

Rapid Communication

Clava multicornis (Forsskål, 1775): rediscovery of a North Atlantic hydroid (Cnidaria, Hydrozoa, Anthoathecata) on the Pacific coast of North America

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Abstract

The shallow-water hydroid *Clava multicornis* is reported from the west coast of North America for the first time in nearly six decades. A North Atlantic species often occurring on intertidal fucoid algae, it had been found elsewhere only in heavily-invaded San Francisco Bay, California, with records dating from the late 19th to mid-20th centuries. The species has not been reported from the Bay Area since 1954, in spite of intensive recent collecting, and it is presumed to no longer exist there. During the winter and summer of 2013, robust colonies (which were fertile in the winter) were discovered in fouling communities on floating docks further north in Coos Bay, Oregon. This estuary harbours a large number of introduced species from both the western Pacific and the North Atlantic. We suspect that *C. multicornis* was introduced to Coos Bay in one of two ways. One means of transport might have been in hull fouling on ships, either directly from the North Atlantic or possibly from another Pacific coast estuary where the species remains undetected. A second possibility is on fucoid algae used in the shipment of polychaete bait worms from the State of Maine, on the Atlantic coast of the United States.

Key words: Coos Bay, Oregon, fouling, Hydractiniidae, introduced species, long-range dispersal, northeast Pacific, San Francisco Bay

Introduction

Commonly known as the club hydroid (Cairns et al. 2002), *Clava multicornis* (Forsskål, 1775) is one of the most familiar species of hydroids inhabiting intertidal shores on both sides of the North Atlantic Ocean. Populations range from the Barents Sea and the White Sea (Naumov 1960) to northern Portugal (Schuchert 2012) in northwest Europe, and from southern Labrador to Long Island Sound on the east coast of North America (Fraser 1944). Frequently used substrates on both sides of the Atlantic include fucoid algae (especially *Ascophyllum nodosum* (Linnaeus, 1753)), rocks, barnacles, wharf pilings, and timbers (Schuchert 2008; personal observations), and it is most prevalent in relatively sheltered areas exposed to tidal currents. The report of a hydroid identified with question as *C. multicornis* from

Puerto Rico in the Caribbean Sea (Wedler and Larson 1986) is discounted given the known geographic distribution and temperature tolerances of the species.

Elsewhere, *C. multicornis* has been recorded only from San Francisco Bay, on the Pacific coast of the United States (Torrey 1902; Fraser 1937, 1938a, 1946; Light 1941; Smith et al. 1954). However, there have been no reports of the species from the Bay Area (or elsewhere on the west coast of North America) in more than 50 years (Mills et al. 2007). The purpose of this account is to document the rediscovery of *C. multicornis* in the eastern North Pacific. Colonies were found during winter and summer 2013 on mussels growing on a floating dock in Coos Bay, Oregon. Voucher material has been deposited in collections of the Invertebrate Zoology Section, Department of Natural History, Royal Ontario Museum (ROMIZ).

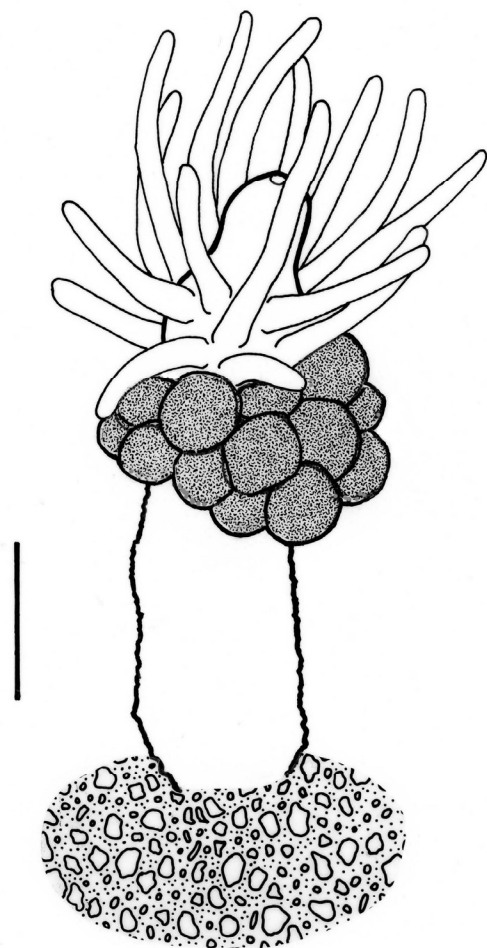


Figure 1. *Clava multicornis*: hydranth with gonophores, Coos Bay, Oregon, USA. ROMIZ B4016. Scale equals 0.5 mm.

Systematic Account

Phylum Cnidaria Verrill, 1865

Class Hydrozoa Owen, 1843

Order Anthoathecata Cornelius, 1992

Suborder Filifera Kühn, 1913

Family Hydractiniidae L. Agassiz, 1862

Species *Clava multicornis* (Forsskål, 1775)

(Figures 1, 2)

Hydra multicornis Forsskål, 1775: 131 [original description].

Clava leptostyla.—Torrey, 1902: 30, pl. 1, figs. 8–12 [original records].—Fraser, 1911: 19 [discussion].—Fraser, 1937: 20, pl. 1, fig. 1 [original records]; 1938a: 40 [discussion]; 1946: 37, 100 [discussion].—Light, 1941: 18, fig. 8A [original record].—Smith et al., 1954: 32, fig. 7c

[original records].—Carlton, 1975: 18; 1979b: 432 [listed].

Not *Clava leptostyla*.—Heath, 1910: 73.

Clava multicornis.—Mills et al. 2007: 153 [discussion].

Material: USA, Oregon, Coos County, Coos Bay, Isthmus Slough, on mussel shells (*Mytilus trossulus* Gould, 1850; identification based upon absence of genetic evidence for *M. galloprovincialis* Lamarck, 1819 or hybrids in Coos Bay, JTC, unpublished) from fouling on a floating dock, 09.iii.2013, colonies with gonophores, coll. J.T. Carlton, ROMIZ B4016.

Remarks

The synonymy list above includes the original description of *Clava multicornis* by Forsskål (1775) from Scandinavia, together with published accounts of the species from the northeast Pacific. All reliable records of *C. multicornis* from the west coast of North America until now have been from San Francisco Bay, California.

Particularly noteworthy contemporary accounts of this species include those of Thiel (1970), Edwards and Harvey (1975) and Schuchert (2008), with synonymy lists being given in the latter two. A biological overview of *Clava multicornis* is also presented in Schuchert (2012). Now considered junior subjective synonyms of *C. multicornis* are the names *C. squamata* (Müller, 1776) and *C. leptostyla* L. Agassiz, 1862.

Another species assigned to the genus *Clava* Gmelin, 1790 from the Americas is *C. parva* Fraser, 1938b from Isla Jicarita, Pacific coast of Panama. That hydroid, known only from its type locality, is described by Fraser (1946) as “a very good miniature” of *C. leptostyla* (= *C. multicornis*). Its polyps are only 2 mm rather than about 10 mm high, and tentacle number is 20 instead of 20–40. More importantly, polyps arise from a thin encrustation, with no stolons visible superficially (Fraser 1938b), rather than from a creeping or anastomosing stolon system as in its supposed congener (Schuchert 2008). It also occurs in deeper water than the typically intertidal *C. multicornis*, having been found on a gastropod shell collected at a depth of 30 fathoms (55 m). Calder et al. (2009) considered the generic identity of *C. parva* to be uncertain, although it was believed to be referable to family Hydractiniidae. *Clava nana* Motz-Kossowska, 1905 from the Mediterranean Sea was regarded by Schuchert (2008) as an indeterminable species of hydractiniid.



Figure 2. *Clava multicornis*: three photographs of living, fertile colonies from Coos Bay, Oregon, USA. Note both salmon-coloured and whitish colonies (Photographs by J.T. Carlton and D.A. Carlton).

Still unresolved is a nomenclatural issue concerning the name of the family to which the genus *Clava* should be assigned. Schuchert (2001) demonstrated that *Clava* is referable to the same family as *Hydractinia* Van Beneden, 1844 and related genera. A recent phylogenetic analysis using a combined dataset of nearly complete nuclear 28S, nearly complete nuclear 18S, and partial mitochondrial 16S rDNA sequences by Cartwright et al. (2008) supports this interpretation. Thus, two well-known names, Clavidae McCrady, 1859 and Hydractiniidae L. Agassiz, 1862, become synonyms. Notwithstanding its status as a junior synonym, the more widely used name Hydractiniidae has been retained for the group in most recent taxonomic works. Meanwhile, the senior synonym, Clavidae, is gradually being abandoned. Potential nomenclatural instability still exists because the case has not yet been submitted to the International Commission on Zoological Nomenclature for a ruling.

Populations from Oregon, examined in March 2013, consisted of two colour morphs (Figure 2): (1) salmon-coloured polyps with light salmon-coloured gonophores, and (2) white polyps with intermixed gonophores of two colours, dark gray and light orange-peach. The significance of these colours is not known, nor does this polymorphism appear to have been remarked upon in previous literature. The two colours of polyps may have been due to feeding differences or to the stage of food digestion in them, but we note that the colour morphs were in distinct clusters, often adjacent, but not intermixed.

Discussion

The first published record of *C. multicornis* on the Pacific coast of North America was by Torrey (1902, as *C. leptostyla* L. Agassiz, 1862), who reported finding it throughout the year in Oakland Harbor within San Francisco Bay. Torrey's record of the species was repeated in an account of west coast hydroids by Fraser (1911). Later, Fraser (1937) observed that *C. leptostyla* was distributed "In much of the shore line, shallow water—10 fathoms or less—of San Francisco bay; from Mare island to Oakland and in the lower section of the bay as far as San Mateo. Off Lime point is the farthest seaward location noted." This account by Fraser was almost certainly based on collections of hydroids made available to him by Dr. C. A. Kofoid of the University of California, Berkeley, and included material from a biological and hydrographical survey of the bay in 1912 and 1913 (Fraser 1937: 5, 9). Light (1941) included "*C. leptostyla*" in a list of hydroids occurring in San Francisco Bay. Smith et al. (1954) noted that the species was abundant during spring on two bridges (Fruitvale and Bay Farm Island) in the Oakland Estuary; these observations would have been made between the late 1940s and early 1950s. Occurrence of *C. multicornis* on the west coast has been attributed to shipping, given its highly restricted distribution there (Fraser 1937, 1938a, 1946; Carlton 1979a, b; Mills et al. 2007).

Meanwhile, Carlton (1979a; subsequently published in Mills et al. 2007) noted that *C. multicornis* is known to have occurred in San

San Francisco Bay as early as 1895. That observation is based on material held in collections at the National Museum of Natural History (NMNH), Smithsonian Institution (*Clava leptostyla*, USNM 43476, Oakland Creek, 05 October 1895). Six other San Francisco Bay lots identified as this species from “Oakland Harbor” or “Oakland Creek” collected between 1896 and 1899 are held at the NMNH (USNM 43469, USNM 43470, USNM 43471, USNM 43473, USNM 43474, and USNM 43475). One additional lot (USNM 43468) is indicated as “San Francisco Bay,” which we assume to be of the same era and site. No collections from California are listed in online catalog records of the museum after 1899.

Online collection records of the California Academy of Sciences revealed three specimen lots of “*Clava*” from the Pacific coast of North America (Monterey Bay, 1922; Mexico, 1974; Alaska, 1975). Photographs provided by C. Piotrowski (February, 2014) demonstrated that these specimens are a non-clavid hydroid, an oceaniid hydrozoan likely referable to *Corydendrium parasiticum*, and unidentifiable hydroid fragments, respectively.

A casual mention of *Clava leptostyla* in a paper by Heath (1910), from an undisclosed location but possibly from Monterey Bay, California (where Heath did much of his work), has been disregarded as a misidentification. The hydroid was reported from the spines of the Pacific coast sea urchin *Strongylocentrotus franciscanus* A. Agassiz, 1863 (now *Mesocentrotus franciscanus*), a species occurring in relatively high energy environments on open rocky intertidal and subtidal shores. This is an anomalous habitat and environment for *C. leptostyla* (= *C. multicornis*), and it was likely a different species. It is unreported from exposed rocky shores of the Pacific coast, and is not known to be a sea urchin associate.

McCormick (1965) reported a hydroid identified as *Clava* sp. from the continental slope off Oregon (44°38.8'N, 124°53.9'W, 500–599 m, on the buccinid gastropod *Mohnia frielei* Dall, 1891; now *Retimohnia frielei*). The depth at which it was found is well below the bathymetric range of *C. multicornis*, which extends from the intertidal zone to depths of only about 20 m (Schuchert 2008).

Several biological surveys during recent years in the heavily invaded and much-studied San Francisco Bay estuary have failed to locate *C. multicornis*. Two of us (JTC, DRC) have searched

unsuccessfully for the species there, including at the bridges in the Oakland Estuary noted by Smith et al. (1954). The last records of *C. multicornis* from any location on the west coast of North America are those of Smith et al. (1954). Thus, with the lack of collections after the earliest 1900s, and the lack of tangible reports for the past 60 years, we conclude that *C. multicornis* no longer exists in San Francisco Bay.

The recent discovery of *C. multicornis* to the north of San Francisco Bay in Coos Bay, Oregon, reported herein, is thus of zoogeographic note, as it re-establishes the presence of this species in the northeast Pacific. On 09 March 2013, robust, fertile colonies, with numerous gonophores (Figures 1, 2), were found in an estuarine backwater region of the bay known as Isthmus Slough, in brackish (salinity 14 psu), cold (~10° C) water. Colonies were found encrusting the native mussel *Mytilus trossulus* on floating docks. On 07 July 2013, colonies were still present in Isthmus Slough (albeit no longer fertile) at a salinity of 19.6 psu and temperature of 22.2° C, and were also discovered on the same day 0.8 km north of Isthmus Slough on the Coos Bay city floating docks at 18.3 psu and a temperature of 21.2° C. *Clava multicornis* was not detected in previous extensive surveys of fouling communities in Coos Bay, including the Isthmus Slough and Coos Bay city docks, between 1986 and 2001 (Hewitt 1993; J.T. Carlton, unpublished data) and thus is unlikely to have been overlooked prior to 2013. This said, we re-examined preserved collections of fouling communities from these sites from 1988, 1997, and 2009, and while hydroids of *Obelia* sp. were present, those of *C. multicornis* were absent.

Clava multicornis has not been historically reported from far eastern seas of the Russian Federation, or from Japan, Korea, or China, and the Coos Bay population is, therefore, unlikely to have been introduced from the western Pacific. Given its abundance in lower intertidal and shallow subtidal waters of the North Atlantic (Fraser 1944; Calder 2012; Schuchert 2012), we predict that the Coos Bay population will be found to genetically match a source population either in the western or eastern North Atlantic.

Prior to the mid-20th century, Atlantic oysters (*Crassostrea virginica* Gmelin, 1790) are believed to have been planted on occasion in Coos Bay (Carlton 1979a), but there have been no recorded importations of Atlantic shellfish into this estuary in recent decades. Introduction into Coos Bay (the largest deep-draft port between

Puget Sound and San Francisco Bay) is likely to have been via ships' hull or sea chest fouling communities, either directly from the Atlantic Ocean, or from another Pacific coast harbour where *C. multicornis* is present but, as a small and often inconspicuous species, undetected.

An additional potential (and currently active) vector for the introduction of *Clava multicornis* to the North American Pacific coast (and to elsewhere around the world) is the polychaete bait worm industry based in the State of Maine (Carlton 2001; Haska et al. 2011; Cohen 2012). Live worms intended for fishing bait are packed in Maine in furoid algae (*Ascophyllum* and *Fucus*) and shipped to many regions. Several successful introductions in San Francisco Bay of crustaceans, mollusks, and algae from Maine have been attributed to this vector (summarized in Cohen 2012). Miller (1969) found *Clava multicornis* (reported as *Clava leptostyla*) on baitworm algae shipped to California. However, we know of no releases of worms and associated algal dunnage in Coos Bay, and no invasions in the bay have been directly associated with this vector.

Clava multicornis is restricted bathymetrically to intertidal and shallow subtidal waters. Hydranths avoid desiccation when exposed at low tide by clumping together into jelly-like masses (Edwards and Harvey 1975). While *C. multicornis* is both euryhaline and relatively eurythermal (Kinne and Paffenhöfer 1965, 1966), its survivability is also enhanced in that the hydroids are capable of undergoing dormancy (diapause) during unfavourable periods (Broch 1925; Kramp 1935; Thiel 1970; Makrushin 1986; personal observations). With the return of favourable environmental conditions, hydranths are regenerated from resting stages ("menonts") in the stolons. Such resistant stages, widespread in hydroids, may also facilitate long-range transport in the group (Calder 1990), such as might occur during open-ocean transits in ship fouling communities.

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References

- Agassiz A (1863) List of the echinoderms sent to different institutions in exchange for other specimens, with annotations. *Bulletin of the Museum of Comparative Zoölogy at Harvard College, in Cambridge* 1: 17–28
- Agassiz L (1862) Contributions to the natural history of the United States of America. Vol. IV. Little, Brown & Company, Boston, 380 pp
- Broch H (1925) Biogeographie vom Tier aus. *Naturwissenschaften* 13: 447–452, <http://dx.doi.org/10.1007/BF01558740>
- Cairns SD, Calder DR, Brinckmann-Voss A, Castro CB, Fautin DG, Pugh PR, Mills CE, Jaap WC, Arai MN, Haddock SHD, Opreko DM (2002) Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora. Second Edition. American Fisheries Society Special Publication, 28, 115 pp
- Calder DR (1990) Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina, U.S.A. *Canadian Journal of Zoology* 68: 442–450, <http://dx.doi.org/10.1139/z90-065>
- Calder DR (2012) On a collection of hydroids (Cnidaria, Hydrozoa, Hydroidolina) from the west coast of Sweden, with a checklist of species from the region. *Zootaxa* 3171: 1–77
- Calder DR, Vervoort W, Hochberg FG (2009) Lectotype designations of new species of hydroids (Cnidaria, Hydrozoa), described by C.M. Fraser, from Allan Hancock Pacific and Caribbean Sea Expeditions. *Zoologische Mededelingen* 83: 919–1058
- Carlton JT (1975) Introduced intertidal invertebrates. In: Smith RI, Carlton JT (eds), *Light's manual: intertidal invertebrates of the central California coast*. Third edition. University of California Press, Berkeley, pp 17–25
- Carlton JT (1979a) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. PhD dissertation, Ecology, University of California, Davis, 904 pp
- Carlton JT (1979b) Introduced invertebrates of San Francisco Bay. In: Conomos TJ (ed), *San Francisco Bay: the urbanized estuary*. Pacific Division, American Association for the Advancement of Science, San Francisco, pp 427–444
- Carlton JT (2001) Introduced species in U.S. coastal waters: environmental impacts and management priorities. Pew Oceans Commission, Arlington, Virginia, 28 pp
- Cartwright P, Evans NM, Dunn CW, Marques AC, Miglietta MP, Schuchert P, Collins AG (2008) Phylogenetics of Hydroidolina (Hydrozoa: Cnidaria). *Journal of the Marine Biological Association of the United Kingdom* 88: 1663–1672, <http://dx.doi.org/10.1017/S0025315408002257>
- Cohen AN (2012) Aquatic invasive species vector risk assessments: live saltwater bait and the introduction of non-native species into California. California Ocean Science Trust, Oakland, California, 58 pp
- Cornelius PFS (1992) Medusa loss in leptolid Hydrozoa (Cnidaria), hydroid rafting, and abbreviated life-cycles among their remote-island faunas: an interim review. *Scientia Marina* 56: 245–261
- Dall WH (1891) Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. No. XX. On some new or interesting west American shells obtained from the dredgings of the U.S. Fish Commission Steamer Albatross in 1888, and from other sources. *Proceedings of the United States National Museum* 14: 173–191, <http://dx.doi.org/10.5479/si.00963801.14-849.173>

- Edwards C, Harvey SM (1975) The hydroids *Clava multicornis* and *Clava squamata*. *Journal of the Marine Biological Association of the United Kingdom* 55: 879–886, <http://dx.doi.org/10.1017/S0025315400017768>
- Forsskål P (1775) Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål. Prof. Haun. Post mortem auctoris edidit Carsten Niebuhr. Mölleri, Hauniae, 140 pp, <http://dx.doi.org/10.5962/bhl.title.2154>
- Fraser CM (1911) The hydroids of the west coast of North America with special reference to those of the Vancouver Island region. *Bulletin from the Laboratories of Natural History of the State University of Iowa* 6: 1–91
- Fraser CM (1937) Hydroids of the Pacific coast of Canada and the United States. University of Toronto Press, Toronto, 207 pp
- Fraser CM (1938a) Hydroid distribution in the north-eastern Pacific. *Transactions of the Royal Society of Canada*, series 3, 5, 32: 39–42
- Fraser CM (1938b) Hydroids of the 1934 Allan Hancock Pacific Expedition. *Allan Hancock Pacific Expeditions* 4(1): 1–105
- Fraser CM (1944) Hydroids of the Atlantic coast of North America. University of Toronto Press, Toronto, 451 pp
- Fraser CM (1946) Distribution and relationship in American hydroids. University of Toronto Press, Toronto, 464 pp
- Gmelin JF (1790) Caroli a Linné, systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima tertia, aucta reformata. Tomus 1, Pars 6. Lipsiae, pp 3021–4120
- Gould AA (1850) Shells from the United States Exploring Expedition. *Proceedings of the Boston Society of Natural History* 3: 343–348
- Haska CL, Yarish C, Kraemer G, Blaschik N, Whitlatch R, Zhang H, Lin S (2011) Bait worm packaging as a potential vector of invasive species. *Biological Invasions* 14: 481–493, <http://dx.doi.org/10.1007/s10530-011-0091-y>
- Heath H (1910) The association of a fish with a hydroid. *Biological Bulletin* 19: 73–78, <http://dx.doi.org/10.2307/1536178>
- Hewitt CL (1993) Marine biological invasions: the distributional ecology and interactions between native and introduced encrusting organisms. PhD Thesis, Biology, University of Oregon, Eugene, 301 pp, <http://hdl.handle.net/1794/9974>
- Kinne O, Paffenhöfer G-A (1965) Hydranth structure and digestion rate as a function of temperature and salinity in *Clava multicornis* (Cnidaria, Hydrozoa). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 12: 329–341, <http://dx.doi.org/10.1007/BF01612558>
- Kinne O, Paffenhöfer G-A (1966) Growth and reproduction as a function of temperature and salinity in *Clava multicornis* (Cnidaria, Hydrozoa). *Helgoländer Wissenschaftliche Meeresuntersuchungen* 13: 62–72, <http://dx.doi.org/10.1007/BF01612656>
- Kramp PL (1935) Polypdyr (Coelenterata) I. Ferskvandspolyper og goplepolyper. *Danmarks Fauna* 41: 1–207
- Kühn A (1913) Entwicklungsgeschichte und Verwandtschaftsbeziehungen der Hydrozoen. I. Teil: Die Hydroiden. *Ergebnisse und Fortschritte der Zoologie* 4: 1–284
- Lamarck JBPA de (1819) Histoire naturelle des animaux sans vertèbres. Edition 2, 6, Paris, 232 pp
- Light SF (1941) Laboratory and field text in invertebrate zoology. Associated Students Store, University of California, Berkeley, 232 pp
- Linnaeus C (1753) Species plantarum, exhibentes plantas rite cognitatas, ad genera relatas, cum differentiis specificis, nominibus trivialibus, synonymis selectis, locis natalibus, secundum systema sexuale digestas. Tomus II. Laurentii Salvii, Holmiae, pp 561–1200
- Makrushin AV (1986) Pokoyashchiesya stadii *Clava multicornis*, *Obelia loveni* i *O. flexuosa* (Hydroidea, Leptolida). Resting stages of *Clava multicornis*, *Obelia loveni* and *O. flexuosa* (Hydroidea, Leptolida). *Zoologicheskii Zhurnal* 65: 1254–1258 (Russian text, English summary)
- McCormick JM (1965) Some aspects of the ecology of hydroids off the Oregon coast. *Northwest Science* 39: 139–147
- McCrary J (1859) Gymnophthalmata of Charleston Harbor. *Proceedings of the Elliott Society of Natural History* 1: 103–221
- Miller RC (1969) *Ascophyllum nodosum*: a source of exotic invertebrates introduced into the west coast near-shore marine waters. *Veliger* 12: 230–231
- Mills CE, Calder DR, Marques AC, Migotto AE, Haddock SHD, Dunn CW, Pugh PR (2007) Combined species list of hydroids, hydromedusae, and siphonophores. In: Carlton JT (ed), *The Light and Smith manual. Intertidal invertebrates from central California to Oregon*. Fourth edition. University of California Press, Berkeley, pp 151–168
- Motz-Kossowska S (1905) Contribution à la connaissance des hydriaires de la Méditerranée occidentale. I. Hydriaires gymnoblastiques. *Archives de Zoologie Expérimentale et Générale*, 4^{me} série, 3: 39–98
- Müller OF (1776) *Zoologiae Danicae prodromus, seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium*. Hallagerii, Hauniae, 282 pp, <http://dx.doi.org/10.5962/bhl.title.13268>
- Naumov DV (1960) Gidroidy i gidromeduzy morskikh, solonovatovodnykh i presnovodnykh basseinov SSSR. *Akademiya Nauk SSSR, Opredeliteli po Faune SSSR* 70: 1–626
- Owen R (1843) Lectures on the comparative anatomy and physiology of the invertebrate animals: delivered at the Royal College of Surgeons, in 1843. Longman, Brown, Green, & Longmans, London, 392 pp
- Schuchert P (2001) Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). *Meddelelser om Grønland, Bioscience* 53: 1–184
- Schuchert P (2008) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera Part 3. *Revue Suisse de Zoologie* 115: 221–302
- Schuchert P (2012) North-west European athecate hydroids and their medusae. *Synopses of the British Fauna*, new series, 59, 364 pp
- Smith RI, Pitelka FA, Abbott DP, Weesner FM (revisers) (1954) Intertidal invertebrates of the central California coast. S.F. Light's "Laboratory and field text in invertebrate zoology." University of California Press, Berkeley, 446 pp
- Thiel H (1970) Beobachtungen an den Hydroiden der Kieler Bucht. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung*, neue Serie, 21: 474–493
- Torrey HB (1902) The Hydroidea of the Pacific coast of North America, with especial reference to the species in the collection of the University of California. *University of California Publications, Zoology* 1: 1–105
- Van Beneden P-J (1844) Sur les genres Eleuthérie et Synhydre. *Bulletins de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles* 11(2): 305–314
- Verrill AE (1865) Classification of polyps: (extract condensed from a synopsis of the Polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S.N.). *Proceedings of the Essex Institute* 4: 145–152
- Wedler E, Larson R (1986) Athebate hydroids from Puerto Rico and the Virgin Islands. *Studies on Neotropical Fauna and Environment* 21: 69–101, <http://dx.doi.org/10.1080/01650528609360698>