

Introduction

* Simultaneous hermaphroditism occurs infrequently among freshwater bivalves of the family Unionidae. It has been documented as the predominant mode of reproduction for only five (*Anodonta imbecilis*, *Lasmigona subviridis*, *L. compressa*, *Carunculina parva* (Sterki, 1898; Van der Schalie, 1969, 1970) and *C. pulla* (pers. obs.)) out of an assemblage of more than 220 (Burch, 1975) North American species, but additionally, hermaphroditic individuals are encountered in low frequencies (about 2% in *Elliptio*; see Heard, 1979) among an appreciable number of predominantly dioecious species. For example, a combination of the general surveys of Van der Schalie (1969, 1970) and more restricted surveys of the genera *Elliptio* and *Anodonta* by Heard (1975, 1979) indicates that a total of 30 species of 101 examined contained some individuals reproducing as hermaphrodites within an otherwise completely dioecious population. This number is likely to increase with larger sample sizes; of 97 species examined by Van der Schalie (1970) more than half are represented by fewer than 10 specimens.

Both the species that reproduce predominantly as hermaphrodites as well as the occasional hermaphroditic individuals in dioecious populations can exhibit considerable variability in the ratio of male : female gametes produced. This variability manifests itself at the level of the population, the individual, or both. For example, both Weisensee (1916) and Bloomer (1930, 1934, 1935, 1939, 1940) report that the Eurasian anodontine *Anodonta cygnea* can occur in populations comprised of males, females, and hermaphrodites, females and hermaphrodites, males and hermaphrodites, and hermaphrodites only. Weisensee (1916) suggested a correlation between habitat type and reproductive mode for this species: * dioecious individuals were sampled predominantly from rivers, while hermaphrodites were encountered mainly in impoundments. Bloomer (1935, 1939) apparently found no such relationships. Similar variability at the population level seems to exist for the North American *A. imbecilis*; Van der Schalie (1970) reports that populations of the species in Michigan are uniformly hermaphroditic (but that "... male elements. . . were not as widely distributed as the acini containing eggs") while Heard (1975) found that lotic populations * in northern Florida contained female hermaphrodites ("ovarian tissue slightly or greatly exceeding quantity of testicular tissue") as well as a large percentage (48.5% and 58.5% for the two populations studied) of individuals reproducing as pure females. While the taxonomy of the Anodontinae has been confused for some time because of excessive reliance on environmentally variable shell characters for species determinations (Kat, 1983), such differences among populations of predominantly hermaphroditic species appear not to result from inadvertent sampling of more than one species.

At the level of the individual, variability has been observed in the ratio of testicular : ovarian tissue among individuals in single populations of predominantly hermaphroditic species as well as among hermaphroditic individuals in single populations of predominantly dioecious species (Van der Schalie, 1970; Heard, 1975, 1979). This is apparently a common phenomenon among the Bivalvia (e.g. Coe, 1943; Kat, 1978), and as Coe (1943, 1945, 1953) has pointed out repeatedly, such wide variation in the expression of sexuality among populations and species of molluscs provides a great deal of raw material for studies concerned with the general question of differential advantages of various reproductive modes. For example, studies by Coe (1940, 1945), Gould (1952), and Hoagland (1978) have been instrumental in contributing towards an understanding of the advantages of protandry and

environmentally—determined sexuality among molluscs. While a complicated life cycle coupled with long maturation times of the Unionidae renders them largely unsuitable for laboratory experiments, a series of natural experiments provide the means of testing hypotheses concerning selective value of different modes of reproduction in a variety of habitat types and population densities. These natural experiments are largely the result of two processes: the establishment of a variety of man-made habitats, and the lingering effects of Wisconsinan glaciation on the geographic ranges of all aquatic bivalves (Clarke, 1973; Kat, 1982a, Kat & Davis, In press).

This paper has two purposes. First, a more extensive study of *Anodonta imbecilis* along its geographic range and in a number of habitats was undertaken to determine which factors potentially can affect the observed variability in the presence of ovarian and testicular tissue among different populations of the species. Second, a similar study was conducted along the geographic ranges of five predominantly dioecious species (*Elliptio complanata*, *Lampsilis radiata*, *L. ochracea*, *Strophitus undulatus*, and *Alasmidonta undulata*) to attempt to determine causes contributing towards the occasional occurrence of hermaphroditism among such species. Data from the present and other studies will be presented with a number of testable hypotheses to encourage further research in this area.

Methods

Hermaphroditic species: Anodonta imbecilis

Density of unionids is difficult to quantify, as individuals are often unpredictably distributed over favorable microhabitats (Kat, 1982b). Consequently, the few estimates of population density available are characterized by large standard deviations about the mean (Ökland, 1963; Negus, 1966; Haukioja & Hakala, 1974). Conventional estimates of population density based on numbers of individuals per unit area might have to be abandoned in most habitats with the possible exception of lakes with rather uniform bottom characteristics. Specimens for this study were collected by hand with the aid of a stout dip net, and density estimates of *Anodonta imbecilis* were based on average numbers of individuals collected with standard equipment over four 15 minute, random area searches. This technique provides an adequate estimate of population density, allows for observation of clumping and is the only practical density estimator in sparse populations. By these estimates, population densities of *A. imbecilis* in rivers are almost an order of magnitude lower than those of lakes and impoundments, a rather common observation for this species (Walter, 1956; Johnson, 1970; Havlik & Marking, 1980; Clarke, unpublished manuscript).

Animals ranging in length from 60 to 70 mm were fixed for 12 h in 10% formalin and preserved in 70% alcohol. Wedges of tissue were cut from the visceral mass at the point where the foot makes its posterior junction with the body (Fig. 1). These wedges were dehydrated, cleared, and embedded by standard histological methods (Humason, 1972). Sections were stained in Harris hematoxylin and counterstained in Eosin Y. The differences in relative male gonadal volume among individuals were quantified by placing a 1 mm grid under 10 slides containing sections from various locations within the wedge of tissue, counting the number of squares filled with each type of gonadal tissue under low magnification, and averaging the ratio over the 10 slides. The number of individuals sectioned was largely determined by the number of individuals found at each sampling location and varied from 4 to 15. It is important to point out that the ratio of male : female gonadal tissue determined by this method is an estimate, and not an indication of the absolute ratio within each individual (even though a number of serial sections through the gonads of several individuals indicates that the ratio is relatively constant from location to location).

Rather, it is indicative of the relative extent to which spermatogenic and oogenic tissue is present

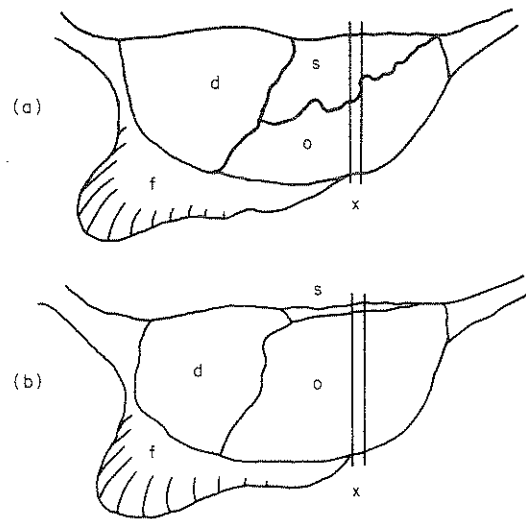


FIG. 1. Ratios of spermatogenic: oogenic tissue among individuals of *Anodonta imbecillis* sampled from populations of different density. Individuals from low-density and newly-established populations (A) exhibit high ratios of spermatogenic (s), oogenic (o) tissue in the gonad and at the section location (x); individuals from high-density populations (B) exhibit low ratios of spermatogenic: oogenic tissue. d = Digestive tissue, f = foot.

at a constant location in the visceral mass. Dissections and serial sections show that as spermatogenic tissue increases in volume, it becomes saddle-shaped and increasingly occupies the dorsal and posterior regions of the gonad. Individuals in which no spermatogenic tissue was detected in the histological sections were all determined to be pure females by dissection.

Any study of reproduction along a geographic range has to consider complications resulting from differences in stages of gonadal maturation caused by differences in local temperatures at the time of collection. If both types of gametes matured at the same rate, a measure expressed as a ratio between spermatogenic and oogenic tissue volumes would compensate for such differences between sites. However, in most bivalves spermatogenic and oogenic regions tend to mature at slightly different rates (Coe, 1943; Galtsoff, 1964; Keck *et al.*, 1975; Kat, 1982*c*), which could lead to inaccuracies in male: female ratios while the gametes are maturing. While some error was doubtlessly introduced from this source, it was kept to a minimum by considering only those specimens which exhibited similar stages of gonadal maturation. This was facilitated by collecting at different times of the year along the geographic range. The sample sites are listed in the Appendix.

Peripheral populations can be identified for those unionids presently expanding their geographic ranges in response to climatic amelioration following the retreat of Wisconsinan glacial ice, and those expanding into recently constructed man-made habitats. Individuals in such peripheral populations might be expected to exhibit variability in reproductive mode associated with colonization and founder events (Allard, 1965; Mulligan, 1965; Zohary, 1965; Ghiselin, 1974) if the genetic or phenotypic potential for such variability exists. For *Anodonta imbecilis*, the Tar River, Loch Raven and Swift Creek reservoirs as well as Lake Osborne and Pickering Creek are considered sites of recent colonization. The reservoir on the Tar River was completed in 1972. In 1977, A. H. Clarke (USNM) collected numerous specimens from the reservoir (unpublished manuscript) while a survey conducted by J. P. E. Morrison (USNM) at the same site in 1971 revealed no specimens of the species (unpublished data). Johnson (1972) reports an absence of the species from Peninsular Florida, but in 1979 it was present

in high densities in Lake Osborne. Fuller & Hartenstine (1980) suspect that the Pickering Creek population is of recent origin, and Tanner (1970) omits it from his Pennsylvania range data. Loch Raven has to my knowledge not been sampled before Long (1979) found evidence of a small population there; it can be considered of recent origin because of the age of the reservoir and its position at the edge of the known geographic range of the species. Swift Creek reservoir was included in a survey by Walter (1956) who found no specimens of the species there at that time.

Dioecious species: Elliptio complanata, Lamprolambis radiata, L. ochracea, Strophitus undulatus, and Alasmidonta undulata.

Specimens of these species were collected by hand from various locations on the Delmarva peninsula and Nova Scotia (see Appendix for locations of the collection sites). Density estimates were again based on average numbers of specimens collected over four 15 minute, random area searches. Histological sections were prepared by the same methods as described for *Anodonta imbecilis*, and the volumes of oogenic and spermatogenic tissue among the occasional hermaphrodites estimated by similar methods.

Wisconsinan glaciers in all likelihood restricted populations of these species to refuges south of the maximal glacial advance such as Maryland, the Delmarva Peninsula, and Virginia (Kat, 1982a, In press; Kat & Davis, In press). Nova Scotia constitutes an area of very recent colonization for these species (Athearn & Clarke, 1961; Kat, 1982a; Kat & Davis, In press), and again, since low founder population density and colonization events have been associated with differential reproductive success of hermaphrodites (Tomlinson, 1966; Baker & Stebbins, 1965; Ghiselin, 1974), ~~peripheral populations of predominantly dioecious species which have recently been established can be expected to exhibit disproportionate frequencies of hermaphrodites~~ if the genetic or phenotypic potential for hermaphroditism exists in such species.

Except in the case of rare species, gonads and structure of the outer demibranchs of 20 individuals from each site were examined histologically. The number of sites sampled for each species depended entirely on how each species was distributed within its geographic range; some species such as *Elliptio complanata* occur in almost every freshwater habitat between Maryland and Nova Scotia, and are thus well represented in terms of number of sample sites. Other species such as *Lamprolambis radiata*, *L. ochracea*, and *A. undulata* occur less frequently and were sampled from fewer sites. The location of the sample sites is listed in the Appendix.

Among the species examined, only *Lamprolambis radiata* and *L. ochracea* exhibit an immediately apparent sexual dimorphism in shell shape and gill structure. The remaining species either exhibit no such macroscopic dimorphism, or possible dimorphism is masked by high levels of phenotypic variability in shell shape common among these unionids. Nevertheless, since all female unionids maintain larvae within variably specialized intralamellar brood spaces, histological examination of the demibranchs can discriminate between males and females (Heard, 1979; Davis & Fuller, 1981). Therefore an examination of the demibranchs of hermaphroditic individuals of predominantly dioecious species allows determination of whether such hermaphrodites have an overall male or female phenotype.

Results

Anodonta imbecilis

Individuals of this hermaphroditic species (Plate I(a)) are bimodally distributed with respect to gonadal volume of male tissue (Tables I & II). A first group can be characterized by low ratios of male : female tissue at the section location ($\bar{x}=0.14$) and the rest of the gonad, while a second contains individuals with significantly higher amounts of spermatogenic tissue

($\bar{x}=0.43$; $P\ll 0.01$, t -test corrected for unequal variances) (Fig. 1). Analysis of variance confirms highly significant differences between sites ($F=141.07$, $P<0.01$).

Low ratios of male:female tissue were found in high density, central range populations in the Suwannee River canal, Lake Talquin, and the Mosquito Creek reservoir. Populations at these localities also contained pure females at various frequencies: 12%, 20%, and 14%, respectively. These populations are thus characterized by very low levels of investment in spermatogenic tissue. High ratios of male:female tissue were found in all populations sampled from creeks and rivers, as well as peripheral populations in reservoirs.

Dioecious species

Results of this study indicate a fundamental stability of the dioecious system of reproduction among unionids; for example, none of the 560 individuals from 28 populations of *Elliptio complanata* examined exhibited any evidence of hermaphroditism, even though these individuals were sampled from a variety of habitats, at two range extremes, and under various conditions of population density. A similar observation applies to *Strophitus undulatus* and *Lampsilis ochracea*.

Lampsilis radiata and *Alasmidonta undulata* were the only predominantly dioecious species in which simultaneous hermaphroditism was occasionally encountered (Table III). Hermaphroditism among *L. radiata* always involved inclusion of various amounts of spermatogenic tissue within discrete follicles (Plate I(b)) within phenotypically female individuals (lampsiline unionids generally exhibit sexual dimorphism in shell shape and gills), and occurred in dense populations on the Delmarva Peninsula and in Lake Memphremagog which were highly infected (up to 85% of the individuals examined) by digenean trematodes (Plate I(c), I(d)) which caused partial or complete castration. Paradoxically, female individuals were much less frequently parasitized than males in these populations. Frequency of hermaphrodites among the populations was 13% in the Sassafras River, 8% in the Andover Branch, 10% in the Chester River, and 15% in Lake Memphremagog. Percentages of male tissue in these hermaphrodites varied from 81.7% to 24.6%, with an average of 67.3% ($n=10$ hermaphrodites).

Two types of hermaphroditism were encountered among the populations of *Alasmidonta undulata* sampled. The first type always involved inclusion of a limited amount (<1% of gonadal volume) of male tissue within female follicles (Plate II(a)) and was encountered in two very low density peripheral populations. The second type was characterized by the presence of discrete male and female follicles (Plate II(b)) and was encountered in a higher density lentic peripheral population. Percentages of male tissue in these hermaphrodites varied from 92% to 62%, with an average of 73.4% ($n=4$ hermaphrodites). Analysis of the demibranchs revealed that the individual with the highest male:female gonadal ratio had an overall male phenotype, while the other individuals had an overall female phenotype. As was the case among *Lampsilis radiata*, gonads of individuals of this population were infected with digenean trematodes (Plate II(c)).

Discussion

Hermaphrodites

Differential allocation of energy to reproductive functions and the resulting differential reproductive success has been a key to the understanding of life-history strategies (Cody,

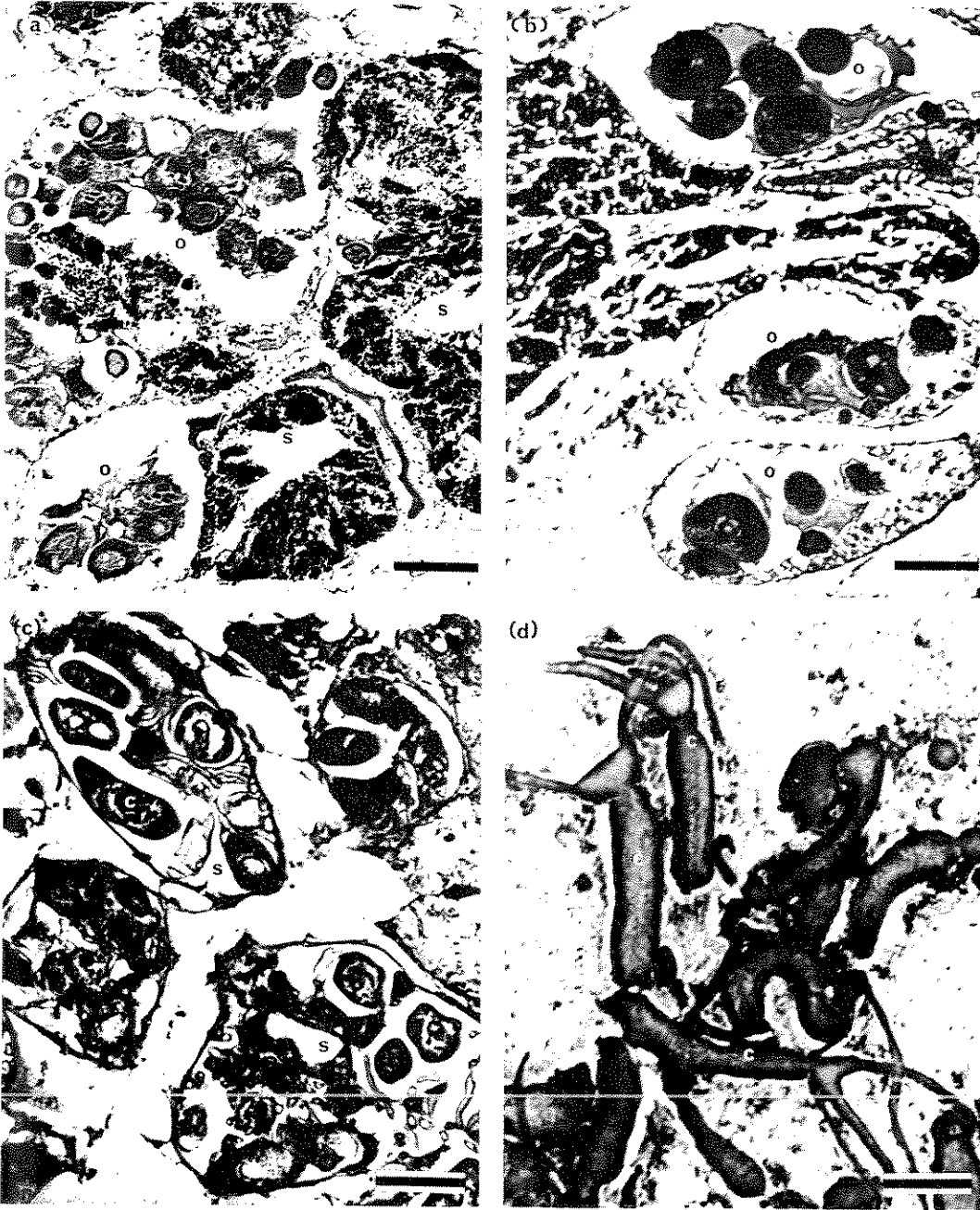


PLATE I(a) Oogenic (O; left) and spermatogenic (S; right) tissue of *Anodonta imbecilis*. Scale bar = 100 μ m. (b) Oogenic (O; right) and spermatogenic (S; left) tissue within an hermaphroditic individual of *Lampsilis radiata*. Scale bar = 100 μ m. (c) Sporocysts (S; top left and bottom right) containing cercariae (C) within the gonadal tissues of *Lampsilis radiata*. Scale bar = 100 μ m. (d) Typical "oxhead" cercariae (C) of trematodes of the family Bucephalidae from *Lampsilis radiata*. Scale bar = 100 μ m.

TABLE I
Variation in the ratio male : female gonadal tissue in central geographic range populations of Anodonta imbecilis

Sample location collection date	Habitat type	Population density	Ratio male : female		N
			\bar{x}	S.D.	
Talquin, 1/79*	Reservoir	21 ind/h	0.09	0.05	15
Suwannee, 1/79, 1/80*	Canal	32 ind/h	0.18	0.06	15
Mosquito, 1/80*	Reservoir	26 ind/h	0.15	0.03	15
House Cr., 1/80	Creek	3 ind/h	0.46	0.08	4
Cedar Cr., 1/80	Creek	6 ind/h	0.43	0.06	5
Ocmulgee R., 1/80	River	4 ind/h	0.47	0.09	7
Altamaha R., 1/80	River	3 ind/h	0.42	0.08	4
Savannah R., 1/79	River	2 ind/h	0.38	0.06	4
Limestone Cr., 1/80	Creek	3 ind/h	0.44	0.07	3
Tarpleys Mill, 4/80	River	4 ind/h	0.40	0.05	7

*Population contains pure females: see text.

TABLE II
Variation in the ratio of male : female gonadal tissue in peripheral or newly- established populations of Anodonta imbecilis

Sample location collection date	Habitat type	Population density	Ratio male : female		N
			\bar{x}	S.D.	
L. Osborne, 1/79	Reservoir	25 ind/h	0.40	0.06	15
Pickering Cr., 5/78	Creek	4 ind/h	0.36	0.05	15
Tar R., 4/79	Reservoir	18 ind/h	0.42	0.09	15
Loch Raven, 4/80	Reservoir	3 ind/h	0.44	0.07	6
Swift Cr., 4/79	Reservoir	8 ind/h	0.38	0.06	12

1966; Tinkle, 1969; Gadgil & Solbrig, 1972; Hirshfield & Tinkle, 1975; Calow & Woolhead, 1977). However, it is only more recently that the more subtle process of differential allocation of energy to male and female gametes among simultaneous hermaphrodites has begun to receive attention commensurate with its importance in understanding sexual strategies (Williams, 1975; Charnov, Smith *et al.*, 1976; Charnov & Bull, 1977; Charnov, 1979a, 1979b; Fisher, 1981; Freeman, McArthur *et al.*, 1981). Williams (1975) and Altenberg (1934) proposed that selection should maximize fertilization efficiency and reduce wasteful sexual competition: hermaphroditic animals which self-fertilize or fertilize internally should spend less on male than female functions. Evidence has been mounting to suggest that sessile, non-selfing hermaphrodites can also alter allocation of resources to male or female reproductive

TABLE III
Occurrence of occasional hermaphroditism and trematodal infections among two predominantly dioecious unionid species

Sample location	# ♂	# ♀	# ♂ ♀	trematodes	N
(a) <i>Lampsilis radiata</i>					
Sassafras	17	6	3f*	+	23
Chester	12	6	2f	+	20
Andover	14	9	2f	+	25
Nanticoke	12	8	—	—	20
Memphremagog	13	7	3f	+	20
Champlain	11	9	—	—	25
French	10	10	—	—	20
Shubenacadie	9	11	—	—	20
Mattatall	13	7	—	—	20
Egmont	12	8	—	—	20
Newville	11	9	—	—	20
(b) <i>Alasmidonta undulata</i>					
Andover	7	5	—	—	12
Norwich	10	8	—	—	18
Newville	4	2	1f	—	7
Gilbert	2	3	1f	—	6
Nine Mile R.	5	7	4m,f	+	16

*f=phenotypically female hermaphrodites, m=phenotypically male hermaphrodites.

functions, suggesting that these hermaphrodites experience unequal reproductive success through male or female gametes depending on environmental conditions (Ghiselin, 1974; Charnov & Bull, 1977; Charnov, Gotshall *et al.*, 1978; Freeman, Klikoff *et al.*, 1976; Freeman, McArthur, *et al.*, 1981). Perhaps the most convincing data emerge from the botanical literature, which indicates that plants show large variations in the sex ratios of flowers on different individuals depending on the quality of the site occupied (Kooistra, 1967; Williams & Thomas, 1970; Freeman, McArthur *et al.*, 1981; Meagher, 1981). The results of this study indicate a distinctly bimodal pattern of allocation of reproductive energy to male gametes in *Anodonta imbecilis* collected from different habitats (Table I). Several non-inclusive hypotheses can be proposed to explain these differences:

(1) For plants, hormonal systems are known to control allocation of resources to different gametes, and these hormonal systems could respond to specific environmental conditions, providing a direct link between allocation ratios and environmental parameters. For example, Freeman, McArthur *et al.*, (1981) showed that three monoecious spinach species altered proportional allocation to gametes depending on the availability of moisture in the soil. In addition, different nutrients are known to affect pollen and ovule production (Charnov, Smith *et al.*, 1976; Freeman, McArthur *et al.*, 1981). It is not known whether different nutrients are involved in the manufacture of sperm and eggs among molluscs, or if environmental parameters can affect hormone activity. Nevertheless, Coe (1938, 1943)

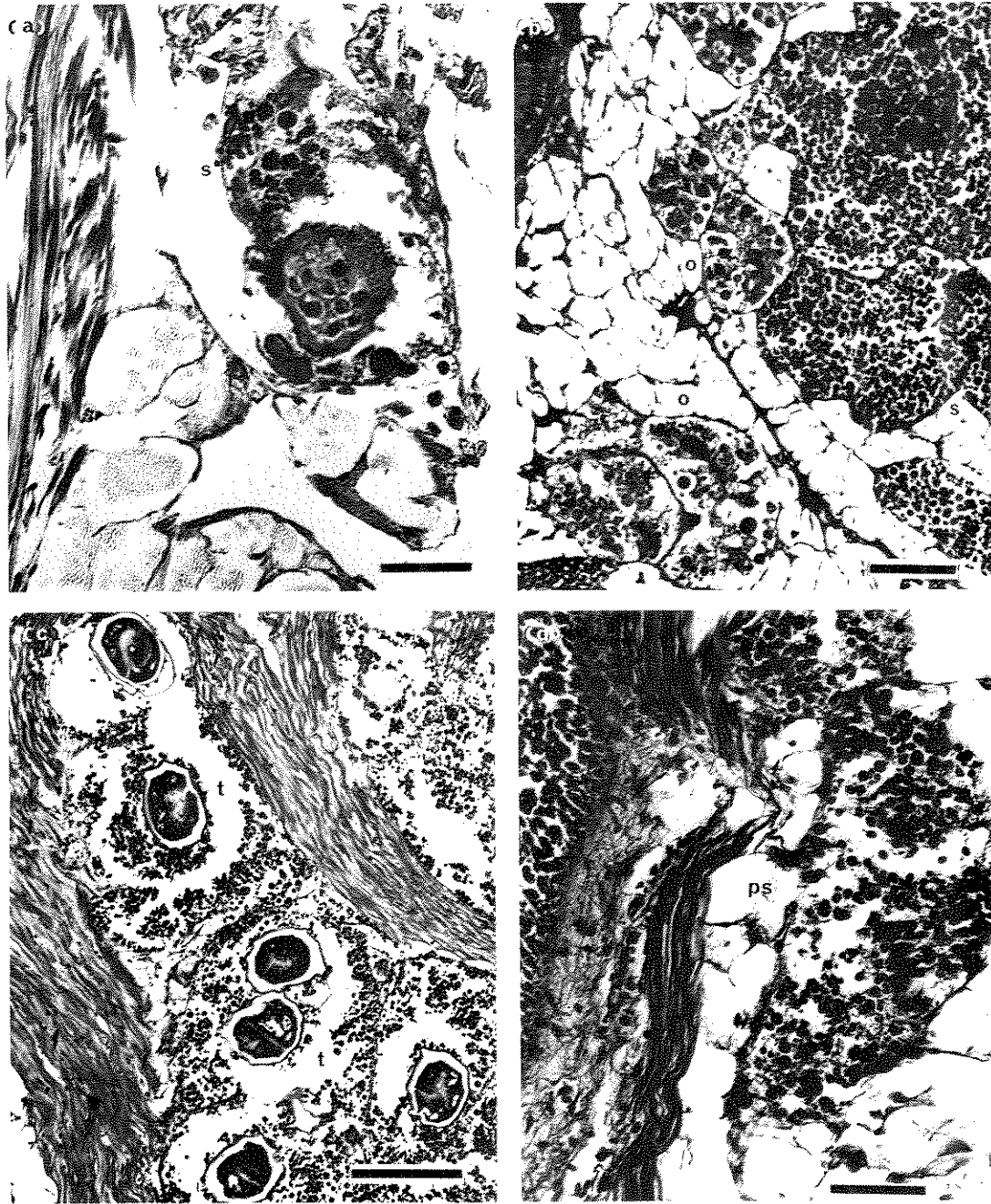


PLATE II(a) A small cluster of spermatogonia and spermatids (s) within a predominantly female individual of *Alasmidonta undulata*. Scale bar = 50 μ m. (b) Oogenic (o; left) and spermatogenic (s; right) tissue within an hermaphroditic individual of *Alasmidonta undulata*. Scale bar = 100 μ m. (c) Individual trematodes (t) within the gonadal tissue of *Alasmidonta undulata*. Scale bar = 200 μ m. (d) Primary spermatogenic tissue (ps) of a juvenile *Anodonta implicata*. Scale bar = 50 μ m.

indicated that among Virginia oysters (which function seasonally as separate sexes) the proportion of yearling females was highest in those localities most favourable for rapid growth, so that temperature and nutrient conditions could have led to differential proliferation of female cells in the early ambisexual gonads. Hormones are known to be implicated in triggering protandric change in gastropods of the genus *Crepidula* for example (Gould, 1952; Coe, 1953; Hoagland, 1978; Le Gall, 1980), and accumulations of metabolic by-products are thought to be responsible for rhythmical sexuality characteristic of many oysters (Orton, 1913; Coe, 1943). While different environmental conditions and/or differential availability of nutrients could have influenced the observed differences in the ratio of male : female gametes among *Anodonta imbecilis*, the relative constancy observed among individuals with high male : female ratios sampled from a variety of habitats and geographic range positions tends to weaken an explanation based only on nutrient-induced patterns of allocation.

(2) There could exist a fundamental difference in mode of fertilization among the populations studied. ~~For example, individuals in populations characterized by low male : female ratios could be primarily self-fertilizing, while individuals with higher male : female gonadal ratios could be predominantly cross-fertilizing.~~ This hypothesis would be in accordance with theoretical studies that propose that investment in male gonadal products should be low in self-fertilizing hermaphrodites since fertilization is efficient (Ghiselin, 1974; Williams, 1975; Charnov, Smith *et al.*, 1976; Charnov, 1979a, 1979b). However, self-fertilization often entails a considerable cost in fertility (Paraense, 1959; Gee & Williams, 1965; Giese & Pearce, 1975), and the populations with reduced male investment were also those populations with the highest density of individuals, a condition in which self-fertilization can be expected to be selected against (Tomlinson, 1966; Ghiselin, 1974; Charnov, Smith *et al.*, 1976). It is important to point out that experimental self-fertilization among *Anodonta cygnea* was accomplished by Bloomer (1940, 1943), and until more data on mode of fertilization are obtained, the possibility that low male-investment populations of *A. imbecilis* are largely self-fertilizing cannot be ruled out. The presence of pure females in such populations could have resulted from selection for outbreeding, as is suggested for gynodioecy in plants (Lewis & Crowe, 1956; Willson, 1974; Bawa, 1980).

(3) Gametes produced by unionids such as *Anodonta imbecilis* fall into two distinct classes, namely those that are broadcast and those that are retained. Sperm are suited for the broadcast category because of the low individual energetic cost involved in their manufacture. In an aqueous environment, sperm which are released into the water column will become more dispersed both by their own swimming movements and water currents with increasing distance from their source. The probability that a xenogamous, sedentary hermaphrodite will gain sufficient spermatozoa to fertilize its eggs thus depends on distances separating individuals, and in habitats with unidirectional currents, position of those individuals. A comparison can be drawn with wind-pollinated plants, but to my knowledge, resource allocation to gametes among populations occurring in sites differing in plant density and wind regimes has not been investigated. However, pollen availability can be a factor determining seed set (Willson, 1982), and competition for pollinators is often used to explain particular reproductive strategies among plants (Stebbins, 1974; Cruden, 1977; Harper, 1977; Waser, 1978). The probability of obtaining male (broadcast) gametes could differ in different habitats, and could constitute directional selection for hermaphrodites which stress either maleness or femaleness.

Population density of *Anodonta imbecilis* varies considerably in the two habitat types from which it was collected. Populations in lakes and reservoirs are characterized by small between-neighbour distances as a result of high population density and some clumping of individuals. Populations in rivers and creeks, on the other hand, are sparse and between-neighbour distances can be considerable. Characteristics of the water currents are also quite different in the two habitat types. In lakes and reservoirs, currents are often weak and non-directional, except where occasionally generated by wind. In rivers and creeks, currents can be strong and are generally highly directional.

Based on these differences in population density and current characteristics, a simple model can be constructed to attempt to predict probability of obtaining broadcast gametes, and consequently, how selection on ratios of allocation differs in each habitat. The assumptions of the model are as follows.

(a) A threshold concentration of spermatozoa per unit volume of water is necessary not only to induce transfer of eggs into brood pouches within the gills where fertilization takes place, but also to achieve fertilization of these eggs.

(b) Spermatozoa remain viable for a limited amount of time. For example, Galtsoff (1964) mentions that dilution of oyster spermatozoa as well as exposure to room temperature limits viability to five hours.

(c) Spermatozoa are effectively neutrally buoyant, and remain suspended for a period greater than the viability time.

(d) In a stream, the flushing time (the amount of time it takes for the effective volume of water containing the spermatozoa to wash over the population) is proportionally more important than the viability time in reduction of fertilization potential of spermatozoa; in a lake, the reverse is true.

(e) spawning of spermatozoa by males is largely synchronous. Thus, to achieve fertilization,

$$\frac{S n e^{-t/Td}}{V} > C.$$

Where S = the total number of spermatozoa contributed by an individual; n = the total number of individuals in the breeding population; V = the effective volume of water, which measures the volume of water around the population by which the spermatozoa are diluted.

$e^{-t/Td}$ = The decay rate of the spermatozoa, where $Td = Tv$, the viability time in standing water, or V/Q , the flushing time in flowing water; t = the time needed to achieve fertilization, a constant; C = the threshold concentration of spermatozoa needed to achieve fertilization.

(1) In cases where the reduction in fertilization potential of the spermatozoa is small, i.e. when Td is effectively large (long flushing time or a long viability maintained by concentrated spermatozoa) then;

$$e^{-t/Td} \rightarrow 1.$$

This simplifies the model to:

$$S > \frac{V C}{n}.$$

In dense populations, V will be relatively small and n relatively large, so that the quantity V/n becomes small. Assuming C to be constant under any set of conditions, the model therefore predicts that the threshold concentration of spermatozoa in such populations can be maintained by low individual input.

- (2) In cases where the reduction in fertilization potential is large, i.e. when Td is small (fast flushing time, short viability time due to dilution) then,

$$e^{-t/Td} \ll 1.$$

This situation pertains in streams and rivers, in which populations generally are sparse. In such sparse populations, V is large and n is small, so that the quantity V/n is large. Consequently,

$$S > \frac{VC}{n e^{-t/Td}},$$

and the number of spermatozoa produced by an individual to maintain a threshold concentration has to be large.

This particular model proposes that the patterns of allocation to male and female gametes by *Anodonta imbecilis* are due to limited sperm availability, which is at odds with current views on sexual selection among simultaneous hermaphrodites (e.g. Charnov, 1979a). In fact, unless sperm competition can be avoided under conditions of high population density, it would seem that increased investment in male gametes in such populations should yield higher fitness returns, especially because of the occurrence of pure females. Nevertheless, reduced sperm availability could well be important in low-density populations in which distances between individuals are large.

Alternatively, rather than only implicating a selective model based on levels of sperm availability, a similar hypothesis based on limitation of brood space could also be applicable. Heath (1977, 1979) developed a general model to explain the evolution of hermaphroditism among organisms which brood their eggs: if the brood space is limited and can hold fewer developing eggs and embryos than the individual can produce, then the remainder of the reproductive resources could profitably be channelled into male gametes which can be broadcast to fertilize another individual's eggs. This model can be extended to apply to variability in ratios of allocation in simultaneous hermaphrodites such as *Anodonta imbecilis*, which are also restricted in the number of embryos that can be maintained within the brood pouches. In a situation where a hermaphrodite is limited in the number of eggs that can be fertilized, and where efficiency of transfer of sperm between individuals is high (such as applies among individuals in lakes, see below), reduced investment in male gametes is selected for compared with individuals in populations where efficiency of sperm transfer is low. In populations of high density where sperm transfer is efficient, fertilized egg production could thus be mainly limited by space available to brood eggs, while in populations of low density with inefficient transfer of sperm, fertilized egg production could be limited by availability of sperm.

The extensive studies of Bloomer (1934, 1935, 1936, 1939, 1940, 1943, 1946) on the simultaneously hermaphroditic *Anodonta cygnea* offer support for these theories. First, Bloomer (1943) noted that some individuals within river populations did not produce young during reproductive seasons, which he attributed to "... want of favorable conditions,

principally warmth, during the critical period", but which could also be contributed to unavailability of foreign sperm, especially since water temperature in flowing rivers tends to be rather uniform. Second, Bloomer (1943) also mentions that "... the products of the gonads very much exceed the quantity requisite for filling the outer gills with ova. All this excess apparently is not discharged and part of it remains unabsorbed in the gonads, more especially in the dorsal portion, for a very long time". Third, individuals within a population vary considerably with respect to the extent to which the demibranchs are filled with larvae, which again supports a hypothesis based on limitation of sperm in some populations (Bloomer, 1934, 1943, 1946).

An interesting correlate emerges from this study in that all peripheral populations, regardless of population density and habitat type, consist of individuals which resemble river and creek populations in ratios of allocation (see Table II). Since unionid habitats are highly discontinuous, colonization of new habitats will probably involve few individuals from single, nearby source populations (Kew, 1893; Ortmann, 1913; Johnson, 1970; Kat & Davis, In press), and reservoirs and lakes are likely to be colonized by individuals from rivers to which these bodies of water are linked. Newly established, high density populations such as those in lake Osborne and the Tar River reservoir also supply evidence for the underlying assumption that the degree of allocation is under genetic control: if production of spermatozoa were phenotypically controlled, all dense populations would resemble those of the Suwannee River canal, Lake Talquin, and Mosquito Creek reservoir in ratios of allocation.

These various hypotheses are not mutually exclusive, and aspects of each could well contribute to the observed variability of allocation to male gametes observed among individuals of *Anodonta imbecilis*. Populations of other predominantly hermaphroditic unionids which occur under similar conditions of population density and habitat variability should be examined to test the generality of observed pattern of allocation, and aspects of each hypothesis should be examined experimentally. For example, information concerning levels of self-compatibility in *A. imbecilis* could cast considerable light on the applicability of hypothesis (2), and much more information is needed about sperm viability, dilution times spawning habits of populations, and brood space limitation.

Dioecious species

This study reveals that occasional hermaphroditism among populations of predominantly dioecious species is generally associated with the presence of digenean trematodes within the gonads. Such trematodes can be locally very common, and affect up to 80% of the bivalves in a population, considerably reducing population fecundity. These trematodes are specific: those that were responsible for very high rates of infection among individuals of *Lampsilis radiata* at Andover Branch did not infect other species such as *Elliptio complanata*, *Anodonta cataracta*, and *A. implicata*, which occurred in high densities at the same site.

Parasitic castration is a relatively common phenomenon among molluscs (McCrary, 1873; Rothschild, 1936, 1938; Rees, 1936; Fretter & Graham, 1962; Robson & Williams, 1971; Cheng *et al.*, 1973; Tripp, 1973), and the presence of parasites within the gonads of molluscs has been implicated as a cause of sex-reversals (Rothschild, 1936, 1938; Fretter & Graham, 1962; Smith, 1980) and hermaphroditism (Tripp, 1973). Why the trematodes cause such partial or complete sex reversals is not understood, but previous hypotheses have included

deprivation of an essential metabolite, disruption of normal hormonal activity or synthesis, mechanical damage, and among protandrous molluscs, premature "ageing" of certain follicles (Cheng *et al.*, 1973; Tripp, 1973).

Hermaphroditic and protandric bivalves, as well as those characterized by rhythmical or alternative sexuality, begin reproduction as primary or ambisexual males, and even dioecious species often have ambisexual primary gonads with oocytes forming within early spermatogenic tissue (Coe, 1943, 1945; Kat, 1978). A limited survey (Kat, unpublished data) of juvenile *Anodonta implicata* ($n=8$), *Elliptio complanata* ($n=15$), and *Lampsilis ochracea* ($n=7$) indicates that primary gonads are all spermatogenic (Plate II(d)). This predominance of male reproduction among juvenile bivalves suggests that sexual determination among such dioecious species could be influenced by hormonal levels. Juveniles in which the gonads were just forming, or individuals in their first reproductive season would tend largely toward maleness due to low levels or absence of either a single or complex of sex-determining hormones; true males would continue with such low levels; and the female condition would result from high levels of such hormones (Fig. 2). Trematode parasites could secondarily or directly alter levels of these hormones within infected dioecious individuals by disrupting hormone synthesis, depleting nutrients necessary for hormone synthesis, and/or releasing metabolites which interfere with the ability of gonadal cells to perceive hormone levels.

Previous studies of occasional hermaphroditism among dioecious species (Van der Schalie, 1966, 1970; Heard, 1979) have made no mention of a relationship between such hermaphroditism and infection by trematodes. This could indicate that trematodes have a residual effect on reproduction after the period of infection, that such infections were overlooked, or that such hermaphrodites resulted from different processes such as developmental errors in sexual determination. In fact, Heard (1979) presents evidence from occasional hermaphrodites of *Elliptio* to suggest that demibranch structure of some individuals was intermediate to that observed among males and females; such phenotypic intermediacy is likely to be the result

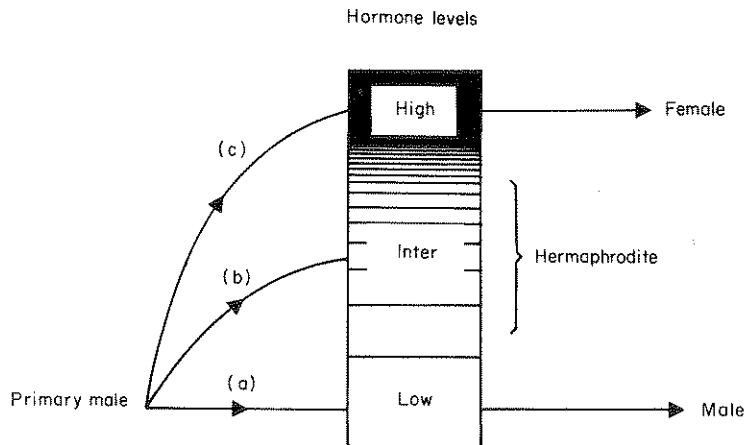


FIG. 2. Proposed mechanism of sexual determination among dioecious unionids. Following an initial primary male phase in juveniles, hormone levels either remain low (a) resulting in adult males, or increase to a high level (c) resulting in adult females. Developmental irregularities environmental stress, and trematodal infections may alter normal hormone concentrations (b) resulting in hermaphrodites with variable ratios of male : female tissue.

of errors in developmental processes. Nevertheless, a number of similarities exist between the results of this study and previous ones. First, hermaphrodites reproducing largely as males are either very uncommon (Van der Schalie, 1970), or when present in appreciable numbers (Heard, 1979), contain less than 5% female tissue. Second, hermaphrodites reproducing largely as females are common (Van der Schalie, 1970), and are highly variable with respect to the amount of male tissue within the gonad. For example, Heard (1979) noted that among *Elliptio* with female demibranchs, the amount of the gonad containing male tissue varied from less than 5% to more than 95%. Such data are largely in accordance with a model based on sexual determination via hormone levels: disruption of such levels by either trematodal infections or developmental error should result in much more variability in male : female gonadal ratios among females since females are hypothesized to be determined by high hormone levels.

A final question about occasional hermaphrodites concerns their functionality. Any individual with a male phenotype which reproduces hermaphroditically will be less fit than an individual which reproduces as a male because of the following: (a) They lack the appropriate demibranch structure to include and perhaps maintain developing larvae (note, however, that Heard (1979) found a phenotypically male hermaphrodite of *Elliptio* with larvae contained in its demibranchs, but gave no indication of their relative density and state of development compared to larvae within gills of females). (b) They could lack mantle modifications (see Kraemer, 1970) and behaviour appropriate for attraction and response to fish hosts necessary for glochidial metamorphosis. Individuals with a female phenotype which reproduce as hermaphrodites could be as fit as other females since they possess both appropriate demibranch structure, mantle modifications, and behaviour if such female hermaphrodites can: (a) prevent loss of fertility through self-fertilization, (b) time the release of sperm to coincide with other males in the population. Female hermaphrodites of both *Lampsilis radiata* and *Alasmidonta undulata* observed in this study were not gravid at the same time as females occurring in the same populations. (Heard (1979) observed an *Elliptio* hermaphrodite that was, but again gave no information on relative density and stage of maturity of the larvae). Obviously, much more information is needed on relative fecundity of occasional hermaphrodites before the question of functionality can be addressed further.

Summary

Data gathered in this and previous studies indicate that members of the freshwater bivalve family Unionidae reproduce dioeciously or as simultaneous hermaphrodites. However, different individuals and populations can display considerable variability within these modes of reproduction.

A simultaneous hermaphrodite, *Anodonta imbecilis*, is bimodally distributed with respect to the ratio of male : female tissue within the gonad, and several hypotheses to account for these differences based on population density, nutrient and spermatozoon availability, mode of fertilization, and limitation of brood space are presented. It is proposed that dense populations in reservoirs and sparse populations in streams are subject to fundamentally different sexual selection pressures acting on ratios of allocation to male and female gonadal products.

A large sample of dioecious species indicates that dioecious reproduction among unionids is relatively invariant among populations differing in density and geographic range position (recency of establishment).

However, occasional hermaphroditism can occur, which in this study is generally associated with infection by digenean trematodes, but previous studies point out that such hermaphroditism can also result from developmental errors. It is proposed that sexual determination following a primary male phase among juveniles is influenced by genetically controlled hormone levels. Trematodal infections are hypothesized to mimic developmental errors by directly or indirectly (by affecting the ability of cells to detect hormone levels) altering hormone levels within affected individuals. Males and females are affected differentially by such changes in hormone levels: phenotypically male hermaphrodites are either rare and/or contain very little oogenic tissue, while phenotypically female hermaphrodites are relatively common and/or contain variable amounts of spermatogenic tissue. This difference in response is proposed to result directly from levels of hormones which determine each sex: males are hypothesized to result from low levels of hormone(s), and females from high levels, which renders females more susceptible to variability in male:female ratios of gonadal tissue.

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Appendix

Collection localities of the populations and species studied

(a) *Elliptio complanata*

- (1) French Lake, Oromocto Sunbury Co., New Brunswick
- (2) Newville Lake, Halfway River East, Cumberland Co., Nova Scotia
- (3) Mattatall Lake, Wentworth Centre, Cumberland Co., Nova Scotia
- (4) First Lake O' Law, Gold Brook, Victoria Co., Nova Scotia
- (5) Blachette Lake, Sydney, Cape Breton Co., Nova Scotia
- (6) Shaw Lake, Arichat, Isle Madame, Richmond Co., Nova Scotia
- (7) Lake Egmont, Cooks Brook, Halifax Co., Nova Scotia
- (8) Nine Mile River, Elmsdale, Hants Co., Nova Scotia
- (9) Shubenacadie Grand lake, Grand Lake, Halifax Co., Nova Scotia
- (10) Nowlans Lake, Havelock, Digby Co., Nova Scotia
- (11) Placide Lake, Havelock, Digby Co., Nova Scotia
- (12) Lac a Pic, Springhaven, Yarmouth Co., Nova Scotia
- (13) Lake St. George, Montville Waldo Co., Maine
- (14) Lake Ossipee, Center Ossipee, Carroll Co., New Hampshire
- (15) Joe's Pond, West Danville, Caledonia Co., Vermont
- (16) Lake Champlain, South Hero, Grand Isle Co., Vermont
- (17) Lake Memphremagog, Newport, Orleans Co., Vermont

- (18) Sassafras River, Sassafras, Cecil Co., Maryland
- (19) Sewell Branch, Chester River, Millington, Kent Co., Maryland
- (20) Andover Branch, Chester River, Millington, Kent Co., Maryland
- (21) Chester River, Millington, Kent Co., Maryland
- (22) Mason Branch, Tuckahoe River, Queen Anne, Queen Anne Co., Maryland
- (23) Norwich Creek, Queen Anne, Queen Anne Co., Maryland
- (24) Watts Creek, Choptank River, Denton, Caroline Co., Maryland
- (25) Concord Pond, Concord, Sussex Co., Delaware
- (26) Deep Creek, Nanticoke Acres, Sussex Co., Delaware
- (27) Little River, Tarpleys Mill, Wake Co., North Carolina
- (28) Bull Run, Manassas, Prince Williams Co., Virginia

(b) *Lampsilis radiata*

- (1) French Lake, Oromocto, Sunbury Co., New Brunswick
- (2) Newville Lake, Halfway River East, Cumberland Co., Nova Scotia
- (3) Mattatall Lake, Wentworth Centre, Cumberland Co., Nova Scotia
- (4) Shubenacadie Grand lake, Grand Lake, Halifax Co., Nova Scotia
- (5) Lake Champlain, South Hero, Grand Isle Co., Vermont
- (6) Lake Memphremagog, Newport, Orleans Co., Vermont
- (7) Sassafras River, Sassafras, Cecil Co., Maryland
- (8) Andover Branch, Chester River, Millington, Kent Co., Maryland
- (9) Chester River, Millington, Kent Co., Maryland
- (10) Norwich Creek, Queen Anne, Queen Anne Co., Maryland
- (11) Deep Creek, Nanticoke Acres, Sussex Co., Delaware

(c) *Lampsilis ochracea*

- (1) Blachette Lake, Sydney River, Cape Breton Co., Nova Scotia
- (2) Placide Lake, Havelock, Digby Co., Nova Scotia
- (3) Lake Waccamaw, Columbus Co., North Carolina

(d) *Strophitus undulatus*

- (1) Shinimecas River, Shinimecas Bridge, Cumberland Co., Nova Scotia
- (2) Norwich Creek, Queen Anne, Talbot Co., Maryland
- (3) Andover Branch, Chester River, Millington, Kent Co., Maryland

(e) *Alasmidonta undulata*

- (1) Gilbert Lake, Lakelands, Cumberland Co., Nova Scotia
- (2) Newville Lake, Halfway River East, Cumberland Co., Nova Scotia
- (3) Kennetcook River, Riverside Corner, Hants Co., Nova Scotia
- (4) Nine Mile River, Elmsdale, Hants Co., Nova Scotia
- (5) Norwich Creek, Queen Anne, Talbot Co., Maryland
- (6) Andover Branch, Chester River, Millington, Kent Co., Maryland

(f) *Anodonta imbecilis*

- (1) House Creek, Bowens Mill, Ben Hill Co., Georgia
- (2) Cedar Creek, Fountain Mill, Pulaski Co., Georgia
- (3) Ocmulgee River, boat ramp at Ben Hill—Coffee Co. line, Georgia
- (4) Altamaha River, Hazelhurst, Jeff Davis Co., Georgia
- (5) Savannah River, Allendale, Allendale Co., South Carolina
- (6) Limestone Creek, Hawkinsville Pulaski Co., Georgia
- (7) Little River, Tarpleys Mill, Wake Co., North Carolina
- (8) Pickering Creek, Phoenixville, Chester Co., Pennsylvania
- (9) Lake Talquin, Talahassee, Leon Co., Florida
- (10) Canal at Suwanee River Campground, Old Town, Dixie Co., Florida
- (11) Lake Osborne, Lantana, Palm Beach Co., Florida
- (12) Mosquito Creek impoundment, Chattahoochee, Gadsden Co., Florida
- (13) Tar River reservoir, Rocky Mount, Nash Co., North Carolina
- (14) Swift Creek reservoir, Raleigh, Wake Co., North Carolina
- (15) Loch Raven reservoir, Baltimore, Baltimore Co., Maryland