Planktonic associations between medusae (classes Scyphozoa and Hydrozoa) and epifaunal crustaceans

Kaden Muffett, Corresponding Author, Maria Pia Miglietta

1 Department of Marine Biology, Texas A&M University - Galveston, Galveston, Texas, United States

Corresponding Author: Kaden Muffett
Email address: kmmuffett@tamu.edu

Jellyfish are known to carry various epibionts, including many of the subphylum Crustacea. However, the associations between gelatinous zooplankton and other invertebrates have been chronically overlooked. Crustacea, a massive clade of economically, ecologically, and culturally important species, includes many taxa that utilize gelatinous zooplankton for food, transport, and protection as both adults and juveniles. Here we compile 211 instances of epifaunal crustaceans recorded on Hydromedusae and Scyphomedusae from a century of literature. These include 78 identified crustacean species in 65 genera across nine orders found upon 37 Hydromedusa species and 48 Scyphomedusae. The crustacean life stage, location, nature of the association with the medusa, years, months, and depths are compiled to form a comprehensive view of the current state of the literature. Additionally, this review highlights areas where the current literature is lacking, particularly noting our poor understanding of the relationships between juvenile crabs of commercially valuable species and medusae.
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Kaden McKenzie Muffett¹, Maria Pia Miglietta¹

¹Department of Marine Biology, Texas A&M at Galveston, TX, USA

Corresponding author:

Kaden Muffett¹

200 Seawolf Parkway, Galveston, TX, USA, 77554

Email address: kmmuffett@tamu.edu
Abstract

Jellyfish are known to carry various epibionts, including many of the subphylum Crustacea. However, the associations between gelatinous zooplankton and other invertebrates have been chronically overlooked. Crustacea, a massive clade of economically, ecologically, and culturally important species, includes many taxa that utilize gelatinous zooplankton for food, transport, and protection as both adults and juveniles. Here we compile 211 instances of epifaunal crustaceans recorded on Hydromedusae and Scyphomedusae from a century of literature. These include 78 identified crustacean species in 65 genera across nine orders found upon 37 Hydromedusa species and 48 Scyphomedusae. The crustacean life stage, location, nature of the association with the medusa, years, months, and depths are compiled to form a comprehensive view of the current state of the literature. Additionally, this review highlights areas where the current literature is lacking, particularly noting our poor understanding of the relationships between juvenile crabs of commercially valuable species and medusae.

Background

An increased focus on ocean climate research in the past twenty years has made clear the fragility of the world's oceans and the organisms that live within them. The rate at which species are disappearing, undergoing climate-related range fluctuations, and experiencing developmental and behavioral changes is unlike anything seen in the time of record (Walther et al., 2002; Guinotte & Fabry, 2008; Comeaux, Allison & Bianchi, 2012). Attempts to model changes in populations, species, and ecosystems have laid bare the degree to which dynamics among many marine invertebrates remain unknown and poorly understood (Uye, 2008; Brodeur, Ruzicka & Steele, 2011; Henschke et al., 2014). This problem is especially apparent in jellyfish of the
phylum Cnidaria, which are chronically understudied and poorly categorized (Riascos et al., 2013; Gambill & Peck, 2014; Sweetman et al., 2016; Gómez Daglio & Dawson, 2017). Long considered a pure pest, the last decade has demonstrated an increasing number of ways in which jellyfish are critical components of the ecosystems they reside in (Cardona et al., 2012; Hays et al., 2018). While they are best known for the vertebrates that depend on them for nutrition, including turtles and birds, they provide a host of ecosystem services unrelated to a "prey" designation. Reef and non-reef fish juveniles readily congregate around large scyphozoans, some hiding within the bell or between tentacles when disturbed (Brodeur, 1998; D'Ambra et al., 2014; Tilves et al., 2018). Large jellyfish can reach sizes that allow them to support independent encrusting organisms, like barnacles and brittle stars (Ohtsuka et al., 2010; Álvarez-Tello et al., 2013; Yusa et al., 2015).

While research has expanded around services jellyfish provide (Riascos et al., 2018), much of this research focuses on benefit and harm to vertebrates (Brodeur, 1998; Cardona et al., 2012; Mir-Arguimbau, Sabatés & Tilves, 2019). However, the relationships between scyphomedusae, hydromedusae and other invertebrates are currently poorly characterized. A prime invertebrate group to analyze through this lens is Crustacea. Crustaceans are some of the most visible and well-studied marine invertebrates. They are present in every region and are integral components of food webs, including species of high commercial value and known ecological significance (Boudreau & Worm, 2012). Ecological processes that impact them are thus relevant to humans. However, studies focusing on epifaunal crustaceans and jellyfish interactions have been scarce, incomplete, and taxonomically imprecise. Moreover, such studies are often narrowly focused accounts of interactions with single individuals (Weymouth, 1910; Reddiah, 1968; Yusa et al., 2015). Some early communications discuss these interactions as
common knowledge that has, however, failed to be recorded in the scientific literature (Jachowski, 1963). This review provides a list of documented crustacean epibionts on medusae of the orders Scyphozoa and Hydrozoa. This work aims to assess the breadth and depth of jellyfish-crustacean interaction and develop a resource for further studies.

**Methodology**

Four independent sets of searches were conducted in Google Scholar using keywords, as described in Fig. 1. All four searches were conducted in early November 2019 and were revisited in January 2021 to include all results through the end of 2019. Searches were performed in English, and as such, only papers published in or with an available translation to English were included. The number of papers yielded by each of the four searches is shown in Fig. 1, ranges from 4,840 articles (for keywords Crustacea, Scyphozoa) to 13,300 (for keywords Crustacea, Jellyfish) (See Fig. 1 for details). Only papers in which the primary focus was associations between medusae (Hydrozoa and Scyphozoa) and crustaceans were further selected.

The four searches performed returned many invariable results. All titles and abstracts were checked for relevance. Results from 161 papers were obtained initially and then narrowed to 81, after excluding repeat papers mistakenly included multiple times and papers on cubomedusae, ctenophores, ascidians, and non-crustacean epibionts. Also, results from six relevant literature reviews were included (Vader, 1972; Pagès, 2000; Towanda & Thuesen, 2006; Ohtsuka et al., 2011; Schiariti et al., 2012; Wakabayashi et al., 2019). These reviews account for 40 interactions from 29 sources (Table 1). The inclusion of the literature reviews was deemed essential to include results from earlier sources and non-English sources not available on Google Scholar. Results from literature reviews that had no information on the nature of the interaction between the medusa and crustaceans (such as taxa identification, location, etc.) were eliminated.
Records were also analyzed for taxon validity using the World Register of Marine Species (WoRMS). Seven papers within the database that referred to invalid taxa with no valid synonymized name in WoRMS were removed. Results from 97 unique sources (68 articles from the Google Scholar search and 29 from literature reviews) were kept. From these 97 sources, 211 distinct interactions were extracted. Details provided by each paper were recorded in Table 1.

Results and Discussion

The final table produced by this review process includes 211 recorded interactions between hydrozoan or scyphozoan medusae and crustaceans, extracted from 97 papers (Table 1). For both cnidarians and crustaceans, order, family, genus, and species are included in Supplementary Materials. Results that lacked taxonomic identification (at least Family level) were not included. The final table (Table 1) provides sampling information, such as year and month of sampling, sampling method, and region of sampling. For crustaceans, records include the life stage involved in the interaction, sex of the epibiont, location on the hosts, and additional notes, if available. In most studies, fewer data were available on the cnidarian hosts, reducing the degree to which these interactions could be analyzed in terms of hydromedusan or scyphomedusan life stage. In the next paragraphs, we discuss the jellyfish-crustacea interactions through all of the categories included.

DIVERSITY

Diversity of scyphozoan hosts

A supermajority of records (70%, or 148/211) involves Scyphomedusae, with 53 records involving just the five most common scyphozoan species: *Lychnorhiza lucerna* (Haeckel, 1880), *Catostylus mosaicus* (Quoy & Gaimard, 1824), *Stomolophus meleagris* (Agassiz, 1860), *Cyanea*
capillata (Linnaeus, 1758) and Rhopilema hispidum (Vanhöffen, 1888). These records are heavily concentrated in the upper water column. Deeper water collections (ROV/HOV) were dominated by hydromedusae (69%, or 27/39), while records involving the upper water column (0-30 m) were more common and dominated by scyphomedusae (78%, or 83/106). Sixty-seven records included no specific sampling depth. These records were generally more than 50 years old. Although they are likely near-surface sampling records and mainly report known shallow-water species, they cannot be verified as such because of the lack of explicit information. Most of these (87%, or 58/67) are records of scyphomedusae. Overall, the diversity of scyphomedusae was low, with only 39 species from 27 genera represented in records (Fig 2a). The genus Chrysaora had the largest contingent of accounts, with 21 individual records of associations across at least seven Chrysaora species. This genus has been reported to interact with 16 different epifaunal crustaceans. The genera Chrysaora, Lychnorhiza, and Catostylus accounted for a third of scyphozoan records. These records originate mainly from the upper water levels of various locations (i.e., the east coast of the United States, the southeast of Brazil, the southern Australian coast, and the western Philippines, Japan and Pakistan).

Diversity of hydrozoan hosts

Twenty-six genera, and six Hydrozoan orders were reported interacting with Crustacea in 63 records (Fig 2b). The order Leptothecata included the greatest number of records (18), with 17 records of Siphonophorae and 12 of Narcomedusae. The diversity of Hydrozoa was significantly limited by region, with 45 of the 63 records (71%) from the Gulf of California. Additionally, those from the Gulf were acquired from primarily deep water ROV missions. The medusae recorded belonged to 28 known species, with twelve records unable to provide higher resolution than genus and a single Prayid siphonophore only identified to the family level. Rosecea
cymbiformis (Delle Chiaje, 1830) (4), Aegina citrea (Eschscholtz, 1829) (5), and Aequorea coerulescens (Brandt, 1835) (6) were the three most common species.

Diversity of crustacean epibionts

The crustaceans included Hexanauplia (reported in 37 discrete observations), Malacostraca (173), and a single representative of Branchiopoda (Evadne sp.) (Fig. 3). Recorded Hexanauplia consisted of mainly specialist groups known to be obligate epibionts and had overall low species resolution, with 13 of the 23 documented associations lacking a species name. The Macrochironidae, a group of known scyphozoan parasites, makes up 12 of the copepod epibiont records. Outside of this family, no additional Hexanauplia epibiont was recorded more than twice. The single reported case of a medusa with Evadne sp. occurred in a broad analysis of items found on a Catostylus medusae (Browne & Kingsford, 2005). As this was not replicated throughout medusae within the study, or in other studies, it is unlikely this is a common or genuine association.

The bulk of the associations involve crustaceans of the class Malacostraca. These 173 records include amphipods and decapods in equal proportion (47%, or 81/173 each), isopods (5%, or 9/173), and mysids (1%, or 2/173). The amphipods are dominated by the parasitic family Hyperidae, recorded in 32 separate encounters. Members of the family of Hyperidae are present across 22 identified scyphozoan and hydrozoan species, making them the most widely distributed family. Hyperia galba (Montagu, 1813) is present in nine records from both surface and deep-water samples, making it the single most plentiful within the amphipods. Outside of the family Hyperidae, Tryphana malmii (Boeck, 1871) is recorded six times in association with deep-sea jellyfish. Most amphipod species recorded were recorded on multiple host species.
Decapod associations (81 records) are separated among twelve families, Epialtidae (17), Portunidae (14), Palaemonidae (12), Hippolytidae (14), Scyllaridae (11) Cancridae (6), Chlorotocellidae (2), Scyllaridae (1), Luciferidae (1), Penaeidae (1), Varunidae (1), and Grapsoidea (1). No decapod was found in association with hydrozoans or in deep-sea records. The representatives of Epialtidae are comprised exclusively of multiple species of the genus Libinia. The Portunidae records are mainly composed of the commercially valuable Charybdis feriata (Linnaeus, 1758) (11 records), Charybdis annulata (Fabricius, 1798) (1) and two Callinectes, Callinectes sapidus (Rathbun, 1896) and an unidentified Callinectes specimen (1). Periclimenes paivai (Chace, 1969) is the most common Palaemonidae, representing three of the twelve records, with six additional Periclimenes species, two Ancylomenes species and one Leander paulensis (Ortmann, 1897). All Hippolytidae associations were between a specimen of Latreutes anoplonyx (Kemp, 1914) or Latreutes mucronatus (Stimpson, 1860) and one of an array of different scyphomedusae in Asia, Australia, and the Arabian Sea-Persian Gulf corridor. The families Scyllaridae and Scyllarinae include seven Ibacus, three Scyllarus, and Eduarctus martensii (Pfeffer, 1881). These associations were all exclusively larval. The majority (4) of Cancridae records involve Metacarcinus gracilis (Dana, 1952) with two unknown Cancer species. These crabs were found on Chrysaora medusae and one Phacellophora camtschatica (Brandt, 1835). Two Chlorotocella gracilis (Balss, 1914) (Chlorotocellidae) were found on Japanese rhizostomes, both in somewhat limited encounters. The last three accounts include a Cyrtograpsus affinis (Dana, 1851) (Family: Varunidae), Lucifer sp. (Family: Luciferidae), and a juvenile Grapsoidea of unknown genus and species. The account of Lucifer sp. was of a record of one specimen on a medusa in New South Wales, and is not likely a common or genuine association (Browne & Kingsford, 2005). Cyrtograpsus affinis and the juvenile of the family
Grapsoidea were also one-off reports found in single medusae (Schiariti et al. 2012; Gonçalves et al. 2016).

Associations that involved mysids or isopods were far fewer than those involving decapods and amphipods. The isopod records include only four species, including the deep-sea parasite *Anuropus* associated with *Deepstaria enigmatica* (Russell, 1967). Besides the in situ accounts of the *Deepstaria* scyphomedusae with an attached *Anuropus*, three Isopoda species were found in association with upper water column medusae. These are *Cymodoce gaimardii* (H. Milne Edwards, 1840) and *Synidotea marplatensis* (Giambiagi, 1922), each recorded three times, and *Cymothoa catarinensis* (Thatcher et al., 2003), found once in association with *Chrysaora lactea* (Eschscholtz, 1829). Within the order Mysida, the two species *Mysidopsis cathengelae* (Gleye, 1982) and *Metamysidopsis elongata* (Holmes, 1900) were recorded on *Chrysaora* during a bloom in the Southern California Bight (Martin & Kuck, 1991).

Three species of cirripeds were recorded 15 times in association with jellyfish, *Alepas pacifica* (Pilsbry, 1907) accounting for twelve of such records, *Conchoderma virgatum* (Spengler, 1789) accounting for two, and a single report of an unidentified *Anelasma* epibiont on a *Pelagia noctiluca* (Forsskål, 1775) from 1902. *Alepas pacifica* has been found on seven separate host species, all scyphozoans. The vast majority of these records came from a single literature review included within an extensive paper from Vader (1972). None of these species were found in deep-sea records.

FIELD COLLECTIONS

Only 58 papers included some explicit method of capture of the jellyfish and its epibiont (Fig 4). Between 1862 and 1962, only seven of the twenty records reported a method of capture.
From 1963 to 1989, this increased to 64%, with 25 of 39 records including the collection method. Since 1990, there have been only seven failures to report collection methods out of 140 accounts. The most common method of collection, used in 31 of the papers, is "by hand", defined as using handheld dip nets, buckets, plastic bags, and, in limited cases, collection of carcasses from beaches. Trawling was first used in 1968 and has remained in use until recently, reported in 17 of the 33 associations after 2010. Although 38 records were obtained through deep water methods (HOV and ROV), these were used scarcely before 1999. Some studies employed multiple methods, with divers and ROV, or dip net and trawl capture, such that it was unclear which associations were found by each collection method. These were listed as "multi-method" and include four papers.

The larger proportion of scyphozoan hosts to hydrozoan hosts may be a sampling artifact. The vast majority of the papers discussed here were only analyzing interactions in the top 30 m of the water column. A fair number, especially earlier texts, involve serendipitous encounters at the water’s edge or within sight of the surface (Bowman, 1963; Jachowski, 1963; Vader, 1972; Martin & Kuck, 1991). The larger, more visible nature of surface water scyphozoans of the rhizostomes and semaeostomes makes them an easier collection target than deep water species. Note that only a single scyphozoan of the order Coronatae, which has no large shallow representatives, was recorded as well. Many elements of the sampling methods impact the scope of this data, and the preeminence of hand collection and papers written on chance occurrences, as opposed to prolonged study, result in a picture that heavily weights organisms more frequently seen or interacted with by humans.

The oldest records of jellyfish-crustacean interaction involved hand collection with buckets and nets, often from shore. These include first accounts of hyperiid amphipod-jellyfish...
associations from the Chesapeake Bay (Bowman 1963). Buckets and nets have remained mainstays, with hand collection accounting for 34 of the 108 post-2000 records and 32 of the 55 pre-2000 records. Buckets and plastic bags are likely preferable to nets, as they may reduce chances of epibiont detachment and medusa damage.

Trawling (by ring nets, otter nets, and bottom trawls), while reported in twelve papers, has been a prominent capture method in South America for the last two decades. However, trawling provides an additional threat, as epibionts may detach, get caught in the bell of a medusa, or move to a different location within the carcass. Given the damage sustained by gelatinous bodies during trawls, and the inability to capture more delicate associations, this is the methodology that seems most likely to provide low-quality relationship information. A focus on a lower number of medusae examined in more detail, may provide more useful information on the ecology of the interaction between jellyfish and their epibionts. Notably, Greer et al. (2017) uses a combination of *in situ* imaging (with an automatic ISHIS imaging system) and trawls. Trawls were used to verify the identity of organisms seen in the captured images. Such a protocol should be considered for future quantitative and qualitative work.

66% of the records (136/211) are from known surface encounters. 18% of the records (38/211) involve deep water accounts using either an ROV/HOV. These records are distributed unevenly across depths with few records below the mesopelagic zone (Fig 5). Most of these records fail to provide epibiont location on the jellyfish but provide the only available information on deep water scyphomedusa and hydromedusa hosts. Most of the deep water records are from the Gulf of California. While this sampling method is useful, the high cost and difficulty of use of ROV and HOV equipment make it unrealistic for the vast majority of researchers. The limited number of deep-water accounts and the novelty of many of the findings
on each dive can be attributed mainly to these limitations (Gasca and Haddock, 2004; Gasca et al., 2007; Gasca et al., 2015).

Given the fragility of scyphozoan and hydrozoan medusae, as well as the delicacy of the interaction with their epibionts, the most precise picture of the jellyfish-crustacean associations has been achieved from dip net, plastic bag, bucket, or other by-hand collection methods. These are not only a cost-effective strategy requiring little additional equipment, they also maintain maximum integrity of the organisms. Hand collection, however, is restricted to analyzing associations that are close to the surface. Trawl sampling provides a reliable way to collect many medusae offshore but sacrifices sample integrity. ROV is an imperfect sampling method, often failing to record epibiont positioning, but allows for the only viewing, documentation, and collection of deep water associations, thereby being uniquely important, especially for hydromedusa research. Moreover, the majority of the records document all symbionts on the target host species, often with little data beyond a name or tentative classification for the epibiont. This lack of closer examination leads to an inability to correctly categorize the nature of the relationship, including positioning, feeding behaviors, and duration of the interaction.

In conclusion, the overall best sampling results come from observation-first methodologies such as collection by-hand while snorkeling and diving, as in Mazda et al. (2019), ROV/HOV in situ underwater photography, as employed by Gasca et al. (2015), or imaging and supplemental trawling as in Greer et al. (2017). Obtaining underwater pictures of medusae and epibiont is crucial to the understanding of the associate placement in relation to host and its behavior. It is also more informative than post hoc in-lab examinations and analysis of trawl contents, because the stress of collection and sampling may impact the epibiont position within the host (Hayashi et al. 2004). As waterproof video equipment becomes less expensive, options
like a simple GoPro may provide clear enough imaging to allow novel *in situ* observations.

Adding an underwater imaging component to sampling may also enable collectors to revisit the ecological context of the association.

**LIFE STAGES**

Age classes and sex, where available, are reported in Table 1. 63% of all records (133/211) reported an age class for the crustacean. 65% of the interactions with a listed age class (65%, or 86/133) reported crustacean juveniles, eggs, larval stages, copepodites, megalopae, or other immature forms. For a minority of records (37%, or 73/211), no information on the crustaceans' age class and sex was available. When individuals were described as "male" or "female" without any qualifier attached, they were catalogued and treated as adult specimens (Table 1). Megalopae were noted only nine times out of the 106 records that reported an age class for the crustacean associate (8%). In these nine records, the megalopae belonged to the genera *Callinectes, Periclimenes, Metacarcinus, Cancer,* and *Charybdis,* and were all in association with Scyphomedusae (Orders: Rhizostomeae and Semaeostomeae). In addition to megalopae, phyllosoma larvae of the families Scyllaridae and Scyllarinae were reported 12 times. The occurrence of larvae of this type associated with medusae and, more generally, with gelatinous zooplankton is well known, especially along the Japanese coast (Wakabayashi et al., 2019). Within and upon the host, juvenile crustaceans were often coexisting with adult forms.

Eighty-one of the associations include juveniles (excluding megalopae, eggs, and copepodites), sometimes embedded in host tissue (Theusen, 2006; Browne, 2015; Towanda & Yusa et al., 2015; Browne et al., 2017; Mazda et al., 2019). The presence of eggs and ovigerous females was reported in 39 cases from 23 different species. In at least three papers, females and ovigerous females were present in exceptionally high proportions relative to adult males (Martinelli-Filho
et al., 2008; Oliva et al., 2010; Mazda et al., 2019). Records of megalopae of the commercial crab, Charybdis feriata were reported in substantial numbers on two separate hosts (Kondo et al., 2014; Boco & Metillo, 2018). In other reports, associations between juvenile Metacarcinus gracilis (Dana, 1852) and medusae are hypothesized to be beneficial to the crab as the medusae supply means of transport and food acquisition, which may be similar across juvenile decapod-scyphozoan associations (Towanda & Thuesen, 2006).

NATURE OF ASSOCIATIONS BETWEEN MEDUSAE AND CRUSTACEANS

There is no agreement between authors on the degree to which medusae and crustaceans' interactions are parasitic, commensal, or otherwise. In the case of the scyphozoan Phacellophora camtschatica and the decapod Metacarcinus gracilis (Dana, 1852), the interaction may involve a mutualistic cleaning relationship as M. gracilis graduates into adulthood (Towanda & Thuesen, 2006). Other reports of megolopae do not suggest any parasitization of the medusae. Weymouth (1910) also indicates that this is a commensal relationship important to M. gracilis megalopae until they reach ~20mm. In other cases, such as the shrimp Perimincles paivai, the commensals seemed to be feeding on the mucus, not the host tissue (Browne & Kingsford, 2005; Martinelli-Filho et al., 2008). Dittrich (1988) demonstrates an aggressive parasitoidism by Hyperia galba in which a large subset of host medusae was so reduced by predation as to lose almost all morphological features. While the ultimate death of these hosts is not recorded within the text, the loss of all tentacular structure and non-mesoglear tissue would make survival nearly impossible. The numbers in which Hyperia can be found on some of the recorded medusae, occasionally upwards of 100 amphipods engaging in host consumption, may lend credence to the parasitoid rather than classically parasitic nature of this relationship in many hosts (Vader, 1972; Dittrich, 1988; Towanda & Thuesen, 2006). However, additional reports on the same species and
other hyperiids reported that this group engages in cradle positioning, facing outwards from the medusa, into the water column with no reported predation, or engage in only limited predation of the gonadal tissue or mesogleal tissue (Bowman et al., 1963; Gasca et al., 2005; Browne, 2015).

Based on this information it seems likely that the family Hyperidae includes a variety of strategies, and the family Hyperia itself may also encompass non-aggressive parasitism, aggressive parasitism, and parasitoidism. In part, this may be due to temporal behavioral differences within species, with more extreme predation in summer and autumn and limited parasitism in spring as populations raise and fall (Bowman, 1963; Dittrich, 1988). "Inverted cradle" positioning is a recurring feature of amphipod associates (Bowman et al., 1963; Condon & Norman, 1999). While some of the crustaceans fed on the medusae themselves, Towanda and Thuesen (2006) primarily recorded crustaceans engaging in theft of prey collected by medusae. Many crustaceans that were reported feeding on the medusae were feeding entirely or in part on the highly regenerative gonadal tissue (Pagès, 2000; Towanda & Thuesen, 2006; Ohtsuka et al., 2009) or engaging in the excavation of small pits in the host mesoglea (Humes, 1953; Jachowski, 1963; Browne, 2015). Reports of Libinia dubia (H. Milne Edwards, 1834) have the greatest agreement on the parasitic nature of the species’ interactions with their medusa host (Jachowski, 1963; Phillips et al., 1969; Schiariti et al., 2012).

The largest exception to the above patterns of limited consumption or longer term residence is the scholarship surrounding phyllosoma larvae on gelatinous zooplankton. These larvae have been reported to stab a pair of pereiopods through the exumbrella or exterior of a nectophore and use the medusa as propulsion and food source. This is a common occurrence both in the northern Gulf of Mexico and at various locations along the Japanese coast (Greer et al., 2017; Wakabayashi et al., 2019). In the review on the subject by Wakabayashi et al. (2019),
it is hypothesized that the flattened body and ventral mouth of these phyllosoma larvae is ideal for consumption of gelatinous zooplankton while attached. The exact length of this parasitoid association is unknown, though it is likely generally ended by the medusa’s eventual death as the larva eats its way through.

The degree to which crustaceans engage in host consumption may be in part obscured by the speed with which medusae regenerate tissues, especially gonadal and oral arm tissues (Towanda & Thuesen, 2006). The number of associates (at least eight crustacean species) found residing within the bell and around the gonads, suggests that gonadal tissue may be common nourishment even when bell and arm tissue is not consumed. Overall, the relationships of crustaceans with their medusa hosts remain largely uncharacterized and require additional study. Few papers have analyzed the gut contents of the epibionts, which would be a helpful tool in determining whether inverted positioning on hosts was actually a signal of lack of consumption, or simply a break from such (Vader, 1972; Pagès, 2000; Towanda & Thuesen, 2006; Oliva et al., 2010; ). Detailed records of the diets of such organisms are difficult to reconstruct. However, specific searches for nematocysts in digestive tract and excretions or stable isotope analysis have proven successful at identifying cnidomedusae as possible food sources (Schiariti et al., 2012; Fleming et al., 2014). Expanding future works to include both these practices, photographs of the host medusae, and notes on swimming strength, tentacular loss and other signs of deterioration would improve our understanding of how detrimental these relationships actually are. This sort of documentation of host condition is impossible when specimens are collected via trawl.

In addition to consumption, the issue of host choice and host specificity has been analyzed only sparsely. There is evidence in multiple studies that while some individual jellyfish host symbionts, others in the same area lack them due to their size or species (Towanda &
Theusen, 2006; Ohtsuka et al., 2011; Boco and Metillo, 2018). While exotic species often have lower amounts of parasitization in their introduced range (Torchin et al., 2003), the degree to which epibionts in medusae are affected by host or epibiont endemicity is unknown. The high number of cryptic species, a history of misidentification, and poor understandings of historical ranges compound issues with sparse research on the topic (Dawson, 2005; Graham & Bayha, 2008; Morandini et al., 2017; De Souza & Dawson, 2018).

Only one study provides an indication of how nuanced the relationship between gelatinous zooplankton hosts and epibionts may be; six years of monthly observation showed that single adult females of the amphipod *Oxycephallus clausi* (Bovallius, 1887) had a broad range of gelatinous hosts, but shifted to primarily *Ocyropsis fusca* (Rang, 1827), a lobate ctenophore, during brood release (Mazda et al., 2019). While ctenophores are not the focus of this review, it shows that the nature of interactions may change during the crustacean lifecycle. These sorts of long-term analyses are hard to pursue, but provide a fascinating look at the range of information that can be collected with observational methods. Uneven sex ratios, such as those seen in the case of *Oxycephallus clausi* (97% female), are present across many associations (Condon & Norman, 1999; Martinelli-Filho et al. 2005; Oliva et al., 2010; Mazda et al., 2019). The most common explanation for this higher ratio of females and often ovigerous females is use of scyphozoan and hydrozoan hosts primarily as nursery habitat for movement and protection of juveniles (Gonçalves et al., 2016; Gonçalves et al., 2017; Mazda et al., 2019). Potential territoriality in some females, like those of *P. paivai*, may help ensure more resources for their brood, and is in line with other symbiont crustaceans (Baeza et al., 2017). For deep sea crustaceans, such as *Pseudolubbockia dilatata* (Sars, 1909), more even sex ratios would be expected, as there is evidence of long-term resident brooding pairs, and mate scarcity is a feature
of deep sea life. Evidence for long-term association and pairing has not been found for other
deep water crustaceans, although understanding these deep sea interactions is generally
hampered but small sample sizes and difficulty of observation (Gasca et al., 2007; Baeza et al.,
2017; Gasca et al., 2018).

YEARS AND LOCATIONS

The oldest records examined were only available from earlier literature reviews (Pagès,
2000; Towanda & Thuesen, 2006; Schiariti et al., 2012). The first record is the Bate (1857)
account of the amphipod *Iphimedia eblanae* on the scyphozoan *Rhizostoma pulmo* (Macri, 1778)
from 1862, also reported in the Vader (1972) review on amphipod associations with medusae.
Thiel (1976) refers to older records from as far back as 1791. Overall, the number of records
detailing interactions has risen over time but has not exceeded ten papers during any five years.
While these numbers are increasing modestly, the number of distinct interactions that any given
paper reports have increased. Pre-1990s articles, on average put forward information on 1.24
associations per paper. In contrast, the average number of associations reported in papers
published from 1990 to 2018 increased more than twofold (an average of 2.83 records per
paper). These surveys provide useful records of separate associations found in one area or on one
organism and are informative of ecosystem features on a regional level. Still, given the studies'
breadth, they often lack depth, not characterizing relationships between individual host species
and their associates.

Records were unevenly distributed globally, with Africa and Europe completely devoid
of records from the past thirty years with the exception of a single note on an accidental
observation from Gran Canaria, Spain. The eastern coast of North America (one record since
1984 (Tunberg & Reed, 2004) and China (no direct records), as well as West Africa (one record
from 1972 (Bruce, 1972)) and the Mediterranean Sea (last collections 1985 (Dittrich, 1988) also lack records from the last 30 years. The areas consistently covered by recent papers are Australia (1968-2009), the Philippines (2014, 2018), the eastern coast of South America (1980-2016), and the western United States (1966-2015). Japanese records represent the longest continuity over time, with 33 records between 1902 and 2019. The association that consistently appears throughout time is that of *Alepas pacifica* (Thoracica, Lepadiformes) with Nomura's Jellyfish (*Nemopilema nomurai*) (Pagès, 2000; Yusa et al., 2015). The first record of this association was in 1902 (Pagès, 2000), and the most recent in 2015 (Yusa et al., 2015). Phyllosoma larvae of multiple species, *Chlorotocella gracilis* (Balss, 1914), and *Latreutes* spp. also have records spanning multiple decades and papers.

It is worth mentioning that the uneven geographic distribution of associations reported herein may be an artifact of lack of readily available English translations of works from some areas. Reports from Japan and China of crustacean and gelatinous zooplankton associations are mentioned by Hayashi et al. (2004) and Wakabayashi et al. (2019), but were not available in English and therefore are not accounted for in this review. Similarly, European records may be underestimated, as non-English records are absent. Other locations’ lack of records may be a more accurate representation of a gap in academic knowledge. Africa’s west and eastern coasts are known to be understudied ecosystems, and so the missing research here is likely not just untranslated (Berkström et al., 2019). As in other ecological inquiries, the expansion of Local Ecological Knowledge into the study of gelatinous zooplankton should be considered, as fishermen and coastal communities often have a deep knowledge of organisms and their associations (Berkström et al., 2019). Fishermen are often well acquainted with specific
gelatinous zooplankton species and know their harms, and may have knowledge of symbionts living upon or within them (Al-Rubiay et al., 2009).

COMMERCIAL SPECIES

Many commercial crustaceans and jellyfish were found to have associations that may be of ecological and commercial importance. Twelve records reported the edible jellyfish *Rhopilema* spp. as hosts (Berggren, 1994; Pagès, 2000; Hayashi et al., 2004; Towanda & Theusen, 2006; Ohtsuka et al., 2010; Ohtsuka et al., 2012; Boco & Metillo, 2018). The commercially harvested shrimp, *Penaeus stylirostris* (Stimpson, 1871), was found on *Stomolophus meleangris* (Riascos et al., 2018). Notably, young *Callinectes sapidus*, the Chesapeake Blue Crab, was reported by Jachowski (1963) as regularly found on *Chrysaora quinquecirrha* (Desor, 1848) medusae without consuming them. This association was reported again briefly in the Mississippi Sound by Phillips et al. (1969). This interaction between a jellyfish and the blue crab has never been corroborated further except for a nonspecific report of a *Callinectes* sp. associated with jellyfish reported by Towanda et al. (2006) as unpublished data. The commercially valuable crab, *Charybdis feriata*, has been reported in association with ten jellyfish species (Berggren, 1994; Towanda & Thuesen, 2006; Ohtsuka et al., 2010; Schiariti et al., 2012; Boco et al., 2014; Boco & Metillo, 2018). These reports involve juveniles (Trott, 1972; Towanda & Thuesen, 2006; Schiariti et al., 2012; Kondo et al., 2014; Boco & Metillo, 2018) and megalopae (Kondo et al., 2014; Boco & Metillo, 2018) of *C. feriata*, and this association has been recorded in Hong Kong, Japan, the Philippines, Mozambique, and Indonesia, suggesting a consistent pattern over time (first record in 1965 (Schiariti et al., 2012) and last record in 2014 (Boco & Metillo, 2018)) and across their range.
Slipper lobster larvae of the genera *Scyllarus* and *Ibacus* have been reported many times across various hosts (Wakabayashi et al., 2019). Some slipper lobsters are commercially fished for consumption, and a large number of these larvae (40% in the Gulf of Mexico) have been shown to live attached to gelatinous zooplankton (Greer et al. 2017).

The consumption of some Scyphozoan hosts, such as *Catostylus mosaicus* and *Rhopilema* spp., makes their records valuable as well. The fishing pressures on the jellyfish populations may significantly impact the crustaceans that rely on their oral arms and bells for transport and nourishment of their juvenile stages. Further understanding of these relationships may be especially important in cases where both the medusae (e.g., *Rhopilema* spp., *Lobonemoides robustus* (Stiasny, 1920) and *Catostylus* spp.) and crustacean (*Charybdis feriata*) are subject to fishing (Boco et al., 2014; Boco & Metillo, 2018, Kondo et al., 2014). Finally, current information on *Callinectes sapidus* and its relationship to and frequency of interaction with host jellyfish is needed, as the blue crab represents a commercially valuable fishery in the Gulf of Mexico and along the Atlantic Coast of the USA.

Understanding the nature of the relationships between economically valuable species of Crustacea and common scyphozoans and hydrozoans can improve fisheries practices and regulation, as already acknowledged for economically important fish and their jellyfish hosts (Tilves et al., 2018). The importance of maintaining juvenile communities for commercially sized adult populations to recruit from is well established and a frequent impetus for marine protection areas. The fishing of medusae is different from most modern vertebrate fishing. It is temporally highly variable, and blooms, when found, are fished as intensely as possible by local fishermen. It is also comparatively new as an export industry, especially in Southeast Asia (Omori & Nakano, 2001). Additional regulation and management should be considered for
jellyfish species known to harbor juveniles of commercially viable crustaceans. It is clear that
many crustaceans, fish, and other organisms live in, upon and around medusae, thus
indiscriminate efforts to remove or destroy blooms of endemic species are likely unwise (Tilves 
et al., 2018; Riascos et al., 2018).

Conclusion

Many of the interactions we reviewed are fragmented and not comprehensive. Studies
covering timing and breadth of infection of commercially valuable crustaceans on marine
scyphozoans are scarce, but may be valuable information to fully understand the complexity of
their life cycle, and thus the species' vulnerability at each life cycle stage. The general picture of
the commensal relationships that arise from this review is complex and emphasizes the diversity
of jellyfish and crustaceans' relationships. Any attempt to paint them as uniformly parasitic fails
to acknowledge the diversity of crustacean host-use strategies. While some seem to be parasitic
or parasitoid, others are life-stage dependent commensals reliant on medusae for transportation.
Some deep water crustaceans may be lifelong commensals (Gasca et al., 2007). In each of these
cases, the work thus far is far from exhaustive. Additional research on seasonality, maternal care,
territoriality, impact on host and other such matters should be further pursued.

The scyphozoans and hydrozoans studied here represent only a small proportion of the
globally recognized species. Even shallow water coastal species are poorly covered. This
research has been restricted to a small selection of near-shore sites over the past 50 years, leaving
inadequate coverage even in regions with a significant scyphozoan research presence (i.e., the
Mediterranean, western Europe, China, northeastern North America). Because much of the
published research focused on single occurrences, this paper's overall results do not necessarily
capture the broader ecology of the species involved (Bowman, 1963; Jachowski, 1963; Suzuki,
Similarly, species descriptions that mention an association without details on the conditions in which it was found offer little insight on the frequency and ecological role of such interactions (Humes, 1953; Reddiah, 1968; Bruce, 1972; Criales, 1984; Bruce, 1988; Bruce, 1995; Bruce, 2005).

Best practices moving forward should include some of the following elements: *in situ* imaging pre-collection, observations on medusa health, analysis of epibiont gut contents when possible, preferential use of non-destructive collection methods, observations on symbiont placement within or upon the medusa, and frequency, geographical and temporal variation of the association.

With this review, we hope to highlight a significant knowledge gap and a lack of formal study on the ecology of the crustaceans residing on and around jellyfish, as well as a glimpse of the ecological complexity of these interactions. We provide easy access to a century of ecological research and a framework for analyzing and contextualizing future research on this topic.

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Figure 1

Summary of Google Search Results

The number of results reported by Google Scholar Advanced Search where both “Crustacea” and one of the four medusa describer terms was included (“Hydrozoa”, “Scyphozoa”, “medusa”, or “jellyfish”) and at least one of the following terms was included (Association, Associated, Symbiotic, Symbiosis, Commensal, Epifaunal, Harboring, Parasitic, Parasitoid, Epibiont or Epibiotic).

| Medusa Describer | Results |
|------------------|---------|
| Jellyfish, Crustacea | 13,300 |
| Medusa, Crustacea | 5,080 |
| Scyphozoa, Crustacea | 4,840 |
| Hydrozoa, Crustacea | 11,500 |
Figure 2

Diversity of Scyphozoa and Hydrozoa species

Rings from innermost to outermost are order, family, genus in the classes (A) Scyphozoa and (B) Hydrozoa as distributed by number of accounts including a host in that group. Families and genera with single reports are whitened.
Figure 3

Diversity of Crustacean epibionts

From innermost ring to outermost ring: Subphylum, Order, Family, Genus. Color coded by classes Malacostraca (orange), Hexanauplia (pink), and Brachipoda (green). Families and genera reported only once are whitened.
Figure 4

Collections information for both number of papers using a collection method and number of associations reported from this collection type

Types are blue water diving (BWD), collection by hand (HC), multiple methods (MULTI), ring net (RN), scuba diving (SC), trawling (TR), in situ observation (OBS) or unknown (Unknown). Associations from papers in which multiple methods were used, but specific methods are known for each association are categorized under the known method. Many papers are comprised of multiple associations, as such, the "Individual" columns include each association separately, "Paper" columns report by paper.
Figure 5

Percent of sampling by depth

The depths of samples with known depths. 68% of samplings had known depth data (pie chart). 74.4% of sampling was done above 30m. Where depth ranges were given (i.e. 8 to 30 meters) the deeper value was used.
Table 1 (on next page)

Associations Reported Organized By Host

Every association in all reviewed papers with details on species and higher order classification of host, species of associate, sex and life stage of associate, notes on association, location on host, location association was recorded, date of record, depth of association and literature source.
| Host Species | Epibiont                | Notes                                                                 | Life Stage and Sex | Location on Medusa | Collection                | Limited | Month/Year | Depth | Reference               |
|--------------|-------------------------|------------------------------------------------------------------------|--------------------|---------------------|---------------------------|---------|------------|-------|-------------------------|
| **Scyphozoa**|                         |                                                                        |                    |                     |                           |         |            |       |                         |
| **Coronatae**|                         |                                                                        |                    |                     |                           |         |            |       |                         |
| *Nausithoe rubra* Vanhöffen, 1902 | *Prohpyeria shihi* Gasca, 2005 | Not visibly parasitizing host, female and male pair | F, M               | EX                  | Gulf of California        | ROV     | L          | 2012 Feb | 907 m | Gasca, 2013             |
| **Rhizostomeae**|                         |                                                                        |                    |                     |                           |         |            |       |                         |
| *Acromitoides purpurus* Mayer, 1910 | *Charybdis feriata* Linnaeus, 1758 | Never more than one per medusa | ?                  | ?                   | Various bays, Philippines | HC      | N          | 2014-2015, Feb-Apr | NS      | Boco & Metillo, 2018    |
| *Acromitoides purpurus* Mayer, 1910 | *Paramacrochiron* sp. | Present 44-100% of medusae depending on location and medusa color morph | ?                  | ?                   | Various bays, Philippines | HC      | N          | 2014-2015, Feb-Apr | NS      | Boco & Metillo, 2018    |
| *Acromitus flagellatus* Maas, 1903 | *Latreutes anoplonyx* Kemp, 1914 | Present throughout the adult medusa population | ?                  | SUM, O              | Chilka Lake, India        | ?       | L          | ?      | ?                      | Hayashi, 2004 |
| *Acromitus sp.* | *Horstionus pusilla* K.H. Barnard, 1916 | Present throughout the adult medusa population | ?                  | ?                   | ?                         | ?       | ?          |       | ?                      | Chilton, 1921 via Vader, 1972 |
| *Cassiopea sp.* | *Ancylomenes aqabai* Bruce, 2008 | Present throughout the adult medusa population | ?                  | OF & O              | Aqaba, Jordan            | L       | 1976 Mar  | NS      | Bruce, 2008            |
| *Cassiopea sp.* | *Ancylomenes holthuisi* Bruce, 1969 | Present throughout the adult medusa population | ?                  | O                   | Zanzibar harbour         | SC      | L          | 1970 Dec | 20-25 m | Bruce, 1972            |
| *Cassiopea sp.* | *Periclimenes pedersoni* Chace, 1958 | Present throughout the adult medusa population | ?                  | OF & M              | Santa Marta, Colombia     | ?       | N          | 3-40 m  | Criales, 1984          |

**Key:**

- **Life Stage and Sex:**
  - **F**: Female
  - **M**: Male
  - **MG**: Megalopa
  - **A**: Adult
  - **E**: Egg
  - **J**: Juvenile
  - **OF**: Ovigerous female
  - **C**: Copepod/Copepodite
  - **I**: Instar
  - **PL**: Phyllosoma larva

- **Location on Medusa:**
  - **EX**: Exumbrella
  - **SUM**: Subumbrella
  - **O**: Oral arms
  - **B**: Bell (undifferentiated)
  - **GVC**: Gastrovascular cavity
  - **SG**: Subgenital pit
  - **MA**: Umbrellar margin
  - **T**: Tentacles

- **Collection:**
  - **HC**: Hand collection (Nets, buckets, bags, etc.)
  - **SC**: Scuba and Blue Water Diving
  - **ROV**: Remote and Human Operated Vehicles
  - **TR**: Boat trawls
  - **MULTI**: Multiple methods used
  - **OBS**: Observational methods with imaging

- **Limited Observations:**
  - **L**: 5 or fewer occurrences catalogued
  - **N**: >5 medusae with this epibiont

- **Depth:**
  - **NS**: Near surface
  - **All**: Data missing

- **Reference:**

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Table 1: Associations Reported Organized By Host
| Cassiopea sp. | Periclimenes tonga | N/A | OF | ? | N/A | ? | L | 1985 Jul | ? | Bruce, 1988 |
| Cassiopea sp. | Periclimenes yucatanicus | N/A | OF & OF & OF | O | N/A | ? | N | ? | 3-25 m | Criales, 1984 |
| Cassiopea sp. | Sewellorschon fidens | N/A | F, M | ? | N/A | ? | N | ? | 1959 | 3 m | Humes, 1969 |
| Cassiopea sp. | Acartia sp. | N/A | C & A | O | N/A | ? | N | ? | 1999-2000 | NS | Browne & Kingsford, 2005 |
| Catostylus mosaicus Quoy & Gaimard, 1824 | Cymodoce gaimardii H. Milne Edwards, 1840 | Autumnal prevalence peak | ? | O, SUM, EX | HC | N | 2009 Aug - 2010 Sep | NS | Browne, 2015 |
| Catostylus mosaicus Quoy & Gaimard, 1824 | Cymodoce gaimardii H. Milne Edwards, 1840 | Highest prevalence in Mar | A & J | B, O | Port Phillip Bay, Victoria | HC | N | 2008 Aug - 2010 Sep | NS | Browne et al., 2017 |
| Catostylus mosaicus Quoy & Gaimard, 1824 | Eudane sp. | Only one specimen | ? | O | Port Phillip Bay, Victoria | HC | L | 1999-2000 | NS | Browne & Kingsford, 2005 |
| Catostylus mosaicus Quoy & Gaimard, 1824 | Hyperia gaudichaudii H. Milne Edwards, 1840 | September prevalence peak, Es and Js embedded in host tissue | E & J | GVC, B & A | Port Phillip Bay, Victoria | HC | N | 2008 Aug - 2010 Sep | NS | Browne, 2015 |
| Catostylus mosaicus Quoy & Gaimard, 1824 | Ibacus sp. | A single specimen from Sydney museum collection | PL | SUB | Hawkesbury River, New South Wales | ? | L | 1925 | ? | Thomas, 1963 |
| Catostylus mosaicus Quoy & Gaimard, 1824 | Latreutes anaplonyx Kemp, 1914 | Found on medusa type specimen from Pakistan | OF & J | O | Port Phillip Bay, Lake Illawarra, New South Wales | HC | L | 1995 | NS | Tahera & Kazmi, 2006 |
| Catostylus mosaicus Quoy & Gaimard, 1824 | Lucifer sp. | Only present on two medusae in one lake | ? | O | Lake Illawarra, New South Wales | HC | L | 1999-2000 | NS | Browne & Kingsford, 2005 |
| Catostylus mosaicus Quoy & Gaimard, 1824 | Oncaea venusta Philippi, 1843 | N/A | ? | O | Port Phillip Bay, Lake Illawarra, New South Wales | HC | L | 1999-2000 | NS | Browne & Kingsford, 2005 |
**Catostylus mosaicus** Quoy & Gaimard, 1824

- **Paramacrochiron maximum** Thompson I.C. & Scott A., 1903
  - Present in hundreds per medusa at all phases of development and size class
  - A & J & OF
  - Botany Bay, Lake Illawarra, New South Wales
  - HC
  - N
  - 1999-2000
  - NS
  - Browne & Kingsford, 2005

- **Pseudodiaptomus sp.**
  - N/A
  - A
  - O
  - Botany Bay, Lake Illawarra, New South Wales
  - HC
  - N
  - 1999-2000
  - NS
  - Browne & Kingsford, 2005

- **Temora sp.**
  - N/A
  - A
  - O
  - Botany Bay, Lake Illawarra, Smiths Lake, New South Wales
  - HC
  - N
  - 1999-2000
  - NS
  - Browne & Kingsford, 2005

- **Tortanus barbatus** Brady, 1883
  - N/A
  - C & A
  - O
  - Botany Bay, Lake Illawarra, New South Wales
  - HC
  - N
  - 1999-2000
  - NS
  - Browne & Kingsford, 2005

- **Catostylus sp.**
  - **Charybdis feriata** Linnaeus, 1758
    - Present from Apr-May
    - ?
    - O, SUM
    - Kolambugan, Lanao del Norte
    - ?
    - N
    - 2013 Dec - 2014 Jul
    - NS
    - Boco et al., 2014

- **Catostylus sp.**
  - **Paramacrochiron sp.**
    - Present from Jan-Mar
    - ?
    - O, SUM
    - Kolambugan, Lanao del Norte
    - HC
    - N
    - 2013 Dec - 2015 Jul
    - NS
    - Boco et al., 2014

- **Cephea cephea** Forskål, 1775
  - **Alepas pacifica** Pilsbry, 1907
    - Barnacles 44 mm wide present on umbrella and oral arms. Additional details absent.
    - ?
    - B, O
    - Japanese Coast
    - ?
    - ?
    - ?
    - ?
    - HIro, 1937 via Pagès, 2000

- **Lobonemoides robustus** Stiasny, 1920
  - **Charybdis feriata** Linnaeus, 1758
    - Present in Gulf of Thailand from July to October as well
    - MG, J
    - ?
    - Carigara Bay, Leyte Island
    - HC
    - L
    - 2013 23 August
    - NS
    - Kondo et al., 2014

- **Lychnorhiza lucerna** Haeckel, 1880
  - **Cyrtoograpsus affinis** Dana, 1851
    - N/A
    - A
    - SG
    - Rio de la Plata Estuary
    - TR
    - N
    - 2006 Mar
    - ?
    - Schiariti et al., 2012

- **Grapsoidae gn sp.**
  - N/A
  - J
  - ?
  - Cananéia, Brazil
  - TR
  - L
  - 2013 Feb-2014 May
  - 5-15m
  - Gonçalves et al., 2016

- **Lychnorhiza lucerna** Haeckel, 1880
  - **Leander paulensis** Ortmann, 1897
    - N/A
    - M
    - ?
    - Cananéia, Brazil
    - TR
    - L
    - 2013-2014
    - 5-15m
    - Gonçalves et al., 2016

  - **Lobinthus dubia de Brito Capello, 1871**
    - N/A
    - M, F, OF, J
    - O, SUB, B
    - Cananéia, Brazil
    - TR
    - N
    - 2012 Jul
    - 5-15 m
    - Gonçalves et al., 2017
| Species                        | Common Name                          | Collector(s) | City, State | Start Year-End Year | Duration | Location    | Reference                  |
|-------------------------------|---------------------------------------|--------------|-------------|---------------------|----------|-------------|----------------------------|
| Lychnorhiza lucerna          |                                      |              |             | 2013-2014           | 5-15 m   | Rio de Janeiro, Macaé | Gonçalves et al., 2016     |
| Libinia ferreirae de Brito    |                                      | N/A          | F, M, J     | ?                   |          |             |                            |
| Capello, 1871                 |                                      |              |             | Cananéia and       | TR       | N           |                            |
|                              |                                      |              |             | state, Macaé       |          |             |                            |
| Libinia ferreirae de Brito    |                                      | N/A          | ? SUM, O    | Maranhão state      | HC       | N           | Lopes et al., 2008         |
| Capello, 1871                 |                                      |              |             |                     |          |             |                            |
| Libinia spinosa Guérin,       |                                      | N/A          | F           | Ubatuba             | TR       | N           | Gonçalves et al., 2016     |
| 1832                         |                                      |              |             |                     |          |             |                            |
| Libinia spinosa Guérin,       |                                      | N/A          | ?           | Rio del Plata       | MULTI    | N           | Schiariti et al., 2012     |
| 1832                         |                                      |              |             |                     |          |             |                            |
| Libinia spinosa Guérin,       |                                      | N/A          | ?           | Punta del Este      | ?        | ?           | Vaz-Ferreira, 1972 via     |
| 1832                         |                                      |              |             |                     |          |             | Schiariti et al., 2012     |
| Periclimenes paivai          |                                      | N/A          | ? SUM, O    | Mar Chiquita Estuary| ?        | L           | Zamponi, 2002 via         |
| Chace, 1969                   |                                      |              |             |                     |          |             | Schiariti et al., 2012     |
|                              |                                      |              |             | Paráiba River estuary| HC       | N           | Baeza et al., 2017         |
|                              |                                      |              |             |                     |          |             |                            |
|                              |                                      |              |             | Sao Paolo           | TR       | N           | de Moraes et al., 2017     |
|                              |                                      |              |             |                     |          |             |                            |
|                              |                                      |              |             | Cananéia            | TR       | N           | Gonçalves et al., 2016     |
|                              |                                      |              |             |                     |          |             |                            |
|                              |                                      |              |             | São Paulo state     | HC       | N           | Martinelli-Filho et al., 2008|
|                              |                                      |              |             |                     |          |             |                            |
| Synidotea marplatensis       |                                      | N/A          | ? SUM, O    | Guaratuba, Paraná   | TR       | L           | Nogueira Junior & E Silva, 2005|
| Giambiagi, 1922              |                                      |              |             | e Barra do Sai,     |          |             |                            |
|                              |                                      |              |             | Santa Catarina      |          |             |                            |
|                              |                                      |              |             |                     |          |             |                            |
|                              |                                      |              |             |                     |          |             | Reddiah, 1968              |
| Paramacrochiron sewelli      |                                      | N/A          | F, M, ?     | Ennore estuary      | HC       | L           | Hayashi and Miyake, 1968   |
| Reddiah, 1968                |                                      |              |             | near Madras Tanabe  |          |             | Hayashi and Miyake, 1968   |
| Chlorotocella gracilis       |                                      | N/A          | M, F, OF    | Bay, Japan          | ?        | N           | Hayashi and Miyake, 1968   |
| Balss, 1914                  |                                      |              |             |                     |          |             | Hayashi and Miyake, 1968   |
| Latreutes anoplonyx          |                                      | N/A          | M, F, OF    | Tanabe Bay, Japan   | ?        | N           | Yusa et al., 2015          |
| Kemp, 1914                   |                                      |              |             |                     |          |             |                            |
| Latreutes mucronatus         |                                      | N/A          | M, F, OF    | Tanabe Bay, Japan   | ?        | N           |                            |
| Stimpson, 1860               |                                      |              |             |                     |          |             |                            |
| Alepas pacifica Pilsbry,     |                                      | N/A          | M, F, OF    | Western Coast of    | HC       | N           | Yusa et al., 2015          |
| 1907                         |                                      |              |             | Japan              |          |             |                            |
| Nemopilema nomurai           |                                      | N/A          | ? SUM, O    |                     |          |             |                            |
| Kishinouye, 1922             |                                      |              |             |                     |          |             |                            |
| Mastigias papua Lesson,      |                                      | N/A          | F, M, O     |                     |          |             |                            |
| 1830                         |                                      |              |             |                     |          |             |                            |
| Mastigias papua Lesson,      |                                      | N/A          | M, F, OF    |                     |          |             |                            |
| 1830                         |                                      |              |             |                     |          |             |                            |
| Mastigias papua Lesson,      |                                      | N/A          | M, F, O     |                     |          |             |                            |
| 1830                         |                                      |              |             |                     |          |             |                            |
| Nemopilema nomurai           |                                      | N/A          | M, F, OF    |                     |          |             |                            |
| Kishinouye, 1922             |                                      |             |             |                     |          |             |                            |
| Species | Author | Habitat | Observations |
|---------|--------|---------|--------------|
| *Nemopilema nomurai* Kishinouye, 1922 | Charybdis feriata Linnaeus, 1758 | 5 juveniles present on one host on the oral arms, one adult present under the bell of a second medusa. | J & M, O, SUM, M, F, O, SUB, M, F, O, J | Mirs Bay, Hong Kong | ? | L | 1970 Oct | ? | Trott, 1972 |
| *Netrostoma setouchianum* Kishinouye, 1902 | Latreutes anoplonyx Kemp, 1914 | Exhibits hiding behavior | ? | Miyazu and Sanriku, Japan Seto Inland Sea, Japan | OBS, HC, L | 2003 Nov | ? | Hayashi et al., 2004 |
| *Charybdis feriata* Linnaeus, 1758 | Latreutes anoplonyx Kemp, 1914 | Single specimen | ? | O, SC, L | 2010 Sep | NS | Ohtsuka et al., 2011 |
| *Netrostoma setouchianum* Kishinouye, 1902 | Latreutes mucronatus Stimpson, 1860 | Mix of sexes and ages of epibiont from two host individuals, 7 on one and 54 epibionts on the other | M, F, OF, J | ? | O, SUM | O, SUB | O, B | OF, A, B | NT Australia | HC, L | 1993 | NS | Bruce, 1995 |
| *Phyllorhiza punctata* von Lendenfeld, 1884 | Charybdis feriata Linnaeus, 1758 | Single specimen from August 2014 | MG | Various bays, Philippines | HC | L | 2014-2015, Feb-Apr | NS | Boco & Metillo, 2018 |
| *Phyllorhiza punctata* von Lendenfeld, 1884 | Latreutes anoplonyx Kemp, 1914 | Two specimens from Leyte Gulf- Guiuan in April 2015 | ? | Various bays, Philippines | HC | L | 2014-2015, Feb-Apr | NS | Boco & Metillo, 2018 |
| *Libinia ferreirae* de Brito Capello, 1871 | Paramacrochiron sp. | Peak in Oct, preference for mature medusae, consume host gonad | J, A | German Bight | HC + SC | ? | 1984-1985 | ? | Dittrich, 1988 |
| *Pseudorhiza haeckeli* Haacke, 1884 | Cymodoce gaimardii H. Milne Edwards, 1840 | Present in the brachial cavities, mouthpart shape leads to speculation that these are semi-parasitic short-term associates | ? | GC, Dublin Bay, Ireland | ? | N | NS | Bate, 1862 via Vader, 1972 |
| *Pseudorhiza haeckeli* Haacke, 1884 | Hyperia gaudichaudii H. Milne Edwards, 1840 | Exhibit cradle positioning for filter feeding | ? | Port Phillip Bay, Victoria | HC | N | 2011 Sep + 2012 Feb | NS | Browne, 2015 |
| *Pseudorhiza haeckeli* Haacke, 1884 | Themisto australis Stebbing, 1888 | | ? | Port Phillip Bay, Victoria | HC | N | 2010 Sep + 2012 Feb | NS | Browne, 2015 |
| *Rhizostoma pulmo* Macri, 1778 | Phyllorhiza punctata von Lendenfeld, 1884 | | N/A | ? | ? | ? | ? | ? | ? | Bate, 1862 via Vader, 1972 |
| *Iphimedia eblanae* Spence Bate, 1857 | Themisto australis Stebbing, 1888 | | ? | ? | ? | ? | ? | ? | ? | Bate, 1862 via Vader, 1972 |
| *Rhizostoma pulmo* Macri, 1778 | Hyperia galba Montagu, 1813 | | N/A | ? | ? | ? | ? | ? | ? | Hayashi et al., 2004 |
| *Iphimedia eblanae* Spence Bate, 1857 | Themisto australis Stebbing, 1888 | | N/A | ? | ? | ? | ? | ? | ? | Hayashi et al., 2004 |
| *Pseudorhiza haeckeli* Haacke, 1884 | Paramacrochiron sp. | | N/A | ? | ? | ? | ? | ? | ? | Hayashi et al., 2004 |
| *Rhizostoma sp.* | Latreutes anoplonyx Kemp, 1914 | | N/A | ? | ? | ? | ? | ? | ? | Hayashi et al., 2004 |
| *Rhizostoma sp.* | Paramacrochiron rhizostomae Reddiah, 1968 | | N/A | F, M, J | ? | ? | ? | ? | ? | Hayashi et al., 2004 |
| *Rhizostomatidae gn. sp.* | Alepopsis pacifica Pilsbry, 1907 | 2 barnacles on the umbrallar margin up to 68 mm in length | ? | Morrison Bay, Mergui Arch | ? | L | 1914 | NS | Annandale, 1914 via Pagès, 2000 |
| Species | Voucher | Host | Location | Date | Notes |
|---------|---------|------|----------|------|-------|
| *Rhopilema esculentum* | Kishinouye, 1891 | *Charybdis feriata* Linnaeus, 1758 | Sagami Bay | October | ? |
| *Rhopilema esculentum* | Kishinouye, 1891 | *Latreutes anoplonyx* Kemp, 1914 | Northeast China | ? | ? |
| *Rhopilema esculentum* | Vanhöffen, 1888 | *Charybdis annulata* Fabricius, 1798 | Palk Bay, Sri Lanka | ? | L |
| *Charybdis feriata* | Linnaeus, 1758 | *Latreutes anoplonyx* Kemp, 1914 | | | |
| *Latreutes anoplonyx* | Kemp, 1914 | | | | |
| *Juvenile transport* | | | | | |
| *Sagami Bay* | | | | | |
| *Northeast China* | | | | | |
| *Palk Bay, Sri Lanka* | | | | | |

| Species | Voucher | Host | Location | Date | Notes |
|---------|---------|------|----------|------|-------|
| *Rhopilema hispidum* | Vanhöffen, 1888 | *Charybdis feriata* Linnaeus, 1758 | Panguil Bay | 2014 Feb-Aug | NS |
| *Rhopilema hispidum* | Vanhöffen, 1888 | *Hippolytidae gn sp.* | Panguil Bay | 2014 Feb-Aug | NS |
| *Rhopilema hispidum* | Vanhöffen, 1888 | *Latreutes sp.* aff. *anoplonyx* Kemp, 1914 | Sichang Island, Thailand | 2009 Oct | ? |
| *Rhopilema hispidum* | Vanhöffen, 1888 | *Latreutes sp.* aff. *anoplonyx* Kemp, 1914 | | | |
| *Charybdis feriata* | Linnaeus, 1758 | *Paramacrochiron sp.* | Panguil Bay | 2014 Feb-Aug | NS |
| *Paramacrochiron sp.* | Vanhöffen, 1888 | | Laem Phak Bia, Thailand | 2010 Oct | NS |
| *Rhopilema nomadica* | Galil, Spanier & Ferguson, 1990 | *Charybdis feriata* Linnaeus, 1758 | Delagoa Bight, Mozambique | 1988 Mar + 1992 Mar | NS |
| *Periclimenes nomadophila* Berggren, 1994 | | | | | |
| *Rhopilema nomadica* | Galil, Spanier & Ferguson, 1990 | *Conchoderma virgatum* Spengler, 1789 | Tranquebar, Bengal Gulf | L | |
| *Libinia dubia* H. Milne Edwards, 1834 | | | | | |
| *Stomolophus meleagris*, Agassiz, 1860 | Agassiz, 1860 | *Charybdis feriata* Linnaeus, 1758 | Hong Kong | ? | ? |
| *Conchoderma cf virgatum* Spengler, 1789 | Agassiz, 1860 | | Gulf of California | L | 2010 Apr |
| *Libinia dubia* H. Milne Edwards, 1834 | | | | | |

References:
- Suzuki, 1965 via Pagès, 2000
- Hayashi et al., 2004
- Panikkar & Raghuv Prasad, 1952 via Towanda & Thuesen, 2006
- Boco & Metillo, 2018
- Ohtsuka et al., 2010
- Boco & Metillo, 2018
- Ohtsuka et al., 2010
- Berggren, 1994
- Fernando & Ramamoorthi, 1974 via Pagès, 2000
- Morton, 1989 via Towanda & Thuesen, 2006
- Álvarez-Tello et al., 2013
- Corrington, 1927
| Species                          | Associated Species                  | Habitat          | Location                      | Age | Month      | Reference                              |
|---------------------------------|-------------------------------------|-------------------|-------------------------------|-----|------------|----------------------------------------|
| Stomolophus meleagris, Agassiz, 1860 | Libinia dubia H. Milne Edwards, 1834 | N/A               | SUM Beaufort, NC              | TR  | N          | 1927 Jul-Oct                           | Gutsell, 1928 |
| Stomolophus meleagris, Agassiz, 1860 | Libinia dubia H. Milne Edwards, 1834 | Juvenile associations, parasitic, transient | Mississippi sound | HC  | N          | 1968 Jul-Oct                           | Phillips et al., 1969 |
| Stomolophus meleagris, Agassiz, 1860 | Libinia dubia H. Milne Edwards, 1834 | Highly variable seasonally, high in July, low in Dec | Wrightsville Beach Jetty NC | HC  | N          | 1983 May-Dec                           | Rountree, 1983 |
| Stomolophus meleagris, Agassiz, 1860 | Libinia dubia H. Milne Edwards, 1834 | Feeding           | ? EXC Onslow Bay, NC          | SC  | ?          | ?                                      | Shanks & Graham, 1988 |
| Stomolophus meleagris, Agassiz, 1860 | Libinia dubia H. Milne Edwards, 1834 | ? ? | Indian River Lagoon, Florida | HC  | ?          | 2003 Mar                               | Tunberg & Reed, 2004 |
| Stomolophus meleagris, Agassiz, 1860 | Penaeus stylirostris Stimpson, 1871 | N/A               | SUM Malaga Bay, Colombia      | HC  | ?          | 2015 Nov + 2017 Apr                   | Riascos et al., 2018 |
| Thysanostoma thysanura Haeckel, 1880 | Paramacrochiron sp. | N/A               | ? ? Sirahama                   | ?   | ?          | 1969                                   | Humes, 1970 |
| Versuriga anadyomene Maas, 1903 | Charybdis feriata Linnaeus, 1758 | Large medusae     | ? ? Leyte Gulf-Guian          | HC  | L          | 2014-2015, Feb-Apr                     | Boco & Metillo, 2018 |
| Versuriga anadyomene Maas, 1903 | Charybdis feriata Linnaeus, 1758 | N/A               | SUM Pari Island, Indonesia    | ?   | L          | 2009 Nov                               | Ohtsuka et al., 2012 |
| Versuriga anadyomene Maas, 1903 | Latreutes anoplonyx Kemp, 1914 | N/A               | A & J NT Australia            | HC  | L          | 1993                                   | Bruce, 1995 |
| Versuriga anadyomene Maas, 1903 | Paramacrochiron sp. | Large medusae     | ? ? Leyte Gulf-Guian          | HC  | N          | 2014-2015, Feb-Apr                     | Boco & Metillo, 2018 |
| Semaeostomeae                   |                                      |                   |                               |     |            |                                        |                        |
| Aurelia aurita Linnaeus, 1758    | Hyperia galba Montagu, 1813          | N/A               | A & J & OF Narragansett Marine Laboratory German Bight | HC  | ?          | 1955 June                              | Bowman et al., 1963 |
| Aurelia aurita Linnaeus, 1758    | Hyperia galba Montagu, 1813          | Preference for mature medusae, infestation increases as gonads develop, peak in Oct, consume host gonad | J, A O | HC + SC | 1984-1985 | Dittrich, 1988 |
| Aurelia aurita Linnaeus, 1758    | Libinia dubia H. Milne Edwards, 1834 | Eating medusa tissue, residence within bell, excavation behaviors | ? EXC Chesapeake Bay | ?   | ?          | 1963 Aug                               | Jachowski, 1963 |
| Aurelia aurita Linnaeus, 1758    | Scyllarus sp.                        | 19.9% of medusae examined 300-500 m from shore had phyllosoma, none on Aurelia near shore, likely parasitoid. | PL EX Bimini, Bahamas | HC  | N          | 1973 Oct                               | Herrnkind et al., 1976 |


| Species | Details | Host | Parasite | Host Details | Location | Host Activity | Host Details | Notes |
|---------|---------|------|----------|--------------|----------|---------------|--------------|-------|
| *Aurelia coerulea* von Lendenfeld, 1884 | Riding small medusae, pierced exumbrella with pereiopods | PL, EX | Yamaguchi, Japan | OBS | ? | ? | Wakabayashi et al., 2017 via Wakabayashi et al. 2019 |
| *Ibacus ciliatus* von Siebold, 1824 | February to May, 97.6% female, largely one female per host, occasionally M/F pair, 1/3 of parasites were ovigerous. No breakdown by specific host. | OF, F, EX | Nagato, Yamaguchi, Japan | OBS | N | 2012-2018 | 0-5 m | Mazda et al., 2019 |
| *Oxycephalus clausi* Bovallius, 1887 | Engage in excavation, many epibionts on a single 5' medusa | N/A, F, M, OF | New Hampshire coast Kuwait Bay | TR | ? | 1981-1982 Aug | Grabe & Lees, 1995 |
| *Chrysaora colorata* Russell, 1964 | Early stages of crabs on medusae | J, MG | Califorina | ? | ? | ? | Graham, 1989 via Schiariti et al., 2012 |
| *Chrysaora fuscescens* Brandt, 1835 | Crabs gain dispersion | ? | Monterey Bay | ? | ? | ? | Graham, 1994 via Schiariti et al., 2012 |
| *Chrysaora fuscescens* Brandt, 1835 | Infestations occur in late summer | ? | NE Pacific, Oregon and northern California NE Pacific "off California" | ? | ? | ? | Larson 1990 |
| *Chrysaora fuscescens* Brandt, 1835 | Peak in Oct, reference for mature medusae, consume host gonad | J, A | German Bight | HC + SC | 1984-1985 | ? | Dittrich, 1988 |
| *Chrysaora lactea* Eschscholtz, 1829 | Parasite | L, J, W, O | Sao Sebastian Channel | TR | L | 2015 Nov | Puente-Tapia et al., 2018 |
| *Chrysaora lactea* Eschscholtz, 1829 | | N/A | Guaruatuba, Paraná e Baia Norte, Florianópolis, Santa Catarina | TR | L | 2003 + 2005, Nov + May | Nogueira Junior & Silva, 2005 |
| Species                        | Location                              | Host                     | Year     | Depth | Reference                              |
|-------------------------------|---------------------------------------|--------------------------|----------|-------|----------------------------------------|
| *Chrysaora lactea* Eschscholtz, 1829 | Periclimenes sp.                       | Facultative commensal, feeding on mucus, large proportion ovigerous females | OF, A, J SUM | SAO Paulo state | HC ? 1999-2002 + 2006 Jul NS Martinelli-Filho et al., 2008 |
| *Chrysaora lactea* Eschscholtz, 1829 | Synidotea marplatensis Giambiagi, 1922 | N/A ? SUM Guaratuba, Paraná e Barra do Sui, Santa Catarina, | TR L | 2003-2004 Aug-Dec 8-14 m | Nogueira Junior & E Silva, 2005 |
| *Chrysaora melanaster* Brandt, 1835 | Hyperia galba Montagu, 1813 | N/A J SUM, O Takehara City (34 18'N, 132 55'E) | ? L | 2009 Apr + Jun | Ohtsuka et al., 2012 |
| *Chrysaora pacifica* Goette, 1886 | Oxycephalus clausi Bovallius, 1887 | February to May, 97.6% female, largely one female per host, occasionally M/F pair, 1/3 of parasites were ovigerous. No breakdown by specific host. | OF, F EX | Nagato, Yamaguchi, Japan | OBS L 2012-2018 0-5 m Mazda et al., 2019 |
| *Chrysaora plocamia* Lesson, 1830 | Hyperia curticephala Vinogradov & Semenova, 1985 | Mean 0f 174.4 amphipods/host, 79% female, ingested mesoglea | M, F, OF W Mejillones Bay | SC N 2005 Feb | NS Oliva et al., 2010 |
| *Chrysaora quinquecirrha* Desor, 1848 | Callinectes sapidus Rathbun, 1896 | Not feeding on medusa | ?? EX Mississippi sound | HC L 1968 Aug | NS Phillips et al., 1969 |
| *Chrysaora quinquecirrha* Desor, 1848 | Libinia dubia H. Milne Edwards, 1834 | Lower incidence rate near surface than bottom trawls, actively feeding on medusae | ?? B, O Mississippi sound | MULTI N 1968 Aug | NS Phillips et al., 1969 |
| *Chrysaora quinquecirrha* Desor, 1848 | Pseudomacrochiron stocki Sars, 1909 | 12 specimens from 10 hosts | F, M ? Madras Marina | HC N 1967, Oct | ? Reddiah, 1969 |
| *Chrysaora sp.* | Cancer sp. cf antennarius* | N/A J, MG ? Southern California Bight | HC N 1989 Jul-Sep | NS Martin & Kuck, 1991 |
| *Chrysaora sp.* | Hyperia medusarum Müller, 1776 | N/A F ? Southern California Bight | HC L 1989. Jul-Sep | NS Martin & Kuck, 1991 |
| *Chrysaora sp.* | Metamyisidopsis elongata Holmes, 1900 | N/A M ? Southern California Bight | HC L 1989. Jul-Sep | NS Martin & Kuck, 1991 |
| *Chrysaora sp.* | Mysidopsis cathengelae Gleyce, 1982 | N/A M ? Southern California Bight | HC L 1989. Jul-Sep | NS Martin & Kuck, 1991 |
| *Cyanea capitata* Linnaeus, 1758 | Alepas pacifica Pilsbry, 1907 | Seven barnacles from 14.5-37 mm in length on the exumbrella and umbrella Margin. | ? MA, EX Marion Bay, Tasmania | ? L 1985 | ? Liu & Ren, 1985 via Pagès, 2000 |
| Species                              | Host                      | Epibiont                  | Location          | Collection Method | Collection Period | Reference                      |
|--------------------------------------|---------------------------|---------------------------|-------------------|-------------------|--------------------|--------------------------------|
| *Cyanea capillata* Linnaeus, 1758     | *Hyperia galba* Montagu, 1813 | Inverted positioning, plentiful in the spring | A & J OF MA, EX, Narragansett Marine Laboratory, Niantic River | August 1954 - August 1955 | NS | Bowman et al., 1963 |
| *Cyanea capillata* Linnaeus, 1758     | *Hyperia galba* Montagu, 1813 | N/A                       | A & J OF ?       | May + June 1960   | NS | Bowman et al., 1963 |
| *Cyanea capillata* Linnaeus, 1758     | *Hyperia galba* Montagu, 1813 | Peak in Oct, reference for mature medusae, consume host gonad | J, A O German Bight, Niantic River | June 1984 - August 1985 | ? | Dittrich, 1988 |
| *Cyanea capillata* Linnaeus, 1758     | *Hyperoche medusarum* Kröyer, 1838 | Single specimen in May | J ? Niantic River | May + June 1960 | NS | Bowman et al., 1963 |
| *Cyanea capillata* Linnaeus, 1758     | *Themisto australis* Stebbing, 1888 | Cradle positioning, no bell damage, all sampled epibionts submature females | JF EX Rye Pier (38°23'S, 144°50'E) | November 1995 - October | NS | Condon & Norman, 1999 |
| *Cyanea nozakii* Kishinouye, 1891    | *Alepas pacifica* Pilsbry, 1907 | Relationship uncharacterized except to note epibiont presence on umbrella and oral arms. | ? B, O Japanese Coast | ? ? ? ? | | Hiro 1938 via Pagès, 2000 |
| *Cyanea nozakii* Kishinouye, 1891    | *Alepas pacifica* Pilsbry, 1907 | 3 barnacles on the umbrella up to a length of 130 mm Substrate | ? EX Shanghai | ? ? | 1946 | Tubb, 1946 via Pagès, 2000 |
| *Cyanea nozakii* Kishinouye, 1891    | *Alepas pacifica* Pilsbry, 1907 | | M, F, OF B Western Coast of Japan | | HC L | 2005-2009 | Yusa et al., 2015 |
| *Deepstaria enigmatica* Russell, 1967 | Anuropidae gn sp. | Two anuropids close to the oral arm base on one medusa Parasitic | ? O, SUM Mutsu Bay, ROV L | | 2002 Apr/May 669 m | Lindsay et al., 2004 |
| *Deepstaria enigmatica* Russell, 1967 | Anuropus sp. | | ? SUM San Diego Trough | | ROV L | 1966 Oct 723 m | Barham & Pickwell, 1969 |
| *Diplulmaris malayensis* Stiasny, 1935 | *Alepas pacifica* Pilsbry, 1907 | 15 barnacles found on 10 hosts, mostly attached to the subumbrellar margins. 1 to 3 epibionts per host. 11 were oriented towards the GVC opening and oral arms of the host. Hypothesized consumption of gonadal tissue by this epibiont. Over 100 barnacles on the umbrella and oral arm regions of an unknown number of medusae. | ? MA 34 29.4N, 138 32.6E | | | Pagès, 2000 |
| *Pelagia noctiluca* Forsskål, 1775    | *Alepas pacifica* Pilsbry, 1907 | | ? B, O Japanese Coast | | ? ? | Hiro 1937 via Pagès, 2000 |
| *Pelagia noctiluca* Forsskål, 1775    | *Alepas pacifica* Pilsbry, 1907 | N/A                       | ? SUM 39N, 52W | | | Madin unpubl data via Pagès, 2000 |
| Taxon | Host | Description | Collection Details |
|-------|------|-------------|--------------------|
| *Pelagia noctiluca* Forsskål, 1775 | *Alepas pacifica* Pilsbry, 1907 | One barnacle 20 mm long, present on an oral arm | ? O Misaki, Japan ? L ? ? Utinomi, 1958 via Pagès, 2000 |
| *Pelagia noctiluca* Forsskål, 1775 | *Anelasma sp.* | Medusae up to 60 mm in diameter, unknown epibiont number, size and position. | ? ? Kuroshio, Japan ? ? ? ? Kishinouye, 1902 via Pagès, 2000 |
| *Pelagia noctiluca* Forsskål, 1775 | *Oxycephalus clausi* Bovallius, 1887 | February to May, 97.6% female, largely one female per host, occasionally M/F pair, 1/3 of parasites were ovigerous. No breakdown by specific host. | OF, F EX Nagato, Yamaguchi, Japan OBS L 2012-2018 0-5 m Mazda et al., 2019 |
| *Pelagia noctiluca* Forsskål, 1775 | *Thamneus rostratus* Bovallius, 1887 | Relatively rare species | A & J SUM Gulf of California SC L 2003 Mar 10 m Gasca & Haddock, 2004 |
| *Pelagia panopyra* Péron & Lesueur, 1810 | *Ibacus sp.* | Each medusa had a phyllosoma larva firmly attached to the bell surface. The larvae were difficult to remove without injuring them, considered parasitoid relationship. | PL EX Sydney Harbor ? L 1960 May ? Thomas, 1963 |
| *Phacellophora camtschatica* Brandt, 1835 | *Alepas pacifica* Pilsbry, 1907 | 2.5-5.1 cm long barnacles on a 50 mm | ? ? Tasman sea ? L 1968 ? Utinomi, 1968 via Pagès, 2000 |
| *Phacellophora camtschatica* Brandt, 1835 | *Hyperia medussarum* Müller, 1776 | Parasitoid, May to Sept, 100s of amphipods, 100% of hosts had infestation in July | M & F O Puget Sound HC N 1994-2003 May-Oct NS Towanda & Thuesen, 2006 |
| *Phacellophora camtschatica* Brandt, 1835 | *Metacarcinus gracilis* Dana, 1852 | Association appears in May, once bell widths of hosts begin to exceed 3 cm, peaks in June/July, few after mid-Oct | MG & I B, O Puget Sound HC N 1994-2003 May-Oct NS Towanda & Thuesen, 2006 |
| *Poralia rufescens* Vanhöffen, 1902 | *Lanceola clausii* Bovallius, 1885 | N/A | F, M, J SUM Suruga Bay ROV L 2002 Apr 867-1697 m Hughes & Lindsay, 2017 |
| *Poralia rufescens* Vanhöffen, 1902 | Lysianassinae gn sp. | Attached at base of oral arms, 1-6 per medusa | ? O, SUM Japan Trench ROV N 2002 Apr/May 500-1000 m Lindsay et al., 2004 |
| *Poralia rufescens* Vanhöffen, 1902 | *Pseudocallisoma coecum* Holmes, 1908 | Only juvenile specimens | J O Japan Trench ROV L 2002 Apr/May 576-732 m Hughes & Lindsay, 2017 |

**Hydrozoa**
### Anthoathecata

#### Bythotiara depressa
- **Scina sp.**
- Naumov, 1960
- **Bythotiara sp.**
- **Minonecetes sphaericus**
- Bovallius, 1885

#### Leuckartiara octona
- **Hyperia medusarum**
- Müller, 1776

#### Leuckartiara zacae Bigelow, 1940
- **Hyperia medusarum**
- Müller, 1776

#### Neoturris sp.
- **Hyperia medusarum**
- Müller, 1776

### Leptothecata

#### Aequorea coerulescens
- **Brachyscelidae gni sp.**
- Brandt, 1835

#### Aequorea coerulescens
- **Brachyscelus crusculum**
- Spence Bate, 1861

#### Aequorea coerulescens
- **Ibacus ciliatus von Siebold, 1824**

#### Aequorea coerulescens
- **Oxycephalus clausi**
- Bovallius, 1887

#### Aequorea coerulescens
- **Saphirina nigromaculata**
- Claus, 1863

#### Aequorea coerulescens
- **Thanoneus rostratus**
- Bovallius, 1887

#### Aequorea euridina* Péron & Lesueur, 1810
- **Hyperia gaudichaudii**
- Milne Edwards, 1840

#### Aequorea macrodactyla
- **Ibacus novemdentatus**
- Gibbes, 1850
| Species | Author & Year | Observations | Location | Date | Depth | Authors |
|---------|---------------|--------------|----------|------|-------|---------|
| *Aequorea victoria* Murbach & Shearer, 1902 | Riding small medusae, pierced exumbrella with pereiopods, attached to a salp as well, parasitoid relationship hypothesized. | PL, EX | Japan | ? | ? | Wakabayashi et al., 2019 |
| *Hyperoche medusarum* Kröyer, 1838 | N/A | OF | Gulf of California | ROV | L | 2003 Mar | 1100 m | Gasca & Haddock, 2004 |
| *Ibacus ciliatus* von Siebold, 1824 | N/A | PL | ? | Yamaguchi, Japan | ? | ? | ? | ? | Wakabayashi et al, 2017 via Wakabayashi et al, 2019 |
| *Clytia hemisphaerica* Linnaeus, 1767 | Association from Oct to March, epibionts passed between medusae. | ? | B, O | West Scotland | ? | N | Oct - Mar | ? | Elmhirst, 1925 via Vader, 1972 |
| *Tryphana malmii* Boeck, 1871 | N/A | ? | ? | Gulf of California | ROV | L | 2006 May | 202 m | Gasca et al., 2015 |
| *Hyperoche medusarum* Kröyer, 1838 | N/A | OF, J | W | Monterey California | SC | L | 2004 May | 10 m | Gasca et al., 2007 |
| *Metopa borealis* G. O. Sars, 1883 | Speculates year-round relationship, mobile on medusa, did not feed on host tissue, fed on mucus | J & A | SUM, O, B, T | Bergen | ? | N | 1970 Apr | ? | Vader, 1972 |
| *Iulopis mirabilis* Bovallius, 1887 | N/A | J & A | ? | Narragansett Marine Laboratory | HC | L | 1954 Sep - 1957 Aug | NS | Bowman et al., 1963 |
| *Simorhynchotus antennarius* Claas, 1871 | N/A | 0F | ? | Gulf of California | SC | L | 2006 Jun | <30 m | Gasca et al., 2015 |
| *Ibacus ciliatus* von Siebold, 1824 | N/A | PL | ? | Nagasaki, Japan | ? | ? | ? | ? | Shojima, 1973 via Wakabayashi 2019 |
| *Scyllarus chacei* Holthuis, 1960 | 30% of phyllosoma attached to at least one GZ species, primarily hydrozoa, parasitoid | PL, EX | Northern Gulf of Mexico | OBS, TR | N | 2015 Oct | 1-31 m | Greer et al, 2017 |
relationship.

| Species                  | Authors                  | Geographical Location         | Mating Activity Description                                                                 | Dates/Depth/Instruments | References                                      |
|--------------------------|--------------------------|-------------------------------|---------------------------------------------------------------------------------------------|-------------------------|------------------------------------------------|
| *Olindias sambaquiensis* Müller, 1861 | *Brachyscelus cf. rapacoides* Stephensen, 1925 | Sao Sebastian Channel | Reduction in mouthpart of epibions higher in females                                              | TR L 2015 Nov  | Puente-Tapia et al., 2018 |
| *Olindias sambaquiensis* Müller, 1861 | *Syndotinae marplatensis* Giambiagi, 1922 | Guaratuba, Paraná e Barra do Sai, Santa Catarina, | | TR L 2003-2004 Aug-Dec 8-14 m | Nogueira Junior & E Silva, 2005 |
| *Narcomedusae*            |                          |                               | Refuge and mating, mating pairs with long residence time evident on more than one occasion | M, F SUM | Gasca et al., 2015 |
| *Aegina citrea* Eschscholtz, 1829 | *Iulopis loveni* Bovalli, 1887 | Gulf of California ROV L 2007 Jan 83 m | | | Gasca et al., 2015 |
| *Aegina citrea* Eschscholtz, 1829 | *Iulopis mirabilis* Bovalli, 1887 | Gulf of California ROV L 2006 Oct 1286-1478 m | | | Gasca et al., 2015 |
| *Aegina citrea* Eschscholtz, 1829 | *Lanceola pacifica* Stebbing, 1888 | Monterey California ROV L 2005 Apr 1322 m | | | Gasca et al., 2007 |
| *Aegina citrea* Eschscholtz, 1829 | *Pseudolubbockia dilatata* Sars, 1909 | Gulf of California ROV L 2007 Aug 554 m | | | Gasca et al., 2007 |
| *Pegantha laevis* Bigelow, 1909 | *Pseudohepieria shihi* Gasca, 2005 | Gulf of California ROV L 2004 May 606-1098 m | | | Gasca et al., 2007 |
| *Solmissus incisa* Fewkes, 1886 | *Brachyscelus sp.* Bovalli, 1887 | Gulf of California ROV L 2006 May 497 m | | | Gasca et al., 2007 |
| *Solmissus incisa* Fewkes, 1886 | *Thamneus rostratus* Bovalli, 1887 | Monterey California ROV L 2005 Apr 243 m | | | Gasca et al., 2007 |
| *Solmissus incisa* Fewkes, 1886 | *Tryphana malmii* Boeck, 1871 | Monterey California ROV L 2004 May 458 m | | | Gasca et al., 2007 |
| *Solmissus incisa* Fewkes, 1886 | *Tryphana malmii* Boeck, 1871 | Gulf of California ROV L 2006 May 295 m | | | Gasca et al., 2007 |
| *Solmissus incisa* Fewkes, 1886 | *Hyperia medusarum* Müller, 1776 | Gulf of California ROV L 2006 Sep 498 m | | | Gasca et al., 2007 |
| *Apolemia sp.*             | *Apolemia sp.* Gasca, 2005 | Gulf of California ROV L 2015 Mar 926 m | | | Gasca & Browne, 2018 |
| *Apolemia sp.*             | *Mimonectes loveni* Bovalli, 1887 | Gulf of California ROV L 2015 Mar 2094 m | | | Gasca & Browne, 2018 |
| *Athorybia rosacea* Forsskål, 1775 | *Parascelus edwardsi* Claus, 1879 | Gulf of California SC L 2003 Mar 10 m | | | Gasca & Haddock, 2004 |
| Species | Description | Collection Method | Location | Date | Depth | Authors |
|---------|-------------|-------------------|----------|------|-------|---------|
| Chelophyes appendiculata | | | Monterey, California | 2004 May | 5-15m | Gasca et al., 2007 |
| | | | | | | |
| Diphyes bojani | | | | | | |
| | | | | | | |
| Nectadamas diomedae | | | Monterey, California | 2005 Apr | 1082 m | Gasca et al., 2007 |
| Bigelow, 1911 | Mimonecetes sphaericus | N/A | | | | |
| | Bovallius, 1885 | M | | | | |
| | | | | | | |
| Nectadamas diomedae | | | Gulf of California | 2006 Jan | 116 m | Gasca et al., 2005 |
| Bigelow, 1911 | Mimonecetes sphaericus | N/A | | | | |
| | Bovallius, 1885 | J | | | | |
| | | | | | | |
| Nectadamas diomedae | | | Monterey, California | 2006 May | 1344 m | Gasca et al., 2015 |
| Bigelow, 1911 | Mimonecetes sphaericus | N/A | | | | |
| | Bovallius, 1885 | | | | | |
| | | | | | | |
| Muggiea sp. | Sclarrus chacei | 30% of phyllosoma attached to at least one GZ species, primarily hydrozoa, parasitoid relationship hypothesized. | Northern Gulf of Mexico | 2015 Oct | 1-31 m | Greer et al. 2017 |
| | Hoffhuis, 1960 | | | | | |
| | | | | | | |
| Physophora hydropoistica | Tryphana malmii | N/A | Gulf of California | 2006 Jan | 116 m | Gasca et al., 2005 |
| Forsskål, 1775 | Boeck, 1871 | | Gran Canaria, Spain | | | Ates et al., 2007 |
| | Scllaridae gn sp | Attached with pereiopods | | | | |
| | | | | | | |
| Resomia ornicephala | Anapronoe reinhardtii | N/A | Gulf of California | 2006 Sep | 254 m | Gasca et al., 2015 |
| Pugh & Haddock, 2010 | Stephensen, 1925 | | | | | |
| | | | | | | |
| Rosacea cymbiformis | Tryphana malmii | N/A | Gulf of California | 2006 May | 204 m | Gasca et al., 2015 |
| Delle Chiaje, 1830 | Boeck, 1871 | | | | | |
| | Brachyscelus crusculum | | | | | |
| | Spence Bate, 1861 | | | | | |
| | | | | | | |
| Rosacea cymbiformis | Eupronoe minutia | N/A | Gulf of California | 2006 Sep | 161 m | Gasca et al., 2015 |
| Delle Chiaje, 1830 | Claus, 1879 | | | | | |
| | | | | | | |
| Rosacea cymbiformis | Paraphronima gracilis | N/A | Gulf of California | 2006 May | 430 m | Gasca et al., 2015 |
| Delle Chiaje, 1830 | Claus, 1879 | | | | | |
| | | | | | | |

**Trachymedusae**

| Species | Description | Collection Method | Location | Date | Depth | Authors |
|---------|-------------|-------------------|----------|------|-------|---------|
| Sulficulolaria quadrivalvis | Simorhynchotus antennarius | N/A | Cabo Frio (RJ) and the Santa Catarina Island (SC) | 1980, 17-23 Jan | ? | Lima & Valentin, 2001 |
| de Blainville, 1830 | Claus, 1879 | | | | | |

**Siphonophorae**

| Species | Description | Collection Method | Location | Date | Depth | Authors |
|---------|-------------|-------------------|----------|------|-------|---------|
| Physophora hydrostatica | Tryphana malmii | N/A | | | | |
| Forsskål, 1775 | Boeck, 1871 | | | | | |
| Prayidae gn sp | Scllaridae gn sp | | | | | |
| | | | | | | |
| Resomia ornicephala | Anapronoe reinhardtii | N/A | | | | |
| Pugh & Haddock, 2010 | Stephensen, 1925 | | | | | |
| | | | | | | |
| Rosacea cymbiformis | Tryphana malmii | N/A | | | | |
| Delle Chiaje, 1830 | Boeck, 1871 | | | | | |
| | Brachyscelus crusculum | | | | | |
| | Spence Bate, 1861 | | | | | |
| | | | | | | |
| Rosacea cymbiformis | Eupronoe minutia | N/A | | | | |
| Delle Chiaje, 1830 | Claus, 1879 | | | | | |
| | | | | | | |
| Rosacea cymbiformis | Paraphronima gracilis | N/A | | | | |
| Delle Chiaje, 1830 | Claus, 1879 | | | | | |

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**Manuscript to be reviewed**

PeerJ reviewing PDF | (2020:12:56424:2:0:NEW 10 Mar 2021)

Manuscript to be reviewed
| Species                        | Genus                     | Location          | Code | Month | Depth | Year   | Refs                  |
|--------------------------------|---------------------------|-------------------|------|-------|-------|--------|-----------------------|
| Haliscera bigelowi Kramp, 1947 | Hyperia medusarum Müller, 1776 | Gulf of California | J    | Sep   | <30 m | 2006   | Gasca et al., 2015    |
| Haliscera bigelowi Kramp, 1947 | Scina spinosa Vosseler, 1901 | Monterey California | M    | Apr   | 394 m | 2005   | Gasca et al., 2007    |
| Haliscera sp.                  | Scina spinosa Vosseler, 1901 | Gulf of California | J    | Oct   | 1263 m| 2006   | Gasca et al., 2015    |
| Haliscera sp.                  | Scina uncipes Stebbing, 1895 | Gulf of California | A    | May   | 449 m | 2006   | Gasca et al., 2015    |
| Pectis tatusnoko Lindsay & Pagès, 2010 | Mimonecetes spandlii Stephensen & Pirot, 1931 | Suruga Bay        | JM   | Apr   | 1967 m| 2002   | Lindsay & Pagès, 2010 |