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Box Jellyfish (Cubozoa: Carybdeida) in Hawaiian Waters, and the First Record of *Tripedalia cystophora* in Hawai'i

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Abstract. Box jellyfish represent an ecologically important component of tropical marine planktonic communities, and certain species are notorious for their potent sting. We describe and review the occurrence of three box jellyfish species previously recorded from the Hawaiian Islands, *Carybdea arborifera* (Maas, 1897), *Alatina moseri* (Mayer, 1906), and *Copula sivickisi* (Stiasny, 1926), and newly report a fourth species, *Tripedalia cystophora* Conant, 1897. The latter two species are likely to have been introduced by shipping to Hawai'i. Although previously reported in Hawai'i, *Carybdea rastonii* was not confirmed from Hawaiian waters in this study and we suggest it may have been misidentified. Instead, DNA sequence fragments from specimens tentatively identified via morphological characters as *C. rastonii* matched the congener *C. arborifera*. Continued surveillance of box jellyfish is warranted, as the Hawaiian Islands have a well-developed ocean associated tourism, introduction of dangerous stinging jellyfish such as those that cause severe "irukandji" syndrome is of primary concern.

Introduction

In the last three decades jellyfish (cnidarian classes Cubozoa, Scyphozoa, and Hydrozoa) have received increased scientific attention due to their fluctuations in abundance that frequently result in population explosions (i.e., blooms) in marine ecosystems worldwide (see Pitt & Lucas 2014). Jellyfish blooms negatively affect fisheries by clogging nets (Nagata *et al.* 2009, Dong *et al.* 2010), pen aquaculture by causing fish death (Doyle *et al.* 2008, Delannoy *et al.* 2011), power generation and desalination by clogging intake screens (Daryanabard & Dawson 2008), and tourism by stinging swimmers (Fenner & Williamson 1996, Fenner *et al.* 2010).

Box jellyfish, or cubomedusae (Cubozoa), represent the smallest cnidarian class with approximately 50 species (Bentlage *et al.* 2010). However, the basic biology, population dynamics and species identity are poorly understood (Kingsford & Mooney 2014). Box jellyfish have complex eyes with sophisticated visual acuity (Martin 2004, Nilsson *et al.* 2005, Kozmik *et al.* 2008) enabling active predation (Hamner *et al.* 1995, Buskey 2003), obstacle avoidance (Garm *et al.* 2007), and even navigation using terrestrial landmarks (Garm *et al.* 2011). Cubomedusae exhibit complex phototactic, courtship and mating behaviors (Lewis & Long 2005), unique to this group. Perhaps their most notorious feature is their extremely dangerous venom (Tibballs *et al.* 2012). Most species within this class can cause medically significant stings (Gershwin *et al.* 2010), and while toxicity varies

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from species to species, the class includes the world's most venomous marine creature, *Chironex fleckeri* (Fenner & Williamson, 1996), which can kill an adult human within minutes. Most box jellyfish prefer calm tropical and subtropical near-shore marine habitats, areas that are frequently shared with tourists, fishermen, surfers and divers. This overlap of recreation with box jellyfish often results in dangerous encounters (Fenner & Williamson 1996, Fenner & Hadok 2002, Huynh *et al.* 2003).

Box jellyfish have been documented in the Hawaiian Islands since 1877 when Theodore Ballieu, a French commissioner to Hawai‘i, collected a specimen in Honolulu reported as *Charybdea alata* (Reynaud, 1830) (Ranson 1945, Kay 1972) and placed it in the Muséum National d'Histoire Naturelle in Paris. In 1891, *Carybdea arborifera* (as *Charybdea arborifera* Maas, 1897) was collected in Honolulu surface waters (Maas 1897). In 1902 a five-month survey of the entire Hawaiian Island chain by the Steamer *Albatross* collected 41 *C. arborifera* (as *Charybdea rastonii* Haacke, 1887) off O‘ahu, Maui and Kaua‘i from 0 to 42 m (Mayer 1906). Twenty-three specimens of a new species, *Alatina moseri* (as *Charybdea moseri* Mayer, 1906) were collected in the same survey from the Northwestern Hawaiian Islands (NWHI) Maro Reef to south of the Island of Hawai‘i at the surface to 46 m (Mayer 1906). Galtsoff (1933) reported *A. moseri* (as *Charybdea alata*) during a 1.5 month survey of Pearl and Hermes, NWHI as a one day occurrence on 18 Aug 1930 "appeared in great numbers near southeast island and caused considerable discomfort (from stings) to our divers".

Night surveys in 1996 and 1998 discovered *Copula sivickisi* (as *Carybdea sivickisi* Stiasny, 1926) on the south shore of O‘ahu in Mamala Bay (Waikīkī Beach area) and on the west coast of O‘ahu in Yokohama Bay (Matsumoto *et al.* 2002), respectively, as well as from Ma‘alaea Harbor on Maui in 2005 (Crow *et al.* 2006). An additional survey in Ma‘alaea Harbor on Maui in 2004 collected *C. arborifera* (as *C. rastoni*) (Crow *et al.* 2006).

Considering the fact that box jellyfish were recorded as far ago as the 19th century in Hawai‘i, surprisingly little information exists regarding their biology and ecology. We summarize here our knowledge of Hawaiian cubomedusae and report the first record of *Tripedalia cystophora* Conant, 1897 in Hawaiian waters.

Methods

We studied the collections of the Bernice P. Bishop Museum (BPBM), Honolulu, the National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., and the Muséum National d'Histoire Naturelle, Paris (MNHN). Additional specimens from the National Marine Fisheries Service (NMFS), the University of Hawai‘i, Department of Oceanography and those of the first author were also added to the BPBM collection. In addition, we reviewed Hawaiian Ocean Safety and Lifeguard Services (OSLS) records, currently available at the OSLS Leahi St. office. Reports were also taken from newspaper accounts and accessed via the printed index to the Honolulu Advertiser and Honolulu Star-Bulletin 1926–1994 based on key word search (jellyfish, box jellyfish, stings). Printed microfilm accounts are available from the first author. In addition, a search was conducted on the Chronicling America, Library of Congress website: http://chroniclingamerica.loc.gov covering Hawai‘i newspapers from 1836–1922 with no reports of box jellyfish in newspaper articles. The website was last accessed on 23 Feb 2014. Newspaper reports were accepted when verification of species identification was possible.

Measurements were made with an analog micrometer (± 0.1 mm) as follows: 1) bell-height (BH): the distance from the upper tip of the bell to velarial turnover, and 2) bell-height to rhopalial opening (BHR): the distance from the upper tip of the bell to the rhopalial niche opening.

We performed preliminary molecular evaluation of each taxon by sequencing one or more DNA markers and conducting BLAST (Basic Local Alignment Search Tool) searches to determine highest probability matches in GenBank.

Table 1. Records of the box jellyfish *Alatina moseri* on Waikīkī Beach, O'ahu, and significant records from two other Hawaiian Islands.

Date(s)	Comments	Source
5 Mar 1948	First time reported in Waikīkī	BPBM D285 records
30 Jun 1951	Swarms on beach;painful stings	Edmondson 1952; BPBM D315
28 May 1962	Queen's surf to Natatorium	Hono. Star Bull. 51:148.
30–31 Dec 1980	First two day episode	BPBM D533
23 Sep 1981	Aggregation over a 4–5 km area	BPBM D555, OSLS
5 Dec 1982	Ala Moana, after Hurricane Iwa	Star Adver. I 13
5 Mar 1988	Mass near Hilton Hawaiian Village	Hono. Advertiser A1/ A3
22 Mar 1990	Hanauma Bay closure	Hono. Advertiser A3
28 Feb 1992	Invasion, Hanauma Bay to Sandy Beach	Hono. Advertiser A1
14 Jun 1993	Invasion, Nanakuli to Makua	Hono. Advertiser A4
15 Jul 1993	3 people stung near Molokini Crater	Hono. Advertiser C6
1998 to 2011	Waikīkī monthly beach counts	Chiaverano *et al.* 2013
3 Dec 2007	Poi'pu Beach, Kaua'i	Hono. Advertiser A1

BPBM = Bernice P. Bishop Museum records; Hono. Star Bull. = Honolulu Star Bulletin; Hono. Advertiser = Honolulu Advertiser; OSLS = Ocean Safety and Lifeguard Services records.

Class CUBOZOA Werner, 1972
Order CARYBDEIDA Gegenbaur, 1857
Family ALATINIDAE Gershwin, 2005
Genus *Alatina* Gershwin, 2005

Family and species diagnosis: T-shaped rhopaliar niche ostia with a single upper and two lower covering scales (Gershwin 2005, Bentlage & Lewis 2012, Kayal *et al.* 2012, Smith *et al.* 2012, Lewis *et al.* 2013).

Alatina moseri (Mayer, 1906)
Fig. 1

Synonyms used in Hawaiian literature: *Carybdea moseri* (Mayer, 1906), *Charybdea moseri* Mayer, 1906; *Carybdea alata* Reynaud, 1830, and *Charybdea alata* (Reynaud, 1830).

ECOLOGICAL AND MORPHOLOGICAL INFORMATION: Mayer (1906) captured large specimens about 80 mm high and 47 mm wide (mature at about 67 mm bell height) throughout Hawaiian offshore waters as far as 520 km from the nearest island. Ranson's (1945) report of *C. alata* (a name used by subsequent Hawaiian authors to refer to what is now known as *A. moseri*) is a misidentification of (at the time) an undescribed specimen of *C. arborifera*, as discussed below. Edmondson (1946) specimens have a bell about 2 in wide and nearly twice that height occasionally observed it on the reefs of O'ahu, this species is typically a pelagic species. The first specimens were reported in Waikīkī on 5 March 1948 with "very powerful stinging cells" (*fide* BPBM Accession Record). Edmondson (1952) reported that "swarms suddenly appeared" at Waikīkī Beach on 30 June 1951 (*fide* BPBM Accession Record). Chu & Cuttress (1954) noted that this species was occasionally encountered on the reefs and unprotected coastline of Hawai'i. Anonymous (1962) reported a "heavy distribution" from Queen's Surf to the Natatorium in Waikīkī on 28 May 1962. This species has appeared in Waikīkī Beach surveys every month since August 1994 (OSLS records). Thomas *et al.* (2001a) discussed an 8–12 day influx cycle, Chiaverano *et al.* (2013) discussed climatic and oceanographic influences on its abundance on Waikīkī Beach, and Carrette *et al.* (2014) reported on its early life history in laboratory cultures. *A. moseri* specimens examined in Hawaii had simple, bi-fork and tri-fork distal ends of the velarial canals (first author data).

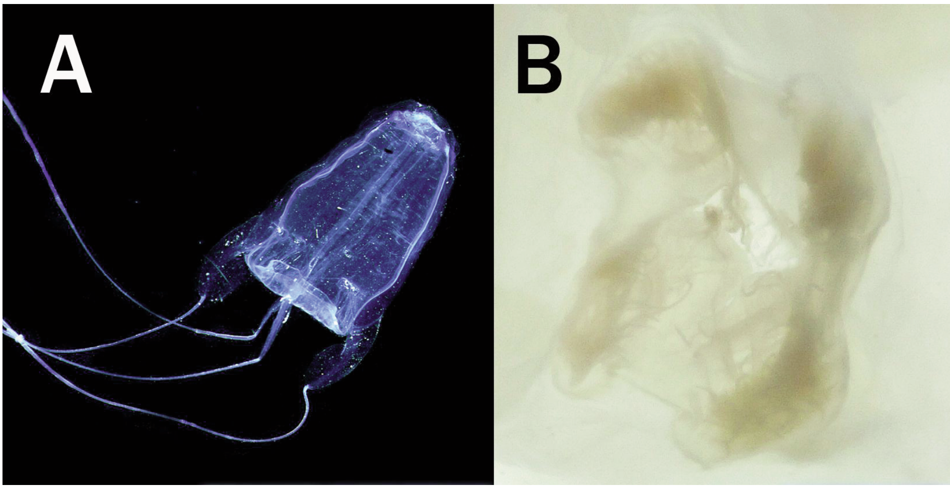

Figure 1. (**A**) Photograph of living *Alatina moseri* collected at Waikīkī Beach, in a kreisel tank, (**B**) Close up of crescentric gastric phacellae.

STINGS AND TOXICOLOGY: References: Tamanaha & Izumi (1996) sting reaction; Thomas & Scott (1997) sting records and first aid; Nagai *et al.* (2000) unique protein sting toxin; Chung *et al.* (2001) venom; Thomas *et al.* (2001a) treatment; Thomas *et al.* (2001b) sting treatment trial; Nomura *et al.* (2002) sting treatment; Yanagihara *et al.* (2002) ultrastructure of nematocyst; Yoshimoto & Yanagihara (2002) heat sting treatment; Ping & Onizuka (2011) sting treatment review 2000 to 2008, and Yanagihara & Shohet (2012) venom cardiovascular effects.

HAWAIIAN SPECIMENS EXAMINED: BPBM D285 Waikīkī Beach 5 Mar 1948; BPBM D315 Waikīkī Beach 30 Jun 1951 (four specimens); USNM 51962 Ala Wai Boat Harbor 1955; BPBM D533 Kūhiō Beach, Waikīkī 31 Dec 1980; BPBM D555 Waikīkī Beach 23 Sep 1981; R V *Oscar Elton Sette* (OES) NOAA/ Pacific Island Fisheries Research Center and UH Manoa, Oceanography night Cobb trawls in the top 200 m of water around Cross Seamount Summit (for trawl details see Drazen *et al.* 2011); BPBM D2302 (BHR 30 mm) < 14 km off Cross Seamount 24 Apr 2008, BPBM D2303 (BHR 23.4 mm) off southwest flank Cross Seamount 30 Apr 2008; BPBM D2304 in cyclonic mid ocean eddy between Cross Seamount and O'ahu 18°N and 158°W 7 May 2008); BPBM D2271 Magic Island, Ala Moana Beach Park 19 May 2009; BPBM D2269 Cobb Trawl southwest of Keāhole Point, Island of Hawai'i SE 12-06 station 30, 21 Aug 2012; BPBM D2270 Waikīkī Beach 24 Feb 2014.

HAWAII DISTRIBUTION: NWHI, Midway Atoll (washed ashore) to Island of Hawai'i (Kona side) and south of Hawaiian Islands over Cross Seamount.

RANGE: Widespread throughout Hawaiian Islands and Osprey Reef on Great Barrier Reef, Australia (Bentlage *et al.* 2010). Considered by Bentlage & Lewis (2012) to be an oceanic species in tropical and temperate waters.

REMARKS: This is a widespread, oceanic species recorded since 1902 throughout the entire Hawaiian Archipelago, as well as on the Great Barrier Reef (Mayer 1906, Bentlage *et al.* 2010). As discussed below, *A. moseri* appears to have increased in frequency on O'ahu since the late 1940s (Table 1). Box jellyfish collections of GLC in 1998 and 2000 along the leeward coastline of O'ahu ranged from 54.6 to 93.3 mm BH and 22.0 to 66.5 g wet weight.

Chiaverano *et al.* (2013) reported records over a 14-yr period (1998 to 2011) for *A. moseri* that had no seasonality at Waikīkī Beach. Rather, box jellyfish abundance at Waikīkī Beach fluctuated monthly and annually, and correlated with the changes in the North Pacific Subtropical Gyre (NPGO) index. This index displayed a strong positive correlation with primary production and >2 mm zooplankton biomass that potentially translated to increased food availability for *Alatina moseri* medusae. There was no abundance link to the Pacific Decadal Oscillation or to the Multivariate El Nino-Southern Oscillation Index (Chiaverano *et al.* 2013). This species now appears off Waikīkī Beach every month of the year eight to 12 days after the full moon (Thomas *et al.* 2001a; Chiaverano *et al.* 2013) close to the late night or early morning high tide. To date, the polyps for this species in Hawai‘i have not been found in the wild. Starting in 31 March 1989, this species began to show up at Hanauma Bay (east shore), appearing on 18 May 1990 on the west shore (several areas) and on 28 August 1997 at Waimea Bay north shore of O‘ahu (OSLS records).

On Waikīkī Beach during 21 and 22 October 2000, adult *A. moseri* were observed in spawning condition from the hours of 2300 to 0400 (Carrette *et al.* 2014). During spawning events witnessed in buckets at Bonaire, Dutch West Indies, male *A. alata* gonads became cloudy and ruptured in several spots along the distal axis releasing spermatozoa into the gastro-vascular cavity that were then shed through the manubrium into the water. Females took up the spermatozoa into the gastro-vascular cavity, their gonads became opaque and also ruptured in several spots while eggs were concurrently ovulated into gastric sacs for fertilization (Lewis *et al.* 2013). Within several hours embryos were seen circulating through the entire gastro-vascular system, the fertilized eggs were released and the planulae settled out after several days to start development as polyps (Lewis *et al.* 2013). The polyps of *A. moseri* (reported as *A.* near *mordens*) survived in the laboratory at temperatures of 18 to 31 °C and salinities of 22 to 40 ppt (Courtney & Seymour 2013), well within the range of Hawaiian waters. In the laboratory, polyps began to start metamorphosis 31 days post fertilization (Carrette *et al.* 2014). Polyp cysts of *A. moseri* were highly resistant to high salinities (39.3 ppt) and starvation for more than 12 months could still regenerate when conditions stabilize (Courtney & Seymour 2013, Carrette *et al.* 2014).

The sting of this species produces a mixture of toxic and allergic reactions and in acute cases results in local painful, pruritic erythematous dermatitis that may persist for seven months (Tamanaha & Izumi 1996). Heat treatment, particularly hot showers at 44 °C, helped reduce pain from stings (Yoshimoto & Yanagihara 2002).

Family CARYBDEIDAE Gegenbaur, 1856

Genus CARYBDEA Peron & Lesueur, 1810

This family has heart-shaped rhopaliar niche ostia (Gershwin & Gibbons 2009; Bentlage & Lewis 2012).

Carybdea arborifera (Maas, 1897)

Fig. 2

Synonyms used in Hawaiian literature: *Charybdea arborifera* Maas, 1897, (non *Carybdea rastonii* Haacke, 1886, *Carybdea rastoni* Haacke, 1887, *Charybdea rastoni* Haacke, 1887), *Procharybdis cuboides* Haeckel, 1880.

Original description (Maas 1897): *"Schirm glockenformig bis prismatisch (bei kleineren Exemplaren mehr das erstere), oben flach gewolbt. Gallerte sehr diinn und schlaff. Exumbrella structurlos. Schirmhohe 15, durchmesser 10 mm. Magenrohr etwa 5 (!) mm. lang mit kurzen Mundlappen. Phacellen ein Baumchen in jedem Interradius bildend. Velarium breit, in jedem Quadranten von 4 symmetrisch liegenden und symmetrisch verastelten Canalen durchzogen. Pedalien kaum hervortretend. Tentakel vielmals langer wie die Schirmhohe.*" [Bell is bell-shaped to prismatic (in smaller specimens more the former), top of dome flat. Jelly is very thin and limp. Exumbrella structureless. Bell height 15, diameter 10 mm. Stomach tube about 5 mm long with short oral lobes. Phacellae dendritic in each interradius. Velarium wide, in each quadrant traversed with four symmetrically placed and symmetrically branching canals. Pedalia barely protruding. Tentacles many times longer than the height of the bell.]

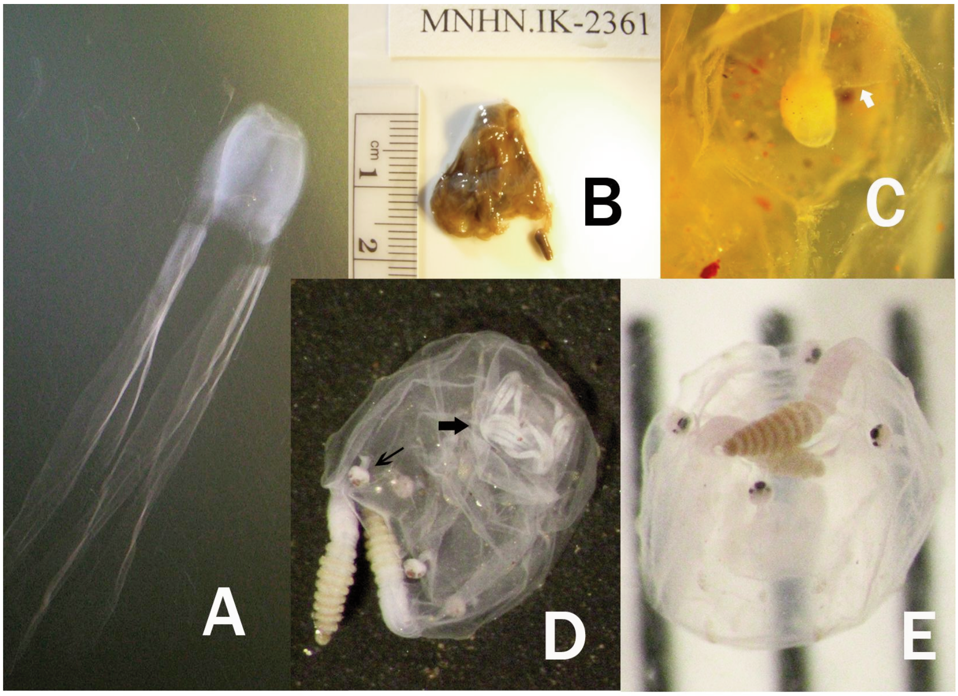

Figure 2. (**A**) Photograph of in situ *Carybdea arborifera* at Kewalo Basin, Oʻahu; (**B**) The 1877 Hawaiian specimen of *Carybdea arborifera* in MNHN; (**C**) Close up of the adult heart-shaped rhopaliar niche ostium of the 1877 *Carybdea arborifera* specimen; (**D**) Juvenile specimen of *Carybdea* from Kāneʻohe Bay, Oʻahu. Note the four gastral filaments in each interradius of juvenile specimen; (**E**) Ventral view of juvenile showing open rhopaliar niche ostium.

Bentlage *et al.* (2010) concluded that *C. arborifera* is a distinct species. Molecular studies (Bentlage *et al.* 2010; this study) have not confirmed the presence of *C. rastonii* in Hawaiʻi. A number of specimens that have been morphologically identified as *C. rastonii* from three Oʻahu localities and were sequenced for this study at two mtDNA loci, 16S and COI (Table 2). However, our 16S gene fragments matched *C. arborifera* in GenBank with a minimum of 99% sequence identity for all specimens, whereas, the match to *C. rastonii* exhibited only 84% sequence identity at maximal query sequence cover (96%) (CQ849116, XQ849117), confirming the identity of the Hawaiʻi specimens as *C. arborifera*. Prior to this investigation, there were no *C. arborifera* COI sequences in GenBank. The top taxonomic match for COI gene fragment was at 81% sequence identity (non-species level match) to the carybdid *Tamoya ohboya* Collins *et al.* (2011), the Bonaire banded box jellyfish.

ECOLOGICAL AND MORPHOLOGICAL INFORMATION: Mayer (1906) reported specimens ranging in size from 11 mm to 35 mm bell height (beginning to mature at about 11 mm bell height) in Hawaiʻi from the 1902 *Albatross* research cruise from Maui, Oʻahu, and Kauaʻi. Crow *et al.* (2006) found *C. arborifera* in Maʻalaea Boat Harbor, Maui by night lighting at the surface.

HAWAII SPECIMENS EXAMINED: MNHN.IK-2361 Iles Sandwich (Hawaiian Islands), 1877, bell height 16.7 mm, labeled as *Carybdea alata*; USNM 52341 (1 specimen) Oʻahu, 3 Jul 1954; USNM 54397 Kāneʻohe Bay, Oʻahu 5 Jul 1972 (5 specimens); BPBM D2272 Kewalo Basin boat harbor, Honolulu, Oʻahu 22 Apr 2004; BPBM D2274 Snug Harbor, Sand Island, Honolulu, Oʻahu 26 May 2004; BPBM D1119 (3 specimens) Maʻalaea Boat Harbor, Maui, 9 Feb 2006; BPBM D1120 (1 specimen) Maʻalaea Boat Harbor, Maui, 7 Feb 2006; BPBM D2273 Lilipuna Pier, Kaneohe Bay, Oʻahu 03 Jul 2013; BPBM D2305 (8 specimens) Kewalo Basin boat harbor, Honolulu, Oʻahu 05 Jul 2006.

HAWAII DISTRIBUTION: Known only from the Hawaiian Islands. Captured at Puniawa Point, Maui in 33 to 77 m, and at Hanalei Bay, Kaua‘i and by surface night lighting in Honolulu Harbor (Mayer, 1906), Kāne‘ohe Bay, Kewalo Basin, Snug Harbor, O‘ahu and Ma‘alaea Harbor, Maui where it was observed feeding on fish on O‘ahu (USNM, and GLC personal observations).

This species appears to have a similar ecological niche as *Carybdea rastonii* in Australia. Matsumoto (1995) reported that adults of *C. rastonii* in Australia have four rhopalia each with six eyes; in the laboratory medusae moved away from dark objects and toward light (white) objects. Medusae were observed near the bottom over sand during daylight and moved to the surface at night or under turbid water conditions (Matsumoto 1995). Stomach contents in Australia consisted of copepods, isopods, amphipods and fishes (Matsumoto 1995).

REMARKS: As noted above, the first specimen of this species from Honolulu (probably Honolulu Harbor) was collected by Ballieu in 1877 and sent to MNHN. The specimen was misidentified as *Carybdea alata*. It is still in the collection (MNHN.IK-2361) and we present photographs of it here (Figs. 2B, C). The species was again captured from Honolulu surface waters in 1891 and described by Maas (1897) as a new species that differs from *rastonii* based on the smooth structure of the bell and the form of gastric phacellae. Mayer (1906) reports *rastonii* from Hawaiian waters (including Honolulu Harbor) but does not discuss *arborifera*. Bigelow (1909) compared specimens from Australia, Tuamotu Archipelago and Hawai‘i and stated that the smooth bell was an artifact of preservation, the gastric phacellae shape represent ontogenetic changes and the similar location data of Honolulu Harbor make it unlikely two species would occur there, therefore, *arborifera* is a probable synonym of *rastonii*. Mayer (1910) stated that *arborifera* was clearly young specimen of *rastonii*. This remained in place until Bentlage *et al.* (2010) showed genetic differences between *arborifera* and *rastonii*.

Family TRIPEDALIIDAE Bentlage, Yanagihara, Lewis, Richards, & Collins, 2010

sensu TRIPEDALIDAE of Conant 1897

Family diagnosis: Sexual dimorphism of the gonads, produces spermatophores and the males have sub-gastric sacs/seminal vesicles (Bentlage & Lewis 2012).

Genus COPULA Bentlage, Yanagihara, Lewis, Richards & Collins, 2010

Copula sivickisi (Stiasny, 1926)

Synonyms used in Hawaiian literature: *Carybdea sivickisi* Stiasny, 1926.

General Description: Key-hole shaped rhopaliar niche ostia (Gershwin, 2005).

ECOLOGICAL AND MORPHOLOGICAL INFORMATION: Matsumoto *et al.* (2002) found this species by night lighting at the surface on the south shore of O‘ahu at the Natatorium (a War Memorial fronting Mamala Bay, Waikīkī) on 8 July 1996, and from the west coast of O‘ahu, Yokohama Bay, on 20 March 1998 at the surface during night collecting and fishing operations 1.3 km offshore over 180 to 550 m of water. Crow *et al.* (2006) reported it from night lighting surveys at the water’s surface in Ma‘alaea Harbor, Maui.

HAWAIIAN SPECIMENS EXAMINED: BPBM D1068 (five specimens) Waikīkī Natatorium, 3 Dec 2001; BPBM D1069 (1 specimen) offshore Yokohoma Bay, O‘ahu, 20 Mar 1998; BPBM D1117 (1 specimen) Ma‘alaea Boat Harbor, Maui, 7 Feb 2006; BPBM D1118 (5 specimens) Ma‘alaea Boat Harbor, Maui, 9 Feb 2006.

HAWAII DISTRIBUTION: O‘ahu and Maui, probably established throughout the main Hawaiian Islands.

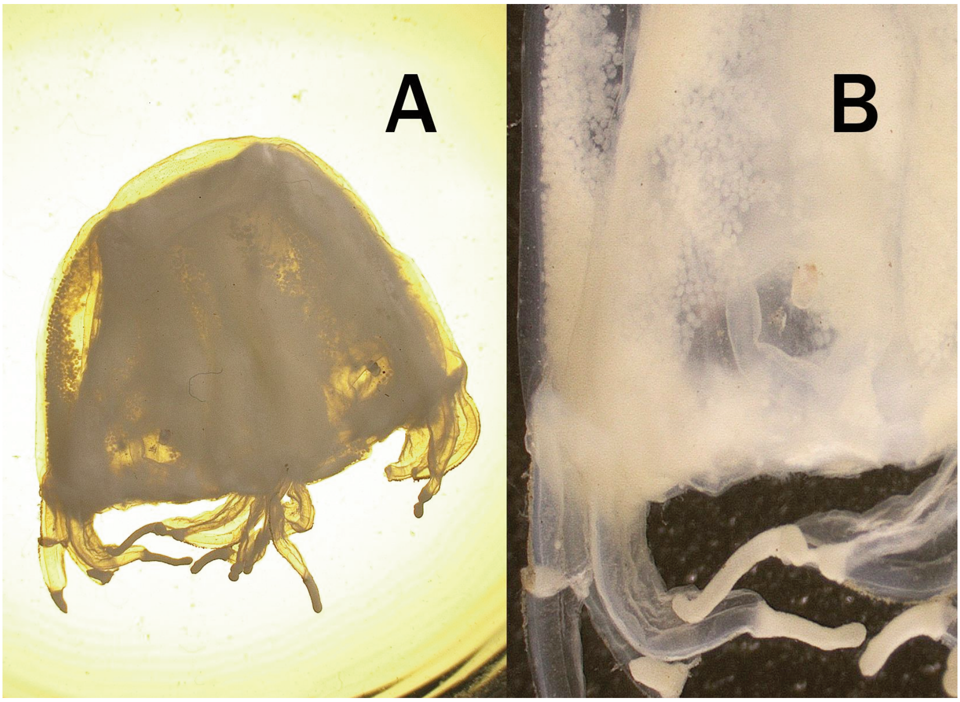

Figure 3. (**A**) Adult female *Tripedalia cystophora* from Enchanted lakes, O‘ahu; (**B**) Close up of eggs in gonadal lamellae of the Hawai‘i specimen.

RANGE: Widespread throughout the Pacific (Philippines, Japan, Hawai‘i, Guam, Vietnam, Thailand, Australia, New Zealand) and Indian Oceans (western Sumatra) (Lewis *et al.* 2008).

REMARKS: *Copula sivickisi* is a small sexually dimorphic cubomedusa ≤14 mm bell diameter with four distinctive adhesive pads that allow attachment to algae, rocks or coral during the day (Hartwick 1991, Long & Lewis 2005). Females with bell diameters larger than 2.5 mm have velar spots and gonads and mature at about 4.5 mm (Lewis *et al.* 2008). During courtship males attach a tentacle to the female and the female is brought in contact with the oral opening of the bell; the male then passes a spermatophore to the female that the female inserts into her manubrium (Lewis & Long 2005, Lewis *et al.* 2008). The female releases an embryo strand to complete reproduction (Lewis & Long 2005). In laboratory culture at 28 °C fertilization to budding was completed in 95 days (Toshino *et al.* 2014). This species is seasonal from May to August in Shirahama, Japan and then presumably dies after reproduction (Lewis & Long 2005). In Hawai‘i, this species was captured in February March, July, and December and probably occurs year round based on capture dates in Matsumoto *et al.* (2002) and Crow *et al.* (2006).

Genus TRIPEDALIA Conant, 1897

Tripedalia cystophora Conant, 1897

Fig. 3

General Description: Medusa with 12 tentacles in four interradial groups with each group having three tentacles. Velarium suspended by four perradial frenula with canals present. Stomach with relatively well developed suspensoria and four horizontal brush-shaped groups of gastric filaments (Conant 1897). Frown-shaped rhopaliar niche ostia (Gershwin 2005).

HAWAIIAN SPECIMENS EXAMINED: BPBM D2256 (9.7 mm BH; 8.3 mm BHR).

HAWAII DISTRIBUTION: A single mature female with eggs was collected 7 August 2011 by Keagan Young at a boat dock near mangroves in the Ka‘elepulu Canal, Enchanted Lakes, O ‘ahu (21°23'25"N, 157°43'45"W). The specimen has been deposited in the Bishop Museum (above).

RANGE: Widespread along tropical and subtropical mangrove habitats: Atlantic (Jamaica, Puerto Rico, Florida, Brazil; Orellana & Collins, 2010), Pacific (Costa Rica; Rodriquez-Saenz & Segura-Puertas 2009), Hawai‘i (herein), Indonesia (Derawan Island, GenBank EU272637, GQ849065) and Indian Oceans (Seychelles, Aldabra Atoll USNM 1078120, USNM 1102214).

REMARKS: Conant (1897) reported this species from the mangrove habitat of Port Henderson and Kingston Harbor, Jamaica. In Puerto Rico, *T. cystophora* feeds on copepods in shafts of daylight within the mangrove prop root forest (Buskey 2003). The visual system is made up of upper and lower lenses, pit and slit eyes (Garm *et al.* 2008). The upper eye lens and pit eye are oriented upward when swimming to help orient to the water surface and terrestrial objects (Garm *et al.* 2008). This allows navigation within the mangrove prop roots and positioning within the canopy (Garm *et al.* 2011). The lower eye lens and slit eye are oriented obliquely downward (Garm *et al.* 2007) presumably for feeding and obstacle avoidance.

Only one specimen of *T. cystophora* is known to date from the Hawaiian Islands. While the single recovered individual was a mature ovigerous female, we do not know if this species is established in Hawai‘i. Since 2011, we have searched for this species in Ka‘elepulu Canal, and nearby regions, both to obtain material for genetic analysis and to determine its status, on 19 August 2011, but without success.

Discussion

Four species of box jellyfish are reported from the Hawaiian Islands: *Alatina moseri*, *Carybdea arborifera*, *Copula sivickisi*, and *Tripedalia cystophora*. *Tripedalia cystophora* actively feeds during the day in the mangroves (Garm *et al.* 2012) while the other three species are nocturnal. *Alatina moseri* is the only species that appears monthly along O‘ahu shorelines and regularly impacts marine recreation, even closing Hanauma Bay on large influx days. Native Hawaiians relied heavily on coastal marine resources and were therefore intimately familiar with nearshore marine flora and fauna of the islands. Using native linguistics as a metric for the presence and importance of various taxa can be instructive, although not definitive, relative to what species were present pre-western contact in 1778. The Hawaiian language includes two names for the Indo-Pacific blue bottle *Physalia utriculus*, *pa‘i malau* and *po‘i malau*, and a generic jellyfish named *pololia*. However, no name was given to the box jellyfish *Alatina moseri* (Pukui & Elbert 1986). It is not clear whether *Alatina moseri* was transported to Hawai‘i with early ship traffic from the western Pacific or it was already wide spread throughout the Pacific basin prior to human mediated transport. Considering the painful nature of the *A. moseri* sting (Tamanaha & Izumi 1996, Yoshimoto & Yanagihara, 2002) it is unlikely that the people of pre-contact Hawai‘i would not have named this animal if it was commonly present in coastal waters.

Alatina moseri is an oceanic species that is present throughout the Hawaiian archipelago and its abundance appears to have increased in the coastal waters of O‘ahu from early 1900s to the late 1980s, including a dramatic increase in abundance since 1948 (Table 1). Beach counts in the 1990s have fluctuated in an oscillating pattern such that its abundance is difficult to predict (Chiaverano *et al.* 2013). Whether coastal alterations on O‘ahu have resulted in increased polyp survival or changing climatic conditions over the 20th century have favored recent proliferation is not clear. Currently, the other populated islands of Maui, Moloka‘i, Kaua‘i, Lāna‘i and Hawai‘i do not experience regular influxes of box jellyfish, although *A. moseri* has been documented offshore throughout the entire archipelago.

Based on genetic data published by Bentlage *et al.* (2010) and this paper, with limited Pacific Ocean sampling *Carybdea arborifera* is currently confirmed only from the Hawaiian Islands.

Table 2. Hawaii molecular systematic data used as a way to confirm the taxonomic identity of box jellyfish in Hawai'i.

All matches to GenBank database had associated expectations values of 0.0 with the exception of COI for *Carybdea arborifera*, which matched *Tamoya ohboya* with an expectation value of 1e-138.

Taxon	Gene Fragment	Locality and date *n* = number of individuals	GenBank accession number; fragment length (base pairs)	Top taxonomic match and percent sequence identity
Alatina moseri	COI	Waikīkī Beach, O'ahu 24 Feb 2014 *n* = 5	KM200330 (637)	*Alatina moseri* 98% identity JN642336
		50 naut. mi off Kona, Big Island , 21 Aug 2012 *n* = 1		
	18S	Waikīkī Beach, O'ahu 10 Aug 2004 *n* = 4	KM200329 (538)	*Alatina mordens*[a] 100% identity GQ849082
		Magic Island, O'ahu 19 May 2009 *n* = 2		
		50 naut. mi off Kona, Big Island , 21 Aug 2012 *n* = 1		
		Waikīkī Beach, O'ahu 24 Feb 2014 *n* = 16		
Carybdea arborifera	COI	Kewalo Basin, O'ahu 22 Apr 2004 *n* = 8	KM200333 (656)	*Tamoya ohboya*[b] 81% identity HQ824532
		Kāne'ohe Bay, O'ahu 3 Jul 2013 *n* = 3		
	16S	Snug Harbor, O'ahu 26 May 2004 *n* = 1	KM200331 (585)	*Carybdea arborifera* 99% identity GQ849096
		Kewalo Basin, O'ahu 22 Apr 2004 *n* = 7		
		Kāne'ohe Bay, O'ahu 3 Jul 2013 *n* = 2		
	18S	Snug Harbor, O'ahu 26 May 2004 *n* = 1	KM200332 (528)	*Carybdea arborifera*, *C. mora*, *C branchii*, *C.* cf *rastonii* 100% identity GQ849091 GQ849094 GQ849093 GQ849089
		Kewalo Basin. O'ahu 22 Apr 2004 *n* = 7		
		Kāne'ohe Bay, O'ahu 03 Jul 2013 *n* = 3		

Although the genes coding for 18S ribosomal RNA (18S rDNA) are widely used in phylogenetic reconstruction, this locus tends to have a relatively slow substitution rate, and therefore is most useful in recovering clades representing class and family relationships. Generally this locus cannot resolve congeneric nodes, therefore it is unable to provide the resolution required for species level recognition, such as within the genus *Carybdea*. In addition, there is increasing support, morphological (Bentlage & Lewis 2012; (capture localities, Mayer 1906, 1910) as well as molecular [data presented here and Bentlage *et al.* (2010)], that *Alatina moseri* is synonymous with *A. mordens* and a widespread lineage in the Pacific Ocean, including Hawaii and Australia.

The Hawaiian Islands are clearly vulnerable to marine introductions via ship traffic (ballast water and hull-fouling) and other sources (Carlton 1987, Apte *et al.* 2001). Eldredge & Carlton (2002) estimated 87% of the introduced marine invertebrates were transported to the Hawaiian Islands via hull-fouling, solid ballast and ballast water. Six primary incoming routes of transoceanic vessel-mediated introductions were detected for Hawai‘i, four from the western Pacific and one each from the eastern Pacific coast of North America and French Polynesia (Carlton, 1987). There is evidence that biogeographically isolated, relatively depauperate marine communities such as those of the Hawaiian Islands are highly susceptible to marine invasions (Hutchings *et al.* 2002). Introduced jellyfish *Cassiopea* spp. from two different ocean basins (Holland *et al.* 2004), *Phyllorhiza* sp. and *Aurelia* sp. from the western Pacific Ocean (Dawson *et al.* 2005; Carlton & Eldredge 2009) and *Mastigias* sp. (GLC pers. observ.) have become established in Hawai‘i. At least two of the box jellyfish in Hawai‘i, *Copula sivickisi* and *Tripedalia cystophora* appear to be introduced. Clearly, Hawai‘i is vulnerable to introduction of jellyfish and constant surveillance is necessary to keep additional species, especially the more dangerous “irukandji” taxa, from becoming established.

Worldwide jellyfish populations received relatively little attention until after the 1950s (Purcell, 2012). Natural jellyfish population fluctuations (including 10 yr and 20 yr cycles) in conjunction with solar and climatic cycles and anthropogenic changes to the environment including climate, eutrophication, overfishing, coastal construction, aquaculture and transport of nonindigenous species may have resulted in jellyfish proliferations (Purcell, 2012; Condon *et al.* 2013; Duarte *et al.* 2013). Detailed oceanographic, climatic, systematic and ecological studies are needed to better understand and predict changes in the distributions and the long-term impacts of cubomedusae on coastal ecology and recreation in the Hawaiian Islands. Such data will provide predictive value in our understanding of range expansion and management of established box jellyfish, as well as potential invasion by additional harmful box jellyfish species.

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Key to Table 2: CO1= mitochondrial cytochrome *c* oxidase subunit I; 16S= mitochrondrial rRNA small ribosomal subunit; 18S= nuclear small subunit (SSU) rRNA ribosomal gene

a. Match used to compare GenBank sample JN642336.1 (Smith *et al.* 2012) to this study sample KM200330.

b. There are no entries for 18S gene fragment from *Alatina moseri* in GenBank; however, 100% match from *A. moseri* from Waikīkī this study GenBank KM200329 to *A. mordens* from Australia GenBank GQ849082.1 supports the conclusion that *A. mordens* and *A. moseri* from Hawai‘i could be the same species as was detailed by Bentlage *et al.* (2010).

c. There are no COI sequences for *Carybdea arborifera* in GenBank; closet match is the sequence for *Tomoya ohboya* with an 81% match.

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