Research

Questions for Further Research

The commercial importance of Crassostrea *virginica* has stimulated much research into its biology and management in North America. Numerous studies of varying degrees of thoroughness and quality have been performed over the past century (Breisch and Kennedy 1980). Yet, many questions, some more important than others, remain.

That we have such a shortfall in knowledge after so much research attests to the immensity of the job of understanding even one species and its niche in nature. The complexity of interaction in a system such as Chesapeake Bay is great. The broad role of a dominant species such as the oyster requires careful, extensive, and lengthy analysis. This creature initially has a role as a pelagic larva which may become food for any of a variety of pelagic or benthic predators. As a pediveliger it competes with other epifaunal species for limited hard substrate. As a settled oyster its shell becomes that hard substrate. As it grows it filters great quantities of water, preys on or at least filters out plankton, consolidates sediment, and produces fecal and pseudofecal material which smothers some creatures and serves as food for others. By concentrating trace materials, it may serve as a sink for pollutants. It is a target for parasites and disease organisms. As a commercial species, its harvest supports an important economic infrastructure involving thousands of people.

These and other facets of the oyster's life and role in estuarine ecology and human culture have formed the basis for this report. We have drawn together a number of questions that remain to be answered, questions that indicate areas that need more study. We have tried to avoid trivial questions but have included a number that are of "academic" or basic interest because, we believe, the best management depends on a great depth of understanding of the oysters' biology and ecological relationships.

The questions are grouped roughly according to the order of sections of our review. However, a number of questions (e.g. the influence of low salinity on feeding and thus on gametogenesis, spawning success and resultant larval vigor) cut across that listing (in the example just given, the question involves salinity,

Scientists an a research vessel obtain a water sample to study the movements of oyster larvae in the plankton.

food and nutrition, reproduction, and larval biology). Such questions appear in the section we think most appropriate. There may be some overlap.

Oyster Biology

There is need for research into physiological adaptations of eastern oysters to various environmental factors throughout their distributional range (Canada to the Gulf of Mexico). The results could be significant for aquacultural activities, if the environmental plasticity and resilience of various oyster stocks can be exploited in culture. Studies might include responses to temperature, salinity, and sediment load. Other studies would consider disease resistance, growth, rapidity of attaining maturity, fecundity, spawning stimuli, larval vigor, feeding efficiency, etc. over a wide geographic range. The genetic exploitability of such adaptations could then be investigated.

Temperature

What are the upper and lower lethal temperature limits for adults, spat, and larvae? How does temperature influence physiology or activity-feeding, growth, condition, susceptibility to disease, larval swimming, and settlement in the field-over the distributional range of C. virginica? In terms of aquaculture, for specific geographic regions or broodstocks of oysters, what influence does temperature have on shell deposition, increase in meat weight, food conversion efficiency, resistance to parasites and disease, sublethal stress in adults and resultant larval vigor?

Is spawning initiated by temperature change, either slow or rapid increase? Is it influenced by temperature only in some areas of the oysters' range and by other factors (e.g. food supply) elsewhere? Why is it apparently easier to spawn oysters from more northerly populations (say New Jersey north) than from more southerly populations (below Chesapeake Bay)?

Salinity

What mechanisms are involved in the apparent influence of adult acclimation salinity on salinity tolerances of larvae? How does salinity affect larval, spat, and adult growth and gametogenesis and spawning in adults? Is it by the imposition of physiological stress, or by some indirect influence either by inhibiting oyster feeding (Butler 1948), or by leading to changes in phytoplankton that are unacceptable to oysters?

In Chesapeake Bay, does recruitment to oyster populations in low salinity regions (<10 ppt) depend on influx of mature larvae from higher salinity areas (Davis 1958)?

Rainfall

In Chesapeake Bay, does copious late winter-early spring rainfall followed by late spring-summer drought conditions lead to enhanced nutrient input and phytoplankton growth, followed by excellent larval survival and retention in good setting areas?

Sediment

In Chesapeake Bay, how does silt affect survival of all life history stages of oysters? Are there seasonal effects which might prove detrimental, for example, by combining stress from high temperature or low salinity with stress from silt coverage? If so, how could this stress be mitigated in oyster farming? Has the apparent increase in siltation in Chesapeake Bay in recent decades been a factor in oyster resource depletion?

Dissolved Oxygen

In Chesapeake Bay, what role do low levels of dissolved oxygen play in affecting larval survival and settlement? Are areas of poor spat settlement success the result of low dissolved oxygen levels during summer?

Light

What is the role of light in stimulating or inhibiting larval behavior? Do larval responses to light alter with age, or with variation in other environmental factors such as temperature, salinity, pressure, etc? Have apparent changes in turbidity and therefore light transmission in Chesapeake Bay altered larval behavior (swimming, settlement) and, if so, how?

pH

Does heavy siltation, which is reputed to result in lowered pH, thereby affect oyster recruitment (Calabrese and Davis 1966)?

Chemicals

The influence of a wide range of anthropogenic chemicals needs to be measured for all life history stages of the eastern oyster. Both direct effects (toxic levels leading to death) and indirect effects through inhibition of feeding or respiration, etc. need to be known. Effects on growth, reproduction, and spat settlement need to be understood. As with natural environmental stress, chemicals may stress adults with resultant production of larvae with reduced vigor. Synergistic effects need to be assessed.

In addition to direct effects on the animals themselves, we need to understand the influence of chemicals on quantity and quality of oyster food. Chemicals which may not directly affect oysters in any measurable fashion may have a major impact if they affect the oysters' food source deleteriously.

Is chlorine so harmful to oysters that its increased use in Chesapeake Bay has contributed to population declines?

What control mechanisms are involved in manganese dynamics in relation to shell deposition, feeding and spawning in oysters (Frazier 1976)?

What are the synergistic effects involving different metals with each other and with other kinds of pollutants (e.g. PCBs, petroleum hydrocarbons, etc.)? What is the role of salinity in such synergisms, or in heavy metal uptake in general? Is there a transfer of metals and accumulated toxins from female oysters to their eggs? If so, what is the result on fertilization and subsequent growth of the young? Ultimately, is the reproductive performance of the population affected? What are the effects on oyster populations of chronic sublethal stress caused by heavy metals and other toxins? Are there mutagenic and other genetic effects as a result of exposure to heavy metals?

Food and Nutrition

What do larval and adult oysters feed on in Chesapeake Bay today? Has their diet changed appreciably from that reported by Morse in 1944? Is there a seasonal pattern of diet with different dominant species of algae? Has there been a change or decline in phytoplankton species, similar to that observed in submerged aquatic vegetation populations? Have conditions favored less nutritious algal species at the expense of "good" algal species? Have suspended silt concentrations in Chesapeake Bay increased over time to the point that they adversely affect oyster feeding mechanisms?

Are there great variations in the carbohydrate content in natural populations of phytoplankton as there are in laboratory cultures? Are these variations seasonal? How do they affect oyster condition and growth? What are the relative food values of both natural and artificial diets? What are the rates of ingestion of these foods?

What are the biochemical aspects of nutritional requirements? Can vitamin supplements of artificial or natural diets increase growth rates and oyster condition? How are dissolved substances accumulated? Do they have an important nutritional role? Are dissolved substances which are adsorbed onto inert suspended particles made more or less accessible to oysters? Can oysters "taste" their food and, if so, how does this ability affect their choice in natural and artificial diets? Is carbohydrate in the diet more important than protein, or are there some other factors involved?

How do larval feeding mechanisms differ from those of adults? How do these mechanisms change in metamorphosis? What is the mechanism of digestion in both larval and adult oysters? Is it mainly intracellular or extracellular? How is it affected by environmental conditions? Are feeding and digestion continuous or is there a rhythmic alternation between these two activities? In the culturing of oysters, is a continuous feeding regime preferable to one employing batch feeding? What is the role of mucus in feeding and how is it affected by environmental factors including pollution?

Does the diet of Crassostrea sp. parent stocks greatly affect the viability of larvae and spat as it appears to do in *Ostrea* sp. (Helm et al. 1973)?

Growth

What causes the differences in average growth rates among different oyster bars within Maryland, or within bars from one year to the next, or among groups of seed from different areas (Beaven 1950, 1953a)? Specifically, with regard to good seed areas such as James River, Va. or Broad Creek, Md., why are the resident oysters stunted and slow-growing (Andrews 1955)?

Reproduction

Given the demonstrated impact on larval vigor of stress on adult *Mytilus edulis* and *Ostrea edulis* during gametogenesis, what are the effects of natural and anthropogenic stresses on adult Crassostrea *virginica* in terms of larval vigor?

What is the role of food in the process of oyster gametogenesis and in stimulating spawning? How does temperature interact with food supply in controlling reproductive activity? If there are interactions, do they vary with latitude?

How do environmental conditions affect sex ratios? It appears that Chesapeake Bay oysters maintain balanced or nearly-balanced sex ratios in the face of long-term diminution of recruitment of young (which are mainly males). How do they accomplish this? What cues are available to indicate sex ratios on established oyster bars? What sex ratios are optimal for spawning and fertilization?

What causes varied widths of gonad layers from year to year (Galtsoff 1938)? Why do some areas such as James River, Va. do so well in producing spat, yet have such apparently poorly conditioned brood stock (Andrews 1951)? Similarly, how do Florida grounds containing oysters with low glycogen content manage to produce so much spat (Ingle 1951)? What is the relationship (if any) between thickness of gonads and reproductive success?

Why are oysters from southern populations (Chesapeake Bay south) so difficult to spawn in the laboratory (Hidu et al. 1969, Dupuy and Rivkin 1973)? Are

their spawning stimuli different in nature from stimuli that cause northern oysters to spawn?

Larval Biology

What is the mortality rate of oyster larvae in Chesapeake Bay (Carter 1967)? How does the rate vary from year to year, or with location? What are the principal causes of larval mortality and do these causes vary annually or are they consistent from year to year? From an oyster farming point of view, can larval survival be enhanced in nature, and if so, at what cost?

How widely are larval broods spread in nature? Do they settle in the vicinity of the adults which produced them? Is there widespread mixing among larvae from different spawning populations, either within a tributary system or up and down the Bay?

How do oyster larvae react to various current speeds? What is their swimming behavior like in the field? Are they able to sense cues that would allow them actively to take advantage of estuarine transport mechanisms and be carried upstream, or are they transported passively?

What factors influence setting in Chesapeake Bay? Why does setting occur at consistently high levels in one area and consistently low levels in another? Why is setting so successful in some years (e.g. 1980) and not in others (e.g. 1978)? Are there features about oyster shells, other than the shell proteins, which attract pediveligers to settle? If so, can settlement be augmented by enhancement of these features? Why are some kinds of bacterial films on cultch apparently attractive to pediveligers while other films are not?

What are the larval concentrations to be found over various kinds of Bay bottom? Are they similar over both good setting areas and barren bottom, indicating that good setting areas have suitable quantities of cultch and barren bottoms do not? If a barren area has sufficient quantities of larvae in the overlying water (how much is sufficient?) does it need only application of cultch to become a good setting area?

Genetics

What trait or traits need to be selected for in Chesapeake Bay oysters? Is there an interaction between traits such that improvement in one, e.g. shell growth, results in loss in another, e.g. meat yield?

Given adequate quantities of cheap wild seed, what is involved (in terms of expense) in developing higher quality hatchery seed that will outperform the wild seed, e.g. in growth, meat yield, survival? How much better than natural seed does hatchery seed have to be in order to justify hatchery production economically?

What level of heterosis ("hybrid vigor") may be expected from crossbreeding different oyster strains for rearing in Chesapeake Bay?

Can we control the sex of oysters so that sterile animals can be produced? If so, would these sterile oysters be superior in growth characteristics or meat quality now that energy would not be diverted to gonad production?

Is it possible to select for low-salinity tolerant oysters so that the Upper Bay could be reseeded? If it were possible, would it be desirable or economically feasible?

Can genetic selection in oysters be enhanced by use of mutagenic agents? Is polyploidization (increase in the number of chromosomal sets) applicable to oysters, and if so, what useful characters (enhanced growth rate, greater mature size or weight, more efficient conversion of food) might result?

We know relatively little about oyster genetics. Research into this field needs to be expanded if aquaculture is to be successful.

Disease and Parasites

For Chesapeake Bay, the long term incidences of diseases and parasites need to be monitored as they are now by Project MADI, sponsored by DNR. In addition, methods of transmittal need to be established for some diseases and parasites. Interaction of certain diseases (e.g. "MSX" and "Dermo") need to be studied. The study of disease should be performed with attention to the-role of disease in the ecology of oysters. Perhaps more understanding of susceptibility on the part of oysters will accrue if the animals' niche is also considered during research into parasites and disease.

Larval diseases, both in the hatchery and in the field, are little known and need attention.

Studies of disease in oysters are in their infancy, yet are of great importance. Monetary support should be adequate and consistent.

Competitors, Predators and Pests

What are the major competitors of larval oysters for food? Is such competition of an intensity to affect larval survival significantly? If so, can these competitors be controlled to ensure an adequate food supply for oyster larvae? Would it be economically possible to do so?

What is the nature and extent of the proposed sea nettle-ctenophore-oyster larvae interaction? If such a relationship exists and if it is deleterious to larval survival, can anything be done to counter the deleterious effect? What is the influ-

ence of potential predators such as filter-feeding fish, moon jellyfish (*Aurelia auri - ta*), mosquito larvae, folliculinids, which are mentioned in the review? In general, how greatly do predators of oyster larvae affect recruitment and population maintenance in Chesapeake Bay?

What effects do chemicals used for predator control, such as quicklime, have on other estuarine organisms? Do chemical barriers or treatments adversely affect other important organisms? What predator and competitor controls are truly feasible for a public fishery where a free resource is less likely to be carefully maintained?

Rehabilitation

What is the abundance of natural brood stock now available in different locations of Chesapeake Bay? Is it increasing or declining? If it fluctuates annually, why, and how important are these fluctuations in affecting future harvests? Is brood stock presently too dispersed in the Bay to allow for adequate stimulation of adults to spawn? Is there an optimal brood stock concentration to ensure adequate spawning (or, how many brood oysters are required for a given area of bottom)? If so, do different areas have different optimal concentrations? Do young or old oysters make the best brood stock?

What is the best position of brood oysters in relation to cultch? On the cultch? Upstream or downstream? Some distance away? What are the best concentrations of cultch shells on different bottom types? Is setting rate enhanced by allowing large brood reserves to accumulate in designated seed areas where dispersal of larvae to other water masses would be at a minimum (assuming they are greatly dispersed at all)?

Why are (or were) certain oyster grounds capable of producing an excellent set consistently (e.g. James River, Holland Straits, St. Mary's River, Eastern Bay, Fishing Bay, Tangier Sound, Broad Creek and Harris Creek in the Choptank River)? Why are some of these setting areas not suitable for rapid growth and fattening of oysters? Why was and is the Chester River a poor setting area? Why are other areas (e.g. Patuxent River) good for growing market oysters but not for spat settlement? (for background—see Galtsoff 1958, Engle 1948). Can any area of the Bay be made into a good seed area, given adequate material to firm up the bottom and adequate cultch for settlement? What is the optimum density for maximum survival and growth of newly settled spat, juveniles or adults? Do such optimal densities vary with region? What are the natural mortality levels for larvae, spat and juveniles in different areas?

How are growth and mortality affected by handling and transporting spat or seed oysters within the Bay? What sort of damage is caused to spat by harvesting activities? In oyster farming, what is the optimum time for harvesting oysters? That is, should they be harvested just after they have first spawned, or would it be better to wait for another year or two? Should they be harvested when they

have reached their maximum growth rate and before it slows? How would the latter affect possible future contributions of these oysters to recruitment?

What is the annual magnitude of recruitment in any area? What is the level of fishing mortality and catch per unit effort in the Bay? Are variable annual quotas more suitable than fixed quotas for management of Bay oysters? Would a limited entry fishery result in better management for greater yield? What is the projected yield that would accrue if widespread rental of oyster grounds was practiced in Maryland?

What kinds of automated systems for handling farmed oysters in the field and for processing them on-shore are economically feasible? If oyster farming were to become a viable enterprise in Maryland, what economic and marketing steps could be taken to prevent an over-supply of oysters?

There is need for development of a wider variety of food products incorporating oysters, in order to stimulate consumer demand.