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Invertebrate introductions in marine habitats: two species of hydromedusae (Cnidaria) native to the Black Sea, *Maeotias inexspectata* and *Blackfordia virginica*, invade San Francisco Bay

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Abstract The hydrozoans *Maeotias inexspectata* Ostroumoff, 1896 and *Blackfordia virginica* Mayer, 1910, believed to be native to the Black Sea (i.e. Sarmatic) and resident in a variety of estuarine habitats worldwide, were found as introduced species in the Petaluma River and Napa River, California, in 1992 and 1993. These rivers are mostly-estuarine tributaries that flow into north San Francisco Bay. Both species appeared to be well-established in this brackishwater habitat. Salinities at the collection sites were about 11‰ during the summer, rising to nearly 20‰ in the early autumn and falling to near 0‰ in the winter. Large numbers of all sizes of both species of medusae were observed and collected, indicating that the hydroid stages of the life cycles of the two are also well-established in these rivers. In the Petaluma River, populations of both species were at maximum in late July, with numbers of individuals declining through August and into September; the Napa River was sampled only in October, and at that time only *B. virginica* was found. Examination of full guts of *M. inexspectata* and *B. virginica* medusae revealed that both species had fed nearly exclusively on small crustaceans, principally barnacle nauplii, copepods and their eggs and nauplii, and crab zoea larvae (*M. inexspectata* only). All the *M. inexspectata* medusae were males, indicating that the population has probably developed from the introduction of perhaps only a single male polyp or polyp bud. In spite of its inability to reproduce sexually, this population appears to be maintained by the prodigious ability of the polyp to bud and reproduce asexually, and is fully capable of invading additional low-salinity habitats from its present Petaluma River site. Male and female *B. virginica* medusae were collected in both the Petaluma River and the Napa River, indicating that *B. virginica* may have been introduced by either the polyp or medusa stage (or both), but that multiple individuals (of both sexes) must have arrived from another port in one or more invasions. As indicated for *M. inexspectata*, the *B. virginica* population will also probably seed new populations in San Francisco Bay and elsewhere. Based on its cnidome as well as the morphology of both medusa and polyp, *M. inexspectata* has been reclassified by moving it from the family Olindiidae, Limnomedusae, to the family Moerisiidae, Anthomedusae.

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Introduction

New appearances of exotic marine species in shoreline and estuarine habitats have become frequent. Since transoceanic shipping began, marine organisms have been transported from their native habitats by way of fouled ships' hulls, or by ballast stones, ballast water and sediment, and introduced into new harbors when this ballast has been dumped. Both the incidence and our awareness of such invasions have greatly increased in recent decades (Carlton 1985, 1989; Hallegraeff and Bolch 1992; Carlton and Geller 1993).

In the United States, San Francisco Bay on the Pacific coast and Chesapeake Bay on the Atlantic coast have long been subjected to invasions of marine and estuarine organisms from around the world (Carlton 1979 and personal communication 1994). In turn, each bay may serve as a new center of dispersal for exotic species. In this paper we chronicle the invasion of two species of hydromedusan jellyfish, both of which have previously been reported from Chesapeake Bay, into tributaries of San Francisco Bay. These jellyfish are the Black Sea species *Maeotias inexspectata* Ostroumoff, 1896 (often misspelled as *M. inexpectata*) and *Blackfordia virginica* Mayer, 1910.

Most hydromedusae, including the two species discussed in this paper, have a complex life cycle. The benthic polyp or hydroid (either male or female) asexually buds medusae of the same sex as the polyp, usually in the spring when available food in the plankton is increasing. Medusae are released at a very small size, typically about 1.0 mm. The single-sex medusae grow up in the plankton, entirely separate from their polyps, attain sexual maturity, and then spawn either eggs or sperm daily for some time. Eggs are fertilized in the water column, and planula larvae settle upon the bottom and develop into polyps. *Maeotias inexspectata* is one of a small number of species in which the polyps can also reproduce by budding small planuloid bits of tissue known as polyp buds (Petersen 1979) that separate from the parent polyp and then rapidly develop into new polyps. Each solitary polyp may also produce several pedal cysts at its basal attachment point; these serve as protective resting stages if the polyps regress in response to unfavorable environmental conditions. Thus, *M. inexspectata* has four independent-living phases capable of being transported to new locations, namely the medusa, polyp, planuloid polyp bud, and resting pedal cyst, whereas *Blackfordia virginica* has two forms capable of colonization, the medusa and polyp. We shall argue that the stage that invaded San Francisco Bay may have been different for *M. inexspectata* than for *B. virginica*.

Materials and methods

Observations of the medusa *Maeotias inexspectata* Ostroumoff, 1896 were made in early June 1992 and in June through September 1993 in the Petaluma River, Sonoma County, California. The original 1992 collection was made by A. Chess of Tiburon, California, and C. Cannon of Petaluma, California, made numerous observations in addition to our own during the summer of 1993. *Blackfordia virginica* Mayer, 1910 was present from June through September 1993 in the Petaluma River and in October 1993 in the Napa River, Napa County, California. Living medusae were further observed and photographed in laboratory aquaria during the summer of 1993. In the laboratory, *M. inexspectata* were fed adult and naupliar brine shrimp, *Artemia* sp., and occasionally guppies. Individual medusae were shaken and probed in the dark in order to determine whether or not they were bioluminescent.

Nematocysts on tentacles and manubria of living and preserved *Maeotias inexspectata* medusae and from preserved *Blackfordia virginica* medusae were examined in squashed preparations using a compound microscope at magnifications of 200 to 600×.

Gut contents of preserved, field-collected medusae were examined. Approximately 120 adult *Maeotias inexspectata* were collected on 6 July 1993 by hand-dipping individuals in the Petaluma River from a floating dock at the Petaluma municipal boat-turning basin. These medusae were immediately preserved in 5% formalin. Approximately 200 adult *Blackfordia virginica* were collected on 5 October 1993 in the Napa River from a floating dock beside the John F. Kennedy Boat Launch at the Napa Municipal Park. Some of these medusae were preserved immediately in 5% formalin and others were preserved several hours later. Gut contents were later revealed by microscopic examination of individual medusae. For *M. inexspectata*, it was necessary to clip off the manubrium of each specimen; using needles and a pipette all prey were then removed from the base of the manubrium and the four perradial stomach lobes, and prey were also teased from the four long, frilly, mouth lobes of each specimen. The lips and manubrium of *B. virginica* were examined using needles on whole, uncut specimens. Extracted prey were examined, measured, and identified using a binocular dissecting microscope. The same samples of medusae that were examined for gut contents were also measured using calipers or the ocular micrometer of a dissecting microscope in order to assess size structure of the population.

Salinities were measured in the field and in the laboratory with a handheld refractometer. Because *Maeotias inexspectata* medusae were restricted in distribution to a rather small portion of the Petaluma River, tolerance by the medusae to various salinities was examined by placing three adult medusae each in six, 1-liter beakers containing pondwater/seawater mixtures at salinities of 30, 20, 16, 6, 2 and 1‰. At the same time, six medusae each from the same collection were held in two larger aquaria (10 and 20 liters) at 13 and 11‰ S. The medusae were kept in the beakers for 5 d and were not fed during this experiment. *Blackfordia virginica* is known to tolerate a wide range of salinities (Moore 1987).

A search for polyps of *Maeotias inexspectata* and *Blackfordia virginica* was made in the Petaluma River on various substrata including sediment samples and scrapings from pilings and from underneath docks. None was found, although one *M. inexspectata* polyp on a bit of floating debris was inadvertently included with a shipment of medusae sent by C. Cannon in several liters of Petaluma River water to the Monterey Bay Aquarium. This polyp was isolated for culture in a glass petri dish and kept at room temperature (20°C). The polyp asexually produced planuloid buds which were kept in similar containers in a mixture of spring water and Monterey Bay seawater at a salinity ranging from 10 to 14‰; they were fed *Artemia* sp. nauplii, with water being changed twice per week. We did not culture *B. virginica* in the laboratory.

Preserved specimens of *Maeotias inexspectata* and *Blackfordia virginica* medusae from San Francisco Bay have been deposited in the California Academy of Sciences, San Francisco (CASIZ #094794), and the United States National Museum of Natural History (Smithsonian Institution), Washington, D.C. (USNM #93894).

All the genus names of hydromedusae and polyps used in this manuscript follow the revisions and conventions of Bouillon (1985) and Petersen (1990).

Results

Maeotias inexspectata from the Petaluma River

The medusa (Figs. 1A,B; 2A)

Maeotias inexspectata were observed and collected in the Petaluma River on 7 June 1992, and from late June into September 1993. Large medusae, described as "in the thousands", were found in the boat-turning basin of downtown Petaluma in late June 1993. By early July (Fig. 3A), most of the medusae were sexually mature, indicating that most budding from polyps had probably ceased several weeks before. Numbers remained high throughout July 1993, and then gradually declined during August. Only a few were seen in early September (C. Cannon personal communication). Since all of the ~200 medusae that we examined microscopically were males, we conclude that no females were present in the population.

The species has probably been established in this location for several years, given its abundance in 1993. According to local fishermen, large numbers were also present in the summer of 1992 (*Blackfordia virginica* is much smaller and is not likely to be noticed by the casual observer). The Petaluma River is brackish where it runs through the city of Petaluma, about 20 km from its mouth in San Pablo Bay at the north end of San Francisco Bay. In Petaluma, the salinity was 10 to 12‰ and the temperature was ~20°C during July and August 1993. A visual transect from a boat along the estuary in early July 1993 revealed

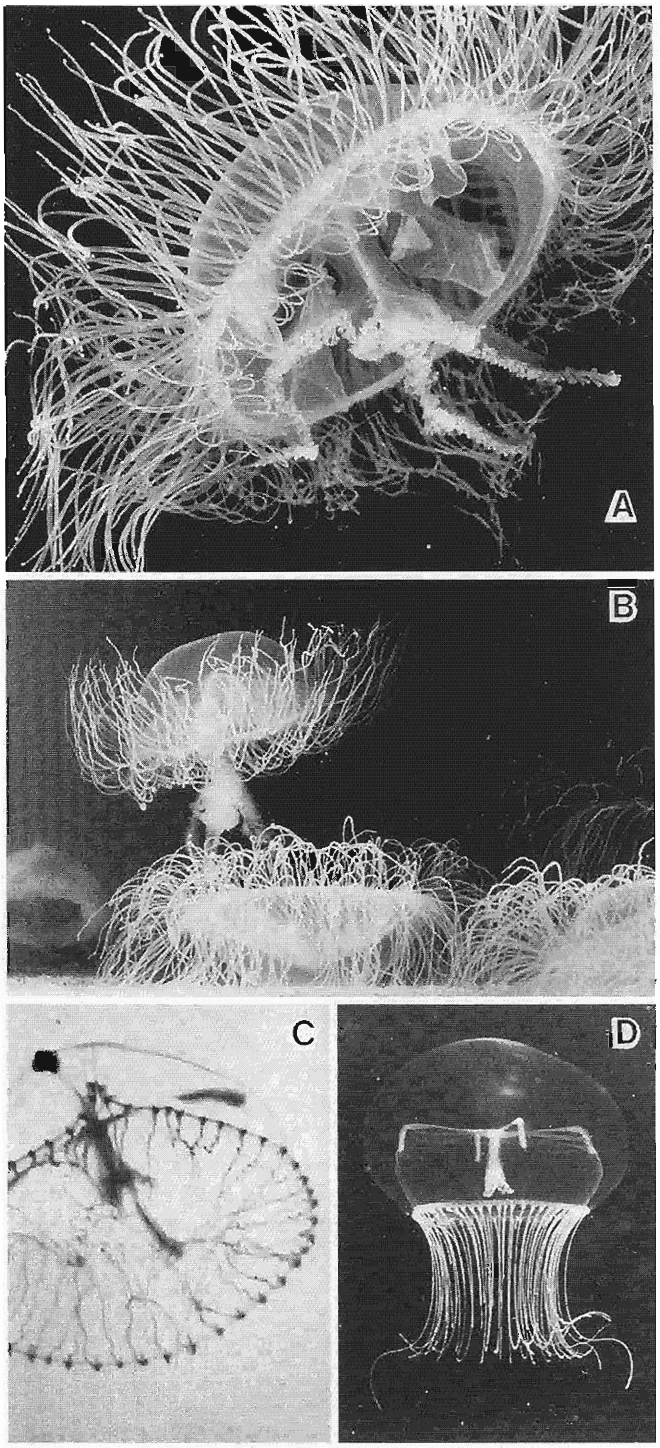

Fig. 1 *Maeotias inexspectata* and *Blackfordia virginica*. Mature living specimens from Petaluma River, California, photographed in aquarium. **A** *M. inexspectata*, 25 mm bell diam, in water column; **B** several *M. inexspectata* in typical postures on bottom; **C** *B. virginica* female from brightfield video; **D** *B. virginica*, 9 mm bell diam, in water column

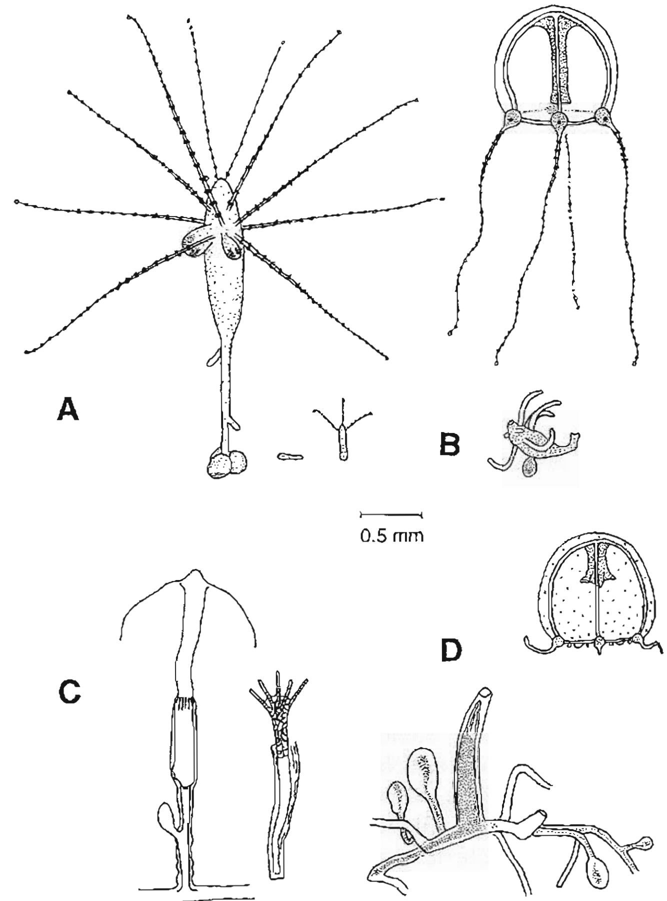

Fig. 2 *Maeotias inexspectata* and *Blackfordia virginica*. **A** *M. inexspectata* polyp producing lateral planuloid buds and newly released medusa from laboratory culture; **B** budding polyp of ?*M. inexspectata* taken from preserved gut of *M. inexspectata* from Petaluma River; **C** *B. virginica* polyp (after Valkanov 1935); **D** budding polyp of ?*B. virginica* taken from preserved gut of *Maeotias inexspectata* from Petaluma River and newly released medusa of *B. virginica* collected in Napa River (Scale bar for entire figure=500 µm)

no medusae downstream of the point in the Petaluma River where the increasing salinity reached 15‰. By early October 1993, when no *Maeotias inexspectata* were seen in Petaluma, the salinity had risen to about 17‰ and the temperature was 17°C. During winters that are very rainy, the Petaluma River runs nearly fresh and its temperature drops to ~10°C; the years 1992 and 1993 were moderately rainy after a 6 yr drought, but how this weather has influenced the *M. inexspectata* population is unknown.

Newly released medusae of *Maeotias inexspectata* (Fig. 2A) are 1.0 mm in height and bell diameter in life, and have four equal perradial tentacles arising from large orange-pigmented bulbs; a deep red-black ocellus is present in each bulb and the exumbrella is sprinkled with nematocysts. Adult *M. inexspectata* medusae (Fig. 1A,B) are somewhat opaquely white, with a pink blush of color around the rim of the bell. The medusae had neither statocysts nor sensory clubs around the bell margin. In addition to four radial canals, *M. inexspectata* develop numerous distinctive cen-

Table 1 *Maeotias inexspectata*. Summary of gut contents of 70 medusae from Petaluma River, California, 6 July 1993

Prey type	Frequency (%)	Total no. in guts
Barnacle nauplii	97	908
Copepods (benthic and planktonic forms)	96	686
Crab zoea larvae	94	644
Copepod egg sacs	51	246
Copepod nauplii	27	31
Tanaids	23	22
Other	41	58

tripetal canals that branch upward from the ring canal. There are up to about 10 centripetal canals in each quadrant of 7 mm-diam medusae, and about 15 centripetal canals per quadrant in a 30 mm-diam medusa.

The nematocysts of *Maeotias inexspectata* medusae were all stenoteles; we expected also to find desmonemes, which often occur along with stenoteles, but a careful search at 600× did not reveal any. On the tentacles, the nematocysts are arranged in tightly packed rings. Undischarged tentacular stenoteles measured 28 to 32×20 to 24 μm; the size did not change measurably upon discharge. On the manubrium, stenoteles were sprinkled throughout the tissue in a loose distribution, and they also occurred in tightly packed clusters of about 50 along the frilly edges of the lips, the tightly grouped clusters giving the lip edges a beaded appearance upon close observation. These manubrial stenoteles were about 20×14 μm, with occasional larger ones (30×24 μm) also present. The nematocysts of *M. inexspectata* have been illustrated in photographs by Denayer (1973), but were erroneously identified as probably microbasic euryteles because they were examined in preserved tissue and none could be made to discharge. The discharged nematocysts have the unmistakable spination pattern of stenoteles on their shafts.

The tentacles in adult medusae are closely packed and very numerous (up to 600 on large specimens), extending outward about one bell-diameter in length when a medusa is in the water column (Fig. 1A), but often draping onto the substratum when the medusa is on the bottom (Fig. 1B). All sizes of *Maeotias inexspectata* (including newly-released medusae) demonstrate a peculiar behavior of frequent twitching of the tentacle tips (about once per second) while the medusa is at rest on the bottom of an aquarium. Tentacle-tip twitching may serve to lure prey, although this function has not yet been confirmed. Shaking and probing individual medusae in a dark laboratory revealed no ability to bioluminesce.

Maeotias inexspectata are very heavy relative to the estuarine water in which they live, so they sink rapidly whenever they are not swimming. In laboratory aquaria, *M. inexspectata* are fairly inactive and spend most of their time on the bottom (see Fig. 1B). Some upward swimming bouts were quite long in duration, while others consisted of only a few pulsations. We believe that most of the *M. inexspectata* population, in its natural habitat on or near the bottom, is not visible to a surface observer, given the turbid estuarine conditions.

In an examination of the gut contents of 71 individual *Maeotias inexspectata* ranging from 7 to 36 mm preserved diameter, 70 of these medusae had prey in their guts (Table 1). Prey taken, in order of decreasing numerical abundance, included barnacle nauplii, copepods, crab zoea larvae of *Rhithropanopeus harrisii* (an Atlantic species introduced years ago to San Francisco Bay), copepod egg sacs (presumably originally attached to copepods, but loose in the guts), copepod nauplii, and tanaids. The category "Other" in Table 1 includes seeds (12), barnacle cyprid larvae (7), crab eggs (7), appendicularians (7), annelids (6), pieces of hydroid (6), fecal pellets (6), ants (2), spider (1), unidentified insect (1), meiofaunal isopod (1), cumacean (1), and nematode (1). The guts of 22 medusae contained filamentous algae. Not counting the algae, *M. inexspectata* medusae contained from 1 to 97 items, averaging 37 items per medusa. Most of the prey were < 1 mm in length, and even the largest items such as polychaete or oligochaete worms were nearly all < 3 mm. Most of the prey were species from the water column, but benthic meiofauna including harpacticoid copepods, tanaids, and annelid worms were also well represented. Some of these benthic organisms may be nocturnal vertical migrators into the water column, but our samples were taken at mid-day, and it seems most likely that the medusae are actually feeding on the bottom when resting there.

Medusae subjected experimentally to various salinities from 30‰ down to 1‰ all survived and continued to pulsate normally for the following 24 h. As described by Mills (1984) for other species, the abrupt transfer to a new salinity initially caused the present medusae to be restricted to either the top or bottom of the beaker-aquaria. All medusae had regained their "normal" buoyancy, usually resting on the bottom of the beakers, within 10 h. By 48 h, medusae in salinities of 30, 20 and 16‰ were cloudy, inactive and moribund. All the medusae in salinities of 13‰ looked healthy after 48 h. By 5 d, all had begun to deteriorate, probably due mostly to lack of food and declining water quality. The ability of the polyp to tolerate various salinities was not examined.

The polyp (Fig. 2A,B)

A single polyp of *Maeotias inexspectata*, about 3 mm long, was found on 29 June 1993 in water in which *M. inexspectata* medusae had been shipped to the Monterey Bay Aquarium. The polyp was attached to a clump of debris, but within a day settled on a glass petri dish. The polyp was fed newly hatched *Artemia* sp. nauplii, and within 2 d began liberating 1 mm-long lateral planuloid polyp buds from the side of the column [as described for *Moerisia horii* (Uchida and Nagao 1959) and in a manner similar to *Craspedacusta sowerbyi*, F. S. personal observations] (Fig. 2A). These buds settled a short distance from the parent, developed tentacles, and within 7 to 10 d began asexually

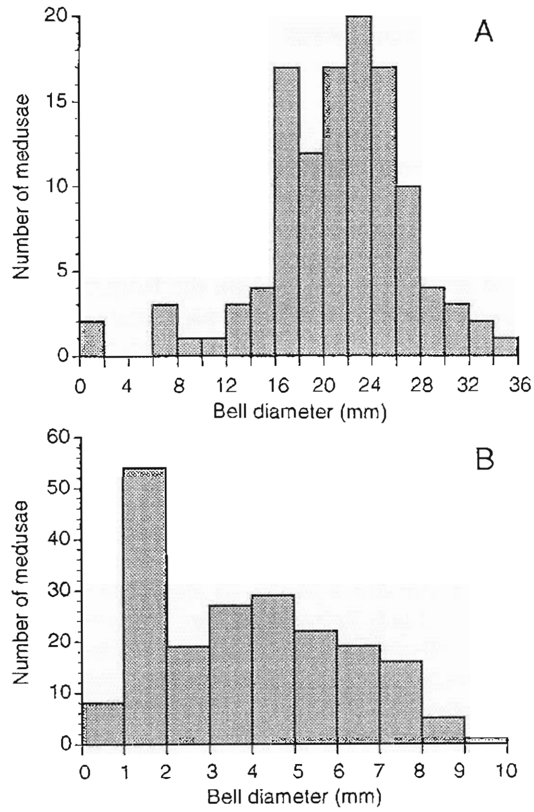

Fig. 3 *Maeotias inexspectata* and *Blackfordia virginica*. **A** Size distribution of 117 *M. inexspectata* in Petaluma River, 6 July 1993; **B** size distribution of 200 *B. virginica* in Napa River, 5 October 1993

producing their own buds. Over a 4 mo period through October 1993, proliferation via polyp budding resulted in the production of over 200 polyps from the original individual and its budded progeny.

The polyps (Fig. 2A,B) are solitary. They are very contractile and can contort into various shapes; their proportions also change as they mature. Polyps usually have 10 tentacles in two cycles of 5, with alternating spacing. The moniliform tentacles have regularly spaced bundles of nematocysts that result in a beaded appearance. The nematocyst-laden mouth is at the end of a cylindrical proboscis some distance above the tentacles. Polyp buds arise from the lower portion of the hydranth, below the region bearing the tentacles. The planuloid lateral buds usually develop as simple elongate projections, but occasionally they develop one or two tentacles prior to detachment from the polyp. Medusa buds arise between the tentacles of the lower cycle, directly under tentacles of the upper cycle (although they arise in irregular positions when the tentacle number is other than 10). Polyps are attached to the substratum by a perisarc-covered pedal disc. Older polyps produce several podocysts at and around the primary point of attachment, as is illustrated for *Moerisia horii* (as *Ostroumovia horii*) by Uchida and Nagao (1959). The slender hydranth base occasionally branches, producing a process that eventually attaches to the substrate in a second location. Older polyps (>2 mo old) can measure up to 15 mm from base to mouth, and each tentacle can stretch to ~10 mm long. Polyps are very slender when fully extended. The entire culture of polyps went into a resting stage in late autumn, suddenly regressing into their basal perisarc-covered podocysts during a week in late fall when they were left in the care of a colleague who apparently (unknowingly) caused a subtle environmental change.

The first medusa was liberated in the laboratory on 4 August 1993 from a polyp 1 mo-old (the original polyp and some of its early asexual progeny had by then succumbed to a ciliate infestation). The same polyp released two more medusae on 6 and 7 August 1993. These newly-released medusae (described above) were compared with living small medusae found in the Petaluma River and found to be the same. Several dozen medusae were produced in the next 3 mo from our laboratory cultures, but efforts to rear them proved unsuccessful.

Blackfordia virginica from the Petaluma and Napa Rivers

The medusa (Figs. 1C,D; 2D)

Numerous medusae of all sizes, ranging from large adult specimens 9 to 10 mm in diameter (Fig. 1C,D) to newly released individuals of < 1 mm (Fig. 2D), were present throughout the summer in the Petaluma River boat-turning basin in downtown Petaluma. Numbers declined rapidly through September, and none was observed by the end of the month. Medusae of all sizes were collected at the Napa River site (14‰ S; 20°C) in early October (Fig. 3B), although none was seen in the Petaluma River (17‰ S; 17°C) at this time. Both male and female *Blackfordia virginica* medusae were collected in the Petaluma River and in the Napa River. Female medusae of ≥6 mm diam were producing eggs. The female gonads are fairly small and probably produce fewer than 100 eggs per female per day. From the size distribution in both locations, we deduce that the hydroids of *B. virginica* were budding medusae continuously all summer. Newly released medusae of *B. virginica* (Fig. 2D) were 0.6 mm in bell height and diameter after preservation (probably ~1.0 mm in life). Each had 2 opposite very short perradial tentacles, 2 opposite longer perradial tentacles, and 4 interradial marginal tentacle bulbs lacking ocelli. The exumbrella was sprinkled with nematocysts.

Blackfordia virginica medusae are transparent, unpigmented, and delicate, with up to 80 very fine tentacles at maturity. They can be distinguished from *Maeotias inexspectata* at all sizes by their general fragility and because they lack centripetal canals arising from the ring canal. *B. virginica* medusae had typically 1, or rarely 2, statocysts containing two otoliths between tentacles, and some specimens also had black pigment granules in the intertentacular marginal region. An endodermal finger-like protrusion, pointing inward toward the subumbrella on each tentacle bulb, is diagnostic. In aquaria filled with Petaluma River water, *B. virginica* were nearly neutrally buoyant

Table 2 *Blackfordia virginica*. Summary of gut contents of 29 medusae containing prey in their guts from Napa River, California, 5 October 1993

Prey type	Frequency (%)	Total no. in guts
Copepods	52	19
Copepod nauplii	45	14
Barnacle nauplii	28	14

and therefore probably occur throughout the water column in nature. Although they swim well at all sizes, in aquaria they were quiescent in the water column most of the time. As for *M. inexspectata*, shaking *B. virginica* medusae in a dark laboratory revealed no ability to bioluminesce.

Nematocysts were examined on the tentacles and manubria of preserved *Blackfordia virginica* medusae. Nematocysts of only one type and size were seen, but never discharged. The elongate capsules measured 21 to 23 μm×5.4 to 6.7 μm, and were scattered thickly along the tentacles and in a row several nematocyts deep along the edge of the lips. We suspect that they were microbasic mastigophores, based on the keys of Mariscal (1974), because the capsules appeared to contain a thickened shaft in addition to a long coiled tubule, but this identification cannot be certain until discharged capsules from living medusae are examined.

Of the 200 preserved *Blackfordia virginica* medusae that were examined from the Napa River collection, 29 had prey in their guts (Table 2). We cannot assess population feeding rates because only some medusae were preserved immediately after collection; the others probably evacuated their guts during the next few hours, before preservation. The individuals that had full guts contained 1 to 3 prey items, with an average of 1.4 prey items per medusa. The prey were exclusively copepods, copepod nauplii, and barnacle nauplii. All were 250 to 700 μm in length and were probably taken from the water column rather than the bottom.

The polyp (Fig. 2C,D)

We did not find any *Blackfordia virginica* polyps in the field. Based on the description of *B. virginica* polyps by Valkanov (1935, and redrawn here in Fig. 2C), we tentatively identify one broken piece of a colony found in the gut of a *Maeotias inexspectata* medusa collected on 6 July 1993 as probably *B. virginica* (Fig. 2D). From the substantial numbers of medusae present, one would expect to find many *B. virginica* hydroids but, as described in Naumov (1969), the hydroids rise < 1 to 2 mm from the substratum, and if they live as part of a fouling surface biota, they are probably very difficult to see in the field.

Discussion and conclusions

Distributions

Prior to the present discovery in California, *Maeotias inexspectata* has been reported from five locations: (1) the mouths of the Don and Kuban Rivers, Sea of Azov, an arm of the Black Sea (Ostroumoff 1896); (2) the Razelm Lake portion of the Danube estuary on the Romanian coast of the Black Sea (Borcea 1928); (3) the Pamunkey River estuary of the Chesapeake Bay in the eastern USA (Calder and Burrell 1969); (4) the estuary of the Loire River, France (Denayer 1973); and (5) the South Edisto River estuary in South Carolina, eastern USA (Burrell and Joseph 1974). *M. inexspectata* has been known since the 19th century in the Black Sea region, and has been collected there at least as recently as 1987 and 1988 (S. D. Stepanyants personal communication 1994). It is considered to be a "Sarmatic" native (i.e. of the Black Sea) – its appearances elsewhere have been noted only in the past 25 yr. *Maeotias* is a monotypic genus. All of the locations where it has been collected are characterized by waters of low salinity; reported salinity, where given, ranged from 4.2 to 10.7‰ and reported temperatures from 11.3 to 27.0°C. Our experiments in which *M. inexspectata* was placed in aquaria at different salinities for several days, combined with field observations, indicate that its upper limit of tolerance is probably ~15‰, and that increasing salinity in the Petaluma River as it approaches San Francisco Bay probably confines the medusa to the Petaluma city portion of the river.

Blackfordia virginica is also thought to be native to the Black Sea, although it was originally described from an estuary near the mouth of the Chesapeake Bay in Virginia, eastern USA, by Mayer (1910). The known distribution of *B. virginica* presently includes sites in North America in the Chesapeake Bay and San Francisco Bay; in South America near Recife, Brazil; in India in the Ganges estuary, near Cochin, and in the Vasishta Godavari estuary; in China in the south China Sea and Fujian Province in the east China Sea; in western Europe in the Loire estuary in France and the Mira estuary in Portugal; and in eastern Europe in the Black Sea, the Caspian Sea, and Lake Belona, Romania (Zhang 1982; Moore 1987; Sai Sastry and Chandramohan 1989; Lin and Zhang 1990). *B. virginica* can tolerate salinities of 3 to 35‰ and is eurythermal (Moore 1987). Thiel (1935), having examined specimens of *B. virginica* from America where it occurs in only localized populations, and from the Mandra swamps on the Bulgarian coast of the Black Sea where it is very abundant, concluded that *B. virginica* is most probably indigenous to the Black Sea and was probably transported to the east coast of North America prior to 1910 by shipping.

This paper represents the first reported observation of *Blackfordia virginica* in the eastern Pacific Ocean. However, specimens on deposit at the California Academy of Science, San Francisco, were found to include two samples of this species collected in the 1970s and misidentified as *Phialidium* sp. (another Leptomedusa). One sample containing 150 to 200 *B. virginica* medusae was collected at another site on the Napa River on 30 September 1970 (13‰ S; 21°C). The second sample contained 8 *B. virginica* medusae collected from the Petaluma River on 10 September 1974 (salinity and temperature not recorded). We conclude that *B. virginica* has probably been present but undetected in the Petaluma and Napa Rivers for >20 yr.

It is of interest that *Maeotias inexspectata* seems to have been introduced to the Petaluma River as a polyp rather than a medusa. We reach this conclusion because the entire medusa population is male and therefore incapable of sexual reproduction. The polyp that we isolated from the Petaluma River has readily reproduced asexually in the laboratory, creating numerous additional polyps which then produced medusae. Since asexual reproduction by the polyps is so prolific, it is inconsequential to this population that the medusae are not able to reproduce sexually. The population of both medusae and polyps may thus be a clone, derived from a single introduced polyp. The invasive potential of this population to other sites is not reduced by this peculiar life-history trait, nor is its significance in the food chain lessened, for predation by mature medusae is presumably much greater than that of the numerous, but tiny, polyps.

Conversely, male and female *Blackfordia virginica* medusae were collected in both the Petaluma River and the Napa River, indicating that *B. virginica* may have been introduced in either the medusae or polyp stage or both, but that multiple individuals (of both sexes) must have arrived from another port. As is possible for *Maeotias inexspectata*, the healthy *B. virginica* population will probably seed new populations in San Francisco Bay and elsewhere.

The Petaluma River, like other navigable tributaries to San Francisco Bay, supports a lot of pleasure-boat traffic. In the summer months, many of these boats are from home marinas elsewhere in San Francisco Bay (C. Cannon personal communication). This circumstance provides a convenient vector for transporting newly settled polyps to other estuarine locations around the Bay, where they will either produce free planuloid polyp buds (*Maeotias inexspectata*) or liberate tiny medusae (*Blackfordia virginica*) to establish new populations. Movement of these species throughout low-salinity habitats in San Francisco Bay as well as elsewhere in the eastern Pacific should be very interesting to follow.

It is possible that, after an initial explosion, the populations of both *Maeotias inexspectata* and *Blackfordia virginica* will be controlled biologically. For example, hydroid populations are often grazed by nudibranchs and it may be that a nudibranch will discover the new hydroid populations in San Francisco Bay estuaries. Presently, the only candidate nudibranch in low-salinity waters in San Francisco Bay is *Tenellia adspersa*, which was itself probably introduced from the Atlantic coast and feeds on the abundant hydroids of (also introduced) *Cordylophora caspia* as well as on other species (T. M. Gosliner personal communication).

Maeotias inexspectata and *Blackfordia virginica* are among a group of estuarine species, native to the Black and/or Caspian Seas, comprising what is sometimes called the Sarmatic fauna. (Both Sarmatae and Maeotae are names of ancient Scythian tribes that once lived in the region of the Sea of Azov.) This group includes a number of Hydrozoa: *M. inexspectata*, *B. virginica*, *Cordylophora caspia*, *Odessia maoetica*, *Moerisia pallasi*, *Moerisia inkermania*, and *Protohydra leuckarti* (Zenkevitch 1940; Kramp 1959; Calder and Burrell 1967; Naumov 1969). All these species have proven to be good invaders (Calder and Burrell 1969; Naumov 1969; D. R. Calder personal communication). The well-known estuarine hydroid *Cordylophora caspia* now occurs in low-salinity waters nearly worldwide, including many estuarine sites on the east coast of North America (Calder 1990) as well as San Francisco Bay (our observations). *Moerisia lyonsi* (originally described from Lake Qurun, Egypt) was found in the Chesapeake Bay (Calder and Burrell 1967) a few years before the related species *Maeotias inexspectata* was discovered there, and we would not be surprised if some species of *Moerisia* is soon found in the estuarine waters of San Francisco Bay.

Systematics

We suggest, based on the presence of stenotele nematocysts in the medusa, and the morphology of the polyp, that the (monotypic) genus *Maeotias* be reclassified in the Anthomedusae, family Moerisiidae. *M. inexspectata* has long been placed in the Limnomedusae, family Olindiidae (Ostroumoff 1896; Kramp 1961; Bouillon 1985), and based on the morphology of the medusa, this has been uncontested. However, nematocysts are good phylogenetic indicators, and no other Limnomedusae have been reported to produce stenoteles, which are nearly universally present among the capitate Athecatae–Anthomedusae. Furthermore, the polyp of *M. inexspectata* is nearly indistinguishable from the moerisiid polyps of *Moerisia horii* (Uchida and Nagao 1959; Petersen 1979) and *Odessia* (as *Moerisia*) *maeotica* (illustrated by Naumov 1969), and is very similar to polyps of other species of *Moerisia* (Rees 1958; Naumov 1969; Petersen 1990).

Borcea (1928) provided perhaps the most complete description of the medusa of *Maeotias inexspectata*, including the long extensions of the stomach lobes, overlying the radial canals, from which the gonads are suspended. The resolution of the remaining discrepancy about placing *Maeotias* in the Anthomedusae – the possession of marginal statocysts as well as secondary marginal clubs – can be made by examining the illustrations of Borcea. The problem seems to be one of histological misinterpretation, for it appears to us that tentacles in random sections have been mistaken for the two kinds of marginal sensory structures. The "statocysts" illustrated by Borcea, matching in number those described by Ostroumoff (1896), seem to be cross-sections of some of the bases of the tentacles, so closely packed as to result in a deformation of some at the margin. Similarly, the marginal sensory clubs are probably oblique sections of other tentacles. Bouillon (1985) mentions a similar problem, in which the described statocysts of *Moerisia* (*Ostroumovia*) could not be found by later researchers.

Rees (1957, 1958) moved the family Moerisiidae from the Limnomedusae to the suborder Capitata of the order Anthomedusae; characters used in that reclassification included the cnidome (nematocyst complement) and morphology of the polyps and medusae. Petersen (1979, 1990), in extensive phylogenetic and cladistic analyses of the Capitata, fully endorsed placement of the Moerisiidae in the Anthomedusae. We assign three genera to the family Moerisiidae: *Moerisia*, in which gonads of the medusa occur on the interradial surfaces of the stomach and continue out onto the stomach lobes; *Odessia*, in which gonads of the medusa occur both interradially on the stomach wall and on the stomach lobes, separated from those on the stomach wall; and *Maeotias*, in which gonads of the medusa occur only on long stomach-lobe extensions overlying the radial canals. *Maeotias* medusae seem to represent an extreme in the evolution of the Moerisiidae, having very numerous tentacles, numerous centripetal canals, long frilly manubrial lips, and gonads restricted to narrow portions of the stomach lobes overlying the radial canals.

Revised from Bouillon (1985) and Petersen (1990), the family Moerisiidae should now be described as follows. Medusae with prismatic stomach with radial lobes along proximal parts of the four unbranched radial canals; with simple, cruciform mouth which, in older specimens, develops four perradial lips; gonads on interradial surfaces of stomach and surrounding stomach lobes, or only on extensions of the stomach lobes overlying the radial canals; (4–) 16–32, or several hundred moniliform or modified moniliform tentacles with adnate bulbs with abaxial ocelli; with or without centripetal canals; without statocysts. Hydroids usually solitary, sometimes colonial; with chordal or hollow, moniliform or modified moniliform tentacles scattered or in one or two whorls around middle part of hydranth; medusa buds borne on short pedicels between or just under tentacles; polyp buds produced from lower part of hydranth; short hydrocaulus ending in pedal-disc forming podocysts, or with short, stolon-like tubes ending in podocysts or hydranths; pedal disc, podocysts and lower end of hydrocaulus either covered by perisarc or naked.

Bouillon (1984, 1985) erected the family Blackfordiidae for the genus *Blackfordia* (in the superfamily Campanulinoidea), which had previously been given only uncertain status among the Thecatae-Leptomedusae (Kramp 1959, 1961). Bouillon et al. (1988) discussed morphology and biogeography of the 3 to 4 species of *Blackfordia*, but no nematocysts have previously been described for this family. Our finding of what appear to be microbasic mastigophores in *B. virginica* medusae is consistent with other medusae in the superfamily, which have microbasic mastigophores and/or haplonemes (Bouillon 1985). Usually at least two kinds of nematocycsts occur in a single medusa, and examination of live material may reveal an additional type in *Blackfordia* spp.

Ecological consequences of invasions

There is no published information about the effects of *Maeotias inexspectata* or *Blackfordia virginica* on surrounding benthic or planktonic communities. Although *M. inexspectata* was able to feed on small fish (guppies) in the laboratory, analysis of the gut contents of both species of alien medusae from the field indicated that they feed nearly exclusively on small crustacean planktonic and infaunal organisms; no fish were seen in any of the stomachs. Stenotele and microbasic mastigophore nematocyst types both correlate strongly with capture of crustacean or other hard-bodied prey; nematocysts may be the agents primarily responsible for diet selection (Purcell and Mills 1988). Feeding rates of *M. inexspectata* are high. Nearly all individuals examined had full guts with many food items. They are likely to be the most important predators of small crustaceans in the Petaluma River in mid-summer.

A dramatic example of the effect that an introduced species can have on its environment is provided by the ctenophore *Mnemiopsis leidyi*, which entered the Black Sea and the Sea of Azov during the 1980s (Studenikina et al. 1991; Travis 1993; Harbison and Volovik 1995). This invasion shows how important a jellyfish or ctenophore may well be in its plankton community. *M. leidyi* had been extensively studied in its native habitat on the east coast of North America (Kremer 1976, 1979, and others), where it often reaches bloom status in bays during the summer, yet since it is an everpresent member of the community, its importance as a keystone predator in shaping the pelagic ecosystem in these bays was not widely appreciated. *M. leidyi* was first seen in the Black Sea in 1982, became noticeably abundant by 1987, and its proliferation has been viewed as a substantial problem for about the past 6 yr. Most probably it was transported in the ballast water of ships arriving at Odessa or another port on the Black Sea from an American port. The further proliferation of *M. leidyi* into the adjacent Sea of Azov (Harbison and Volovik 1995) has apparently caused the collapse of two commercial fisheries, with profound biological, economic and social impacts.

The Sea of Azov is a body of water with low salinity in which zooplankton production has been nearly totally utilized by planktivorous fishes (Studenikina et al. 1991). Over the past 20 to 30 yr, pollution combined with decreased freshwater inflow have taken their toll on the region. With increased salinity came the scyphomedusa *Aurelia aurita*, first spotted in 1978. By the mid-1980s, *A. aurita* was responsible for decreasing fish production by 24% by consuming a large percentage of the zooplankton, and was viewed at the time as a serious problem. In the 1980s the freshwater input to the Sea of Azov was increased, having the effect of eliminating virtually all of the *A. aurita*, but at the same time the more euryhaline *M. leidyi* appeared (in 1988), an invasion which eventually made that of *A. aurita* seem minor. Within a couple of years, the *M. leidyi* population grew so large that it consumed 82% of the summer zooplankton production. This almost complete depletion of the food supply so devastated the populations of two fishes (anchovy and Azov kilka) that these commercial fisheries have ended. This rapid change in the planktonic community in this arm of the Black Sea is thought to be irreversible (Studenikina et al. 1991).

It is unlikely that the appearance of *Maeotias inexspectata* and *Blackfordia virginica* in tributaries of San Francisco Bay will lead to such dramatic changes. The fact that there is no mention of deleterious effects of these species years after their first appearances in the Chesapeake Bay seems to be a good sign. Still, such introductions should be monitored with vigilance. In fact, many other introduced species of hydromedusae (as well as other invertebrates) are presently establishing viable populations in bays and estuaries throughout the world, but few will be reported because local plankton faunas are usually poorly known. Living medusae have been found in the ballast water of cargo ships prior to the release of this water at shipping ports (Carlton and Geller 1993). It will be difficult to regulate alien hydroid/medusa populations that invade new shoreline habitats by human intervention. The need for faunistic studies and regulation of ballast water dumping has perhaps never been greater than at the present time.

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ERRORS IN PUBLISHED PAPER - note from Claudia Mills, 1998

Somehow, I managed not to see statocysts around the bell margin of *Maeotias inexspectata* (see p. 281) by the time this paper was published. My most careful examinations were of formalin-preserved specimens, in which the otoliths dissolve, rendering marginal statocysts very difficult to see - maybe that is how I missed them. My further observation of living specimens in August 1995 showed unquestionably that *Maeotias* does have numerous marginal statocysts.

The presence of marginal statocysts puts into question placement of *Maeotias* within the Anthomedusae. As there are exceptions to many of the morphological characteristics that are grouped together to put hydromedusae into families and classes, I am not all that dismayed by an Anthomedusa having statocysts, but the Limnomedusae may at this point be a more appropriate location for *Maeotias* until more is known.

In September 1997, *Maeotias* medusae were found in another low-salinity location in San Francisco Bay, along with a yet-unidentified species of *Moerisia* (another alien hydromedusa of Sarmatic origin!). Relationships between the two genera and their taxonomic positions (both have been moved from the Limnomedusae to the Anthomedusae) are presently under study by John Rees and Lisa Gershwin.

We found *Blackfordia* polyps in the field during the September 1997 collections, on barnacle shells. We also found polyps similar to those described in this paper as *Maeotias*. It has been brought to our attention that these polyps might be those of *Moerisia* rather than *Maeotias*. More lab and field work need to be done to elucidate differences between the polyps of these 2 species.

SEE ALSO:

Mills, C.E. and J.T. Rees, 2000. New observations and corrections concerning the trio of invasive hydromedusae Maeotias marginata (= M. inexpectata), Blackfordia virginica, and Moerisia sp. in the San Francisco Estuary. Scientia Marina 64 (Suppl. 1): 151-155.