Electronic Supplementary Material

A SYSTEMATIC REVIEW OF THE EVOLUTION OF JELLYFISH BLOOMS: ADVANTAGEOUS AGGREGATIONS AND ADAPTIVE ASSEMBLAGES

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Appendix A: Contextualistic analyses indicate that hydromedusae, in comparison to scyphomedusae, relatively rarely bloom or swarm

Is the conclusion that hydromedusae generally do not bloom or swarm biased because they have been systematically overlooked due to their small size? To answer this question, we conducted three preliminary *ad hoc* contextualistic analyses.

Hypothesis 1. Historically, there has been no systematic research bias against hydromedusae.

We suggest this hypothesis is generally true, on several grounds. Historically many of the influential researchers who have studied Scyphozoa have also studied Hydrozoa. For example, Ernst Haeckel, Paul L. Kramp, Robert Lendlmayr von Lendenfeld, Alfred Goldsborough Mayer, Frederick Stratten Russell, and others. Oceanographic cruises often collected both hydromedusae and scyphomedusae (e.g. the Albatross, Challenger, Dana, and Siboga expeditions). The Hydrozoan Society, which was founded in 1985 (Boero & Mills, 1999), convened its fourth meeting in 1998 with 54 attendees (approximately 24 working to some extent with hydromedusae) and its sixth and most recent meeting was attended by circa 40 members. Although there is currently no society for scyphozoan researchers, two jellyfish blooms symposia have been convened (2000, 2007) attracting circa 70 and 61 participants respectively. These two groups share some members in common. Reports on jellyfish blooms have considered both hydromedusae and scyphomedusae (e.g. Mills, 1995, 2001; Purcell 2005; Purcell et al., 2007). If there has been a bias, it is indicated to be small (less than double in favor of scyphomedusae).

Hypothesis 2. Researchers who have studied hydromedusae and scyphomedusae find that hydromedusae are, on a percentage basis, approximately as frequently aggregators, bloomers, or swarmers as Scyphomedusae.

We suggest this hypothesis is false, on the basis of thorough readings of two texts.

(i) In his carefully structured 1910 monograph "*Medusae of the World*" A. G. Mayer (1910) repeatedly uses terms describing abundance of hydromedusae – e.g. single specimen found, several specimens, rare, quite common, common, very common, abundant, very abundant, extremely/exceedingly abundant, small swarms, vast swarms – in a paragraph on spatial distribution, abundance, and temporal occurrence included within separate entries on a species-by-species basis. From his usage, it is clear that Mayer distinguished a species geographic distribution from its abundance at any particular time or its temporal pattern of occurrence. Mayer (1910) makes three comments that indicate how these terms should be interpreted quantitatively: "*Pseudoclytia pentata* … In 1905 was relatively rare, and only 3 specimens seen throughout the summers of 1906 and 1907 despite extensive searching with net" (p. 278), "*Staurodiscus tetrastaurus* … is common on the surface at Tortugas, Florida, in July and August … I have seen hundreds of specimens at Tortugas" (p. 214), "*Pseudoclytia pentata* … exceedingly abundant at Tortugas … June-August 1897-1904 … At times during 1898 these medusae were so abundant that one could not dip up a bucketful of water without capturing several specimens" (p. 278).

Of records for 1,248 species and varieties of hydromedusae, Mayer (1910) reported that six were exceedingly or extremely abundant, one occurred in vast numbers, one in small swarms and five in vast swarms. That is, Mayer considered that 1% of hydromedusae occurred *en masse*; this figure rises to 1.5% after adjusting for the modern estimate of ~850 species of hydromedusae.

Regarding Scyphozoa, Mayer (1910) made general statements about mass occurrences of families and genera within Scyphozoa which he supplemented with examples for particular species. He evidently considered mass occurrence characteristic of the medusae within each of these higher taxa. Mayer (1910) documented swarms of *Linuche unguiculata* (Swartz), *Linuche aquila* Haeckel, many Pelagiidae, *Cyanea capillata*, *Aurelia aurita* (Linné), *Cephea cephea* (Forsskål), and *Catostylus mosaicus*. Thus, assuming approximately half the number of Pelagiidae is something close to "many" species, we conservatively estimate that Mayer considered circa 11% of scyphomedusae to occur *en masse*; this fraction would increase to ~14% adjusting for the modern estimate of ~200 species of scyphomedusae (with many more species of *Aurelia* occurring *en masse*).

It is important to note that Mayer (1910) seems to have been applying relatively consistent estimates of numerical abundance to both hydromedusae and scyphomedusae.

For example, the small scyphomedusa *Linuche* is the only scyphozoan he thought occurred in 'vast swarms', the term he applied to five or six species of small hydromedusae. In contrast, he considered the widespread and familiar *Aurelia* to be "common from Greenland to the West Indies" (p. 625), and "abundant in the lagoons of the atolls of the Maldives" (p. 629) but mentioned only one swarm; similarly he described the large hydromedusae *Aequorea* as "common" (pp. 325, 331), "abundant" (p. 332), "very abundant at Tortugas" (p. 329). That the large medusae were not also recorded systematically as the most numerous indicates Mayer's estimates of abundance were not confounded by size. Consequently, the biomass of medusae present documented by Mayer (1910) oftentimes must be several orders of magnitude greater for events involving Scyphozoa than events involving Hydrozoa with concomitant differences in ecological impact (see Dawson & Hamner, this volume).

Mayer (1910) makes several other comments notable in the context of our current study. "Anthomedusae … thrive in harbors" (p. 18), "*Limnocnida tanganjicae* Günther … is exceedingly abundant in the fresh-water Lake Tanganyika" (p. 371), and "*Olindias sambaquiensis* F. Müller … is abundant upon the surface during calm days" (p. 354) indicating mass occurrence is favored in enclosed or semi-enclosed and hydrographically benign situations. He noted that "large swarms of [*Dipleurosoma ochracea* Mayer] appeared at Tortugas, Florida, between July 5 and 24, 1907, but no mature specimens could be found" (p. 226) consistent with oceanographic processes impacting occurrences as opposed to growth of a local population. Mayer also reported that "a hydroid of [*Bougainvillia britannica* Forbes] from the Eddystone, English Channel, … liberated 4,450 medusae in 3 days" but does not record them ever as swarming (p. 162), which indicates survivorship and growth, in addition to hydrography and reproduction, are important processes in bloom and swarm formation.

(ii) F. S. Russell's (1953, 1970) monographs on "The Medusae of the British Isles" carefully details "distribution" and "seasonal occurrence" in subtitled sections for each species of hydromedusa. His reports on 92 species of hydromedusae included only three in his highest categories "exceedingly abundant" or having "remarkable … abundance" (Russell 1953, pp. 88, 147, 315). Additionally, *Tima bairdi* (Johnston) were reported to "appear quite suddenly in great hosts" (Russell 1953, p. 381) and *Liriope tetraphylla*

Gegenbaur to be "controlled by hydrographic conditions … irregular … extremely abundant" (Russell 1953, p. 427) indicating apparent rather than true blooms. Thus, according to Russell (1953) only 3-5% of hydromedusae occur *en masse* in British waters. Yet, like Mayer, Russell chose to describe the occurrence of scyphomedusae generically, illustrated with specific examples. Russell (1970) wrote that "there are many records … of Scyphomedusae in great abundance and swarms … often over large areas" (pp. 11-12). He considered *Pelagia noctiluca* (Forsskål) as generally occurring in "large swarms" (p. 85), *Chrysaora hysoscella* (Linné) as seasonally very abundant and possibly swarming, *Cyanea capillata* (Linné) as having "occasional occurrence in large swarms" (p. 124), *Aurelia aurita* as occasionally occurring in "immense numbers … so abundant oars pushed down between them remained … upright" (p. 167), and that "Bauer … repeatedly observed … swarms of *Rhizostoma*" (p. 195). Thus, Russell (1970) considered five of 13 (~40%) scyphomedusae to occur *en masse*.

Russell, like Mayer (1910), appears to have applied terms of abundance consistently to hydromedusae and scyphomedusae. Certainly, Russell was aware of the potential for size to lead to biased accounts, noting that the 1 mm high *Agastra mira* Hartlaub "is probably overlooked on account of its small size" (Russell 1953, p. 304). Yet he made no such comments for *Lizzia blondina* Forbes, which could attain a bell height of 2.0 mm and be "exceedingly abundant" (p. 148). Russell (1953, 1970) therefore clearly distinguished numerical abundance from size, as illustrated in the closing paragraph of his Preface which is quoted in our *Introduction*.

Hypothesis 3. The recent literature indicates hydromedusae and scyphomedusae occur en masse approximately equally frequently.

We suggest the data reject this hypothesis, and support the alternative that hydromedusae occur *en masse* less frequently than scyphomedusae. A search of the *Web of Science* database (on 26th April 2008) found 5273 publications on "Hydrozoa", 710 publications on "hydromedusa*", 1999 on "Scyphozoa", and 1120 on "scyphomedusa*". Considering there are circa 3000 species of Hydrozoa (Schuchert, 1998) and 200 species of Scyphozoa, and that hydromedusae are approximately 4-fold more speciose than scyphomedusae, this represents an approximately 6-fold higher per-species-publicationrate (pspr) for Scyphozoa than Hydrozoa and an approximately 7-fold higher pspr for scyphomedusae than hydromedusae. This represents a baseline for reporting on these two classes against which the relative proportions of reports on blooming or swarming in the two classes can be used to infer relative rates of occurrence of blooms and/or swarms.

Searching *Web of Science* for the keywords (bloom* OR swarm*) AND relevant systematics terms recovered 13 publications for "hydromedusa* OR hydrozoa*" compared to 32 publications for "scyphomedusa* OR scyphozoa*". In total, there were 39 different publications: 6 hydro* + scypho*, 7 hydro* only, and 26 scypho* only. This distribution of recent papers is consistent with the aforementioned difference in size of recent research communities and also illustrates crossover of researchers between classes of medusae. The 2.5-fold imbalance in number of papers does not reflect the larger 10-fold difference in the frequency of blooms documented by Mayer (1910) and Russell (1953, 1970). The approximately 9-fold higher pspr for blooms and/or swarms of scyphomedusae compared to hydromedusae is consistent with the estimates of Mayer (1910) and Russell (1953, 1970) and therefore fewer mass occurrences of hydromedusae than scyphomedusae. Concomitantly, the 39 unique publications indicate blooming or swarming of 19 different species of scyphomedusae (9.5% of all known species) but only 15 species of hydromedusae (1.8% of all known species) even though the total number of scyphozoan species considered in these publications was less than half the number of hydromedusae, suggesting ~10-fold more scyphomedusans than hydromedusans occur *en masse*, again consistent with the estimates from contextualistic analyses of Mayer (1910) and Russell (1953, 1970).

The preliminary evidence indicates hydromedusae have not been systematically overlooked due to their small size. We conclude that the weight of available evidence objectively demonstrates that hydromedusae do not bloom or swarm to the extent that scyphomedusae bloom and swarm, a result important for our understanding of both the systematic distribution of mass occurrences and the evolution of characteristics that promote aggregations, blooms, and swarms (Dawson & Hamner, this volume). Our analyses have, however, only scratched the surface of the rich literature available. Rigorous contextualistic analysis of a more complete set of recent and historical texts, including perhaps original logs and reports from oceanographic cruises, was beyond the scope of this study but may provide almost 150 years of reliable information on the relative abundances of medusae globally.

Appendix B: Intensity of sampling of mesopelagic medusae

Is the conclusion that deep sea medusae generally do not bloom or swarm due to undersampling of a fauna that is, compared to coastal medusae, relatively inaccessible? In addition to life-history data that speak strongly against deep-water medusae having the potential to bloom or swarm, comparison with transects and trawls made in other locations indicate that the deep sea has been surveyed sufficiently intensively to reasonably conclude that mesopelagic medusae generally do not occur *en masse*. Here we preliminarily compare a reference publication on deepwater medusae (Larson, 1986), the principal source on deepwater medusae for our study and Dawson & Hamner (this volume) with publications on coastal and oceanic medusae selected *ad hoc* solely on the basis of their employing rigorous quantitative sampling (i.e. with no *a priori* consideration of survey results).

Reference publication on deepwater medusae (Larson, 1986)

Larson (1986) reported the results of nearly 500 two-hour 3 m Isaacs-Kidd midwater trawls (7.5 m^2 mouth area, ~ 7 kmh^{-1}; ~100,000 m^3 sampled per tow) by the USNS Eltanin made between 10 July 1962 and 29 September 1968. *Periphylla periphylla* (Péron & Lesueur)was caught in 230 trawls, *Atolla wyvillei* Haeckel was caught in 112 trawls, *Atolla chuni* Vanhöffen in 164 trawls, *Atolla gigantea* Maas in 26 trawls, *Atolla vanhoeffeni* Russell in 9 trawls, *Nausithoe* sp. and *Palephyra indica* Vanhöffen in two trawls, and *Pericolpa quadrigata* Haeckel and three species of *Nausithoe* each in one trawl. In total, 6000 medusae were collected. The highest densities were observed for the most common species: *Periphylla periphylla* occurred at up to 51 specimens per 100,000 m^3 (mean 10 medusae per 100,000 m^3), *A. wyvillei* occurred at up to 47 specimens per 100,000 m^3 (mean 21 medusae per 100,000 m^3), and *A. chuni* occurred at up to 65 specimens per 100,000 m^3 (mean 7 medusae per 100,000 m^3).

Comparison 1: <u>Catostylus mosaicus</u> (Pitt & Kingsford, 2000)

Pitt & Kingsford (2000) assessed abundances of *Catostylus mosaicus* (Quoy & Gaimard) using six transects, each sampling 1500 m^3, at six sites within 6 locations in New South

Wales, Australia, at four-monthly intervals between March 1996 and December 1997. The mean maximum number of *Catostylus mosaicus* medusae for any set of 36 transects recorded during any any sampling period at all locations ranged between ~43 and ~265 per 1500 m^3. The smallest mean maximum abundance of *C. mosaicus* is four to six times greater than the maximum density of the deepwater medusae; the largest mean maximum abundance of *C. mosaicus* is 27-fold to 38-fold greater than the maximum density of the deepwater species. The peak density of *C. mosaicus* in each location therefore exceeded the maximum for any deepwater species by an even greater factor.

Comparison 2: ICES North Sea surveys (Hay et al., 1990)

The International Council for the Exploration of the Sea (ICES) International 0-group Gadoid Surveys conducted 43 to 215 trawls, each sampling approximately 65,000 m^3 of the North Sea, every year between 1971 and 1986, except 1984; mesh size was 100 mm tapering to 10 mm in the cod-end (full details provided by Hay et al., 1990). The survey captured ~430,000 medusae (Lynam et al., 2004), dominated by *Aurelia aurita* (total 282,788 medusae, median number per trawl calculated for each year was <1 to 1332 medusae), *Cyanea lamarckii* (Péron & Lesueur) (99,245 medusae, median per trawl per year <1 to 900 medusae), and *Cyanea capillata* (49,387 medusae, median per trawl per year <1 to 242 medusae). Hay et al. (1990) note that the medians do not reflect that individual trawls frequently caught more than 1000 *Aurelia* per 65,000 m^3. The mean number of medusae caught per trawl over the entire sample period is 139 *Aurelia aurita*, 49 *Cyanea lamarckii*, and 24 *Cyanea capillata*. *Aurelia aurita* was therefore at least 10-fold to 30-fold more abundant, on average, than any of the deepwater medusae. *Cyanea lamarckii* was at least 4-fold to 11-fold more abundant, on average, than any of the deepwater medusae. *Cyanea capillata* was at least 2-fold to 5-fold more abundant, on average, than any of the deepwater medusae. In the case of *Aurelia aurita*, the maximum densities (assuming 1000 medusae per trawl) were at least ca. 22-fold to 43-fold greater than the maximum densities of any deepwater medusa.

Comparison 3: GLOBEC Northeast Pacific surveys (Suchman & Brodeur, 2005)

The US Global Ocean Ecosystems Dynamics program in the Northeast Pacific conducted trawls in the California Current during two cruises between 29 May and 12 August 2000 and another two cruises between 01 June and 18 August 2002; mesh size was 163 cm tapering to 8 mm in the cod end (full details provided by Suchman & Brodeur, 2005). Large hydromedusa and scyphomedusae were commonplace, at least one species being caught in 63% to 88% of each cruise's trawls. *Aequorea* sp. was caught in 33%-74% of trawls, with maximum 1.9-11.7 medusae per 1000 m^3. *Aurelia labiata* Chamisso & Eysenhardt was caught in 35%-49% of trawls, with maximum 0.32-10.3 medusae per 1000 m^3. *Chrysaora fuscescens* Brandt was caught in 29%-61% of trawls, with maximum 2.3-76.8 medusae per 1000 m^3. *Phacellophora camtschatica* Brandt was caught in 1%-39% of trawls, with maximum 0.004-2.4 medusae per 1000 m^3. Suchman & Brodeur (2005) noted that actual abundances were likely higher than these recorded due to five limitations, including avoiding some inshore stations where medusae were particularly dense.

Abundances of *Aequorea* sp. were therefore 18-fold to 25-fold greater than the maximum abundances of *Periphylla periphylla* or either *Atolla* species recorded by Larson (1986). Abundances of *Aurelia labiata* were 16-fold to 22-fold greater than the maximum abundances of *Periphylla periphylla* or either *Atolla* species. Abundances of *Chrysaora fuscescens* were 118-fold to 163-fold greater than the maximum abundances of the deepwater species. Abundances of *Phacellophora camtschatica*, a non-blooming and non-swarming species, were only 4-fold to 5-fold greater than the maximum abundances of the deepwater species.

This preliminary survey therefore shows that corrected for differences in effort, shallow-water species that we consider blooming or swarming species (*Aequorea* sp., *Aurelia* spp., *Chrysaora fuscescens*, *Catostylus mosaicus*) are typically one- to two orders of magnitude more abundant than deepwater species. Shallow-water species that we consider non-bloomers and non-swarmers (e.g. *Cyanea* spp., *Phacellophora camtschatica*) are typically several-fold more abundant than deepwater species. Thus, available evidence demonstrates that even the most commonplace and abundant deepwater medusae are neither bloomers nor swarmers and indeed very rarely occur at densities of more than 1 per 10,000 m^3 (see Larson, 1986).

This conclusion is consistent with the independent assessment of earlier researchers. For example, Russell (1953, 1970) tended to employ the phrase "likely to be found in any collections" for deepwater species of hydromedusae and scyphomedusae, indicating mesopelagic medusae were widespread and commonplace but never abundant. Russell (1970) therefore found it notable, while reporting on five species of deepwater coronate, that "*Paraphyllina ransoni* … must be very rare … only been caught on two occasions … evidently were in swarms … forty-five specimens … on 28 April 1955 … 610 specimens … on 24 April 1963" (p. 56). While these records obviously represent accumulations of above-average densities of *P. ransoni*, it is difficult to assess whether these were aggregations or swarms *per se* as the catches represent the totals collected during each trawl. The issue concerns all deepwater trawls. The many observations made by remotely operated vehicles globally (e.g. Monterey Bay Aquarium Research Institutes [MBARI's] *Tiburon* has ca. 1000 dives averaging 12 hours duration and the *Ventana* ca. 3000 dives averaging 6 hours duration [G. Matsumoto, pers. comm.]), however, have not led to any general sense that mesopelagic medusae aggregate, bloom, or swarm. Querying MBARI's online database, for example, demonstrates that *Periphylla periphylla* principally are encountered singly (based on a random survey of ~20 video captures from 361 distinct records for *Periphylla periphylla* between 08 March 1993 and 11 April 2005). Indeed, occasional aggregations of benthopelagic medusae (e.g. *Poralia rufescens* Vanhöffen, see main text, and the hydromedusa *Benthocodon*) remain remarkable, the exceptions suggesting an emerging rule.

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