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FIELD STUDIES OF BIVALVE LARVAE AND THEIR RECRUITMENT TO THE BENTHOS: A COMMENTARY

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ABSTRACT A list of factors influencing the recruitment of bivalve larvae might include, but not be limited to, the following: egg quality, physical environment, food availability, loss to predation and disease during larval development, interplay of passive dispersal (horizontally) by water currents and depth regulation by active swimming, proximity of suitable and available substratum as metamorphic competency is achieved, and availability of sufficient metabolic reserves to complete metamorphosis to the benthic form. While tractable methods exist to quantify aspects of certain members of the above list, the focus of such work has usually been biased towards laboratory experiments or hatchery production. The purpose of this commentary is to suggest that a refocussing of efforts in bivalve larval biology on natural systems is both timely and needed.

KEY WORDS: Bivalve larvae, recruitment

COMMENTARY

There is no question that laboratory work has allowed us to make many advances in the understanding of bivalve larval ecology; however, this work has often focussed on the culture of bivalves for economic purposes rather than examination of interesting ecological questions per se. Indeed, it was the intent of the original "laboratory" work of Brooks (1890) not to provide greater understanding of the ecology of oyster larvae but to provide a culture method for that species so that a repopulation of the Chesapeake Bay could be effected. Nonetheless the products of years of laboratory work suggest that we should again seriously consider field programs to examine larval biology and recruitment to the benthos. After several years of editing the *Journal of Shellfish Research* and even more years of reading the literature relating to bivalve larval biology an impression remains that the option for intensive field work is usually countered by comments such as: "too difficult, too much variability, too little control, and too time consuming." Consequently, we remain in the laboratory.

A list of factors which influence recruitment—here defined as successful metamorphosis from the pelagic pediveliger larva (sensu Carriker 1961) to the benthic, generally attached, feeding juvenile—of bivalve larvae might include, but not be limited to, the following: egg quality as influenced by the availability of food to the parent organisms, physical environment and food availability during larval development, the interplay of passive dispersal (horizontally) by water current and depth regulation by active swimming, loss to predation and disease, proximity of suitable and available substratum as metamorphic competency is achieved, and availability of sufficient metabolic reserves to complete metamorphosis to the attached benthic form. The list is not intended to be definitive or infer that the factors are listed in order of importance. It is, however,

comprehensive. I wish to proceed through this list and demonstrate that we have the ability to quantify (to a variable degree) all of these factors. Consequently, it seems reasonable to suggest that we attempt such a quantification in a known field situation as part of a comprehensive examination of larval survival. I know of no case where this has been attempted for bivalve larvae.

The first item to be considered is egg quality. It has been documented for some time that a strong relationship exists between broodstock condition and larval viability in the flat oyster, *Ostrea edulis* L. (Helm, Holland and Stephenson 1973). More recently, Gallager and Mann (1986) have demonstrated similar strong relationships between broodstock condition and lipid contents of eggs in both *Mercenaria mercenaria* L. and *Crassostrea virginica* Gmelin. We offer a simple technique, based on the lipid specific stain Oil-Red-O, for assessing egg lipid content. Although developed and used in both the laboratory and commercial hatcheries, there is no reason why this cannot be used for field collected specimens. Indeed, we examined bivalve larvae using this technique in a preliminary manner during a field study of larval distribution on the Southern New England Shelf in 1981 and found it tractable and informative.

The second item is the physical environment during larval development. There is a considerable volume of literature on this subject although it is not always presented in a manner that is easily interpreted when attempting to apply the laboratory generated data sets to field situations. The data should be examined and used in models of field situations. Here, I offer two such examples. Lough (1974) examined the data of Brenko and Calabrese (1969) on the influence of temperature and salinity on *Mytilus edulis* L. larvae using response surface techniques. Immediately evident from this approach is the optimal physical environment for growth and survival. Yet, this approach is rarely

used. It is simple to interpret these data in concert with temperature and salinity values from the field. By contrast the tabular data of Davis and Calabrese (1964) for *Crassostrea virginica* Gmelin and *Mercenaria mercenaria* L., although informative, are considerably more difficult to use. An alternative approach, one that I have used in modelling occurrence and growth of *Arctica islandica* L. larvae on the New England Shelf (Mann, 1986a), involves stepwise integration of such data into more complex models. I will address this in my discussion of larval dispersal later in the text. When discussing the physical environment for developing larvae it is also relevant to include the presence of toxic materials. These may originate from natural sources, for example the exudates of blooms of the microorganism *Phaeocystis pouchetii*, or from waste disposal activities. In coastal areas adjacent to urban development the latter can be alarming in volume and variety of composition. Nonetheless progress is being made by toxicologists in quantifying the impact of selected toxic materials on larval molluscs.

The third item is food availability. Even though we can culture larvae in the laboratory on diets of phytoplankton, there is still no definitive statement on what larvae can and cannot eat in the field. How do we determine if enough food is present? Examine a worst case scenario; exclude dissolved organic carbon (D.O.C.), which Manahan (1983a, 1983b) and Manahan and Crisp (1982, 1983) have shown to be available for use by invertebrate larvae, and exclude non-phytoplankton particulate organic carbon (P.O.C.). The latter may be considerable; for example, work by Hugh Ducklow at the University of Maryland has shown that in the upper Chesapeake Bay bacterial biomass may be equal to that of phytoplankton. This leaves only phytoplankton in our examination. If larvae can survive on this, they can certainly survive when all the other carbon sources are also made available to them. Mann (1985) offers a series of calculations examining food availability at a station on the New England Shelf—a station where chlorophyll *a* concentration is probably well below that of inshore and estuarine regions where oyster and clam larvae are expected to grow and metamorphose. The calculation is simple and the result suggests that an estimated standing stock of cell concentrations in the range 0.54 cells/ μ l (obtained using very conservative conversion factors) to 67.7 cells/ μ l (using more reasonable conversion factors) is present during the summer and fall in the waters of the shelf environment. With the exception of the lowest estimates (0.54 cells/ μ l) of food concentration there is generally enough food present for larval development based upon laboratory estimates of bivalve larval requirements (see Walne 1965; de Schweinitz and Lutz 1976; Lutz et al. 1982). In essence we need worry only about atypical rather than typical events with respect to food impacting larval survival. As an example here, I offer the "brown tide" phenomena which Southern New England and Long Island

have recently experienced—essential monocultures of apparently unpalatable phytoplankton. My point, however, is that it is generally difficult to make an argument that food quantity is ever limiting to larval growth.

The fourth item is larval dispersal. Is this an active or passive process? I have recently addressed this subject (Mann 1986a) and reviewed the literature (Mann 1986b). In regions of intense vertical mixing the weak swimming ability of larvae is overwhelmed and dispersal is passive. Consequently, if you want to know where the water (and therefore the larvae) is going you must consult your friendly, local physical oceanographer. To quote Andrews (1979): "Usually hydrographic regimes have not been known or appreciated to plan sampling of larvae." Fortunately, the trend toward active development of programs in collaboration with physical oceanographers is changing rapidly. In coastal systems seasonal stratification can be intense irrespective of whether estuaries or the inner shelf is being examined. In such regions, larval behaviour, a component that can be easily quantified in the laboratory, can be important and is amenable to modelling. The models can also be tested for validity in the field. The point that I wish to make is that we can use simple laboratory experiments in conjunction with field data, both physical and biological, to build testable computer models of larval dispersal. Physical scientists are progressing in the development of three dimensional, finite difference models of currents and sediment transport in coastal regions (see Sheng 1983). The modelling of sediment particle dynamics has many analogies with the modelling of larval behaviour. The problem is large but tractable and we, as bivalve ecologists, should address it.

The fifth item is disease and predation. We have a host of methods to examine disease in the stressful environment of a commercial hatchery operation (see Elston 1984 and references therein). While not all of these can be easily utilized on field collected specimens, due to small numbers of larvae collected, observational techniques such as electron microscopy can be used and draw upon the data provided by laboratory culture procedures. Castagna (personal communication) comments that in laboratory cultures significant numbers of larvae fail to metamorphose or develop very slowly. In the field these larvae would have increased susceptibility to predation. In a review by Gibbons and Blogaslowski (in press) a listing of predators on larvae include *Aurelia*, *Balanus*, *Brevortia*, *Chrysaora*, *Chthalamus*, *Diadume*, *Mnemiopsis*, *Noctiluca*, *Polydora*, *Sphaeroides* and a host of filter feeding bivalves and fish. Such impacts are potentially quantifiable using a combination of laboratory experiments and field collections. It would be particularly profitable here to coordinate efforts with larval fish ecologists (whose activities are considerable in the coastal regions) interested in fish feeding, diet and stomach contents.

The sixth item is substratum availability. Certain bi-

valves, notably oysters, exhibit substratum specificity. While the practice of provision of substratum to enhance settlement of commercially valuable bivalves can be traced back to Roman times and the writings of Plinius, and has been practiced extensively since the 1850's on the U.S. east coast, surprisingly (appallingly) little quantitative information exists on the fate of that substratum, over time, and its availability as a substratum to oysters in the face of competition for that substratum by what we term "fouling" species. In 1985 Richard Rheinhardt and I attempted to quantify the temporal and spatial development of fouling communities on clean shell substratum in the James River, Virginia. Our focus was, in part, to provide managers with a time window for optimal planting of shell to maximize oyster larval settlement and minimize prevention of settlement by fouling organisms. We used point sampling techniques to quantify our data—again illustrating that we must be prepared to look outside of our classical discipline to seek guidance from others in developing our field. The resultant manuscript is in review; however, to summarise, we illustrate that differences in rate of development and extent of areal coverage of fouling communities can be quantified. We also demonstrated that changes in the community structure could be elucidated using detrended correspondence analysis (Hill and Gaugh 1980). Examination of the predominant fouling species over time can give some insight into their potential impact on settlement of bivalves on adjacent, available substratum.

The final item is the assessment of whether or not morphologically competent-to-metamorphose larvae have sufficient energy reserves to complete that same metamor-

phosis. It is now accepted that metamorphosis is an energy consuming and thus critical period of the life cycle for a multitude of marine fishes and invertebrates. The importance of lipid reserves to this process in bivalves has been reported by Gallagher, Mann and Sasaki (1986). As with egg quality we demonstrate that larval quality, including pediveliger larvae, can easily be assayed using a lipid specific stain. As I noted earlier, this technique is both simple and quantifiable. It can and has been used in the field and on other species. We have no excuse not to examine the viability of larvae in the field.

In summary then, I hope that this commentary has convinced you that we have at our disposal viable methods to examine many of the factors influencing larval survival and recruitment in the field. It is time to address the problem at hand.

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