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Combined effects of temperature-salinity on larval survival of the Eastern oyster *Crassostrea virginica* in the Maryland portion of the Chesapeake Bay (U.S.A.)

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ABSTRACT

Oyster landings in the Maryland portion of the Chesapeake Bay have declined by more than 50-fold since the early part of the century, despite intensive management efforts. The annual shell repletion program is the most critical programmatic element to effect recovery of the ailing Eastern oyster *Crassotrea virginica* stock and fishery. The overall efficacy of shell repletion management depends primarily on the success of spat settlement on the planted shell, and furthermore on their survival rate. The Operations Research techniques and mathematical programming developed by Rothschild *et al.* (1991) attempt to maximize spat recruitment to the oyster stock subject to a series of operational constraints. Allocation and timing of shell deployment are the most critical issues. To be truly efficient, this approach should incorporate the principal biological constraints affecting oyster production. A modelling approach is proposed to consider the spatial and temporal distribution of temperature - salinity over the Maryland portion of the Chesapeake Bay. We defined three models according to geographic regions in the Bay (i.e., Upper, Middle, Lower Bay) to characterize the specific pattern of potential larval survivorship. Stations located in Lower Bay on both Eastern and Western shores show the highest potential for larval survivorship. Higher percentages, also maxima, are reached earlier in the season and last longer at southern locations. The sharp ascending phase in survivorship in May-June tends to decline with increasing latitude in the Lower Bay region. Mid-Bay locations rarely reached the 100% of larval survivorship and maxima are reached later in the season than at southern locations. Descending phase is similar on both Lower and Mid-Bay regions with a sharp decline in September. In Upper-Bay, Eastern locations are more favorable than Western areas. Larval survivorship on oyster bars located north from the Chesapeake Bay Bridge is particularly low with a 45% maximum. These areas are unlikely self-sustainable in spat recruitment and probably rely on episodic transport of older larvae from southern areas.

Then, recommendations are proposed to maximize the yield of the current shell and sanctuary programs, and also to define the future research priorities. Modelling streamflow into Chesapeake Bay would likely allow salinity prediction so as to determine optimum sites and timing for shell planting on a yearly basis. Stock assessment and larval monitoring are also strongly recommended to maximize the current management cost-effectiveness.

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INTRODUCTION

The Eastern oyster *Crassostrea virginica* (Gmelin, 1791) population in the Maryland portion of Chesapeake Bay has declined from 15 million bushels in 1884 to about 300,000 bushels in 1992 (Figure 1). Rothschild *et al.* (1992) show that the long-term decline of oysters largely results from habitat loss associated with intense fishing pressure early in the century, and stock overfishing early in the century through recent times (Figure 2). The oyster population is currently at historically low level of spawning stock biomass. The decline is also thought to have affected the biota and chemistry of Chesapeake Bay thereby altering its ecological structure (EPA, 1983; Kemp and Boynton, 1984; Newell, 1988).

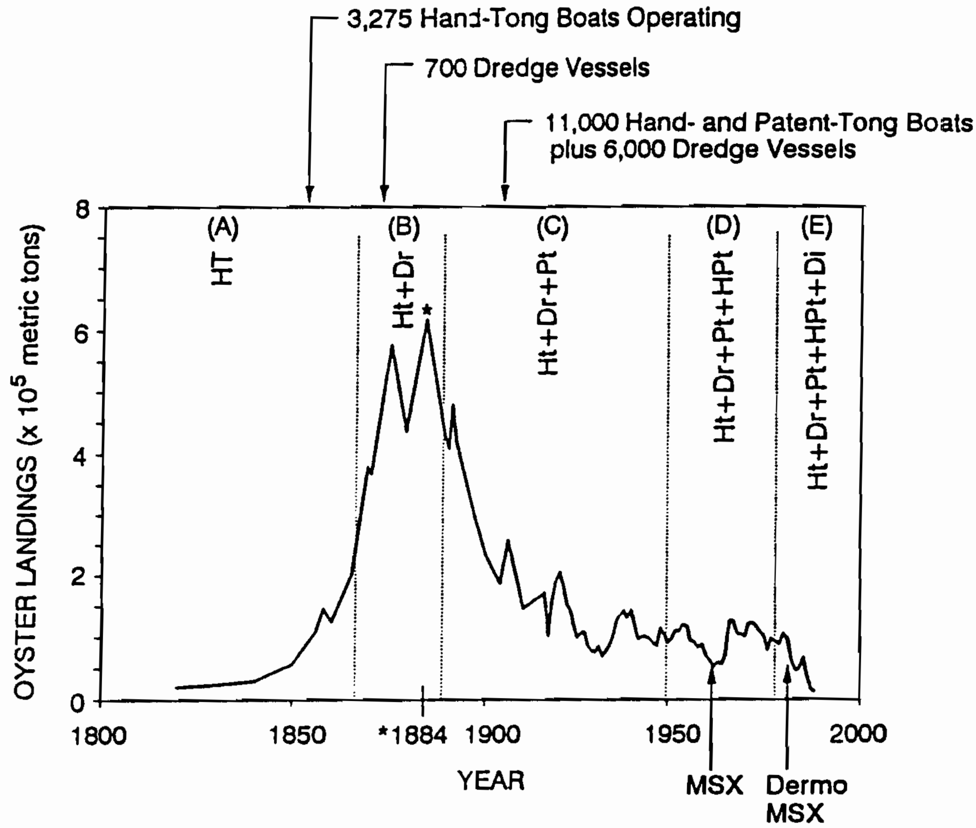

Figure 1. Time series of Maryland oyster landings. The panel segments show corresponding evolution of oyster fishing gears: (A) use of hand-tongs (Ht); (B) introduction of dredges (Dr) (note peak in production occured in 1884); (C) introduction of patent-tongs (Pt) which corresponds with the beginning of the catch decline; (D) introduction of the hydraulic patent-tongs (Hpt) in 1950; (E) the addition of diver harvesting (Di) in 1980. One Maryland bushel equals 0.041 metric ton (from Rothschild *et al.*, 1994).

To effect some habitat replacement and support commercial landings, the Maryland Department of Natural Resources has for years been operating a shell repletion program. The repletion strategy consists on two components: (1) placing shell cultch on depleted oyster bars to provide suitable habitat for oyster spat settlement; and (2) transplanting spat into areas to improve growth and survivorship. Although shell repletion and seed transplanting programs are efficient to sustain locally the oyster population, the program has not reversed the historical landings trends (Abbe, 1987; Kennedy, 1989). Rothschild *et al.* (1990, 1991) have demonstrated that the program cost-effectiveness can be improved using operations research (LP model) and system analysis techniques to optimize shell allocation and oyster production. However, one of the key element of this model is based upon the "attractiveness" index for each bar. This measure relies on historical data and should be updated with regards to the recent and drastic environmental and oyster population changes.

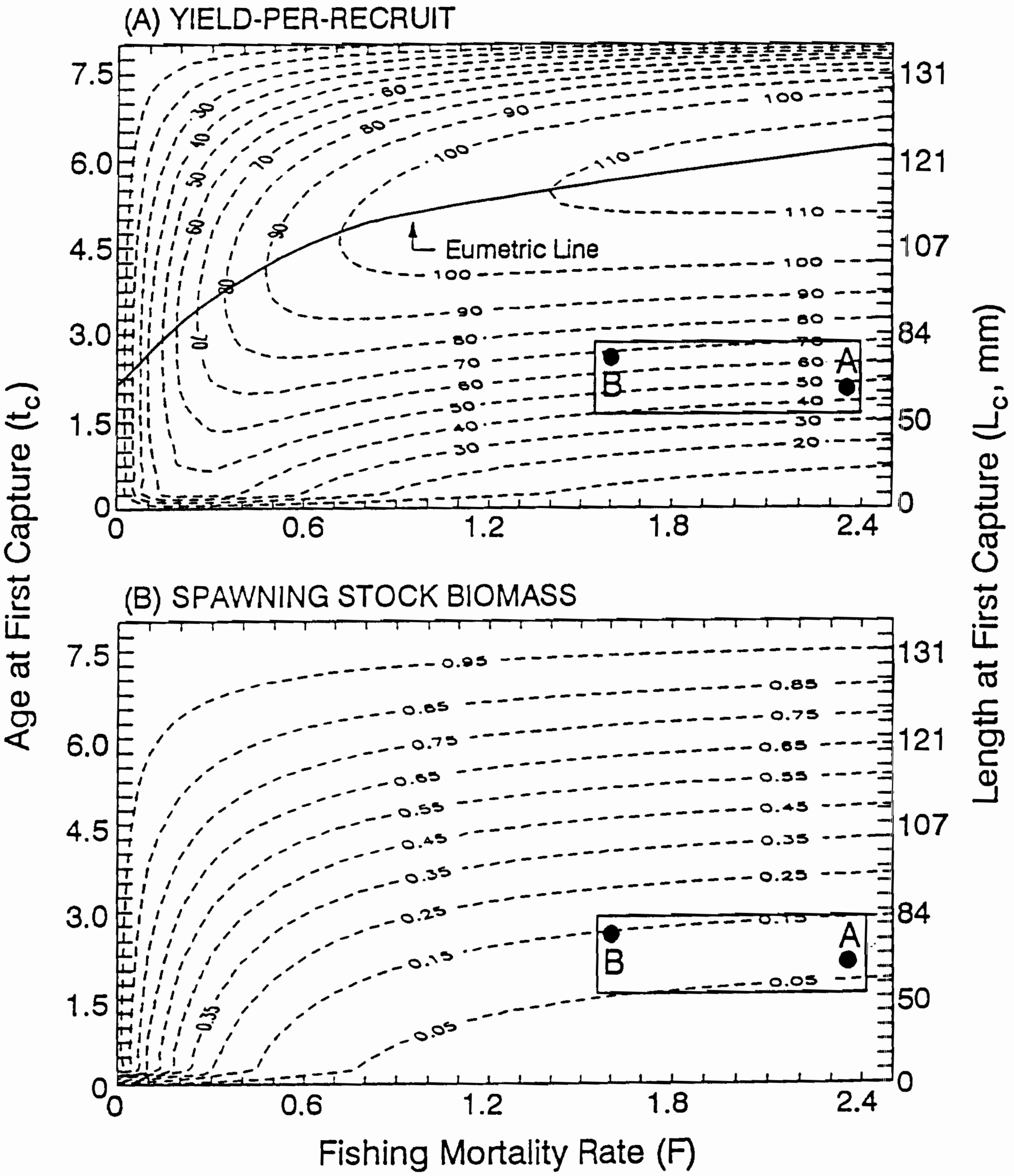

Figure 2. Yield-per-recruit isopleths expressed as a function of fishing mortality rate F and age of first capture tc for the Chesapeake Bay oyster stock (A≈1900, B≈1990 fishery position) (from Rothschild *et al.*, 1994).

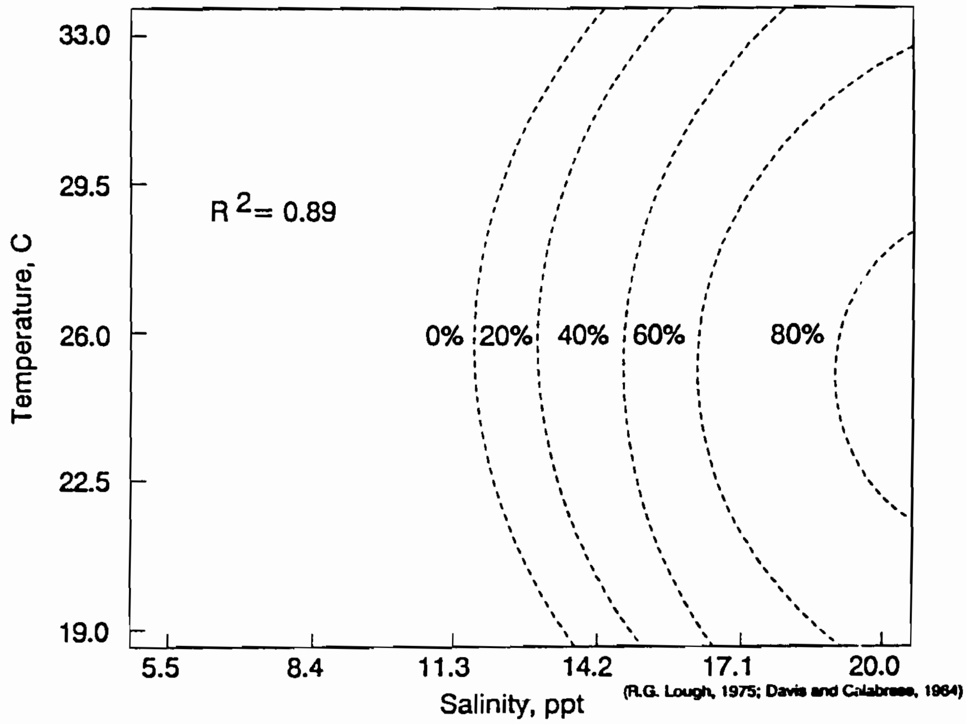

Figure 3. Percent larval survivorship of *Crassostrea virginica* function of temperature and salinity after 2 days of development (Lough, 1975).

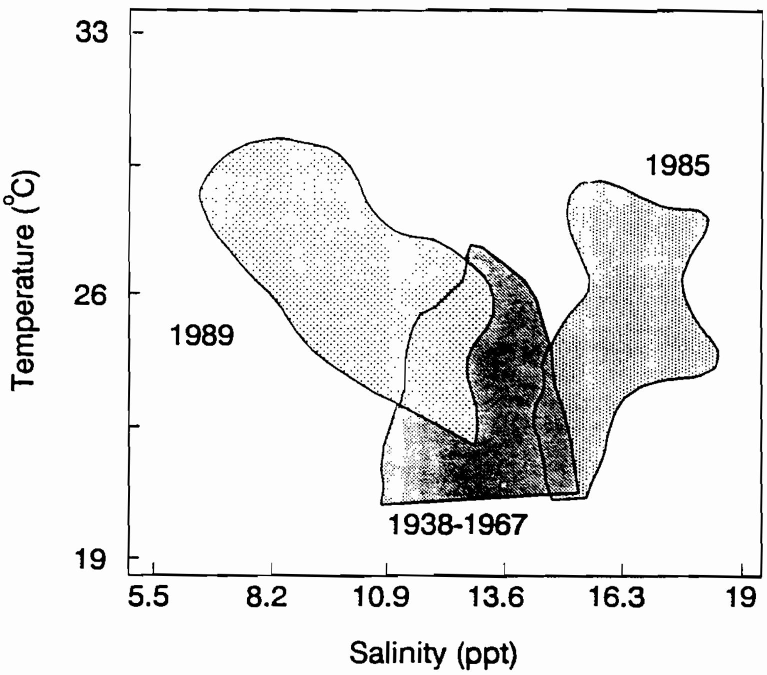

Figure 4. Comparison of salinity - temperature distributions at the CBL pier monitoring station, middle reach of Chesapeake Bay, in 1985, 1989 and an average based on 30 years.

Currently, no spatial and temporal constraints are considered by the shell repletion program to maximize the yield and no permanent habitat restoration allows a permanent recovery. Although aiming to limit diseases effects, the long term impact on local oyster population of transplanting operations, consisting on moving spat from southern to northern areas has not yet been assessed, particularly regarding the spawning stock biomass efficacy. The program aims specifically to sustain commercial landings, limiting the effect on permanent oyster population recovery.

To complement the shell repletion program, the Maryland Department of Natural resources has developed since 1986 a sanctuary program consisting of "off-limit" areas. Although limited to 357 acres, less than 1% of the official total bar acreage, sanctuary areas might be particularly efficient to restore oyster population if locations are appropriate and suitable habitat provided for massive spat settlement. Consequently, efficacy of current selected areas for oyster rehabilitation must be demonstrated. In fact, sanctuaries, mostly located in Upper and Mid-Bay, were not selected so that environmental conditions would maximize reproduction. Thus, they might be of limited efficacy even though planted with oyster shell and seed through the shell repletion program.

Therefore it appears critical to improve and complement both the shell repletion and the sanctuary programs to maximize the management yield while sustaining a long-term recovery. To begin to address the issue, a comprehensive plan has been proposed incorporating the fishery and oyster population management (Rothschild *et al.*, 1990). Four programs were defined involving (1) fishery management, (2) shell repletion program, (3) sanctuaries, and (4) habitat rehabilitation. This study aims to provide quantitative information on bio-physical constraints affecting the shell repletion program efficacy as well as optimum sanctuaries distribution.

Extensive literature reviewed qualitatively habitat oyster requirements and experimentally, factors limiting oyster recruitment (Davis and Calabrese, 1964; Lough, 1975; Abbe, 1986; Kennedy, 1991). While the effect of climatic factors on shellfish population dynamics is widely recognized, only few studies established quantitative relationships between those factors and shellfish recruitment. Ulanowicz *et al.* (1980) regressed spat density against environmental variables in Chesapeake Bay using stepwise multiple regression. Twenty-one percent of the variation was explained by a positive correlation with the cumulative excess salinity. This was in agreement with the notion that spawning seasons with higher salinities tend to be more productive of spat. However, this approach was flawed by underlying assumptions and the variables considered (e.g., spat density estimates). By way of example, environmental variables from the extensive CBL data set were considered as representative of Chesapeake Bay. Its use for management purpose was limited since no spatial variability was considered.

Using a different approach, we also have shown that salinity level is critical for larval survivorship and sufficient to explain the recent 1985 and 1989 yields (Rothschild *et al.*, 1991) (Figures 3, 4). However, our approach used also the CBL data set without spatial variability consideration. We now intend to consider this spatio-temporal variability of salinity-temperature distribution to describe the potential larval survivorship among geographical regions.

MATERIAL AND METHODS

Larval Survivorship in 1985 and 1989

Larval survivorship was first calculated as a function of salinity and temperature using response surface techniques defined by Lough (1975). Because larvae are most sensitive to environmental conditions during the first hours of living, survivorship was calculated using the 2-days development model parameters (Davis and Calabrese, 1964) (Figure 4). Moreover, this approach limited the bias of larval transport. A bay-wide approach was developed using the extensive EPA data set covering Chesapeake Bay main stem and tributaries stations (Figure 5). We stratified the stations among three sections Upper Bay, Mid-Bay and Lower Bay, respectively.

were computed using models from each region. Environmental data (i.e., temperature-salinity) in 1985 and 1989 were first considered to calibrate our previous results (Rothschild *et al.*, 1991). Although we have demonstrated that the MDNR fall survey cannot estimate quantitatively the spat density, estimates were compared from both approaches (MDNR, 1985, 1989; Rothschild *et al.*, 1990; Chai, 1988, 1992).

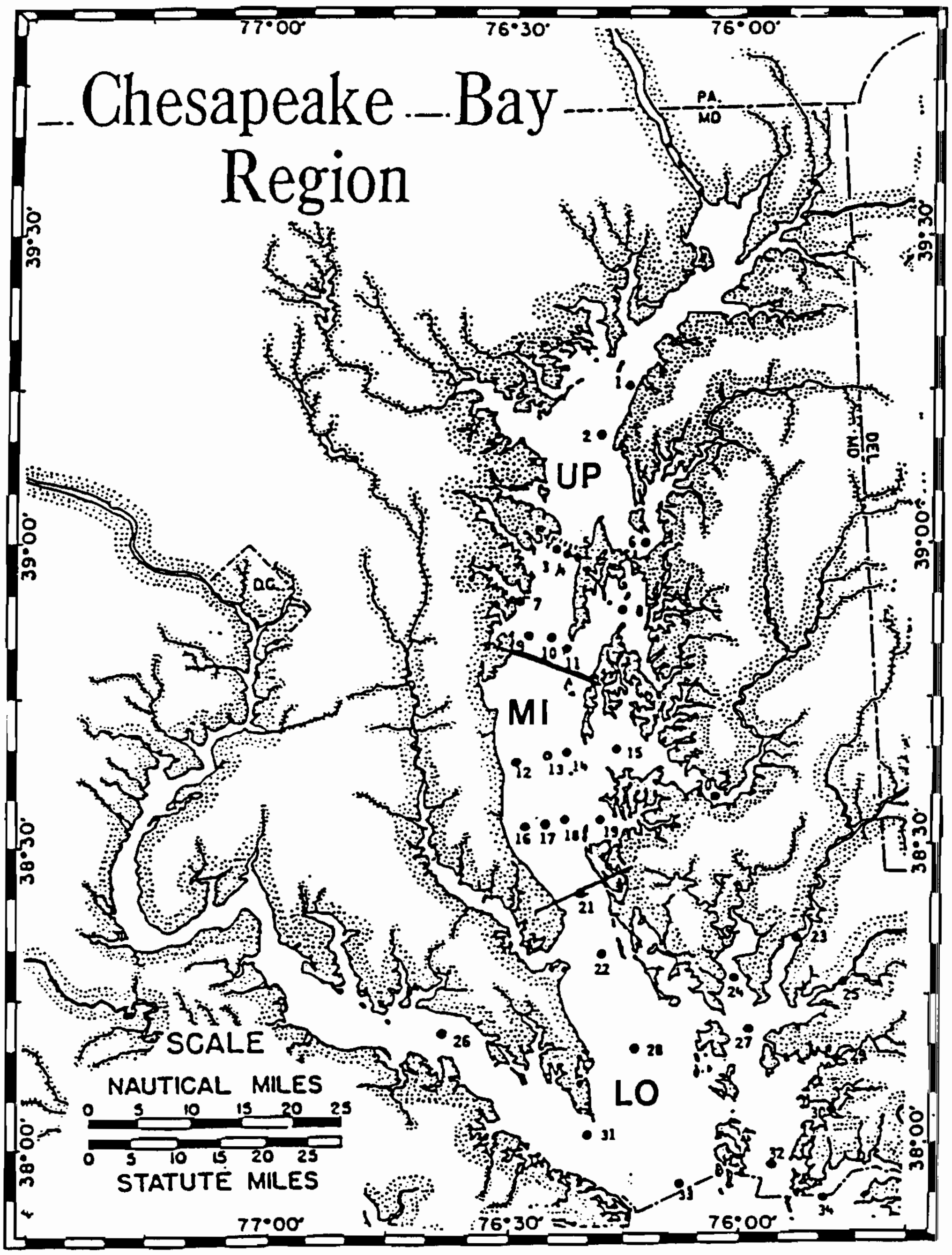

Figure 5. Bay-wide distribution of EPA monitoring stations in Upper, Mid- and Lower Bay.

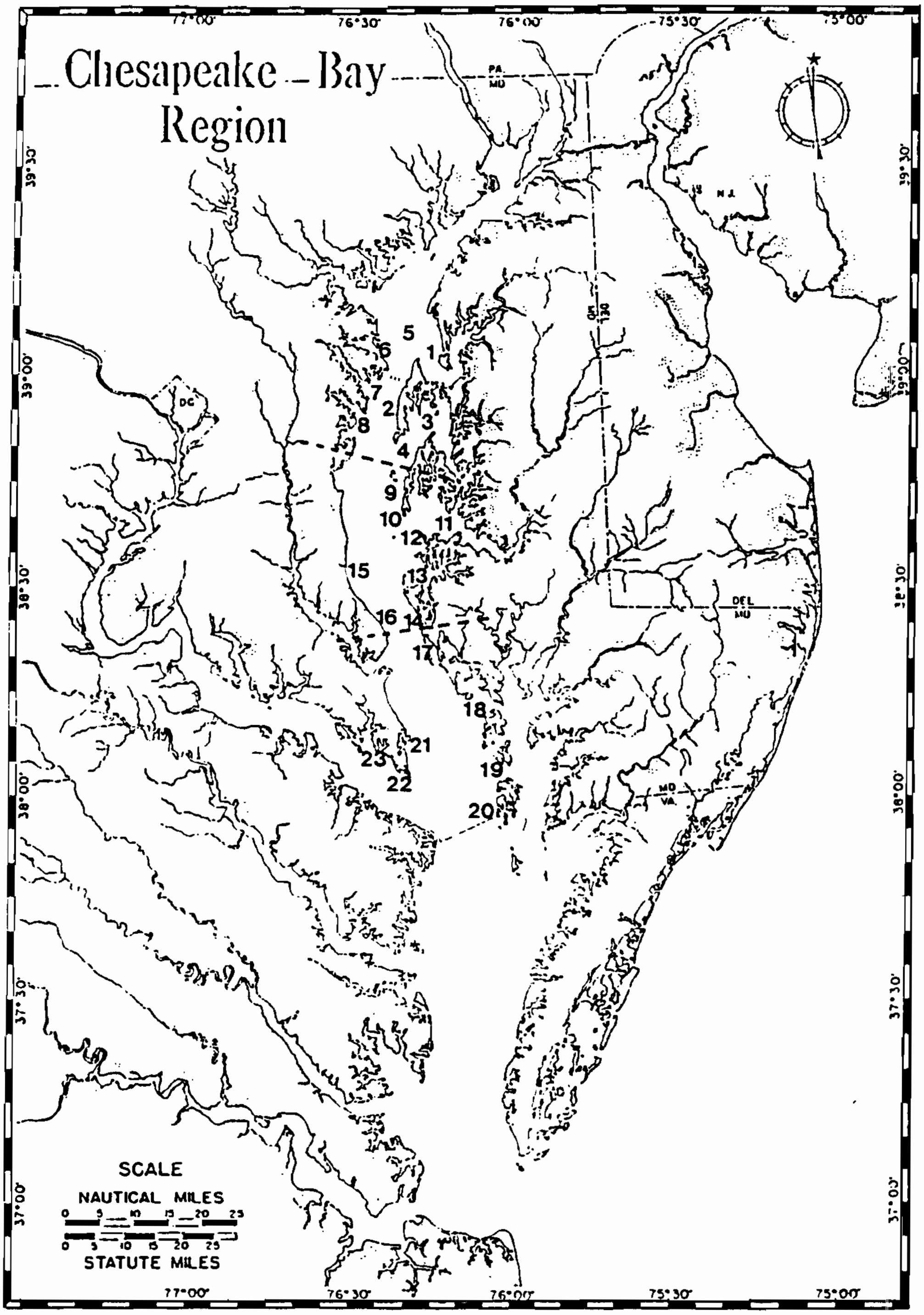

Figure 6. Bay-wide distribution of experimental sites in Maryland Upper, Mid- and Lower Bay selected for larval survivorship computations.

Region	Bar Name	Latitude (degree)	Longitude (degree)	Depth (feet)	Code
Upper Bay					
Eastern Shore					
Lower Chester	Love Pt.	39.04	76.18	18	1
Kent Shore	Gum Thicket	38.53	76.23	10	2
Eastern Bay North	Sow Mill Creek	38.56	76.14	10	3
	Bedkin Shoals	38.52	76.19	10	4
Western Shore					
Upper Bay West	Man-o-War	39.11	76.23	10	5
Anne Arundel Sh.	Graighill Lumps	39.05	76.22	12	6
Magothy River	Persimmon	39.03	76.26	12	7
Low Anne Arundel	Under the Gum	38.55	76.27	15	8
Middle Bay					
Eastern Shore					
Eastern Bay South	Marys Delight	38.49	76.19	18	9
Talbot Shore	Stone Rock	38.39	76.23	15	10
Middle Choptank	Green Marsh	38.34	76.03	8	11
Lower Choptank	Cook's Point	38.39	76.17	18	12
Littler Choptank	Tobacco Spike	38.31	76.14	10	13
Dorchester Shore	New Discovery	38.21	76.17	8	14
Western Shore					
Upper Calvert	Plum point	38.37	76.29	18	15
Lower Calvert	Emmanuel	38.30	76.29	18	16
Lower Bay					
Eastern Shore					
Tar Bay	Tar Bay	38.19	76.14	5	17
Hooper Straits	Applegarth	38.14	76.06	18	18
Kedges Straits	Kedges Straits	38.03	76.07	18	19
Lower Bay East	Southwest Mid.	38.00	76.10	18	20
Western Shore					
Lower Calvert	Emmanuel	38.30	76.29	18	16
St Marys Shore	Butler	38.06	76.19	12	21
Low Potomac	Cornfield Harb.	38.02	76.20	15	22
St Marys River	Chicken Cook	38.07	76.26	10	23

Table 1. Experimental sites characteristics in Maryland Upper, Mid- and Lower Bay selected for larval survivorship computations.

Larval Survivorship Models

We generalized our approach by computing larval survivorship on 23 selected oyster bars using temperature and salinity models (Figure 6) (Table 1). Sites were mostly selected in the main stem of the Chesapeake Bay or at the mouth of tributaries since topography may interact with sea water stratification and larval distribution (Seliger *et al.*, 1982). Also frontal system in tributaries may effect larval transport (Mann, 1988). The 1984-1989 EPA data set was used to establish relationships between temperature-, salinity- and time. A temperature model was computed for each region Upper, Mid- and Lower Bay using

$$y = b+a \sin(\omega t+c) \qquad \text{with } \omega = 2\pi/365$$

Salinity models were described by Wang *et al.* (1991). One regression model was established per region incorporating latitude, longitude, depth effects, time and interactive terms.

RESULTS

Larval Survivorship in 1985 and 1989

Potential larval survivorship in 1985 and 1989 at these stations are presented comparatively on figure 7. An obvious spatial pattern is observed for both years: larval survivorship declines in duration and also in intensity from southern to northern areas. Larval survivorship is particularly low in Upper Bay compared to Lower Bay stations. The favorable survivorship duration as well as intensity present a large yearly variability. Potential survivorship was larger in 1985 than in 1989, and the 60% level was reached earlier in 1985 in Lower than in Mid- or Upper Bay stations. Larval survivorship last from May through November 1985. Except for tributary locations in 1985 (i.e., station No 4 versus No 6; station No 15 versus No 20), no specific pattern between Western and Eastern parts of the Chesapeake Bay was observed. This might be due to the near vicinity of monitoring stations located in the bay main stem. Unfavorable conditions in 1989 led to a low potential of larval survivorship for all three sections. No more than 80% of survivorship in the lower part of the Bay was observed and the maximum survivorship was delayed until October. A significant decline was also observed in lower stations in July and conditions were unfavorable for almost all summer.

The 1985-1989 differences were logically explained by the salinity-temperature trends (Figure 4). A slight delay in temperature increase and a particularly significant decline in salinity in June-August were the causes for the low survivorship potential in 1989.

The overall pattern of spat recruitment observed by the MDNR monitoring must support these trends. Estimate comparisons from both approaches showed that in all cases reported by MDNR but one (i.e., Miles River), spat range counts were greater in 1985 than in 1989 (Table 2). Except Eastern Bay, spat counts in Upper Bay were lower than in southern areas for both years. Therefore this pattern can be considered as consistent with our estimates.

Larval Survivorship Models

The estimated relationships for regressions of the date (t)-temperature (y) were $y = 14.75-12.30 \sin(\omega t + 1.095)$, d.f.= 1,863; $y=14.26-12.46 \sin(\omega t + 1.060)$, d.f. = 1,219, and $y = 14.16-12.43 \sin(\omega t + 1.060)$, d.f. = 1.427 for Upper, Mid- and Lower Bay respectively. Correlation coefficients for each regression was significant; ($r = 0.98$), ($r = 0.98$), and ($r = 0.98$) respectively (Figure 8). Correlation coefficient for each salinity model was also significant; ($r = 0.80$), ($r = 0.80$) and ($r = 0.75$) respectively (Table 3).

Potential trends of larval survivorship are described on figure 9. Stations located in Lower Bay on both Eastern and Western shores show the highest potential for larval survivorship. Higher percentages, also maxima are reached earlier in the season and last longer at southern locations. The sharp ascending phase in survivorship in May-June tends to decline with increasing

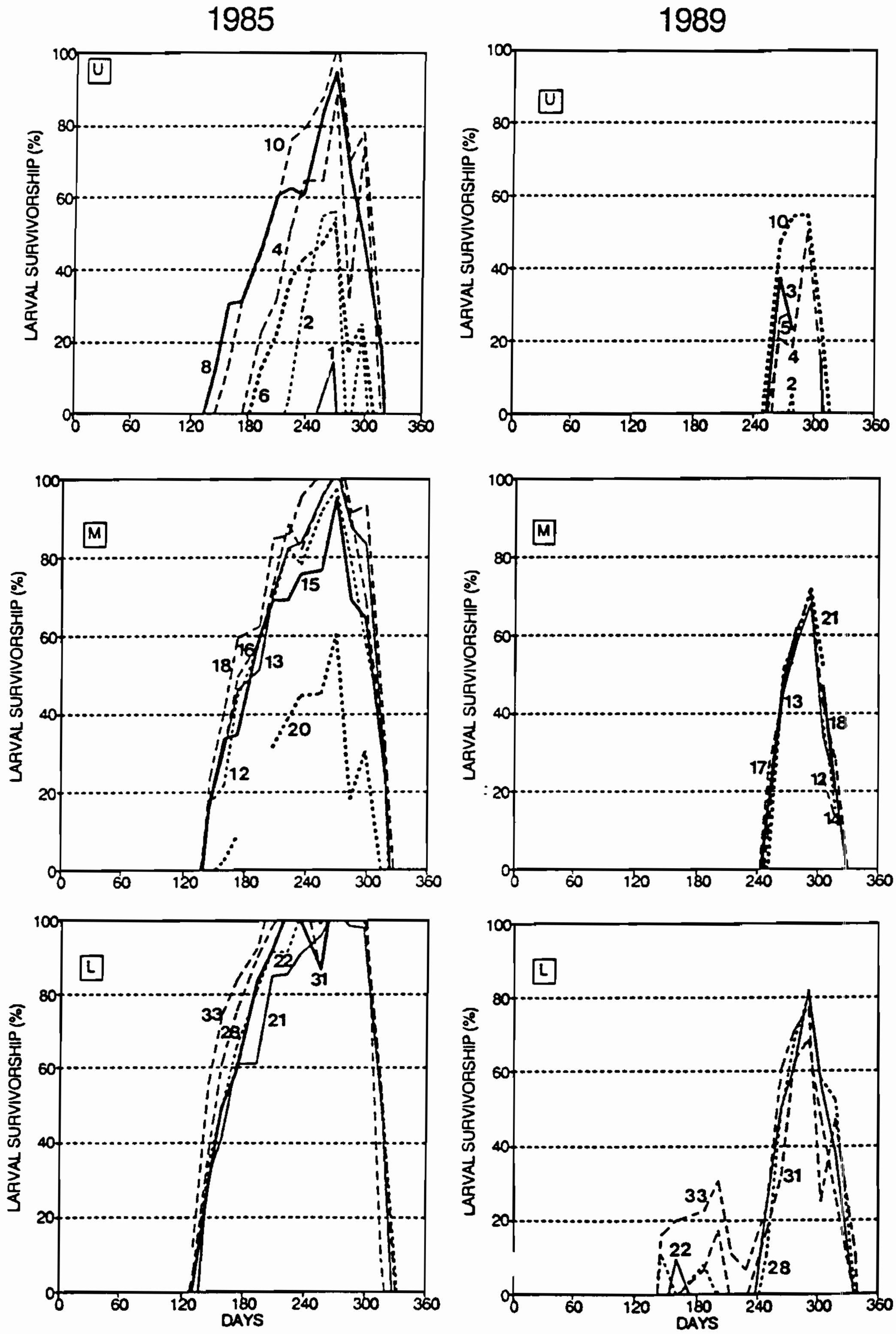

Figure 7. Estimated larval survivorship for Upper, Mid- and Lower Bay stations in 1985 and 1989. Computations based upon EPA data, Chesapeake bay Program (for station N°, see figure 5).

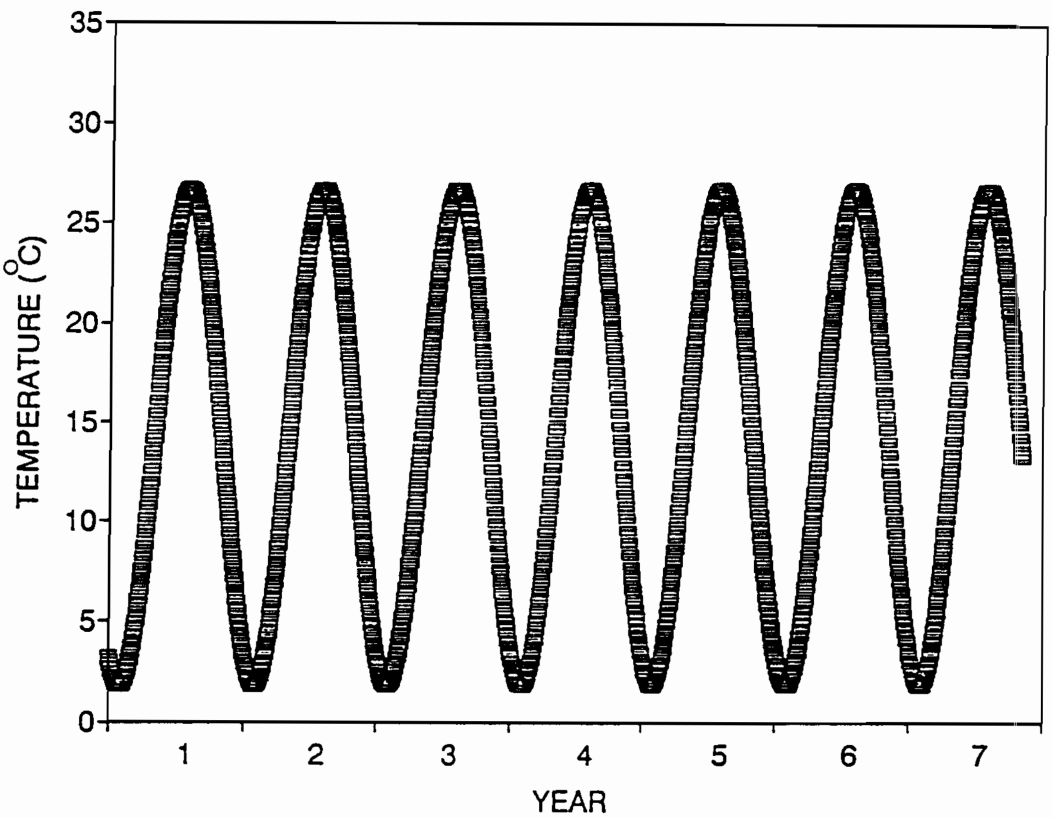

Figure 8. Yearly temperature simulation based on the regression model using the EPA 1984-1990 data.

Location	Spat Range (number)		Location	Spat Range (number)	
	1985	1989		1985	1989
Upper Bay East	0-6	0-4	Fishing Bay	0-186	0-22
Chester River	2-42	0	Nanticoke River	0-216	0-20
Kent Shore	0-76	0-12	Holland Straits	14-528	6-14
South River	0-104	0	Kedge Straits	42-946	18-22
Wye River	6-80	0-30	Lower Bay East	86	32
Miles River	0-30	0-68	Wicomico River	16-38	0-6
Eastern Bay	20-554	0-12	Tangier Sound	0-866	2-136
Talbot Shore	36-96	0-22	Manokin River	16-518	10-72
Choptank River	4-868	0-4	Pocomocke Sound	24-448	0-82
Tred Avon	152-724	0-4	Lower Patuxent	54-56	0-6
Broad Creek	116-4270	0-94	Wicomico	0-12	0-8
Harris Creek	84-1120	0-6	St Georges Creek	14-54	2-8
Little Choptank	38-5358	0-2	St Marys River	20-272	0-32
Honga River	24-652	2-44	Smith Creek	212	2-4
Hooper Straits	92	8-28	Lower Potomac	184	0-28

Table 2. Range of spat counts reported by the MDNR during the 1985 and 1989 fall surveys.

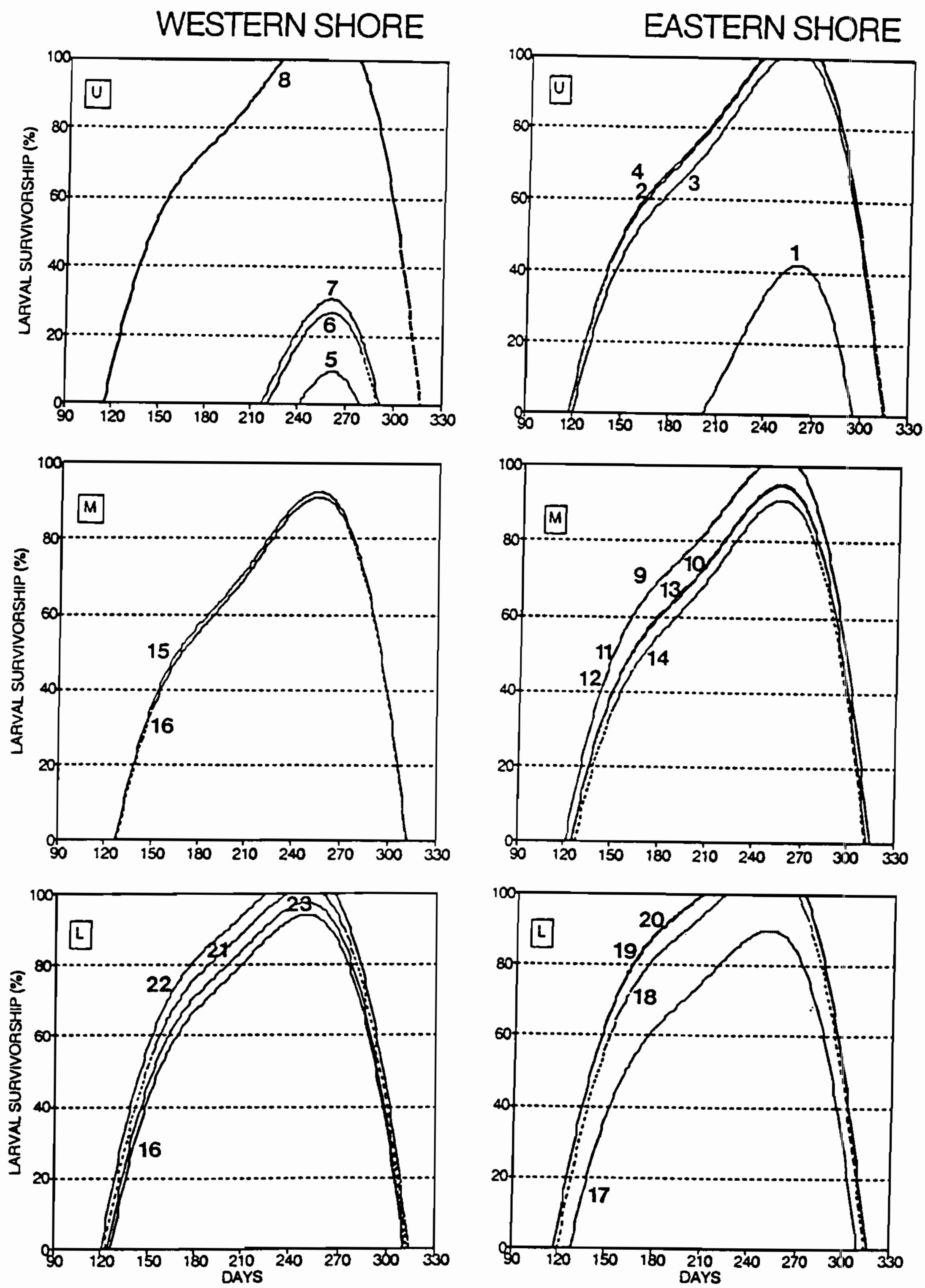

Figure 9. Computed larval survivorship trends (%) in Upper, Mid- and Lower Bay oyster bars (for station N°, see figure 6).

Model	Upper Bay	Middle Bay	Lower Bay	Lower Tributaries	Entire Bay
R^2	.64327	.64002	.55753	.68125	.64920
n	8,775	11,853	8,566	7,054	36,248
Depth	.56444	.29040	.24699	NA	.28291
Latitude	-11.04498	-3.66362	-3.75243	-17.55915	-4.86291
Dlongitude	NA	NA	-2.48042	-.92687	-1.54336
Days	-.00276	NA	NA	.007211	NA
De*Lo	NA	NA	NA	NA	NA
La*Lo	NA	-.17642	NA	NA	NA
Detr	4.02134	NA	NA	NA	NA
Lotr	NA	-36.00600	-10.66990	-26.02528	-13.40169
Dat1	-1.52346	-1.04898	-1.11795	-.83975	-1.154078
Dat2	1.48209	1.30348	.85064	.75632	1.16093
Constant	436.23316	153.78287	157.58367	686.30504	199.83933

Table 3. Results of salinity regression models for Upper, Mid- and Lower Bay. Dlongitude of P represents the longitude of P minus the longitude of the referenced station calculated by using a polynomial regression. De*Lo and La*Lo are interactive terms. Detr = cos (depth $\times \pi/36$), where depth $\leq$ 36m. Dat1 = sin (days $\times \pi/183$), 1 cycle a year. Dat2 = sin (days $\times \pi/122$), 1.5 cycle a year.

latitude in the Lower Bay region. Eventually a similar pattern to those of Mid-Bay locations is observed. Mid-Bay locations rarely reached the 100% of larval survivorship and maxima are reached later in the season than at southern locations. Descending phase is similar on both Lower and Mid-Bay regions with a sharp decline in September. In Upper-Bay, Eastern locations are more favorable than Western areas. Larval survivorship on oyster bars located north from the Chesapeake Bay Bridge is particularly low with a 45% maximum. These areas are unlikely self-sustainable in spat recruitment and probably rely on episodic transport of older larvae from southern areas. Moreover, these results are consistent with the aforementioned 1985-1989 results.

CONCLUSION

This approach permits to estimate and describe the average spatio-temporal pattern of potential larval survivorship of *C. virginica* in the Maryland portion of the Chesapeake Bay. Moreover, similar approach might be used for assessing the associated risk to exotic species introduction such as *Crassostrea gigas* (Thunberg, 1793) and *Dreissena polymorpha* (Pallas, 1754).

These results might be affected by larval transport, particularly from older larval stage, and likely by broodstock size. The mechanisms of dispersal and recruitment of estuarine larvae are still unclear (for review, see Epifanio, 1988; Boicourt, 1988). Local phenomenon of larval retention are generally observed and have been explained by "passive" transport induced by physical factors, by an "active" process involving larval swimming, or a combination of both. In all cases these phenomenon tend to limit the larval distribution. Since our estimates are consistent with field observations and historical data (MDNR, 1985), we can assume that our approach is not drastically affected by larval transport. This might be explained by larval survivorship calculations which are based on the early stage of life (i.e., 48 hours). In fact, the calculations assess the potential efficacy of local broodstock as well as management options to sustain oyster population. With respect to local and currently unknown broodstock, a comprehensive sampling strategy for oyster stock assessment has been developed by Rothschild *et al.* (1991) and Chai (1992). Field implementation would provide significant information on the current status of the oyster population per region and would allow (1) weighing potential larval survivorship estimates, and (2) indexing the LP bar attractiveness measures.

The large yearly variability observed between the 1985 and 1989 seasons demonstrate that an optimum management would consider the salinity threshold on a monthly basis in Upper and Mid-Bay regions before any site selection and timing decision for shell deployment. However, the 1989 salinity record low level and quick decline in Lower Bay would not have been predicted by the salinity model; therefore impeding decision-making to postpone shell deployment. Salinity level and consequently spat recruitment, are directly related to the monthly streamflow into the Chesapeake Bay. By way of example, the highest spat recruitment observed for the last 25 years is linked to a record low mean streamflow in June 1991 (Figure 10). Modeling streamflow into Chesapeake Bay would allow salinity prediction so as to determine site and timing for shell planting.

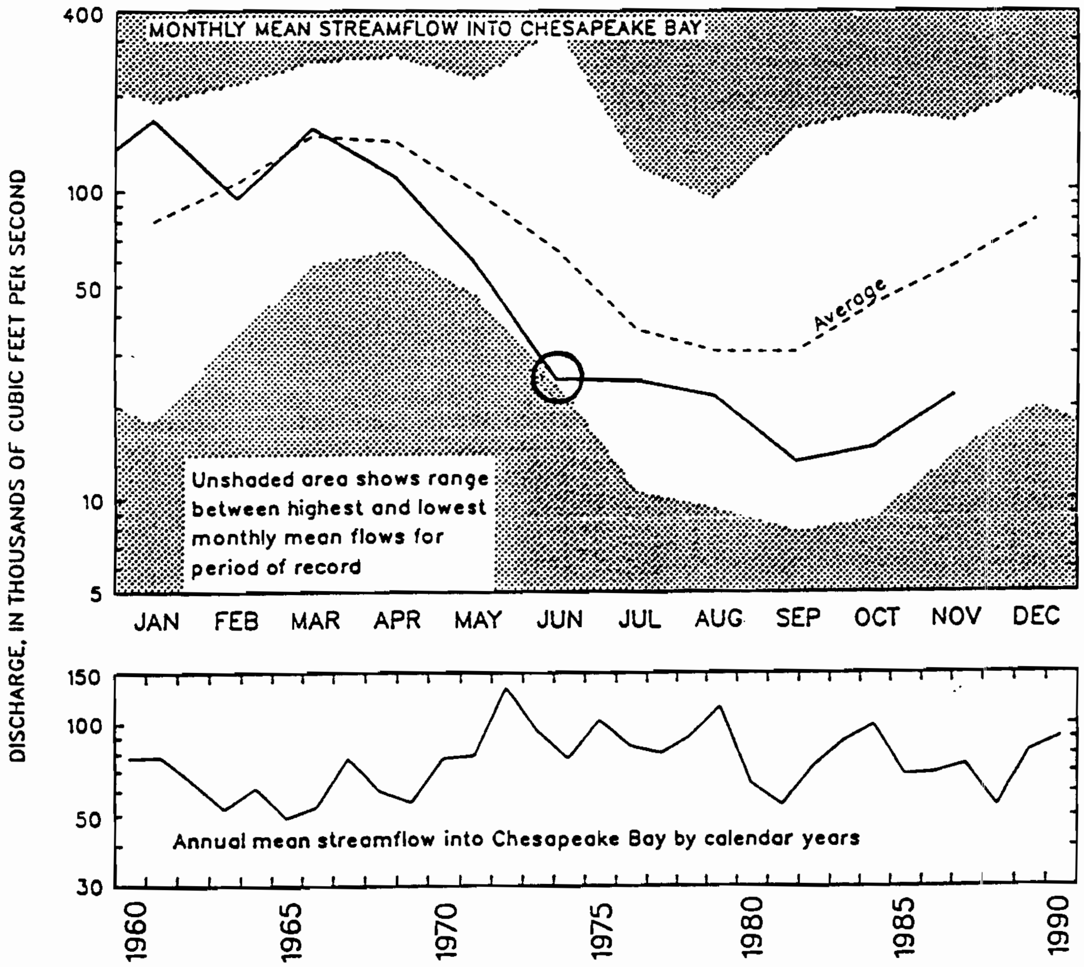

Figure 10. Monthly mean streamflow into Chesapeake Bay in 1991 (US Geological survey, 1992).

Our modeling results do not provide information for optimum-timing for shell planting since no assumption is made concerning spawning events. Kennedy and Krantz (1982) and Kennedy (1986) reported large variability over time and space of spawning patterns as well as peak settlement periods. However, based on our results the spat recruitment would be maximized if spawning occurs in August. This support the need for monitoring spawning and larval development on a yearly basis (Kennedy, 1980). Therefore, a sampling strategy aiming to determine the larval presence/absence and broodstock assessment in targeted strata, combined to the streamflow modeling approach, would be predictive and is likely to largely improve the optimal-timing for oyster shell deployment.

Our results support the current MDNR site selection for the shell repletion program, mostly located on the Eastern shore of the Lower Bay (e.g., Kedge Straits). However, seed transplanting operations from southern to northern locations aiming to limit the disease impacts limit the reproductive efficacy of seed oysters and also decrease the broodstock in Lower Bay. Broodstock has been likely affected since this management has been operating for decades. Therefore, since the shell repletion program is critical to sustain the fishery, an urgent need for additional management is required in the lower portion of the Maryland Chesapeake Bay to compensate for the negative effect of seed moving. Such management might involve broodstock sanctuaries and reef rehabilitation, considering diseases occurrence. The later issue is critical and should prompt managers to also consider flexible management based on results from epidemiologic monitoring.

Broodstock sanctuaries have been established by the MDNR since 1986. However, there are of limited extent and located in Chester River, Upper Bay, Eastern Bay, Mid-Bay, Tred Avon River, and Lower Bay. Locations in Chester River and Upper Bay appear to be of limited efficacy. More recently in 1991, a reef habitat restoration program has been launched by the MDNR. The project is designed to rely on the natural reproduction of oysters for the benthic community development. Four sites were selected using a process of exclusion mapping. This process considers as equal the spat recruitment probability throughout the Maryland portion of Chesapeake Bay. The selection resulted in two stations located north of the Chesapeake Bay Bridge, at the mouth of the Patapsco River and North Kent shore, where spat recruitment is unlikely to occur on a regular basis. In contrast, only one site is located in the Lower Bay in Potomac River. Therefore, site selection based on potential larval survivorship is likely to improve the overall efficacy of the reef rehabilitation program.

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