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# THE POSTLARVAL PHASE OF BIVALVE MOLLUSKS: A REVIEW OF FUNCTIONAL ECOLOGY AND NEW RECORDS OF POSTLARVAL DRIFTING OF CHESAPEAKE BAY BIVALVES

*Patrick Baker and Roger Mann*

## ABSTRACT

Many bivalve mollusks have one or more separate post-metamorphic stages which are functionally distinct from the late juvenile or the adult. The benthic plantigrade and the planktonic postlarva are defined and reviewed here. The plantigrade is a developmentally obligatory stage in most bivalves. Various anatomical or conchological features, depending on taxa, are intermediate between the veliger and the juvenile. The plantigrade is benthic but highly mobile, via the foot and byssus, relative to the adult, although in some highly mobile bivalves, the plantigrade is functionally similar to the adult. The plantigrade may enter the water column briefly, but not nearly to the extent that the postlarva does. The planktonic postlarva is a non-obligatory stage, usually developmentally synonymous with the plantigrade, but functionally distinct. A specialized byssus or similar drogue is used by the postlarva for extended planktonic drifting. The plantigrade may serve simply as a developmentally intermediate stage between the larva and the juvenile, it may increase a species' options when selecting a habitat by its ability to relocate, or it may occupy a different habitat than later stages. The planktonic postlarva can either increase the dispersal ability of a bivalve, or, like the plantigrade phase, it can permit an ontogenetic niche shift. Planktonic postlarvae for three species not previously shown to exhibit this phase (*Anadara transversa*, *Geukensia demissa*, and *Tellina agilis*) are reported and described here.

The classical model of the life cycle of benthic marine invertebrates includes a planktonic larval stage, followed by a benthic juvenile-to-adult stage. The larval stage is the primary dispersal period, and is followed by settlement and metamorphosis to a sedentary juvenile. This model is based in part on early descriptions of the life cycle of oysters (Prytherch, 1934; Cole and Knight-Jones, 1939). In oysters, a planktonic veliger is the primary dispersal stage, and the late-stage, or "competent-to-settle" pediveliger exhibits settlement behavior, followed by metamorphosis to a sessile juvenile (Kennedy, 1996). There is a period of up to several days before internal morphology is similar to that of the adult oyster (Baker and Mann, 1993), but this may be regarded as a continuation of metamorphosis. With minor modifications, this model can be applied to some other groups as well, such as barnacles (Knight-Jones and Stevenson, 1950; Crisp, 1961) hermatypic corals (Lewis, 1974; Morse et al., 1988), and ascidians (Havenhand and Svane, 1988; Worcester, 1994).

As researchers have examined the transition from larva to juvenile, however, it has become clear that some taxa do not neatly fit the classic life history model. For example, some new recruits of a hermatypic coral have been shown to reverse metamorphosis, abandon their skeletons, and re-enter the plankton (Richmond, 1985). Not all invertebrates are as developmentally plastic as corals, but colonial ascidians can disperse as small colonies, via passive rafting on seagrass blades, to a greater extent than the short-lived planktonic larvae (Worcester, 1994). In both of the above cases, the function of the initial dispersal stage, and of settlement and metamorphosis, have become ambiguous.

Furthermore, the secondary dispersal stage is "optional," in the sense that not all recruits are involved.

It is now known that many bivalve mollusks have a life cycle more complex than that for oysters. In fact, it appears that oysters are atypical in this regard. In this manuscript, we will review evidence for two functional life history stages intermediate between the pediveliger larva and the sedentary juvenile. These two stages, which may either alternate or occur exclusively, include the benthic plantigrade (Carriker, 1961) and the planktonic postlarva (Sigurdsson et al., 1976). We will argue that these stages, like other stages in the life history of bivalve mollusks, are better defined by function than by morphology.

*Historical Development of Concepts.* — The plantigrade stage was first clearly defined by Carriker (1961), for a functionally distinct stage of the clam *Mercenaria mercenaria*. Behavior, habitat, and morphology are unique in combination to this stage, and intermediate between the larva and juvenile. The plantigrade *M. mercenaria* lacks a velum, so is clearly post-metamorphic. Unlike the juvenile, which burrows and seldom moves, the plantigrade crawls between sand grains and across surfaces, using the foot and byssal attachment. The byssus becomes less used in juveniles, and is lost in adults. There is no sharp transition between the plantigrade and the juvenile, but the modal behavior and anatomy of the plantigrade is distinct. There is recent evidence of limited resuspension and movement of plantigrade or juvenile bivalve mollusks via bedload transport (Emerson and Grant, 1991; Cummings et al., 1993; Rankin et al., 1994), but this, as discussed later, differs both in mechanism and in magnitude of potential relocation from true planktonic resuspension.

Planktonic postlarvae were observed many decades ago, but their significance was not immediately understood. Nelson (1928) found post-metamorphic mussels (*Mytilus edulis*) in the water column, and referred to them as "dissoconch" stage juveniles, a malacological term for the juvenile or adult shell. Nelson (1928) observed air bubbles within the mantle cavity (a frequent sampling artifact; Sigurdsson et al., 1976), which he interpreted, probably incorrectly, as the floating mechanism. Baggerman (1953) observed post-metamorphic cockles (*Cerastoderma edule*) in the water column, and Williams and Porter (1971) recorded a variety of post-metamorphic bivalves in plankton samples; those researchers attributed juvenile swimming or sediment scour for the presence of post-metamorphic animals in the plankton. Regardless of the precise lifting mechanism, however, the role of the larva as the primary dispersal stage was challenged by these findings.

Bayne (1964) was apparently the first to realize that post-metamorphic *M. edulis* enters the plankton on a population-wide scale, using long byssal threads. Bayne (1964) used the term "plantigrade" for this stage, a point which we will discuss later. *Mytilus edulis* retains the byssal gland and is somewhat motile even as adults (Petraitis, 1987; Wayne, 1987), so the behavioral shift from plantigrade to juvenile is considerably less marked than for the clam *M. mercenaria*. The use of byssal threads to enter the plankton, however, is dramatically different from later juvenile behavior, and increases the dispersal ability over crawling plantigrades by many orders of magnitude.

Sigurdsson et al. (1976) demonstrated that post-metamorphic byssal drifting is widespread among bivalve mollusks, and can be induced under certain conditions. The byssal threads used in drifting are longer than those used for attachment, and act as a drogue in water currents (Sigurdsson et al., 1976; de Blok and Tan-Maas, 1977). Sigurdsson et al. (1976) used the term "postlarva," which has been widely applied to any post-metamorphic bivalve.

The planktonic postlarva has recently been shown to be important on a population scale. Beukema and de Vlas (1989) and Armonies and Hellwig-Armonies (1992) studied recruitment of the clam *Macoma balthica* in the Wadden Sea, and found large location shifts in populations of post-metamorphic animals. Post-metamorphic clams apparently re-entered the plankton from initial settlement sites, and drifted up to 15 km to new recruitment areas. *M. balthica* to 5 mm in shell length were observed in the plankton, although mean size decreased with water velocity, and some of these may have been juveniles suspended as a part of bedload transport. Beukema and de Vlas (1989) used the older term "spat" for byssal drifting postlarvae. Newell et al. (1991) observed population-wide resuspension from seagrass and resettlement to mussel beds by postlarval *M. edulis*. In some bivalves, at least, post-metamorphic dispersal is important on a population scale, and initial settlement of pediveligers may permit no prediction of adult distribution.

Post-metamorphic planktonic drifting now appears to be a widespread phenomenon among bivalves (Table 1). The proposed mechanism of planktonic drifting varies with taxa (discussed below), but in all cases it permits a dispersal phase in addition to the planktonic larvae. In a few viviparous bivalves, passive drifting is the only planktonic dispersal mode; as in the very small clams *Gemma gemma* (Rankin et al., 1994), and *Tranzenella tantilla* (Martel and Chia, 1991a). Post-metamorphic drift is thought to be locally important to *M. balthica* and *M. edulis*, as discussed above, the cockle *C. edule* and the razor clam *Ensis directus* (Armonies, 1992), and the zebra mussel (*Dreissena polymorpha*), a freshwater species with planktonic larvae (Martel, 1993). For most other species, the importance of post-metamorphic drifting on a population scale has not been studied. Nonetheless, it is clear that for many bivalve molluscan taxa, there is a non-obligatory intermediate stage, following larval metamorphosis, and preceding the juvenile/adult stages.

For the remainder of this discussion, the immediate post-metamorphic, planktonic stage of bivalves will be referred to as postlarvae, or planktonic postlarvae, after Sigurdsson et al. (1976). The term "plantigrade" (Carriker, 1961) refers specifically to a creeping mode of locomotion, and non-planktonic postlarvae will be referred to as plantigrades.

The term "postlarva" is used widely for post-metamorphic bivalves, although often without intent to refer to a distinct stage (Ramorino and Campos, 1983; Fuller and Lutz, 1989; Goodsell et al., 1992). The term is also broadly applied for the first post-zoeal instar of decapod crustaceans, during which recruitment to the benthos occurs (Gurney, 1948; Lyons, 1980; Felder et al., 1985). Harvey and Gage (1984) described the behaviorally distinct "postlarva" of a burrowing sea urchin, while Hindler (1975) used the term to refer to both planktonic and benthic post-metamorphic stages of different species of brittle stars. Thiébaud et al. (1996) used the term "postlarva" to refer to the post-metamorphic stage of a sedentary polychaete annelid which, like some bivalves, uses a long thread as a drogue. Copp and Kováč (1996) used the same term to describe an intermediate stage between larva and juvenile in fish larvae.

*Morphological Distinctions of Post-Metamorphic Stages.* — Although we intend to argue in this manuscript that bivalve plantigrades and planktonic postlarvae are best defined functionally, we will present what evidence exists for morphological distinction. The transition from plantigrade or planktonic postlarva to juvenile, as discussed below, is usually gradual rather than rapid, but the modal morphology of the two stages can differ significantly.

The presence of a byssal planktonic stage probably implies a plantigrade stage as well. The byssal thread used for resuspension in the postlarva is produced by a foot gland (Gruffydd et al., 1975, Lane and Nott, 1975; Yankson, 1986), which suggests that this stage is also capable of crawling and byssal attachment. Furthermore, apart from possibly distinct byssal thread structure (Lane et al., 1985), there have been no morphological traits which have been ascribed to planktonic postlarvae and not to plantigrades. For these reasons, morphological distinctions discussed below will refer to plantigrade bivalves, unless otherwise specified. The foot and byssus, which are important to both plantigrade and postlarval function, will be discussed separately.

In many taxa, shell morphology and adductor placement of the plantigrade stage differs from that of juveniles. Juvenile and adult mussels of the subfamily Mytilinae (e.g., *Mytilus* spp.) are strongly heteromyarian; that is, the anterior adductor muscle is greatly reduced, as opposed to the more isomyarian character of most bivalves. In addition, the umbonal region (hinge) is nearly at the anterior tip of the shell, an extreme form of inequalaterality. As larvae, *Mytilus* spp. are nearly isomyarian, and there is a transitional period following settlement, until the juveniles reach the final heteromyarian configuration, at a size of 1-2 mm (Lutz et al., 1982; Ramorino and Campos, 1983; Fuller and Lutz, 1989). Zebra mussels (Dreissenidae) undergo a similar myarian shift (Meisenheimer, 1901; Morton, 1993; Ackerman et al., 1994), as do pen shells (Pinnidae) and members of the genus *Cardita* (Carditidae) (Allen, 1985). Scallops and related families (Pectinacea), pearl oysters (Pteriidae) and giant clams (Tridacnidae) shift from isomyarian to monomyarian (only one adductor muscle), although the shells do not become strongly inequilateral (Allen, 1985; Alagarwami et al., 1989; Fuller et al., 1989; Bower and Meyer, 1990; Bellolio et al., 1993; Rose and Baker, 1994). Jingle shells (Anomiidae) have only one true adductor muscle as adults, but the pedal retractor develops into a functional adductor muscle, due to the location of the byssus (Yonge, 1977).

There are various additional anatomical or conchological shifts, during or following the postlarval stage, in some other bivalve taxa. The plantigrade of the clam *M. mercenaria* lacks distinct siphons, while the juvenile develops long, fused siphons (Carriker, 1961); this is probably true of many burrowing species. The jingle shell, *Anomia simplex*, has a distinctive byssal foramen, or byssal gape, in the right valve as a juvenile and adult, but not as a larva (Fuller et al., 1989). Prezant (1990) found shell differences between the postlarva and juvenile of the brooding bivalve *Lissarca notorcadensis* (Philobryidae). Le Pennec and Jüngbluth (1983) reported an intermediate, "primitive" ligament which arises following metamorphosis from the glochidium larva of the freshwater bivalve *Margaritifera margaritifera* (Unionacea), but which is lost by the time the shell is 2 mm in length. Several researchers have shown a gradual, if continuous, evolution of the hinge teeth in postlarval bivalves (Lutz et al., 1982; Le Pennec and Yankson, 1985; Fuller and Lutz, 1989; Kennedy et al., 1989). More research will no doubt reveal further conchological features unique to the post-metamorphic period in bivalve mollusks.

Histology or internal anatomy of the post-metamorphic stage may also differ significantly from the juvenile. Lucas (1975) defined the post-metamorphic stage of various bivalve taxa on the basis of gonadal development. In the plantigrade, the undifferentiated gonia, or primary germinal cells, are in the pericardial region, but in the juvenile, they have begun to differentiate and migrate to the pedal region. The pigmented eyespot of the oyster, *Crassostrea virginica*, lingers following metamorphosis, but disappears in the ju-

venile, and other anatomical aspects of metamorphosis (complete loss of the larval velum and assumption of gill activity) only gradually occur (Baker and Mann, 1993).

There are many differences between postlarval bivalve mollusks, and the adjoining stages. As the above discussion illustrates, however, there are probably no unifying themes, at least in morphology, anatomy, or histology. Even within families, changes from postlarva to juvenile may not be consistent. For example, although adult mussels of the genus *Mytilus* are strongly heteromyarian and extremely inequilateral, those of the related genera *Modiolus*, *Geukensia*, and *Musculista*, among others, are much closer to postlarvae in morphology (Morton, 1974; Stanley, 1988). Thus, although plantigrades or postlarvae may differ physically from juveniles, general physical definitions of these stages are not practical.

*The Foot and Byssus.* — In bivalves with a plantigrade or planktonic postlarval period, the presence or morphology of either foot or the associated byssal glands may sometimes be used to distinguish the postlarval stage. Behavior involving the foot and byssus will be discussed separately.

In some taxa, early byssal-assisted postlarval motility is terminated in the juvenile when the byssus becomes a massive, permanent attachment, and the foot is reduced to a byssal retractor. Examples of this change in byssal function are found among jingle shells, Anomiidae (Yonge, 1977) and giant clams, Tridacnidae (Allen, 1985). In jewel box clams (Chamidae), there is apparently a brief byssal stage, followed by cementation, loss of the byssus (LaBarbera and Chanley, 1975), and reduction of the foot (Allen, 1985). The extreme case is represented by true oysters (Ostreidae) in which cementation occurs immediately upon settlement, with no plantigrade stage and rapid degeneration of the foot (Cranfield, 1973b; Baker and Mann, 1993).

In some bivalve taxa, motility is lost through the secretion of a permanent tube or the excavation of a permanent burrow. The most highly derived examples are found among the superfamilies Pholadacea, Clavagellacea, and Gastrochaenacea, reviewed by Savazzi (1982) and Morton (1985). The foot, if retained, serves to modify the burrow rather than for locomotion. Larval biology of most tube dwelling species has not been studied. Mussels of the genus *Lithophaga* (Mytilidae) spend most of their life in a permanent burrow, but retain both the foot and byssus (Scott, 1988).

In the many lamellibranch taxa, adults appear to lose the byssus entirely, but retain the foot. The change or loss of the byssus may functionally distinguish the plantigrade or postlarva from the juvenile, but not morphologically, except on a histological level (Carriker, 1961). In an extreme case, the clam *Mulinia lateralis* may not have a functional byssus even as a plantigrade (Calabrese, 1969). The role of the foot in adult locomotion is reviewed by Morton (1975) and Allen (1985).

Many taxa retain the ability to secrete or detach individual byssal threads well into adulthood. Examples are found among marine mussels (Mytilidae), ark clams (Arcidae), pearl oysters (Pteriidae), scallops (Pectinidae), file shells (Limidae), pen shells (Pinnidae), carditid clams (Carditidae), zebra mussels (Dreissenidae), and pandora clams (Pandoracea) (Allen, 1985; Morton, 1985; Newell, 1989; Rzepecki and Waite, 1993). In the majority of these taxa, the foot is retained primarily as an organ to attach the byssal threads.

Waite (1983) has provided a general review of byssal threads and attachment in bivalve mollusks, and the larval byssal glands have been described for a number of species (Cranfield, 1973a; Gruffydd et al., 1975; Lane and Nott, 1975; Lane et al., 1982; Yankson, 1986). Lane et al. (1982) present evidence that in *M. edulis*, there are unique glands for

the production of byssal threads during “byssopelagic migration” or postlarval planktonic drifting. Lane et al. (1985) described the byssal drifting threads of *M. edulis*, which appear to be morphologically distinct from the attachment byssus. The chemical composition of the drifting thread has not been determined; the adult byssus is composed primarily of polyphenolic proteins (Waite, 1983), but Sigurdsson et al. (1976) reported staining postlarval threads with Alcian blue, selective for acid mucopolysaccharides. Small gastropod mollusks use mucous strands to drift in the plankton (see reviews by Martel and Chia, 1991a; 1991b), and Beukema and de Vlas (1989) reported that the clam *M. balthica* (Tellinidae) uses hyaline mucous threads for byssal drifting. Prezant and Chalermwat (1984) demonstrated that the drifting threads of juveniles of the freshwater clam *Corbicula fluminea* (Corbiculidae) are mucous threads produced by the gills. It is thus possible that the drifting threads of at least some bivalve postlarvae are muciferous rather than proteinaceous.

One difficulty for researchers studying bivalve post-metamorphic bivalves is that the byssus or mucous threads, whether for benthic attachment or planktonic drifting, are often not visible under light microscopy, even under high magnification (Cranfield, 1973b; Lane et al., 1985; Beukema and de Vlas, 1989; Beaumont and Barnes, 1992; Cummings et al., 1993). Postlarvae are also able to detach drifting threads at will (Sigurdsson et al., 1976; Lane et al., 1985). It has thus been difficult for researchers to verify that drifting postlarvae are indeed attached to byssal threads. No researcher, apparently, has duplicated the use of Alcian blue to stain byssal drifting threads (Sigurdsson et al., 1976). Prezant and Chalermwat (1984) used carbon black to reveal the mucous threads of *C. fluminea*. Lane et al. (1985) used transmission electron microscopy to view *M. edulis* byssal threads, but other researchers have relied upon the ability of plantigrades to cling to vertical surfaces to detect byssus production (Castagna and Kraeuter, 1981; Yankson, 1986), or have dragged the postlarva via the unseen thread, using a fine probe (Beaumont and Barnes, 1992).

A few bivalves may not even use threads, byssal or otherwise, to drift in the water column; buoyancy by trapped gas has been reported as a passive dispersal means in some bivalves. Nelson (1928) reported this in postlarval *M. edulis*, although subsequent researchers have found byssal drifting to be the primary means of postlarval drift for this species (Lane et al., 1985). *Macoma balthica* up to 14 mm in shell length appear to be able to increase buoyancy of the extended foot to permit brief flotation (Sörlin, 1988); however, the underlying physiological mechanisms are poorly understood.

As a consequence of the difficulty in observing postlarval byssal threads, some researchers have not reported byssal threads as a dispersal mechanism where they probably did occur. Nelson (1928) and Bayne (1964) both reported postlarval *M. edulis* in the plankton, but did not recognize trailing byssal threads. Byssal drifting has subsequently been shown to be the major postlarval dispersal mechanism for this species (Lane et al., 1982, 1985). Baggerman (1953), Williams and Porter (1971), and Grigor'eva and Regulev (1992) found planktonic postlarvae of a variety of species, but proposed other dispersal mechanisms. Subsequent evidence has shown that at least some of the species or closely related taxa they observed do enter the plankton by means of byssal threads (Frenkiel and Mouëza, 1979; Yankson, 1986; Beukema and de Vlas, 1989; Beaumont and Barnes, 1992).

*Ecological Function of the Plantigrade.* — The majority of bivalves studied appear to have a plantigrade post-metamorphic stage, as defined by Carriker (1961); exceptions include oysters (Kennedy, 1996), and shipworms (Culliney, 1975), and possibly some

viviparous freshwater clams (Heard, 1977). Of those taxa with a plantigrade larva, somewhat fewer are known or suspected of having planktonic postlarvae (Table 1). As discussed below, however, the functional definition of a plantigrade is complicated by the range of juvenile and adult behavior and mobility observed across taxa. Specifically, when does a plantigrade stage give way to a juvenile? For some groups, there appears to be a distinct plantigrade stage, but in others, there is no satisfactory difference between plantigrades and juveniles.

The plantigrade of the clam *M. mercenaria* metamorphoses from the veliger larva at about 200  $\mu$  in shell length (Carriker, 1961). At this size, even if it burrows, the plantigrade is as much interstitial as infaunal, because it is smaller than many sand particles. The plantigrade is very active at this stage, crawling across surfaces or between sand grains, and producing a series of byssal thread attachments. The juvenile develops a long, fused siphon that permits it to burrow to a depth of over twice the shell length, and the byssus is eventually lost, at about 7-9 mm in shell length. In the case of *M. mercenaria*, at least, morphology and habitat are inextricably linked; the plantigrade must attach byssally because it lacks either the size or the morphology to burrow. In a related genus, the byssus of *Meretrix lamarckii* is lost by about 10 mm shell length (Narihara and Morisue, 1991). The differences in morphology between plantigrade and later juvenile stages reflect the differences in behavior and microhabitat. It has never been demonstrated, however, that either *M. mercenaria* or *M. lamarckii* exhibit planktonic postlarval relocation and secondary recruitment, although related taxa do (Sigurdsson et al., 1976).

In the burrowing clams *Mya arenaria* and *Panope generosa*, the plantigrade is very active and uses both the foot and byssus, to a size of about 10-12 mm, but adults gradually lose mobility, and the foot serves primarily to position the animal in the burrow (Goodwin and Pease, 1989; Baker and Mann, 1991); this trend is also true of *M. mercenaria* (Stanley and DeWitt, 1983). In more extreme cases of burrowing bivalves, mobility outside the burrow is completely lost, such as in burrowing and boring bivalves in Pholadacea, Clavagellacea, and Gastrochaenacea (Savazzi, 1982; Morton, 1985). In these cases, the degree of mobility is a functional difference between the plantigrade and the later stages. The plantigrade can be defined as a "fine-tuning" stage, before the juvenile becomes permanently committed to a single site.

Plantigrade bivalves may be found either in the water column or as part of bedload sediment transport, without the aid of byssal threads or a similar drogue-like mechanism. This phenomenon must be reviewed, and compared to planktonic postlarval drifting. Williams and Porter (1971) observed a variety of post-metamorphic bivalves in the water column. A few may be attributed to byssal drifting (Table 1), but others are clearly not. More recently, Emerson and Grant (1991) and Roegner et al. (1995) have shown that early juveniles of the clam *Mya arenaria* are transported on a population-wide scale as small juveniles that retain a high ability to reburrow. In this scenario, the site of initial settlement and metamorphosis is not the recruitment site. Functionally, this may be similar to the relocation of *M. balthica* plantigrades; some relocation of post-metamorphic stages is clearly via planktonic postlarvae (Beukema and de Vlas, 1989), but older *Macoma* may also be transported shorter distances (Sörlin, 1988; Beukema and de Vlas, 1989). For *Macoma*, the juvenile habitat is clearly different from the plantigrade habitat, and relocation of plantigrades permits an ontogenetic niche shift (Armonies and Hellwig-Armonies, 1992; Beukema, 1993). Other documented examples of the transport of early juveniles include the tellinid clam *Macomona liliana* (Cummings et al., 1993), and the

Table 1. Occurrence of postlarval byssal drifting in Bivalvia. For *Mytilus edulis* and *Macoma balthica*, only the most important references are listed; see text for further references.

Taxa	References
SOLEMYACEA	
<i>Solemya velum</i> * ‡	Porter and Williams, 1971
NUCULACEA	
<i>Nucula tenuis</i>	Sigurdsson et al., 1976
ARCACEA	
<i>Anadara transversa</i>	this manuscript
MYTILACEA	
<i>Geukensia demissa</i>	this manuscript
<i>Modiolus</i> sp.	Sigurdsson et al., 1976
<i>Musculus marmoratus</i> ( <i>Modiolarca tumida</i> )	Sigurdsson et al., 1976
<i>Musculus</i> sp.*	Martel & Chia, 1991a
<i>Mytilus edulis</i>	Sigurdsson et al., 1977; de Blok & Tan-Maas, 1977; Board, 1980; Lane et al., 1982, 1985; Newell et al., 1992
<i>Mytilus trossulus</i> ‡	Grigor'eva & Regulev, 1992
ANOMIACEA	
<i>Heteranomia squamata</i>	Sigurdsson et al., 1976
PECTINACEA	
<i>Aequipecten opercularis</i>	Beaumont & Barnes, 1992
<i>Pecten maximus</i>	Beaumont & Barnes, 1992
<i>Patinopecten yessoensis</i> ‡	Grigor'eva & Regulev, 1992
VENERACEA	
<i>Austrovenus stutchburyi</i>	Cummings et al., 1995
<i>Gemma gemma</i> * ‡	Sellmer, 1967; Rankin et al., 1994
<i>Petricola pholadiformis</i> ‡	Baggerman, 1953; Williams and Porter, 1971
<i>Tranzenella tantilla</i> * ‡	Martel and Chia, 1991a
<i>Venerupis pullastra</i>	Sigurdsson et al., 1976; Armonies, 1994
CYAMIACEAE	
<i>Turtonia minuta</i> * ‡	Sigurdsson et al., 1976
DREISSENACEA	
<i>Dreissena polymorpha</i>	Martel, 1993
GALEOMMATACEA	
<i>Lasaea</i> sp.*	Martel and Chia, 1991a
<i>Mysella ferruginosa</i>	Sigurdsson et al., 1976
<i>Montacuta substriata</i>	Sigurdsson et al., 1976
CARDIACEA	
<i>Cardium echinatum</i>	Sigurdsson et al., 1976
<i>Cerastoderma edule</i>	Baggerman, 1953; Yankson, 1986; Armonies, 1992
<i>Cerastoderma glaucum</i>	Yankson, 1986

small clam *Gemma gemma* (Rankin et al., 1994). In the case of *Gemma*, which is viviparous, there is no other mode of transport, aside from pedal crawling.

We argue that bedload sediment transport, or even swimming assisted transport, differs both in mechanism and magnitude of transport. Transport by these mechanisms appears

Table 1. Continued

Taxa	References
MACTRIDAE	
<i>Mactra corallina</i>	Sigurdsson et al., 1976
<i>Paphies australis</i>	Hooker, 1995
<i>Spisula</i> sp.	Sigurdsson et al., 1976
SOLENAEAE	
<i>Ensis directus</i>	Williams and Porter, 1971; Armonies, 1992
<i>Ensis</i> sp.	Sigurdsson et al., 1976
<i>Cultellus pellucidus</i>	Sigurdsson et al., 1976
TELLINAEAE	
<i>Abra alba</i>	Sigurdsson et al., 1976
<i>Donax variabilis</i> ‡	Porter & Williams, 1971
<i>Donax vittatus</i>	Sigurdsson et al., 1976; Frenkiel & Mouřza, 1979
<i>Gari fervensis</i>	Sigurdsson et al., 1976
<i>Gari stangeri</i>	Hooker, 1995
<i>Macoma balthica</i>	Beukema & de Vlas, 1989; Armonies, 1992; Armonies and Hellwig-Armonies, 1992
<i>Macomona liliana</i>	Cummings et al., 1993; Hooker, 1995
<i>Scrobicularia plana</i>	Frenkiel & Mouřza, 1979
<i>Soletellina</i> sp.	Hooker, 1995
<i>Tagelus plebius</i> ‡	Porter and Williams, 1971
<i>Tellina agilis</i>	this manuscript
<i>Tellina tenuis</i>	Sigurdsson et al., 1976
MYAEAE	
<i>Corbula gibba</i>	Sigurdsson et al., 1976
<i>Mya arenaria</i>	Baggerman, 1953; Sigurdsson et al., 1976
HIATELLAEAE	
<i>Hiatella arctica</i>	Sigurdsson et al., 1976
<i>Hiatella gallicana</i>	Sigurdsson et al., 1976

\* Lacks a free-swimming larval stage. ‡ Drifting mechanism not shown, but byssus probable.

to rely on strong current velocities, in addition to the low specific gravity of living bivalves relative to sediment (Robinson and Chandler, 1993), and this mode of transport relocates juveniles meters to hundreds of meters in episodes lasting no more than one tidal cycle (Emerson and Grant, 1991; Beukema, 1993). In contrast, byssal-drifting postlarvae can remain in the plankton weeks to months, and are transported as much or more than veliger larvae (reviewed below). Having said this, we admit that bedload transport of plantigrades represents a functional gradation between benthic plantigrades and planktonic postlarvae.

Some bivalves retain high mobility throughout their life. Bivalves that reside on high-energy sandy beaches, such as the coquina clams of the genus *Donax*, and the razor clams *E. directus* and *Siliqua patula*, exhibit very high pedal motility (Williams and Porter, 1971; Ansell and Trueman, 1973; Lassuy and Simons, 1989). Cockles of the genus *Cerastoderma* are active both as a byssal plantigrades and as non-byssate adults (Yankson, 1986). Only the presence of an attachment byssus, if it exists, can morphologically sepa-

rate plantigrades from juveniles. It is not yet known whether, as for *M. balthica* (Beukema, 1993), there are different larval and juvenile recruitment habitats in the above taxa. If not, given the unstable nature of the juvenile habitat, byssal attachment may not be important, and there may be no functional difference between the plantigrade and juvenile. It may be possible that, as for the small, active clam *M. lateralis*, the plantigrade does not have a functioning byssus (Calabrese, 1969).

A different sort of shift between plantigrade and juvenile motility is demonstrated by species that are epifaunal throughout life. As for burrowing bivalves, adult mobility of epifaunal bivalves ranges from completely sessile to highly mobile, but the byssus is retained in all but a few taxa. Researchers have noted mobile and byssally attaching (or "sticky") post-metamorphic stages of otherwise fairly sedentary epifaunal species; examples include the ark clams *Anadara transversa* (Loosanoff et al., 1966) and *Noetia ponderosa* (Chanley, 1966) and the pearl oyster *Pinctada maxima* (Rose and Baker, 1994). There are almost certainly many more, but descriptions of larvae or postlarvae in the literature seldom describe behavior. In these taxa, the plantigrade may be thought of as a highly motile stage compared to a sedentary juvenile or adult, but the transition may be gradual.

Like infaunal species, however, some epifaunal bivalves remain motile throughout their lives. Plantigrade motility and function has been studied in the blue mussel *M. edulis* (Lane et al., 1982; Eyster and Pechenik, 1987), the zebra mussel *Dreissena polymorpha* (Ackerman et al., 1994) and the scallop, *Pecten maximus* (Gruffydd et al., 1975). In all three taxa, the plantigrade foot is large and active, with a well developed byssus. *Pecten* loses the use of the byssus prior to maturity (Minchin, 1992), but the related genus *Argopecten* retains the ability to secrete a byssus throughout life (Haderlie and Abbott, 1980; Garcia-Esquivel and Bricelj, 1993), as do the unrelated *M. edulis* and *Dreissena polymorpha* (Newell, 1989; Ackerman et al., 1994). Furthermore, all of these taxa remain mobile as adults (Morton, 1964, 1975; Petraitis, 1987; Wayne, 1987), and while the locomotory mode of adult scallops (swimming) differs from that of juveniles (crawling), dispersal ability actually increases. In *Argopecten irradians*, there is a distinct ontogenetic habitat shift between the early juveniles and the adults, but this shift is actually correlated with an increase in mobility over the earlier post-metamorphic stages (Garcia-Esquivel and Bricelj, 1993). In *M. edulis* and *D. polymorpha*, adult locomotion does not appear to differ functionally from that of the plantigrade, so it could be argued that for these taxa, the creeping plantigrade is functionally synonymous with the juvenile.

In summary, therefore, the concept of a benthic plantigrade as a distinct life stage is very useful when describing some taxa, such as *M. mercenaria* or *M. arenaria*, but of little value when describing other taxa such as *M. edulis*, with a full range of intermediate forms. Furthermore, the role of a plantigrade may differ between taxa, such as *M. mercenaria*, with a creeping plantigrade, and *M. arenaria*, with a sediment-transported plantigrade. We propose that the plantigrade life stage is a valid concept when the mode or degree of mobility distinctly differs from that of the adult, and permits an ontogenetic niche shift. We further distinguish the plantigrade from the byssal-drifting planktonic postlarva, discussed below. Although morphology or gonadal development may be distinctive, the above definition of a plantigrade is not dependent upon them, apart from constraints due to morphology or small size.

*Ecological Function of the Planktonic Postlarva.* — The planktonic postlarva is functionally distinct from other stages, but is not developmentally obligatory. Planktonic

postlarval motility probably infers plantigrade byssal motility as well, but this is not certain. *Mytilus edulis* byssal drifting threads arise from separate glands than attachment threads (Lane et al., 1982, 1985), so it is conceivable that a postlarva could have a drifting byssus, but not an attachment byssus. Furthermore, there is evidence that some drifting threads are polysaccharides, rather than proteins, and hence not byssal at all (Sigurdsson et al., 1976; Prezant and Chalermwat, 1984; Beukema and de Vlas, 1989). However, even with the unique glands or threads, there is no evidence that the planktonic postlarval stage is obligatory to any taxon; species known to exhibit a planktonic postlarva can be reared in the laboratory without it (Loosanoff and Davis, 1963; Loosanoff et al., 1966).

Entry of the postlarva into the water column has a behavioral component, even though the drifting is considered "passive." Sigurdsson et al. (1976) reported that byssal drifting thread production was controlled by the postlarvae in the water column. Small *M. lilliana* moved out of the sediment and positioned themselves, prior to byssal drifting (Cummings et al., 1993). Planktonic postlarvae of *Cerastoderma* spp., *E. directus*, and *M. balthica* migrate in and out of the water column both on a diurnal basis and in semi-lunar or similar length cycles; tides or current velocity may also be cues (Armonies, 1992, 1994). It is not known whether postlarval drifting behavior permits positional control in the water column, such as used by veliger larvae (Mann, 1986a, 1986b). Positional control even of larvae is strongly limited by water turbulence, however, so the difference in control may be minor (Mann, 1988).

For bivalves which lack a widely dispersing veliger larva, the postlarva is clearly an important means of dispersal. Functionally, the drifting byssal threads of postlarval bivalves are similar to "ballooning" threads used for dispersal by many juvenile spiders (Foelix, 1982; Decae, 1987), and the mucous threads used for aquatic drifting by the polychaete *Pectinaria koreni* (Thiébaud et al., 1996) and some small gastropods (Martel and Chia, 1991a, 1991b). Adults of very small viviparous bivalves, such as *Musculus* sp. (Mytilidae), *Lasaea* sp. (Lasaeidae), and *Transenella tantilla* (Veneridae), are able to enter the plankton via byssal threads (Martel and Chia, 1991a). It can be argued that these taxa are neotenous, because the adults mimic the behavior of postlarvae of other taxa. The concept of neoteny has been reviewed for another small brooding bivalve, *Turtonia minuta* (Turtoniidae), by Ockelmann (1964), which has subsequently been shown to be able to drift via byssal threads (Sigurdsson et al., 1976). Sellmer (1967) observed byssal production in *Gemma gemma* (Veneridae), another small brooding bivalve, and collected juveniles from the water column, although it is suspected that this species can be transported as part of bedload sediment (Rankin et al., 1994).

The function of a prolonged byssal drifting stage for bivalve mollusks that already have a planktonic larval stage is more complex. Beukema and de Vlas (1989), Newell et al. (1991), and Beukema (1993) suggested that primary settlement requirements are different than requirements for growing juveniles, and that therefore the drifting postlarval stage is needed to transport the successfully metamorphosed postlarvae. *Macoma balthica* shifts from one type of substrate to another as a consequence of postlarval movements (Beukema, 1993), while *M. edulis* relocates from seagrass or algae to shell or rock (Newell et al., 1991). The role of the environmental factors that would cause this relocation are only hypothetical, and have not been tested. If this model is correct, however, then the role of the drifting postlarva is not so much dispersal (in the sense of colonizing new habitats and increasing genetic exchange) as it is the ability to perform an ontogenetic habitat shift.

Mortality factors for postlarval drifting bivalves have not been studied. *Macoma balthica* can grow to 5 mm while drifting (Beukema and de Vlas, 1989), which may put it in a different class of planktonic predators than veliger larvae (maximum of about 350  $\mu$ ). Long-term byssal drifting in *M. balthica* occurs during the winter months, while larval development occurs in the summer and early fall (Beukema and de Vlas, 1989). Environmental pressures and the abundance and taxonomic composition of planktonic predators would be different between these two periods. During secondary settlement, however, the juveniles are still vulnerable to benthic planktivores (Elmgren et al., 1986; Ejdung and Bonsdorff, 1992).

The byssal gland of most bivalve larvae is well-developed prior to metamorphosis (Cranfield, 1973a; Gruffydd et al., 1975; Lane and Nott, 1975; Lane et al., 1982; Yankson, 1986), so it is possible that metamorphosis can occur in the plankton, for some species. Byssal drifting may act as a mechanism to move postlarvae a relatively short distance from a primary, "nursery" site to a final settlement site (Newell et al., 1991), or it may last for a period of months (Board, 1983; Beukema and de Vlas, 1989). Following this period, the postlarva may reattach briefly before drifting again (de Blok and Tan-Maas, 1977), but will eventually select a final site in what has been termed "secondary settlement" (Bayne, 1964). Ontogenetic habitat shift has also been observed for plantigrade *M. balthica*, but for this species at least, there are clearly two major ontogenetic habitat shifts after metamorphosis; one involving byssal drifting, and a later, more local shift involving plantigrade transport, possibly involving brief plantigrade floating episodes (Sörlin, 1988; Beukema, 1993).

The function of a planktonic postlarva for bivalve mollusks blurs for some taxa, if large juveniles and adults are able to disperse in the water column. The best-known examples are scallops (Pectinidae) and file shells (Limidae) (Morton, 1964), which are able to swim for short distances. *Pecten maximus* swims as an adult, but also disperses as a planktonic postlarva (Beaumont and Barnes, 1992). Williams and Porter (1971) reviewed swimming in non-pectinid bivalve mollusks, and found juvenile *E. directus* and *Solen viridis* in the water column, as well as several other taxa. Swimming, however, even in a relatively poor swimmer like *E. directus*, is functionally different from passive drifting, and clearly occurs during the juvenile or adult stages, not the postlarval stage.

The planktonic postlarva in bivalves can be defined as a distinct but developmentally non-obligatory life history stage, occurring after metamorphosis from the larva, which includes potentially long-term planktonic resuspension via a byssal or mucous drogue. The planktonic postlarva is further defined as functionally and behaviorally separate from the plantigrade, even though developmentally, the two may be synonymous. The ecological function of the postlarva may be to provide dispersal in species that lack larvae, such as *T. tantilla* or *Lasaea* sp.; or to permit an ontogenetic habitat shift, such as in *M. balthica* or *M. edulis*; or possibly simply to increase a species' options for dispersal and habitat selection.

In the preceding review we have proposed that postlarval drifting may be more widespread among the bivalve taxa than previously acknowledged. We add support to this proposal by describing, in the remainder of the text, the first record of postlarval drifting by three bivalve species from Chesapeake Bay, Virginia.

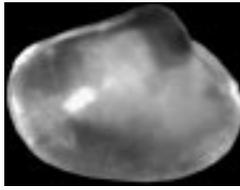


Figure 1. Postlarva of *Anadara transversa* collected from the plankton in the York River, VA. Shell length is 470  $\mu\text{m}$ .

## MATERIALS AND METHODS

The sampling site was in 3 m of water, off the end of a pier in Chesapeake Bay, at Gloucester Point, Virginia. The tidal range was about 1 m, and mean near-bottom ebb tidal current velocities were about 8  $\text{cm s}^{-1}$ . In 1990, a single pump was used near the bottom of the water column, sampling four times daily from July 5 to August 9. In 1991 to 1993, a series of three pumps were used, near the bottom, near the surface, and midwater. Near-bottom samples were about 20 cm above the substrate, and did not entrain bottom sediments. Sampling occurred primarily from late May to late September, with irregular sampling other times of the year.

Larvae and postlarvae were retained on a 150  $\mu\text{m}$  mesh, and identified under a dissecting microscope in the laboratory. The following references were used in aid of identification of larvae and postlarvae: Jørgensen (1946); Sullivan (1948); Rees (1950); Loosanoff et al. (1966); Chanley, (1970); Chanley and Andrews (1971); Culliney (1975); Webb (1986); Fuller and Lutz (1989); and Kennedy et al. (1989). In some cases, larvae and postlarvae were cultured to juveniles, using techniques modified after Loosanoff and Davis (1963), Kennedy et al. (1989), and Gustafson et al. (1991), allowing more positive identification. The presence of shell growth rings past the prodissoconch (larval shell), and shell outline were normally sufficient to distinguish postlarvae from late-stage veliger (pediveliger) larvae, but in some instances, careful observation and a good deal of patience was required to detect the presence or absence of a velum.

Byssal threads could not readily be seen under light microscopy, but their presence could sometimes be detected by dragging a fine probe gently through the water in a circle around a suspected postlarva, without touching the shell. If a byssus was present, the probe would catch it and the attached bivalve. Sigurdsson et al. (1976) used Alcian blue (selective for acid mucopolysaccharides) to stain byssal threads, but this effect could not be duplicated by these researchers.

## RESULTS

Eleven species of bivalve larvae and postlarvae were identified from plankton samples (Table 2). Postlarvae were clearly identified, by shell growth and morphology, to the following taxa: the ark clam *Anadara transversa*; the mussel *Geukensia demissa*; and the tellinid clams *Tellina agilis* and *Macoma* spp. The presence of a byssus was confirmed at least once for all for postlarval taxa. All other bivalves observed in the plankton were veliger larvae, confirmed by the presence of a velum. *Mulinia lateralis*, *Cyrtopleura costata*, *A. transversa*, and *G. demissa* were reared in the laboratory to juveniles for positive identification. Other bivalves were occasionally observed in the plankton, but not identified.

*Anadara transversa* (Fig. 1) reached a maximum density of about 4  $\text{m}^{-3}$  in early July, 1992. In July 1992 most individuals were veliger larvae, but in August 1992 and July 1990 and 1991, most were postlarvae. Larvae attained a shell length of about 300  $\mu\text{m}$ ,

Table 2. Pediveliger larvae and postlarvae collected in plankton samples. Dates are not meant to be exclusive, but only record times when each species was observed by these researchers.

Species	Period observed as pediveliger	Period observed as postlarva
<i>Anadara transversa</i>	June - August	July - mid Sept.
<i>Anomia simplex</i>	July	not observed
<i>Bankia gouldi</i>	June - Sept.	not observed
<i>Crassostrea virginica</i>	June - Sept.	not observed
<i>Cyrtopleura costata</i>	late May - Sept.	not observed
<i>Ensis directus</i>	March	not observed
<i>Geukensia demissa</i>	June - early Sept.	July - Sept.
<i>Macoma</i> spp.	late May - Sept.	August - Feb.
<i>Mulinia lateralis</i>	April	not observed
<i>Mytilus edulis</i>	March	not observed
<i>Tellina agilis</i>	June-July	July

and postlarvae attained a length of about 500  $\mu\text{m}$ . Pediveliger larvae had an eyespot and a foot; postlarvae retained the foot but lost the eyespot. By late September 1992, when large numbers of newly recruited benthic juveniles were found attached to oyster shells collected by a diver, *A. transversa* was absent from the plankton. Juvenile *A. transversa* in the field were observed attached directly to shells, primarily of the oyster *C. virginica*, while individuals cultured in the laboratory from field-collected individuals initially attached to filamentous substrates such as dead hydroid tubes (*Halocordyle distichus*), or byssus threads of the mussel *G. demissa*.

*Geukensia demissa* was present throughout the summers of 1990 to 1992, but rarely exceeded 2 individuals per  $\text{m}^3$ . About 90% of specimens observed were veliger larvae, with a shell length of about 250  $\mu\text{m}$ . The remainder were postlarvae, with a shell length rarely exceeding 350  $\mu\text{m}$ . Adequate photomicrographs of distinct *G. demissa* postlarvae could not be obtained at this time. Both pediveliger larvae and postlarvae had a well-developed foot and eyespot (although eyespot was relatively smaller than that of *C. virginica* pediveligers). No larvae or postlarvae remained in the plankton by late August 1990 or 1991, or late September 1992.

*Tellina agilis* (Fig. 2) was rare to absent except in early July, 1990, when abundances reached more than 30 individuals per  $\text{m}^3$ . The prodissoconch of this genus contains clearly visible annuli, which complicates differentiation of larvae from postlarvae. At least half of the specimens observed appeared to lack a velum, and had a well-developed, broadly triangular foot, and a byssus. These were about 400-450  $\mu\text{m}$  in shell length. Of the remainder that displayed a foot, some as small as 250  $\mu\text{m}$ , several were observed to have a velum, but the status of the rest could not be determined satisfactorily. No *T. agilis* of any size had a visible eyespot.

*Macoma* spp. (Fig. 3) were the most abundant bivalve larvae or postlarvae during summer and autumn. In October 1990 abundances exceeded 1000 per  $\text{m}^3$ , although in summer abundances were typically closer to 100 postlarvae per  $\text{m}^3$ . In summer, *Macoma* spp. larvae and postlarvae were observed together, but in October 1990 and other winter samples, only postlarval *Macoma* were observed. Postlarval *Macoma* were present but rare (1-2 per  $\text{m}^3$ ) in February and March 1992. Veliger larvae as large as 400  $\mu\text{m}$  in shell length

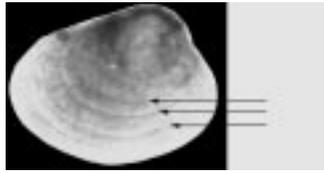


Figure 2. Postlarva of *Tellina agilis* collected from the plankton in the York River, VA. Note the annuli in the prodissoconch (arrows). Shell length is 440  $\mu\text{m}$ .

were observed, but most *Macoma* in the plankton larger than 330  $\mu\text{m}$  in shell length appeared to be post-metamorphic. The largest postlarvae observed were about 500  $\mu\text{m}$  in shell length; most were closer to 450  $\mu\text{m}$ . It was often difficult to distinguish large pediveligers from postlarvae, but postlarvae had a large, broadly triangular foot and a byssus. Neither pediveligers nor postlarvae had visible eyespots.

In this study, attempts to induce juvenile growth of *Macoma* spp. in the laboratory, using methods described by Kennedy et al. (1989), were unsuccessful. Flow-through, ambient York River water flumes in an adjacent laboratory, with 1-2 cm of sediment, however, experienced recruitment of both *M. balthica* and *M. mitchelli* between November and February, in all years of this study.

*Cyrtopleura costata* was the most abundant bivalve after *Macoma* spp., attaining a peak abundance of about 3800 late-stage larvae per  $\text{m}^3$  in August 1992, although typical summer abundances were 10-100 per  $\text{m}^3$ . Evidence of postlarval growth or byssal threads were not seen in any *C. costata*. *Crassostrea virginica* and *Bankia gouldi* were both present throughout summers in all years, and reached peaks of about 140 and 90 per  $\text{m}^3$ , respectively, although normal levels were under 10 per  $\text{m}^3$ . All specimens were veliger larvae.

## DISCUSSION

This was the first record of planktonic postlarvae for *A. transversa* and *G. demissa*. Both species have a functioning byssus throughout their life, and are largely epibenthic even as adults (Turgeon, 1968), so a high degree of post-metamorphic motility is not unexpected. Furthermore, *G. demissa* is in the same family (Mytilidae) as *M. edulis*, for which postlarval drift has been well described (de Blok and Tan-Maas, 1977; Board, 1983; Lane et al., 1982, 1985; Newell et al., 1991). What is perhaps more surprising, given the above literature, is that while veligers of *M. edulis* were observed in winter in this study, no planktonic postlarvae of this species were found. Chesapeake Bay is near the southern extreme of the western Atlantic distribution of this species, and it may be that conditions that favor postlarval migration are absent.

Successive dominance of first larvae, and then postlarvae, in the plankton by *A. transversa* in 1992, raises the possibility that for this species, postlarval drifting is an integral part of the life cycle. This may be similar to the life cycle observed for *M. edulis* in Maine by Newell et al. (1991), in which larvae recruit to seagrass, and then as postlarvae transfer to the adult habitat. It is not known whether *A. transversa* settles before metamorphosing. Pediveliger larvae produce byssal threads (Lane and Nott, 1975), so it is possible that some species begin byssal drifting prior to metamorphosis, and metamorphose in the water column. Nelson (1925) reported that larvae of *M. edulis* could maintain them-



Figure 3. Postlarva of *Macoma* sp. collected in the plankton in the York River, VA. Note the anterior adductor muscle, visible through the shell (arrow). Shell length is 450  $\mu$ m.

selves in the water column while they metamorphosed, but the evidence for this was not presented.

Planktonic postlarvae of *T. agilis* have not been reported as such, but illustrations of *Tellina* species captured in the plankton by Sullivan (1948) and Rees (1950) resemble postlarvae observed in this study, in both shape and size, and Webb (1986) illustrated similar non-planktonic postlarval *Tellina* species. *Macoma mitchelli* postlarvae superficially resemble *Tellina* postlarvae, but do not develop the highly visible annuli as a veliger (Kennedy et al., 1989).

The *Macoma* specimens were probably a mixture of *M. balthica* (Linné, 1758) and *M. mitchelli* Dall, 1895. Both were present as adults at the sampling site and abundant in tidal creeks several km upstream of the sampling site; *M. balthica* adults were about twice as common as *M. mitchelli* in benthic surveys. Both species recruited in the winters into seawater flumes connected by flowing, unfiltered seawater, to the York River (these authors, unpubl. data). Blundon and Kennedy (1982) observed juveniles of *M. balthica* primarily in the spring and juveniles of *M. mitchelli* throughout the year, in the Choptank River in northern Chesapeake Bay; however, Shaw (1965) reported two annual recruitment periods, in spring and fall, for *M. balthica* in the same region. Illustrations of larvae and postlarvae of *M. mitchelli* (Kennedy et al., 1989) closely resemble those of *M. balthica* (Chanley and Andrews, 1971), and hinge characteristics of *M. balthica* have not been published. *Macoma* spp. individuals could not be reared to juveniles in the laboratory for further identification.

The presence of large numbers of *Macoma* spp. planktonic postlarvae in Chesapeake Bay suggests a system similar to that described for *M. balthica* in the Wadden Sea, in which larvae recruit to one habitat, and then migrate via postlarval drifting to another habitat (Beukema and de Vlas, 1989; Armonies and Hellwig-Armonies, 1992; Beukema, 1993). The known adult habitat in the York River of Chesapeake Bay is in mesohaline, highly depositional portions of the estuary (these authors, unpubl. data), a distance of several km from the plankton sampling collection site. If there is a separate larval recruitment site for either species of *Macoma* in the York River, however, it has not been recorded. In the Wadden Sea, planktonic *M. balthica* postlarvae up to 5 mm in length were recorded, but the largest specimens caught in this study were under 500  $\mu$  shell length. The Wadden Sea, unlike the Chesapeake Bay, is characterized by very large tidal excursions and extensive open intertidal mud and sand flats. The rapid movement of water with the incoming tide, local currents, and vertical mixing associated with wind stress may well contribute to a physical environment (see comments in Beukema and de Vlas, 1989) that is conducive to initiating and maintaining suspension of larger postlarval forms in the water column than occur in Chesapeake Bay.

Byssal drifting in postlarvae has been reported in the genus *Ensis* (Sigurdsson et al., 1976) and Williams and Porter (1971) found juveniles of this genus commonly in plankton samples, although they attributed this to swimming, not drifting. The relatively few *E. directus* seen in this study in the York River were all veliger larvae, however. Juvenile *A. simplex* possess a byssus (Fuller et al., 1989), and byssal drifting in postlarvae was reported in the related genus *Heteranomia* (Sigurdsson et al., 1976), but the very few specimens observed in the York River were all veliger larvae. It is possible that postlarval drifting of *M. edulis*, *E. directus*, and *A. simplex* occurs in Chesapeake Bay, despite not having been observed during this study.

No planktonic postlarvae or byssal threads have been reported for any members of the families Pholadidae, of which *C. costata* is a member, or Teredinidae, of which *B. gouldi* is a member. No evidence for planktonic postlarvae in either *Cyrtopleura* or *Bankia* was noted in this study, despite large numbers of animals observed. It is probable that this phenomenon does not exist in these taxa.

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