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12	<b>RH</b> : Goose herbivory on wild rice • Haramis and Kearns
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14	Herbivory by resident geese: the loss and recovery of wild rice along the tidal
15	Patuxent River
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23 24	Abstract: Well known for a fall spectacle of maturing wild rice (Zizania aquatica) and
25	migrant waterbirds, the tidal freshwater marshes of the Patuxent River, Maryland,
26	experienced a major decline in wild rice during the 1990s. We conducted experiments in
27	1999 and 2000 with fenced exclosures and discovered herbivory by resident Canada
28	geese (Branta canadensis). Grazing by geese eliminated rice outside exclosures, whereas
29	protected plants achieved greater size, density, and produced more panicles than rice
30	occurring in natural stands. The observed loss of rice on the Patuxent River reflects both
31	the sensitivity of this annual plant to herbivory and the destructive nature of an
32	overabundance of resident geese on natural marsh vegetation. Recovery of rice followed

2 management actions: hunting removal of approximately1,700 geese during a 4-year
period and re-establishment of rice through a large-scale fencing and planting program.
Key words: *Branta canadensis*, Chesapeake Bay, herbivory, Patuxent River, resident
Canada geese, wild rice, *Zizania aquatica* var. *aquatica*

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38 The high productivity of wild rice, smartweeds, and millet makes the tidal marshes of 39 the upper Patuxent River an important fall stopover site for many migrating waterbirds 40 (Meanley 1975, 1996). Wild rice is a preferred food of soras (*Porzana carolina*), 41 bobolinks (Dolichonyx oryzivorus), red-winged blackbirds (Agelaius phoeniceus) (Meanley 1961, 1965; Webster 1964), and numerous ducks (McAtee 1911, 1917; Martin 42 43 and Uhler 1939; Moyle and Hotchkiss 1945). Along the Patuxent River, American black 44 ducks (Anas rubripes), wood ducks (Aix sponsa), green-winged teal (A. crecca), and 45 blue-winged teal (A. discors) occur most frequently. Soras were formerly so abundant in 46 these marshes that in the early twentieth century the Jug Bay portion of the upper 47 Patuxent River became one of the most famous rail hunting areas in the region (Mitchell 48 1933). Soras aggregate in these marshes for an extended fall stopover to fatten before 49 continuing migration (G. M. Haramis, U.S. Geological Survey, unpublished data). In this 50 way, the migratory fitness of soras and other water birds may be intrinsically linked to 51 wild rice.

52 The importance of these marshes to fall migrant birds led to a growing concern over the 53 widespread decline of wild rice in the 1990s. This loss was confirmed by aerial 54 photographic records, our casual observations accumulated over 15 years of field study of 55 soras, and discussions with B. Meanley, retired U.S. Fish and Wildlife Service biologist, who has been familiar with these marshes for over 50 years (Meanley 1975, 1996). Most
apparent was the loss of river-bordering rice that was most visible during maturation in
late summer and fall.

59 The loss of rice was enigmatic and might have been the result of a number of inter-60 related environmental factors. Germination and seedling survival is potentially sensitive 61 to a number of physical, chemical, and biological factors including sediment type, water 62 depth, turbidity, temperature, salinity, ice scouring in winter, and to consumption by 63 birds, fish, semi-aquatic mammals, and other aquatic life (for general discussion of 64 factors, see Martin and Uhler 1939:116-142; see also Lee and Stewart 1984; Stevenson 65 and Lee 1987; Day and Lee 1989; Baldwin et al. 2001). In fall, red-winged blackbirds 66 are so numerous that they appear to strip plants of seed before they mature and shatter 67 (Meanley 1961,1996). Seasonal variations in numbers of carp (*Cyprinus carpio*), or the 68 possible effects of spawning or foraging activities of an abundance of estuarine fishes 69 that move to the fresh tidal river each spring (e.g., white perch [Morone americana], 70 striped bass [M. saxatilis], yellow perch [Perca flavescens], and shad [Alosa spp.]), might 71 explain the loss of germinating rice seedlings (G. M. Haramis, U.S. Geological Survey, 72 personal observation). Waterfowl, especially resident mallards (Anas platyrhynchos) and 73 Canada geese (*Branta canadensis*), also could potentially be damaging to rice. The 74 objective of our study was to investigate and identify factors causing the decline of wild 75 rice along the Patuxent River and to prescribe and implement methods for its restoration. 76 **Study Area** 

The tidal marshes of the upper Patuxent River at Jug Bay, near Upper Marlboro, MD
(38° 47' N, 76° 42'W), were classified as fresh estuarine river marshes (Stewart 1962,

79	Cowardin et al. 1979). They were bordered downstream by slightly brackish (oligohaline)
80	marshes, upstream by tidal freshwater swamps, and were characterized by a highly
81	diverse assemblage of freshwater emergent plants (Anderson et al. 1968, Tiner and Burke
82	1995). The principal marshes, about 500 ha in extent, have long been known for nearly
83	monotypic stands of the tall, broadleaf coastal form of wild rice, known as southern wild
84	rice (Zizania aquatica var. aquatica; Oelke et al. 2000). In addition to wild rice, the
85	marshes contained such broad-leaved emergents as spatterdock (Nuphar advena),
86	pickerelweed (Pontederia cordata), arrow arum (Peltandra virginica), and arrowhead
87	(Sagittaria latifolia), which dominate deeper zones, and rice cutgrass (Leersia oryzoides),
88	Walter millet (Echinochloa walteri), river bulrush (Schoenoplectus fluviatilis), dotted
89	smartweed (Polygonum punctatum), arrowleaf tearthumb (P. sagittatum), halberdleaf
90	tearthumb (P. arifolium), tidemarsh waterhemp (Acnida cannabina), jewelweed
91	(Impatiens capensis), cattail (Typha spp.), and marsh beggartick (Bidens laevis), which
92	occur in higher marsh. Wild rice typically occurs in river-bordering pure stands or in
93	mixed vegetation at intermediate depths. The pristine nature and high diversity of these
94	marshes led to their inclusion as a component of the Chesapeake Bay National Estuarine
95	Research Reserve (CBNERR).
96	Methods

## **Experiments with Small Exclosures**

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99 In April 1999, we placed small-(1.3 cm by 1.3 cm), medium-(2.5 cm by 2.5 cm), and 100 large-(5.1 cm by 10.2 cm) mesh fenced exclosures to test the possible effect of fish or 101 other aquatic organisms on survival and growth of germinating rice. We placed replicate 102 sets of circular 1.5-m-high, 1-m<sup>2</sup> exclosures and an unfenced control plot at 6 randomly

103 selected locations on river-bordering tidal mudflats where an even distribution of 104 naturally germinating rice occurred. Exclosure mesh size was small enough to exclude 105 ducks, geese, muskrats (Ondatra zibethicus), beaver (Castor canadensis), large turtles, 106 and fish. Because of the inherent link between site-specific factors and plant growth, we 107 adopted a completely randomized block design. We assumed that all experimental units 108 within blocks were homogeneous with respect to herbivory if we assigned them within 109 broad areas of naturally germinating rice. To measure differences in rice growth and 110 productivity, we made a total count of rice stalks, panicles, plants, and tillers within 111 exclosures and controls at the end of the growing season. We also subsampled plant 112 growth variables to test for effects of mesh size. We measured a systematic sample of 10 113 plants per experimental unit for height, panicle length, and stem diameter (nearest mm). 114 We measured stem diameter at the nearest mid node at half the height of each stalk. We 115 used SAS/STAT Proc Mix to conduct ANOVA and Proc Univariate Procedures to 116 confirm model residual distributions and homogeneous variance (SAS Institute, Inc. 117 2002). We made a comparison of rice density in natural stands from panicle counts 118 around buckets (see below) and we measured tiller production from a systematic sample 119 of 100 stalks taken at each of 3 random locations in natural marsh. 120 An exceptional growth response inside exclosures in 1999 prompted us to test the role 121 of large fish on the survival of rice seedlings. We repeated the previous experiment to 122 include exclosures staked 25 cm off the bottom to allow access by fish. We placed a full 123 exclosure, a fish-accessible exclosure, and an unfenced control at 6 river-bordering 124 mudflat sites with naturally germinating rice. All exclosures were constructed of large-125 mesh (5.1 cm by 10 cm) wire.

## 126 **Experiments with Large Exclosures and Plantings**

127 In spring 2000, we used 5 large fenced plots of various sizes, the largest being a 100-m 128 linear exclusion fence along river-bordering rice, to study the effect of fencing on 129 survival and growth of wild rice. We planted 2 5 m by 20 m exclosures with rice seed in 130 April to explore restoration potential. We collected seed from rice plants during the 131 previous fall and maintained it in cold storage over winter (McAtee 1917). We worked a 132 small amount of rice seed into a mud ball (50 balls per site) and threw it into each 133 exclosure. We expanded the planting experiment during the 2001 growing season with 1 134 set of 6 circular, 9.7-m-diameter plots placed on each of 2 barren mud flats formerly 135 occupied by wild rice. In addition, we expanded 1 5 m x 20 m plot planted in 2000 by 136 about 33% in 2001, and we lengthened the large linear exclusion fence along the river 137 from 100 m to 250 m.

## 138 Rice Production and Estimates of Seed Consumption by Blackbirds

139 We estimated avian seed loss to large flocks of red-winged blackbirds that appear in 140 Patuxent marshes as early as mid August, by subtracting an estimate of seed fall from an 141 estimate of seed production. During fall 1998 and 1999, we estimated seed 142 production/panicle by bagging a sample of maturing panicles to exclude feeding birds 143 and capture all seed produced. In a nearby rice marsh, we also staked buckets at random 144 locations to sample seed fall from maturing panicles. Each bucket opening was 28 cm in diameter  $(0.062 \text{ m}^2)$  and we fitted them all with a 1.3 cm by 1.3 cm-mesh wire screen to 145 146 allow passage of seed but exclude birds and rodents. We estimated panicle density around buckets by counting the number of panicles within a 1-m radius ( $3.14 \text{ m}^2$  area) of each 147 bucket. We multiplied average panicle density/ $m^2$  by the average seed production/panicle 148

to estimate seed production/ $m^2$ . The difference between seed production/ $m^2$  and seed fall/ 149  $m^2$  yielded an estimate of avian seed consumption. 150

#### 151 **Techniques for Restoring of Wild Rice**

152 From 2001 to 2004, restoration efforts focused on use of extensive fencing to protect 153 both natural stands and large planted areas from goose herbivory. We expanded many of 154 these plots from year to year as rice filled available space. During this period, we 155 deployed over 6 km of fencing to protect rice from grazing geese. While seed planting 156 was our primary method of rice re-establishment, we also transplanted rice plants and 157 used this restoration method until mid summer. To obtain adequate seed for restoration 158 planting, we maximized seed capture by bagging panicles during late development. For 159 this purpose, we used a tough, high-density polyethylene fabric (Tyvek, manufactured by 160 Dupont Company, Richmond, VA) to prevent blackbirds from pecking through the 161

# material and eating the seed.

### 162 **Controlling Numbers of Resident Geese**

163 Once we knew that the loss of rice was related to an overabundance of resident geese, it 164 was clear that any imperative to restore rice to its former prominence would require 165 action to not only plant and protect rice with fencing, but to mediate herbivory by 166 reducing the resident goose population. We developed a goose reduction plan through 167 collaborative input and consensus of local jurisdictional land and state waterfowl 168 managers to 1) addle eggs to reduce recruitment, and 2) to use Maryland's September 169 resident goose hunting season to reduce the population. The program sought cooperation 170 from local land managers to access areas where geese were concentrated, many of which 171 were formerly closed to hunting. The hunt would be managed by park staff to assure

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maximum public participation and effectiveness in harvest of geese in the short 2-weekSeptember season.

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## Results

During 1999, the growth response of rice within 1-m<sup>2</sup> full exclosures was uniform and 175 176 striking whereas unprotected rice was virtually eliminated by grazing (Fig. 1A). The 18 177 fenced exclosures at 6 sites contained 1,907 panicled stalks (mean = 105.4 + 6.3 SE 178 panicles/exclosure: Table 1), whereas the 6 controls at those sites contained no panicles 179 and only 16 plants which were stunted (mean = 2.7 + 2.3 SE stalks/exclosure). The 180 virtual elimination of rice at unfenced controls produced an over-riding treatment effect of exclosure on rice abundance as measured by the number of stalks ( $F_{(3,15)} = 60.4$ , P <181 182 0.001). We tested for the effect of mesh size on rice abundance by deleting controls from 183 the data set and found no difference with regard to the number of stalks ( $F_{(2,10)} = 1.2, P >$ 184 (0.3). This lack of difference in numbers of stalks indicated that all mesh sizes were 185 effective in deterring grazing by a large and likely numerous herbivore. Although we 186 immediately suspected geese, any associated sign, such as droppings, tracks, feathers, or 187 down, had been washed away by the tide. At 1 observation site, we fenced grazed rice 188 plants in mid-June to protect them from further damage. These plants achieved about 189 two-thirds the height of protected plants and seed development was delayed from late 190 August until mid September.

191 The fish-accessible exclosure experiment that we conducted in 2000 was terminated 192 because we observed geese reaching beneath the wire at ebb tide and grazing rice plants 193 within exclosures. Although we took no plant measurements, we noted that full 194 exclosures produced abundant rice whereas the controls were virtually destroyed by 195 geese. The response of rice in large fenced and planted plots was equally successful (Fig.

196 1C, D): rice grew wherever it was protected by fencing, including plots where we

197 expanded the fencing from 1 year to the next (Fig. 1E).

198 In 1998, seed counts from bagged panicles revealed an average rice production of  $625 \pm$ 

199 76.7 SE seeds/panicle (n=29). Based on a mean panicle density around buckets of  $14.9 \pm$ 

200 1.7 SE panicles/m<sup>2</sup> (n=26), we estimated a seed production of 9,300 seeds /m<sup>2</sup> (95% CI:

201 5,300-14,400) or 93 million seeds/ha. We determined the mean dry weight of rice seed

from a sample of 100 seeds from each of 11 panicles to be  $1.445 \pm 0.084$  SE g. This

203 yielded a point estimate of rice seed production in natural marsh (dry weight) of 1,350

kg/ha. We estimated seed fall from bucket collections in 1998 at  $2,650 \pm 476$  SE

seeds/m<sup>2</sup>. The large difference between production and seed fall yielded an estimate of

avian consumption of 72% (95% CI: 31% – 89%). In 1999, mean seed production was

similar to 1998 at  $528 \pm 31.4$  SE seeds/panicle (n = 35), but panicle density was higher at

208  $26.4 \pm 3.0 \text{ SE /m}^2$  (n= 39). These figures yielded a seed production estimate of 13,940

seeds/m<sup>2</sup> (95% CI: 9,439 -19,212) or a dry weight production of 2,014 kg/ha. Subtracting

estimated seed fall from bucket collection  $(3,999 \pm 642 \text{ SE seeds/m}^2, n=33)$  resulted in an

estimate of avian seed consumption of 71% (95% CI: 44% - 86%).

212 Rice productivity within natural marsh paled by comparison to that within exclosures.

213 Panicle density within natural marsh as measured around buckets (14.9  $\pm$  1.7 SE and 26.4

 $\pm 3.0$  SE panicles/m<sup>2</sup> in 1998 and 1999, respectively) was but a fraction of that within 1-

215  $m^2$  exclosures (105.4  $\pm$  6.3 SE panicles/ $m^2$ : Table 1). Mean tiller production within

216 natural marsh also was lower than within exclosures (1.4  $\pm$  0.4 SE /100 plants vs 8.4  $\pm$ 

1.5 SE /100 plants, respectively; *t*-test with unequal variance: t = 4.6, 19 df, P < 0.001).

Statistical tests based on the subsampling of rice within exclosures revealed mesh size to affect plant height ( $F_{(2,10)} = 4.5$ , P < 0.05), but not panicle length ( $F_{(2,10)} = 0.26$ , P > 0.7) or stem diameter ( $F_{(2,10)} = 2.53$ , P > 0.1). There also was no effect of mesh size on the number of tillers ( $F_{(2,10)} = 0.51$ , P > 0.4). Plant height varied inversely with mesh size

222 (Fig. 2).

In September 2001, resident goose hunting was offered to the general public for the first time within the boundaries of the CBNEER, a wetland sanctuary where waterfowl hunting is normally prohibited. Five hundred geese were harvested in the first season and approximately 1,700 over a 4-year period. This marked reduction in geese, combined with efforts to re-establish rice with the use of 6 km of fencing and widespread seeding and planting, accelerated a major recovery of rice and other vegetation along the 10-km section of the upper Patuxent River.

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### Discussion

The magnitude of goose grazing along the Patuxent River and the response of rice to exclosure were 2 striking outcomes of this study. A third striking outcome was the widespread recovery of rice and other marsh vegetation following the major reduction in the numbers of geese. Although we suspected geese as a possible cause of the loss of rice, only through direct surveillance were we able to confirm the magnitude and speed with which geese could graze emerging rice plants, leaving stubble that appeared as if mowed mechanically (Fig. 1B).

It became apparent that numbers of geese and their grazing had increased unnoticed for well over a decade. This was perhaps because most grazing occurred early in the growing season when few people were in the marsh to notice it. River-bordering rice incurred the 241 most damage and virtually was eliminated by geese. Remaining rice was patchily 242 distributed behind protective barriers of vegetation, most commonly spatterdock and 243 pickerelweed. In the few areas where broad stands of rice still existed on river-bordering 244 mud flats, the plants often appeared terraced in height with the tallest plants at the most 245 interior locations (Fig. 1F). Because this is opposite the normal growth pattern where 246 river-bordering rice is most robust, we believe this terracing effect is a visible record of 247 grazing activity and confirms goose access from the open river channel. 248 Although goose herbivory has emerged as a major factor in reducing wild rice along the 249 Patuxent River, we recognize that numerous interrelated factors also influence 250 establishment, growth, and survival of rice (e.g., see Martin and Uhler 1939:116-142; Lee 251 and Stewart 1984). The striking growth response of rice within exclosures attests to a 252 large degree on the ability of rice to stool out and thus fill exclosures by vegetative 253 means. However, this robust growth also appeared aided by a fertilizing effect of 254 exclosure (i.e., the wire and plants acting as a sediment trap [cf. Meeker 1999]). On 255 removal of exclosures in September, sediment height within exclosures was several 256 centimeters above that of adjacent tidal flats and our finding of an inverse relationship of 257 plant height and wire mesh cross-sectional area (Fig. 2) is consistent with the notion of 258 increased fertility. We also note that most exclosures were located in deeper water zones 259 that generally are more fertile for rice growth and free from competition with other 260 emergent plants. We conclude that the greater productivity of plants inside exclosures is 261 primarily a result of protection from herbivory, along with the aforementioned benefits of 262 fertility and site placement.

263 Wild rice is highly vulnerable to goose grazing during a long early-growth period from 264 germination in April through emergence from the water column (floating leaf stage) in 265 mid May and June. This period coincides with the nesting and brood rearing stages of 266 geese, a time when females must acquire nutrients for eggs and goslings feed voraciously 267 to achieve adult size in about 10 weeks. Breeding adults and growing goslings require 268 large amounts of protein-rich foods (Buchsbaum and Valiela 1987), and early-growth 269 wild rice appears as one of few and the most nutritious of graminoids in the emergent 270 zone of the Patuxent marshes. Adult geese uprooted germinating rice plants on exposed 271 mud flats as soon as they appeared in spring, and by May and June flightless goslings 272 browsed developing plants as they foraged along the river in crèches (Fig. 1B). By mid-273 to-late June, most rice had grown beyond the reach of geese. Adult geese that entered 274 molt on the river in July and August generally had little further grazing effect on rice. 275 Why the resident goose population expanded in the 1990s to overwhelm the rice 276 resource along the Patuxent River is unknown. We speculate that several years of closed 277 or limited hunting on migratory geese during this period was a major contributing factor 278 (Hindman et al. 2003*a*). It was during this decade that surveys documented resident 279 goose numbers in the Atlantic Flyway to rise sharply and exceed an unprecedented 1 280 million birds (Atlantic Flyway Council 1999, Hindman et al. 2003b). Presently, the 281 Maryland resident goose population, as estimated from the Atlantic Flyway breeding 282 waterfowl plot survey, is about 86,500 (Serie and Raftovich 2005). 283 Although imprecise, our 2 estimates of blackbird consumption of rice seed (71% and 284 72%) are consistent and provide some evidence of the magnitude of rice loss to these

285 large flocks of birds. Despite this loss of seed, the rapid return of rice that accompanied

286 restoration efforts and reduction in geese vindicates blackbirds as the cause of the rice

287 decline. In a larger ecological context, we suggest that wild rice has evolved to

accommodate high seed mortality and even be dependent on it as a process to thin and

thus maintain more robust natural populations (Weiner and Whigham 1988).

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## Management Implications

291 Our experience on the Patuxent serves to alert managers to the potential threat of over 292 grazing by resident geese on our mid latitude marshes, and perhaps more importantly, 293 demonstrates a course of successful remedial action. Fortunately the loss of wild rice on 294 the Patuxent was an obvious and striking change to which managers could justify 295 corrective action. Goose herbivory was severe along the Patuxent and might have 296 eventually extirpated rice and possibly other palatable species. Just as seriously, intertidal 297 mud flats left barren of rice were vulnerable to invasion by undesirable species, such as 298 *Phragmites.* The event of such colonization would have rendered rice recovery difficult, 299 perhaps impossible, and radically altered the vegetative composition of the marshes into 300 the future. Loss of rice to resident geese is not unique to the Patuxent River (e.g., see 301 Nichols 2004) and the possibility of a widespread decline of rice in estuaries of the 302 Atlantic seaboard could affect the fall food base of many migrant marsh birds and pose 303 deleterious effects on migration and ultimately populations. In addition we note that 304 many wildlife refuges and wildlife management areas have long harbored resident geese 305 as a result of their management focus on this important game species. We recommend an 306 evaluation of the grazing effects of these birds on local marsh vegetation and especially 307 with regard to the status of wild rice and other palatable grasses. Finally, we could not 308 have predicted better success in both our approaches to rice restoration and a publicly

309	compatible goose reduction plan. Although our plan to reduce numbers of geese was
310	successful, we note that the outcome may have been less so in the face of more stringent
311	management constraints. We believe as numbers of resident geese continue to grow in the
312	Atlantic Flyway, managers will need more options to meet the challenges of resolving
313	resident goose conflicts. Our success in restoring rice along the Patuxent and affecting a
314	solution to an overabundance of resident geese underscores the value of stewardship and
315	collaborative commitment to maintaining our natural wetlands.
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Table 1. September 1999 measurements of mature wild rice plants grown within sets of
1-m<sup>2</sup> exclosures, 1 small-(1.3 cm by 1.3 cm), 1 medium-(2.5 cm by 2.5 cm), and 1 largemesh (5.1 cm by 10.2 cm) fencing, replicated (n=6) on tidal flats of the Patuxent River.

423

		Small		Medium		Large			
	n <sup>a</sup>	Mean	SE	Mean	SE	Mean	SE	Mear	
No. plants per exclosure	6	100.7	7.0 A <sup>b</sup>	89.8	10.4 A	99.7	11.2 A	96.7	
No. panicles per exclosure	6	108.0	8.0 A	98.5	12.7 A	109.7	13.1 A	105.4	
No. tillers per exclosure	6	7.3	1.6 A	9.0	2.8 A	10.0	4.0 A	8.8	
Stalk height <sup>c</sup> (cm)	60	326.2	5.1 A	311.2	5.4 B	292.7	5.6 C	309.3	
Panicle length <sup>c</sup> (cm)	60	63.5	1.2 A	62.6	1.4 A	61.0	1.4 A	62.4	
Stem diameter <sup>cd</sup> (mm)	60	8.5	1.9 A	7.5	0.2 B	7.4	0.2 B	7.8	

<sup>c</sup> Measurements of stalk height, panicle length, and stem diameter are from a systematic
 437

438 sample of 10 rice plants taken from each exclosure.

439 <sup>d</sup> Measured at nearest mid node at half the height of the stalk.

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441 Figure 1. An August 1999 photo taken on the Patuxent River (A) reveals the marked 442 contrast of maturing wild rice inside exclosures and virtually no survival of rice outside 443 (note stake marking control plot). Rice inside exclosures grew robustly and achieved 444 heights up to 4 m. Grazed rice (B) appeared as if it had been cut mechanically. Large 445 fenced plots of naturally germinating rice (C) and planted circular plots (D) produced the 446 same dramatic effect. Extensive river-bordering stands of rice (E) returned quickly once 447 protected by fencing. A single grazing would set back the growth of rice significantly as 448 contrasted by the rice inside and outside this exclosure (F). This often produced a 449 noticeable terracing effect between river-bordering rice and less accessible rice in the 450 interior of the marsh. 451 452 Figure 2. The relationship between height of wild rice stalks (mean + SE) and exclosure mesh size cross-sectional area. Points are means of large- $(5.1 \text{ cm by } 10.2 \text{ cm}, \text{ or } 52 \text{ cm}^2)$ , 453 medium-(2.5 cm by 2.5 cm, or  $6.3 \text{ cm}^2$ ) and small-(1.3 cm by 1.3 cm, or  $1.7 \text{ cm}^2$ ) mesh 454

455 exclosures taken across 6 randomly selected locations (blocks) on intertidal mud flats of

456 the Patuxent River with 10 measurements per block (n = 60 per mesh size) in 1999.