (2000) Review of fish associative behaviour: toward a generalization of the meeting point hypothesis. *Rev Fish Biol Fish* 10: 183–207
- Fujita T, Namikawa H (2006) New observations of *Ophiocnemis marmorata* (Echinodermata: Ophiuroidea) associated with *Rhopilema esculentum* (Cnidaria: Scyphozoa: Rhizostomeae) in the Philippines and Japan. *Memoirs of the National Science Museum of Tokyo* 44: 31–37

- Galil BS, Spanier E, Ferguson WW (1990) The scyphomedusae of the Mediterranean coast of Israel, including two Lessepsian migrants new to the Mediterranean. *Zoologische Mededelingen* 64 (7): 95-105.
- Gemmell BJ, Costello JH, Colin SP, Stewart CJ, Dabiri JO, Tafti D, Priya S (2013) Passive energy recapture in jellyfish contributes to propulsive advantage over other metazoans. *Proc Natl Acad Sci USA* 110 (44): 17904-17909
- Gershwin L (2003) Scyphozoa and Cubozoa of Guam. *Micronesica* 35-36: 156-158
- Golani D, Fricke R, Appelbaum-Golani B (2011) First record of the Indo-Pacific slender ponyfish *Equulites elongatus* (Günther, 1874) (Perciformes: Leiognathidae) in the Mediterranean. *Aquat Invasions* 6 (Suppl. 1): S75-S77
- Gordon AL, Sprintall J, Field A (2011) Regional oceanography of the Philippine Archipelago. *Oceanography* 24 (1): 14-27
- Gul S, Morandini AC (2013) New records of scyphomedusae from Pakistan coast: *Catostylus perezii* and *Pelagia cf. noctiluca* (Cnidaria: Scyphozoa). *Marine Biodiversity Records* 6: e86
- Haddad MA, Nogueira Júnior M (2006) Reappearance and seasonality of *Phyllorhiza punctata* von Lendenfeld (Cnidaria, Scyphozoa, Rhizostomeae) medusae in southern Brazil. *Revista Brasileira de Zoologia* 23 (3): 824-831
- Hanaoka KI, Ohno H., Wada N, Ueno S, Goessler W et al (2001) Occurrence of organo-arsenicals in jellyfishes and their mucus. *Chemosphere* 44 (4): 743-749
- Hayashi KI, Miyake S (1968) Three caridean shrimps associated with a medusa from Tanabe Bay, Japan. *Publications of the Seto Marine Biological Laboratory* 16 (1): 11-19
- Heeger T, Piatkowski U, Möller H (1992) Predation of jellyfish by the cephalopod *Argonauta argo*. *Mar Ecol Prog Ser* Series 88: 293-296
- Heeger T (1998) Quallen. Gefährliche Schönheiten. Stuttgart, Wissenschaftliche Verlagsgesellschaft mbH, Stuttgart, Germany
- Iwatsuki Y, Kimura S (1996) First record of the carangid fish, *Alepes djedaba* (Forsskal) from Japanese waters. *Ichthyological Res* 43 (2): 182-185

- Iyengar EV (2008) Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. *Biol J Linn Soc* 93: 745–762
- Kaburaki T (1923) The polyclad turbellarians from the Philippine Islands. US Government Printing Office.
- Karplus I (2014) Symbiosis in fishes: the biology of interspecific partnerships. John Wiley and Sons. United Kingdom
- Kitamura M, Omori M (2010) Synopsis of edible jellyfishes collected from Southeast Asia, with notes on jellyfish fisheries. *Plankton and Benthos Res* 5: 106-118
- Kondo Y, Ohtsuka S, Nishikawa J, Metillo E et al (2014) Associations of fish juveniles with rhizostome jellyfishes in the Philippines, with taxonomic remarks on a commercially harvested species in Carigara Bay, Leyte Island. *Plankton and Benthos Res* 9 (1): 51–56
- Kramp PL (1961) Synopsis of the medusae of the world. *J Mar Biol Assoc UK* 40: 7-382
- Lebrato M, Pitt KA, Sweetman AK et al (2012) Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia* 690: 227–245
- Light SF (1914) Some Philippine Scyphomedusae, including two new genera, five new species, and one new variety. *Philipp J Sci* 9D: 195-231
- Light SF (1921) Further notes on Philippine scyphomedusan jellyfishes. *Philipp J Sci* 18: 25-32
- Lo CM, Morand S, Galzin R (1998) Parasite diversity\host age and size relationship in three coral-reef fishes from French Polynesia. *Int. J. Parasitol* 28: 1695–1708
- Mansueti R (1963) Symbiotic behavior between small fishes and jellyfishes, with new data on that between the stromateid, *Peprilus alepidotus*, and the Scyphomedusa, *Chrysaora quinquecirrha*. *Copeia* 1963: 40-80
- Martinelli Filho JE, Stampar SN, Morandini AC et al (2008) Cleaner shrimp (Caridea: Palaemonidae) associated with scyphozoan jellyfish. *Vie et Milieu* 58 (2): 133-140
- Masuda R, Yamashita Y, Matsuyama M (2008) Jack mackerel *Trachurus japonicas* juveniles use jellyfish for predator avoidance and as a prey collector. *Fisheries Sci* 74: 276-284

- Masuda R (2009) Ontogenetic changes in the ecological function of the association behavior between jack mackerel *Trachurus japonicus* and jellyfish. *Hydrobiologia* 616: 269–277
- Mayer AG (1910) The medusae of the world. Volume III. The scyphomedusae. Carnegie Institution of Washington publication 109 III: 499–735
- Mayer AG (1915) VII. Medusae of the Philippines and of Torres Straits – Report upon the Scyphomedusae collected by the United States Fisheries Bureau Steamer “Albatross” in the Philippine Islands and Malay Archipelago, 1907–1910, and upon medusae collected by the expedition of the Carnegie Institution of Washington to Torres Straits, Australia in 1913. Papers of the Department of Marine Biology, Carnegie Institute Washington 8: 157–202
- McCloskey L, Muscatine L, Wilkerson F (1994) Daily photosynthesis, respiration, and carbon budgets in a tropical marine jellyfish (*Mastigias* sp.). *Mar Biol* 119 (1): 13-22
- Mebs D (1994) Anemonefish symbiosis: vulnerability and resistance of fish to the toxin of the sea anemone. *Toxicon* 32 (9): 1059-1068
- Mebs D (2009) Chemical biology of the mutualistic relationships of sea anemones with fish and crustaceans. *Toxicon* 54 (8): 1071–1074
- Miller MJ (2009) Ecology of anguilliform leptocephali: remarkable transparent fish larvae of the ocean surface layer. *Aqua-BioSciences Monographs* 2 (4): 1-94
- Miller MJ, Tsukamoto K (2004) An introduction to leptocephali: biology and identification. Tokyo, Japan: Ocean Research Institute, University of Tokyo
- Mortensen T (1917) Observations on protective adaptation and habits, mainly in marine animals. In Papers from Dr. T. Mortensen's Pacific Expedition, 1914-16. *Videnskabelige meddelelser fra Dansk Naturhistorisk Forening i København* 69: 57-96
- Nagelkerken I, Pitt KA, Rutte MD et al (2016) Ocean acidification alters fish – jellyfish symbiosis. *Proc R Soc Lond [Biol]* 283: 20161146
- Nañola Jr. CL, Aliño PM, Carpenter KE (2011) Exploitation-related reef fish species richness depletion in the epicenter of marine biodiversity. *Environ Biol Fishes* 90:405–420.
- Nedosyko AM, Young JE, Edwards JW et al (2014) Searching for a toxic key to unlock the mystery of anemonefish and anemone symbiosis. *PLoS ONE* 9 (5): e98449

- Nishikawa J, Thu NT, Ha TM (2008) Jellyfish fisheries in northern Vietnam. *Plankton Benthos Res* 3 (4): 227-234
- Nogueira M, Haddad MA (2005) *Lychnorhiza lucerna* Haeckel (Scyphozoa, Rhizostomeae) and *Libinia ferreirae* Brito Capello (Decapoda, Majidae) association in southern Brazil. *Revista Brasileira de Zoologia* 22 (4): 908-912
- Ohtsuka S, Koike K, Lindsay D et al (2009) Symbionts of marine medusae and ctenophores. *Plankton Benthos Res* 4: 1-13
- Ohtsuka S, Kondo Y, Sakai Y et al (2010) *In-situ* observations of symbionts on medusae occurring in Japan, Thailand, Indonesia and Malaysia. *Bulletin of the Hiroshima University Museum* 2: 9-18.
- Ohtsuka S, Boxshall GA, Srinui K (2012) A new species of *Paramacrochiron* (Copepoda: Cyclopoida: Macrochironidae) associated with the rhizostome medusa *Rhopilema hispidum* collected from the Gulf of Thailand, with a phylogenetic analysis of the family Macrochironidae. *Zool Sci* 29 (2): 127-133
- Ohtsuka S, Kondo Y, Nishikawa J et al (2013) Symbiotic relationships among jellyfish, fish and invertebrates in Asian waters. Fourth International Jellyfish Bloom Symposium. Hiroshima, Japan
- Ohtsuka S, Metillo EB, Boxshall GA (2015) First record of association of copepods with highly venomous box jellyfish *Chironex*, with description of new species of *Paramacrochiron* (Cyclopoida: Macrochironidae). *Zool Sci* 32 (2): 195-203
- Omori M, Kitamura M (2004) Taxonomic review of three Japanese species of edible jellyfish (Scyphozoa: Rhizostomeae). *Plankton Biology and Ecology* 51: 36-51
- Omori M, Nakano E (2001) Jellyfish fisheries in southeast Asia. *Hydrobiologia* 451: 19-26
- Pagliawan HB, Metillo EB, Ohtsuka S (2015) Post-harvest and trading practices of giant jellyfish (*Lobonemoides robustus*) in Palawan, Philippines. 13th National Symposium on Marine Science, General Santos City, Philippines
- Panikkar NK, Prasad RR (1952) Interesting association of ophiuroids, fish and crab with the jellyfish *Rhopilema hispidum*. *Journal of the Bombay Natural History Society* 51: 295-296

- Peach CW (1855) Notes on the habits of medusae and small fishes. *Proc Linn Soc* 2: 280-281
- Pohnert G (2004) Chemical defense strategies of marine organisms. *The Chemistry of Pheromones and Other Semiochemicals I* 179-219
- Poore G (2004) Marine decapod crustaceans of southern Australia: A guide to identification. CSIRO Publishing, Victoria, Australia
- Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451: 27–44
- Reitzel AM, Sullivan JC, Brown BK et al (2007) Ecological and developmental dynamics of a host-parasite system involving a sea anemone and two ctenophores. *J Parasitol* 93: 1392–1402
- Rountree RA (1983) The ecology of *Stomolophus meleagris*, the cannon ball jellyfish, and its symbionts, with special emphasis on behavior. Honours Thesis, University of North Carolina
- Rózsa L, Reiczigel J, Majoros G (2000) Quantifying parasites in samples of hosts. *J Parasitol* 86: 228-232
- Sal Moyano MP, Schiariti A, Giberto DA et al (2012) The symbiotic relationship between *Lychnorhiza lucerna* (Scyphozoa, Rhizostomeae) and *Libinia spinosa* (Decapoda, Epialtidae) in the Río de la Plata (Argentina–Uruguay). *Mar Biol* 159: 1933-1941
- Sanciango JC, Carpenter KE, Etnoyer PJ, Moretzsohn F (2013) Habitat availability and heterogeneity and the Indo-Pacific warm pool as predictors of marine species richness in the tropical Indo-Pacific. *PLoS One* 8 (2) p. e56245
- Shanks AL, Graham WM (1988) Chemical defense in a scyphomedusa. *Mar Ecol Prog Ser* 45: 81-86
- Strickland JD, Parsons TR (1972) A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board of Canada* 167: 1-293
- Soria M, Dagorn L, Potin G et al (2009) First field-based experiment supporting the meeting point hypothesis for schooling in pelagic fish. *Animal Behaviour* 78 (6): 1441-1446
- Spotte S, Heard RW, Bubucis P, et al (1991) Pattern and coloration of *Periclimenes rathbunae* from the Turks and Caicos Islands, with comments on host associations in other anemone shrimps of the West Indies and Bermuda. *Gulf Res Rep* 8 (3): 301-311
- Stiasny G (1924) Rhizostomeen von Manila. *Zoologische Mededelingen* 8: 39-53

- Stiasny G (1926) Über einige Scyphomedusen von Puerto Galera, Mindoro (Philippinen). Zoologische Mededelingen 9 (12): 239-248
- Swift HF, Gomez Daglio L, Dawson MN (2016) Three routes to crypsis: Stasis, convergence, and parallelism in the *Mastigias* species complex (Scyphozoa, Rhizostomeae). Mol Phylogenet Evol 99: 103-115
- Thiel ME (1976) Wirbellose Meerestiere als Parasiten, Kommensalen oder Symbionten in oder an Scyphomedusen. Helgoländer wissenschaftliche Meeresuntersuchungen 28: 417-446
- Towanda T, Thuesen EV (2006) Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. Mar Ecol Prog Ser 315: 221-236
- Tunberg B, Reed SA (2004) Mass occurrence of the jellyfish *Stomolophus meleagris* and an associated spider crab *Libinia dubia*, Eastern Florida. *Florida Scientist* 67 (2): 93-105
- Vollrath F (1984) Kleptobiotic interactions in invertebrates. In: Barnard CJ (ed) Producers and scroungers; strategies of exploitation and parasitism. Chapman and Hall, New York, pp 61-94
- Wirtz P (1997) Crustacean symbionts of the sea anemone *Telmactis cricoides* at Madeira and the Canary Islands. J Zool 242: 799-811

Figure Captions

Fig. 1 Map of the survey stations in the Philippines. The scyphomedusae and symbionts were observed at the stations (numbers 1-7) located in the three biogeographic zones (see Nañola et al. 2011): Panguil Bay (1) and Iligan Bay (2) of the Southern Philippine Sea zone; Illana Bay (3) of the Celebes Sea zone; and Carigara Bay (4), Leyte Gulf (Marabut (5) and Guiuan (6), Samar Island) and Lipusan Bay (7) of the Visayan Region

Fig. 2 Rhizostome medusa hosts found in the embayments in the Philippines. **a** live *Acromitoides purpurus* blue morph, **b** *A. purpurus* orange morph, **c** *A. purpurus* burgundy morph, **d** subumbrellar view of burgundy *A. purpurus*, **e** stained canal system of live burgundy *A. purpurus* medusa in subumbrellar view placed on a lighted glass plate to illuminate its canal system, **f** *A. purpurus* white

morph, **g** *Phyllorhiza punctata* medusa, **h** *Mastigias* sp. medusae, **i** *Versuriga anadyomene* medusa, **j** *Rhopilema hispidum* medusa, **h** *Rhopilema hispidum* medusa (1 lappet, 2 oral arm) in the field, **i** stained canal system of live *Rhopilema hispidum* medusa. Scale bars: a-g 20 mm, h-l 60 mm

Fig. 3 Symbionts of scyphozoan medusa hosts in the Philippines. **a** shrimp scad *Alepes djedaba*, **b** crucifix crab *Charybdis feriata*, **c** ponyfish *Equulites elongatus*, **d** *C. feriata* megalopa, **e** female *Paramacrochiron* sp. copepod, **f** black *Alepes* sp., **g** turbellarian flatworm symbiont, **h** male *Paramacrochiron* sp., **i** eel larva, **j** shrimp of Family Hypollitidae. Scale bars: a-c, f, i-j 10 mm, d 0.5 mm, e, g, h 1 mm

Fig. 4 Habitat of *Mastigias* sp. medusae in Illana Bay, Zamboanga del Sur, Philippines. **a** image of a seagrass-dominated reef flat in the municipality of Dimataling, Zamboanga del Sur where the medusae of *Mastigias* sp. was observed on 18 May 2014; **b** medusa of *Mastigias* sp. with subumbrella resting on the substrate surrounded by shoots of the seagrass *Enhalus acoroides*

Table Titles

Table 1. Oceanographic values (means $\pm$ standard deviations) recorded during the surveys of jellyfish medusae in various embayments in the Philippines

Table 2. Symbiotic relationship of scyphomedusae with fish and invertebrates in the embayments in the Philippines

Table 3. Records of fish and invertebrate symbionts of jellyfish in the Philippines