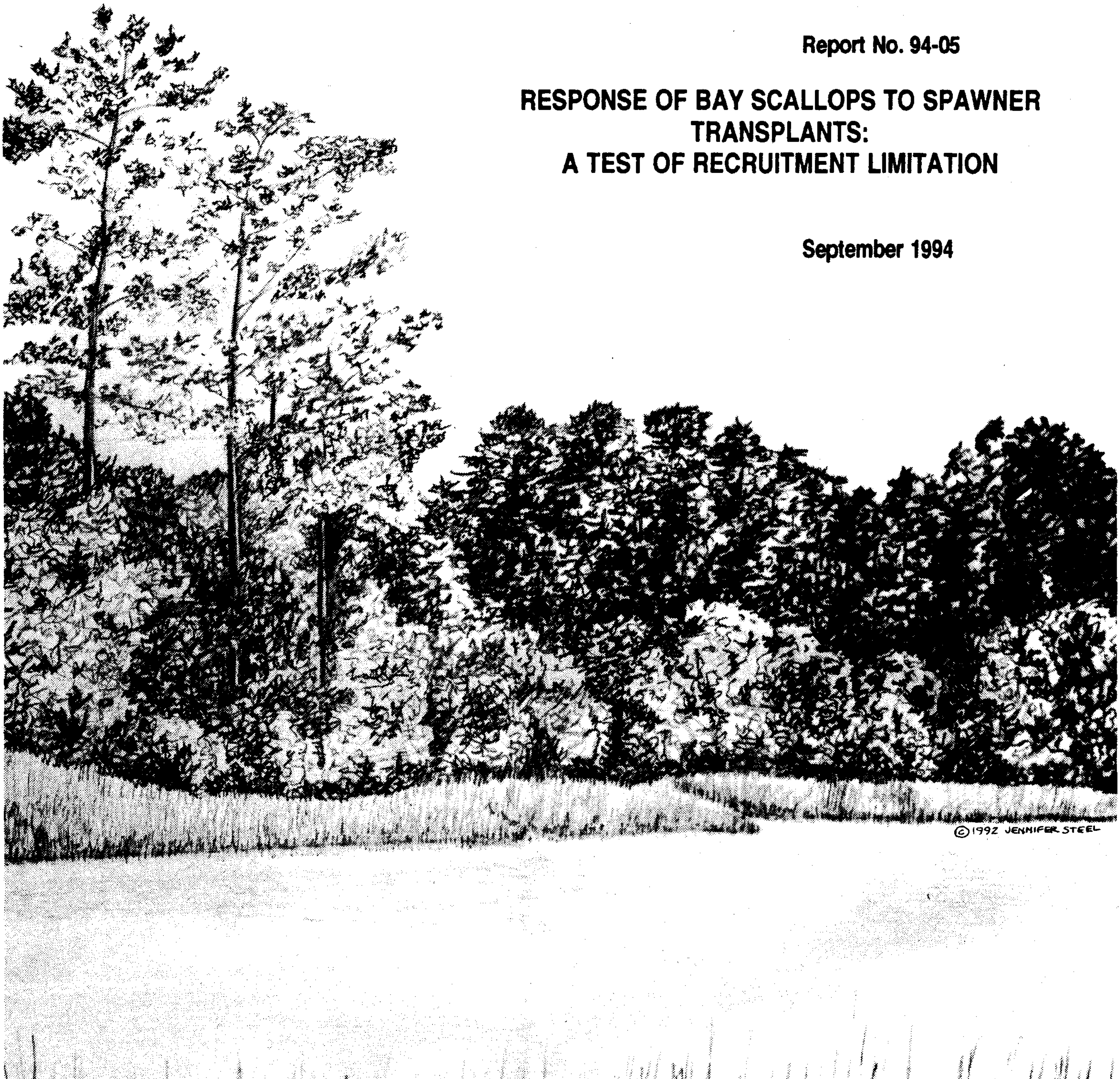
Report No. 94-05

RESPONSE OF BAY SCALLOPS TO SPAWNER TRANSPLANTS: A TEST OF RECRUITMENT LIMITATION

September 1994



ALBEMARLE-PAMLICO ESTUARINE STUDY

NC Department of
Environment, Health,
and Natural Resources

Environmental
Protection Agency
National Estuary Program

ALBEMARLE/PAMLICO ESTUARINE STUDY (APES) REPORT NO. 94-05

RESPONSE OF BAY SCALLOPS TO SPAWNER TRANSPLANTS: A TEST OF RECRUITMENT LIMITATION

Charles H. Peterson, Henry C. Summerson, Richard A. Luettich, Jr.

University of North Carolina at Chapel Hill, Institute of Marine Sciences, Morehead City, North Carolina 28557, USA

Correspondence: CH Peterson
Tel - 919-726-6841
FAX - 919-726-2426

ABSTRACT: Adult bay scallops were transplanted prior to spawning in summers of 1992 (135,000) and 1993 (100,000) from a donor site in Back Sound where scallops were abundant to receiver sites in western Bogue Sound, an estuarine water basin where scallops had not initiated recovery since their virtual elimination by a red tide outbreak in 1987-88. These transplants were intended as a test of the hypothesis that bay scallop populations are recruitment-limited on a basin scale within sounds, consistent with the limited physical transport of their short-lived pelagic larvae. This intervention also represents an empirical test of a process-based restoration option (spawner transplantation) with broad significance to managers of shellfisheries resources. Initial tests of alternative methods for transporting adult scallops during summer heat revealed that transport out of seawater but under moist conditions inside insulated coolers induced only 1.5 % mortality, independent of holding time ranging from 1.75 to 4 hr. In contrast, scallops maintained for 6 hr in flow-through seawater tanks exhibited between 10 and 50 % mortality, with losses increasing with decreasing flow rates and oxygen concentrations. Although fewer than 2.5 % of available adult bay scallops were removed from the donor site of Oscar Shoal, the numbers of remaining adult scallops fell to near zero by early December each year. In contrast, mortality and emigration were both negligible from August to December for scallops at each of the 4 receiver sites in western Bogue Sound. Consequently, transplantation had the effect of protecting those adult scallops from high autumn rates of natural mortality at Oscar Shoal and allowing them to survive until winter, when the fishing season begins. On average, recruitment of scallops at two study sites in western Bogue Sound following the transplants in 1992 and 1993 was 654 % greater than in 1988 and 1989 when no transplantation had occurred. At two control sites in Back and Core Sounds, the average increase in recruitment was only 54 % from 1988 and 1989 to 1992 and 1993. This temporal increase in recruitment of bay scallops to natural seagrass beds was significantly larger in western Bogue Sound than in the control sounds, demonstrating a positive effect of the transplant on bay scallop restoration. Larval settlement onto spat collectors at three of those same study sites did not correlate well with the recruitment data and failed to reveal enhancement in western Bogue Sound following the transplants. Thus, our data cannot confirm that the transplant succeeded through the mechanism of enhancing larval abundances. Nevertheless, settlement of scallop spat onto settlement bags deployed along a transect in the channel revealed a pattern of decreasing settlement with distance from Bogue Inlet, consistent with the hypothesis that scallop larvae become depleted with distance from their source and thus limit population size in this system. Furthermore, larval settlement onto collector bags and recruitment to natural seagrass beds was negligible during both years at a site in central Bogue Sound. Physical current-meter data on water transport show that this site lies outside the influence of tidal forcing from Bogue Inlet and thus is disconnected hydrographically from the source of competent larvae near Bogue Inlet in western Bogue Sound. Thus, transplant of pre-spawning

adult bay scallops proved to be a successful restoration action in this system, probably because it enhanced otherwise limited abundances of larvae, although spat collector results do not unequivocally support the inference that larval enhancement was the mechanism by which increased recruitment was achieved.

INTRODUCTION

The emerging field of restoration ecology places great demands on the basic science of ecology, demands that often quickly expose the limits of our ecological understanding. Restoration ecology requires sufficient knowledge of the processes that organize communities and limit population sizes to generate reliable predictions of the consequences of potential interventions proposed as restoration alternatives (e.g., Jordan et al. 1990). Because of the extent of our present ignorance about population and community controls in nature, a legitimate concern is commonly expressed that restoration actions may do more harm than good in degraded ecosystems and that allowing natural recovery to take place represents the wisest policy. Unfortunately, this attitude of caution and distrust fails to exploit the wisdom that has been gained from fundamental advances in basic ecology.

We propose one resolution of this dilemma over whether to conduct no active restoration and thereby avoid further unexpected ecological damage or to try to apply what is known about ecology and intervene in the natural system to promote recovery. We suggest that basic ecology can be properly used to generate restoration options in the form of testable hypotheses about the consequences of potential restoration interventions and that the methodologies of basic ecology can then be further employed to develop tests of those hypotheses. Such an approach of feasibility testing represents a melding of basic and applied ecology in that the scientific activity is motivated by societal interest in some ecological goods or services, which then stimulates the development and testing of hypotheses that not only address the practical restoration issue but also advance basic ecological understanding. Such an approach is the basis of adaptive management (Walters 1986).

We previously used arguments developed from "supply-side" ecology (Underwood and Fairweather 1989) and the theory of recruitment limitation (Gaines and Roughgarden 1985) in population ecology to propose an explanation for the failure of the bay scallop in North Carolina to recover from the toxic effects on its population caused by the red tide outbreak of 1987-88 (Peterson and Summerson 1992). This outbreak of Ptychodiscus brevis from October 1987 through February 1988 was not uniformly distributed among the scallop grounds of North Carolina (Tester et al. 1991). Instead, the Ptychodiscus bloom was most intense and most prolonged in Bogue Sound and Back Sound, much less pervasive in Core Sound, and essentially absent from Pamlico Sound (Fig. 1). The resulting pattern of adult mortality and immediate recruitment failure of bay scallops matched this geographic pattern of red tide intensity (Summerson and Peterson 1990). From 1987 until 1991, bay scallop abundance in western Bogue Sound remained grossly depressed without signs of even the initiation of recovery, despite persistence of normal populations in Pamlico and Core Sounds and recovery in Back Sound. Peterson and Summerson (1992) suggested that this basin-scale coherence of population dynamics of bay scallops might best be explained by assuming that bay scallop abundances are limited by recruitment and that the bay scallop population in hydrologically isolated western Bogue Sound was slow to recover from the effects of the red tide because the effective spawning stock for that basin was too depleted to provide an adequate supply of larvae for population recovery. This explanation is based upon the growing scientific understanding of the importance and role of recruitment limitation among marine animals (e.g., Underwood and Denley 1984, Gaines and Roughgarden 1985, Butman 1987, Eckman 1987, Doherty and Williams 1988, Sammarco and Andrews 1989, Doherty and Fowler 1994).

Here we provide results of one test of the hypothesis that recruitment limitation exists on a basin scale for bay scallop populations within estuarine water basins and is a substantial cause of the multi-year failure of bay scallops to recover in western Bogue Sound from damages inflicted by the 1987-88 red tide outbreak. We describe how bay scallop recruitment changed after transplanting adult scallops into western Bogue Sound prior to spawning in each of two successive summers. As a control for natural temporal variation in recruitment of bay scallops, we also made and present the same sets of observations at control sites in Core and Back Sounds where no adult transplants took place. Results of this experiment represent simultaneously a test of the fundamental ecological question of whether recruitment limits abundance of bay scallops in this system and also a test of feasibility of a restoration intervention designed to promote recovery of an important fishery resource previously damaged by a natural disaster.

METHODS

Testing alternative transplantation techniques. To minimize or avoid mortality of adult bay scallops (<u>Argopecten irradians concentricus</u> Say) during transplantation among sounds, we first tested how scallops survived each of several conceivable alternative transplant methods. Bay scallops are relatively sensitive to dying from environmental stresses, such as high turbidity (Duggan 1973), salinity reduction (Mercaldo and Rhodes 1982, Tettelbach et al. 1985), and temperature extremes (Belding 1910, Gutsell 1930), so we were concerned with developing a transplant process that would avoid mortality induced by exposure to the typically warm air temperatures of summer in North Carolina.

We measured the mortality rates of adult bay scallops collected from Oscar Shoal in Back Sound (see Irlandi 1994: Fig. 1) and held under 5 different sets of environmental conditions for a period of 6 h, the approximate maximal length of time needed to complete transfer from Back Sound to western Bogue Sound. Scallops were collected by hand from Oscar Shoal, transported for 1 h by boat in plastic coolers, and then held either: (1) out of water under refrigeration at 10 ^{0} C; (2) in mesh bags used as controls suspended in the waters of the estuary from the dock on which flow treatments were also established; (3) in a flow-through seawater system with flow rate of 0.267 l sec^{-1} sufficient to retain ambient O_2 concentrations; (4) in the same flow-through seawater system but with flows reduced to 0.028 l sec^{-1} so that O_2 concentrations were allowed to fall by 50 percent; or (5) in the same flow-through seawater system with a flow (0.067 l sec^{-1}) and O_2 concentration intermediate between the fast- and slow-flow conditions. These alternative methods mimic the conditions that bay scallops would experience under transport in refrigerated trucks (#1) or in transport on a barge or boat with a flow-through seawater system, where water was pumped at various alternative rates (#3-5).

Varying flow treatments were achieved by using a battery-run bilge pump to pump seawater from beneath a dock on Bogue Sound via hoses with a series of T-connectors and valves to control flow rates. Ends of the hoses fed three 5-gallon plastic buckets, each of which held 300 adult-sized bay scallops. Flow entered at the bottom of each bucket and overflow left over the top edge. Two separate runs of this test were conducted, on 12 and 13 July 1992, providing replication for analysis. Flow rate, water temperature, and O_2 concentration were measured at hourly intervals during the course of the second run for all treatments in seawater. Scallops were shaded from direct exposure to sunlight in all 5 treatments. All treatments were tested simultaneously employing 300 replicate scallops in each treatment. At the termination of both runs of this experiment, 10 individual scallops from each treatment were opened and their gonads examined for evidence of induction of spawning. Fewer than 20 percent of scallops had advanced beyond the slightly ripe stage at this time and none showed signs of having spawned, implying that our transplant procedures did not induce spawning.

An additional test was conducted to evaluate the mortality rate for adult bay scallops kept out of water and transported inside insulated plastic coolers. Scallops were collected on July 16, 1992 from Oscar Shoal in Back Sound for this experiment: 120 scallops were placed into each of 8 coolers, representing 2 replicates for each of 4 holding time treatments (1.75, 2.5, 3.25, and 4 hr). Scallops inside the coolers were kept moist by use of wetted cloths and cool by inclusion of a frozen "blue ice" container in each cooler. Care was taken that no scallop lay in contact with the ice. Two control groups of 120 scallops each were placed inside plastic mesh enclosures and retained on the seafloor at a shallow subtidal location at Oscar Shoal. The scallops in the cooler treatments were all transported by boat to a location in Bogue Sound to simulate the transport itself. After the assigned holding times had elapsed, scallops in each cooler were transferred to separate plastic mesh enclosures (one for each cooler) identical to the one used to hold control scallops. Mortality of the scallops was assessed by examining the condition of each scallop in every mesh enclosure after 1 and 2 days had passed. A hand-held thermometer was used to measure the air temperature inside the coolers upon their reopening and in the ambient seawater at those same times. On the second day after transport upon termination of this experiment, 8 replicate scallops from each replicate of each treatment were opened and examined for evidence of spawning. None showed visible signs of induced spawning.

Fates of adult scallops at donor and receiver sites. Transplants of adult bay scallops from a single donor site at Oscar Shoal in Back Sound into sites in western Bogue Sound were conducted in mid summer during both 1992 and 1993. In each year, the scallops were moved on 2 occasions, about half in late July (26-30) and the rest in mid August (10-13). The total number of bay scallops moved was 135,000 in 1992 and 100,000 in 1993. The transplantation method chosen on the basis of results of testing among the 5 alternatives was to place the scallops moist but out of water inside insulated coolers for the 2-4 h move in a motorboat from the estuarine seafloor at Oscar Shoal to the receiver sites. In 1992, 3 receiver sites (Guthrie Point, Goose Creek, and Saunders Creek) were located in seagrass beds in a transect along the north side of the Intracoastal Waterway, spaced at about 1.5 km intervals, while the fourth site (Emerald Isle) was located in an embayment near Bogue Banks where the highest concentration of bay scallops traditionally had occurred (Fig. 1). In 1993, all 4 receiver sites (Emerald Isle, Piney Island, Wood Island, Bean Island) were located on the south side of Bogue Sound in that same embayment between the dredge spoil islands along the Intracoastal Waterway and the Bogue Banks shore (Fig. 1). Each receiver site contained an extensive seagrass meadow within which rectangular plots of 1,200 m^2 were marked off with metal stakes to denote the specific transplant location.

In both 1992 and 1993, sampling was conducted within several seagrass beds in western Bogue Sound in early June to estimate the densities of adult bay scallops in the relevant seagrass habitat within this estuarine basin prior to transplantation. Sampling was carried out by counting the numbers of adult bay scallops inside 5-7 haphazardly placed replicate 2-m^2 quadrats at sites distributed from Dog Island to the Emerald Isle bridge (Fig. 1). In 1992, the average density of bay scallops at each of 15 seagrass beds ranged from 0 to 1.8 m^{-2}, with a mean of 0.7. In 1993, the average density of bay scallops at each of 24 seagrass beds ranged from 0 to 3.9 m^{-2}, with a mean of 0.9.

Sampling was conducted at the donor site and each receiver site to assess population changes of adult scallops. In 1992, the donor site of Oscar Shoal in Back Sound was sampled in June before conducting the transplant by counting scallops at low tide inside 2-m^2 quadrats and again in early December by suction dredge sampling from 0.5-m^2 cylinders haphazardly located within the entire seagrass bed (methods described in detail by Peterson et al. 1989). In 1993, these same samplings were conducted as well as an additional sampling using the 2-m^2 quadrats in mid August shortly after removing scallops for the transplants. At each receivor site scallops were placed within the perimeter of the rectangular 1,200 m^2 area of seagrass (mostly _Halodule wrightii_ with some _Zostera marina_) measuring about 30 m x 40 m (except at Emerald Isle, where the shape of the seagrass bed required use of a 20 m x 60 m plot). At each receiver area, sufficient numbers of transplanted adult bay scallops were added to bring the densities after transplantation to a level of approximately 15 m^{-2}. Mortality of the scallops resulting from the stress of handling during transport was estimated by placing a subset of 300 scallops inside plastic mesh holding trays at every receiver site (2 per site in 1992 and 1 in 1993) and assessing their survivorship for 48 hr after transplantation.

In 1992 intensive sampling of bay scallops in and around the immediate transplant area was conducted to assess the fate of the scallops. Sampling was conducted in early July 2 weeks before and on 7 occasions after transplanting began, ending in early December. Sampling was achieved by counting the numbers of adult bay scallops inside 2-m^2 quadrats haphazardly positioned at low tide inside the transplant perimeter. Additional sampling by the same method was also conducted on those same sampling dates in a perimeter strip of the seagrass bed of equal area that surrounded the transplant site on all sides. This supplemental sampling was intended to test for evidence of any emigration of the scallops, so as to permit mortality to be distinguished from emigration if numbers within the transplant site were observed to decline.

Effectiveness of the spawner transplants. To assess whether the transplants of pre-spawning adult bay scallops made any contribution to the restoration of succeeding generations of the bay scallop population in western Bogue Sound, we conducted two types of sampling. First, we fabricated and deployed scallop spat collector bags identical to those that we had used previously to provide a quantified index of bay scallop settlement intensity (Ambrose et al. 1992, Peterson and Summerson 1992). These spat collectors consisted of an "onion bag" of 5-mm mesh containing a 0.23-m^2 piece of 4-mm black polyethylene mesh, which was attached by rope to a cement anchor. Each bag was held vertical in the water column by enclosed floats that maintained it at an elevation of 0.5 m above the bottom. Twenty replicate spat collector bags were deployed at 1 location in western Bogue Sound (Emerald Isle) and 1 location in both Core Sound (Yellow Shoal) and Back Sound (Banks Bay) (see Fig. 1). This design represents 1 treatment site in western Bogue Sound, where impact of the transplants may be evidenced, and 2 control sites in Core and Back Sounds, where no transplant took place.

Deployment of the spat collectors occurred in the first week of September (3-8) with retrieval in the last week of October

(28,29) each year. This timing matches identically the timing of deployment of identically constructed spat collectors in 1988 and 1989 at those same 3 sites. At retrieval, all bags were marked to indicate source location and moved to a protected location in eastern Bogue Sound where no further scallop settlement occurred. Over the succeeding 2 months, all bay scallops that had settled in the bags were counted, with bags drawn equally from each location on every counting day. This design therefore precisely replicates the design used in both 1988 and 1989, which represent 2 years following the red tide damage to the bay scallop population but lacking any transplant efforts. Consequently, our test of the impact of the adult transplants on the index of scallop settlement represents a comparison of 2 replicate years before transplants and 2 replicate years after transplants at 1 transplant site in western Bogue Sound and 2 replicate control sites in other sounds. This design permits any effect of the transplant to be identified, unconfounded by natural temporal variability.

Our second means of assessing the effectiveness of the transplant of pre-spawning adult bay scallops was to evaluate the abundance of newly recruited bay scallops in natural seagrass beds in both western Bogue Sound and in control sites in the two other sounds. Sampling of abundance of that year's recruits was achieved by suction dredging 40 replicate 0.5-m^2 plots at each of the same 5 study sites where spat collectors were also deployed. This sampling was done in the last week of November and the first week of December in 1992 and 1993, thereby repeating precisely the methodology and timing of sampling at these same 5 sites in 1988 and 1989 (although 60 replicate samples were taken at each site in those years). At this time of year, the 0-year-class recruits and adult scallops are readily separated by size (Peterson et al. 1989, Peterson and Summerson 1992), so analyses can be conducted separately on new recruits and the previous year-class adults. This design thereby permits the assessment of the effectiveness of the transplants on bay scallop recruitment to natural seagrass beds, analogous in design to the test conducted on spat settlement. The design for this assessment of recruitment differed from the design of the settlement bag experiment by including 2 replicate treatment sites in western Bogue Sound (Emerald Isle and Salter Path) along with the same 2 replicate control sites in other sounds (Yellow Shoal and Banks Bay). Comparisons of temporal change in abundance of scallop recruits between the transplant sites in western Bogue Sound and control sites in Core and Back Sounds allows separation of natural temporal variation from true effects of the transplants. In addition, we also sampled a site in central Bogue Sound (Dog Island), which is not a location where traditionally high abundances of bay scallops have occurred. This site was chosen simply to provide an indication of the degree to which the limited spatial scale of larval transport isolates the bay scallop population in western Bogue Sound from other populations to the east in Back and Core Sounds.

Physical transport of scallop larvae In addition to these means of evaluating the impacts of the adult transplants, in 1992 we also deployed and sampled bay scallops that settled on spat collector bags and sampled recruits in natural seagrass beds at 9 sites along a transect in the Intracoastal Waterway that spanned our transplant sites, ranging from behind Bogue Inlet to just east of our most easterly transplant site (Fig. 1). Three of the sites for spat collector deployment were the actual receiver sites where transplants were located in 1992 (M#40A at Guthrie Point, M#36 at Goose Creek, and M#31 at Saunders Creek). This contrast was designed to provide a better understanding of the physical transport and source of bay scallop larvae in western Bogue Sound. Twenty replicate spat collectors of the identical construction described above were deployed in September and recovered in October at each site on the same dates as the spat collectors used to evaluate the effectiveness of the transplants. Sampling procedures were also identical. Suction dredging to sample scallops recruited to the natural seagrass beds was done in December on the same dates and using the same methodologies as in the sampling of recruits for evaluation of the results of the transplants. This effort provided information on how bay scallop settlement and recruitment varied as a function of distance from the ocean inlet in the region where transplants were conducted.

In 1993, 20 replicate spat collector bags were deployed at each 4 additional sites within western Bogue Sound to assess potential spatial patterns in larval settlement in that year. These additional deployments spanned almost the full range of 1992 deployments along the Intracoastal Waterway channel, by locating one set at Marker #42 and another at Marker #28 (Fig. 1). On the southern side of western Bogue Sound deployment locations ranged from a site at the Emerald Isle bridge to a site at Long Island to the east (Fig. 1). When combined with the traditional deployment site of Emerald Isle, this site selection represented a suite of 5 sites scattered across western Bogue Sound. No dredge sampling of natural recruitment into seagrass beds at these 4 supplemental sites was conducted in 1993. Deployment and recovery of these supplemental spat collectors occurred on the same days in 1993 as at the other spat collector sites in that year.

To provide a better physical context in which to understand the transport of scallop larvae, physical oceanographic sampling was conducted along the Intracoastal Waterway in autumn 1992. During the period of deployment of the spat collectors and while bay scallop larvae were presumably developing in the water column, we measured vertical profiles of current velocity, water temperature, and salinity at 3 locations along the transect of spat deployment locations (Fig. 1). At each location, profiles were collected using an Inter-ocean S4 electromagnetic current meter that was raised and lowered over the side of a moored boat. Measurements were averaged for 1-2 min at 8-10 depth levels (depending upon depth) at 0.5 m increments through the water column. A profile was initiated every 30 min for a complete semi-diurnal tidal cycle at each sampling location. Full moon occurred on 11 October, and sampling was conducted on 12 (Marker

#28), 13 (Marker #36), and 14 (Marker #42) October. In addition, water level, temperature, and salinity data were collected continuously from 8 September to 4 November 1992 at the Goose Creek transplant receiver site.

RESULTS

Testing alternative transplantation techniques

Our manipulation of flow rates through the holding tanks fed by seawater taken directly from Bogue Sound was effective in altering the dissolved oxygen content of the water in the tanks (Fig. 2). The high-flow treatment successfully retained oxygen concentrations at levels of 7-7.5 ppm, essentially identical to those observed simultaneously in the sound over the 6-hr experiment. Oxygen concentrations in the low-flow treatment quickly reached and remained at about 4 ppm for the duration of the experiment, whereas the intermediate-flow treatment exhibited oxygen concentrations of 5.5-6.5 ppm (Fig. 2). Water temperature in the sound and in the tanks remained at about 31.8^{0} C during the experiment, while the air temperature varied from about 30 to 32^{0} (Fig. 2).

Mortality rates of the adult bay scallops after 6 hr varied significantly with holding conditions (ANOVA $p = 0.01$). This test was conducted on the 4th root of the number of dead scallops, a transformation that produced the smallest and statistically non-significant difference in variance among treatments by Cochran's test. Mortality rate was significantly higher by a factor of between 8 and 45 ($p < 0.05$ in Duncan's test) than the 1 percent observed in the controls held in the sound for each of the 4 treatments (Fig. 3). Mortality rate varied inversely with flow speed and therefore oxygen concentration in the 3 flow treatments, with a maximum of 46 percent in the low-flow treatment and a minimum of 9 percent in the high-flow treatment (Fig. 3). Average mortality under refrigeration at 10^{0} C was 8.5 percent. Duncan's test revealed that the difference in scallop mortality between the high- and low-flow treatments was significant ($p < 0.05$) but the medium-flow treatment could not be distinguished between either of the two extremes. Mortality in the refrigeration treatment was not significantly different from observed mortality in the low- or medium-flow treatments (Fig. 3).

In the experiment assessing the survivorship of adult bay scallops stored out of water in plastic coolers, mortality was negligible and did not vary significantly with time of storage in the experimental range of 1.75-4 hr ($p > 0.05$ in ANOVA on untransformed counts: Fig. 4). On average about 1.5 percent of the scallops died during this experiment, independent of holding time. Air temperatures within the coolers ranged from about 25-27^{0} C, while ambient water temperatures in the sound were about 31^{0} C (Fig. 4).

Fates of adult scallops at donor and receiver sites

In both 1992 and 1993, the numbers of bay scallops removed from the donor site of Oscar Shoal were set at levels such that no more than 2.5 percent of the adult scallops present would be removed. This upper limit on numbers of scallops was estimated from mapping the seagrass habitat on Oscar Shoal, calculating its area, and sampling by suction dredge from haphazardly located plots within the seagrass bed. In 1992, we estimated a total abundance of adult bay scallops over the 180,000 m^2 of this donor site of 8,973,000. In 1993, we estimated that 4,170,000 adult bay scallops were present on Oscar Shoal in June prior to initiation of our transplant. From these, we removed 135,000 (1.5 %) in 1992 and 100,000 (2.4%) in 1993. Sampling later in autumn of each year revealed that the densities of adult bay scallops declined precipitously to a density of zero by mid December each year (Fig. 5). This decline was not a consequence of our removal of scallops for transplants, as shown not only by our calculations of available adult scallops but also by resampling soon after completion of the transplants in 1993 (Fig. 5). In each year, the commercial and recreational fishing season for bay scallops had not yet opened by mid December. Natural predators such as cownose rays (Peterson et al. 1989) and herring and ring-billed gulls (Prescott 1990) are abundant and potentially significant sources of adult scallop mortality during this period.

In contrast to the virtual disappearance of those adult bay scallops left behind in the seagrass bed at Oscar Shoal, the scallops survived in 1992 at each of the 4 transplant sites in Bogue Sound without any obvious detectable mortality (Fig. 6). Density estimates produced by visual counting of adult bay scallops inside haphazardly positioned 0.5-m^2 sampling quadrats at low tide revealed an immediate increase in abundance of adult bay scallops after completion of the transplants and no subsequent decline, except possibly at Guthrie Point (Fig. 6). Our assessment of the incidence of handling mortality resulting from the transplant itself also revealed negligible mortality during transplant: 99.8 percent of the scallops transplanted into plastic mesh enclosures at each of the receiver sites were alive 2 days after completion of the transplant. In addition, sampling of the ring of seagrass around the perimeter of the transplant area demonstrated no evidence of migration of scallops even on this local scale away from the transplant site (Fig. 6), consistent with maintenance of the numbers inside the boundaries of the transplant sites. No analogous sampling of the survivorship of transplanted scallops was conducted in 1993, when the transplant sites were chosen in even lower-energy environments.

Effectiveness of the spawner transplants

Our data on settlement intensity onto spat collectors reveal a pattern of apparent increase in settlement at the 2 control sites in Back and Core Sounds from 1988 and 1989 to 1992 and 1993 (Fig. 7). The settlement results at the one site in western Bogue Sound where settlement was monitored, Emerald Isle, revealed more temporal variability in bay scallop settlement, with settlement intensity highest in 1989 (Fig. 7). A two factor ANOVA performed on 4th root transformed counts revealed significant effects of site, year, and their interaction (all at $p < 0.001$). However, a pre-planned contrast (Day and Quinn 1989) of whether the mean settlement was increased after transplants at Emerald Isle relative to the temporal change observed at the 2 control sites was non-significant.

Data on recruitment of bay scallops into natural seagrass beds were taken from 2 sites within western Bogue Sound, the same 2 control sites in Back and Core Sounds, and a site in central Bogue Sound. Recruitment into the natural seagrass beds showed a pattern of temporal increase from 1988 and 1989 to 1992 and 1993 at all sites except that in central Bogue Sound, where recruitment was consistently very low (Fig. 8). A two-factor ANOVA performed on 4th root transformed counts revealed significant (all at $p < 0.001$) effects of site, year, and their interaction in this data set, excluding the site in central Bogue Sound from analysis (Table 1). A pre-planned contrast on mean numbers of recruits revealed (using methods of Day and Quinn 1989) that the increase in density after transplants at the sites in western Bogue Sound was significantly ($p < 0.01$) greater than the temporal increase observed simultaneously at the 2 control sites that did not receive transplants. From 1988 and 1989 to 1992 and 1993, western Bogue Sound sites exhibited a 654 percent increase in bay scallop recruitment, while the sites in the control sounds showed only a 54 percent increase (Table 2).

Since the suction dredge sampling done in early December also samples adult bay scallops, it is also possible to use the results of this sampling to assess the effect of the transplants on adult scallop numbers in natural seagrass beds. For this contrast (Fig. 9), only one year (1993) represents adults that were produced after the transplants, while the other 3 years represent pre-transplant values. Again, the two-factor ANOVA performed on 4th root transformed counts revealed significant ($p < 0.001$) effects of site, year, and their interaction, excluding again the central Bogue Sound site of Dog Island (Table 3). An analogous contrast of means (by the Day and Quinn 1989 methods) revealed that the average increase in adult density from 1988, 1989, and 1992 to 1993 after transplants at the 2 western Bogue Sound sites was significantly ($p < 0.001$) greater than the average increase in adult bay scallop density at the 2 control sites in that same period. From 1988, 1989, and 1992 to 1993, western Bogue Sound sites exhibited a 125 percent increase in density of adult bay scallops, while the sites in the control sounds showed a 92 percent decrease (Table 4).

Physical transport of scallop larvae

The pattern of bay scallop settlement onto spat collectors and the pattern of recruitment of bay scallops to the natural seagrass beds at those same 9 sites along the Intracoastal Waterway transect established in 1992 were similar (Fig. 10). Both settlement and recruitment were highest at the M#42 location, the one second from the westernmost (Fig. 1). The settlement data showed higher recruitment at the 3 westernmost locations with declining intensity to the east (Fig. 10). The recruitment data differed somewhat in that recruitment at the eastern end of the transect was somewhat greater than would have been expected from the settlement pattern (Fig. 10). A Pearson product-moment correlation on these untransformed means was significant ($p < 0.05$) when performed on only the 9 sites along the transect on the Intracoastal Waterway. When repeated using also the Emerald Isle site on the southern side of western Bogue Sound, this relationship disappeared ($p > 0.20$). In 1993, when only 5 spat collector sites were used in western Bogue Sound and no sampling of recruitment into natural seagrass beds was conducted except at the traditional Emerald Isle site (Fig. 1), densities of scallop settlers was uniform ($p > 0.40$ in a one-factor ANOVA) among sites, ranging only from 9.7 at Marker #42 and 12.2 at Marker #28 to 13.3 at Long Island and 15.6 settlers per bag at the Emerald Isle bridge site.

The water level measurements made at Goose Creek (Fig. 11) show that the system is characterized by a semi-diurnal variation of approximately 30 cm due to forcing from the coastal ocean. Energy is also present at the diurnal frequency and has the effect of accentuating every second high and low associated with the semi-diurnal tide as well as creating a fortnightly variation in water level. The tidal fluctuations are superimposed upon non-tidal fluctuations in water level of as much as 30 cm (Fig. 11). The largest of these occurred from 17-26 September and suggests a net transport of shelf water into the sound.

Although vertical profile measurements were made on 3 different days, the water level record in Fig. 11 suggests that these days (12-14 October) were typical of the average conditions in the sound. Therefore, we compare the results of all 3 days directly and use them to characterize the tidal transport in the main channel of the sound, the Intracoastal Waterway. Figures 12-14 present velocity, temperature, and salinity profiles at 2 selected times (near slack high tide and near maximum ebb tide) from each station. Maximum along-channel velocities were 40-50 cm sec^{-1} at Marker #42 closest to Bogue Inlet, 20-30 cm sec^{-1} at Marker #36, and less than 10 cm sec^{-1} at Marker #28 furthest to the east. The velocities measured at Marker #28 were not much larger than the expected accuracy of our measurement instrument and methodology. No significant cross-channel velocities were detected at any site (Figs. 12-14). Temperature and salinity profiles were essentially uniform with depth at all sites throughout the tidal cycle. By integrating the along-channel velocities through half a tidal cycle at each site, it is possible to calculate the tidal excursion or maximum travel distance of a hypothetical free-drifting larva, assuming it was subjected for the full half cycle to the flows prevailing at that site. In reality, of course, transport would carry it to different sites along the channel where different velocities would prevail, but this calculation serves to translate observed velocity records into a realistic excursion scale for each site. These calculations suggest a maximum transport distance of about 5 km, 2.5 km, and 0.5 km at the 3 sites. Flux calculations made by integrating the along-channel velocity profiles across the channel cross section, assuming uniform flow across the channel and using measurements of bank-to-bank bathymetry taken separately at each station for the cross-sectional area, indicate a decrease in maximum flux along the channel from 100-150 m^3 sec^{-1} at Marker #42 to approximately 25 m^3 sec^{-1} at Marker #36 (Fig. 15). At Marker #28, the flux appears to be 180 ^{0} out of phase with the the other 2 locations. This pattern implies that the water at Marker #28 was draining at this time primarliy through Beaufort rather than Bogue Inlet.

DISCUSSION

Despite the physiological sensitivity of bay scallops (Belding 1910, Gutsell 1930, Mercaldo and Rhodes 1982, Tettelbach et al. 1985), we were able to find a means of transporting adult bay scallops during the daytime heat of summer that caused negligible mortality during travel times of up to 4 hours (Fig. 4). Given the absence of any trend of increasing mortality with longer holding time in these experiments, it is conceivable that the animals can survive much longer periods of transport. We did not seek to identify the limits to this process because the 4-hour period sufficed for our needs. In winter, when temperatures are cooler and physiological rates are reduced, scallops may be even less susceptible to stress and mortality from handling and transport. Further tests of transplant methods might include evaluating the effects of season and temperature if transplants over greater distances are contemplated. If bay scallop populations are indeed recruitment-limited within water bodies on the scale of sounds, longer-distance transplants may be a reasonable means of restoring bay scallops to localities in many areas where scallops have virtually disappeared (e.g. Tettelbach and Wenczel 1993) but where seagrass habitat seems adequate.

In the course of identifying a means of transplanting adult bay scallops in summer with acceptably low handling mortality, we collected interesting basic data on one additional type of physiological stress on bay scallops, the impact of low oxygen levels. As oxygen levels in our experiment fell below 7 ppm, bay scallop mortality rose. At around 4 ppm, mortality approached 50 percent during a period of only 6 hours (Fig. 3). Since oxygen concentration covaried with flow rate and other unmeasured variables in our experimental regime, these data do not represent a pure, unconfounded test of the effects of oxygen reduction on adult bay scallops. Nevertheless, the increases in mortality of these adult bay scallops coincides with the decline in oxygen concentration to levels that define hypoxia and are typically considered by water quality managers capable of degrading aquatic communities.

Independent of whether the spawner transplant had its intended effect of enhancing the recruitment of the subsequent generation of bay scallops, the transplant proved to be a useful means of protecting the adult scallops from mortality. The scallops left behind at the donor site at Oscar Shoal in Back Sound suffered almost complete mortality between summer and early December in both 1992 and 1993 (Fig. 5). In contrast, those adult bay scallops that were transplanted into western Bogue Sound exhibited no detectable mortality over this same period (Fig. 6). The commercial and recreational fishing season on bay scallops does not open until some time after the first week of December (Peterson 1990), so the scallops that died on Oscar Shoal made no contribution to the commercial or recreational fishery, whereas those that were transplanted into western Bogue Sound did.

We have no compelling evidence to explain the observed difference in natural mortality rates between these sites. Autumn is a period characterized by often intense predation by both cownose rays and herring and ring-billed gulls on adult bay scallops in North Carolina (Peterson et al. 1989, Prescott 1990). This predation may differ consistently among localities, in which case transfer of scallops during summer from the more intensely visited areas to the more lightly visited areas might represent a sensible management strategy. Alternatively, the fishing season on bay scallops could be opened early in just those areas where natural mortality is known to be predictably intense. However, if recruitment limitation is indeed a factor that can limit bay scallop population size, any substantial harvest in late summer before spawning was complete would need to be effectively limited to just those areas where the scallops would die anyway before spawning.

Alternatively, the transplanted scallops may have survived much better than the scallops left behind at the donor site because the predators exhibit density-dependent predation on a large spatial scale (Peterson 1990, Eggleston et al. 1992). It is possible that the effective predators on scallops prey most intensely where bay scallop densities are greatest, which happened to be Oscar Shoal in late summer and autumn of 1992 and 1993. This explanation, however, does not appear to be consistent with the high survivorship of even greater densities of bay scallops in Core Sound around Yellow Shoal in each of those two years. Nevertheless, additional information on the nature of bay scallop mortality during late summer and autumn and the predictability of the site-specific mortality patterns is needed before erecting a management plan that allows pre-spawning harvest that may endanger future production.

The impact of our transplants of adult scallops into western Bogue Sound during summers of 1992 and 1993 on the recruitment of bay scallops into seagrass habitat was clear. Recruitment into natural seagrass beds showed a dramatic 654 percent increase in western Bogue Sound from 1988-89 to 1992-93 after adult scallop transplantation, a change significantly and substantially greater that the 54 percent increase observed in the control sounds over this same time period (Table 2). This effect on recruitment was also evident when adult scallop numbers are examined: adult bay scallops in 1993, resulting from the recruitment in 1992, were enhanced in western Bogue Sound by 125 percent over levels observed in 1988, 1989, and 1992, while adult densities actually declined by 92 percent in the 2 control sites over this same time period (Table 4).

Since numbers of recruits in natural bottom habitats represents the variable of most direct relevance to the actual population in nature, it seems appropriate to conclude that recruitment was enhanced and recovery thereby promoted by the transplant of adult spawners into the depleted region of western Bogue Sound. However, our inability to demonstrate a strict correspondence between these recruitment data measured by sampling the natural seagrass habitat in December and the settlement data collected by counting recruits on artificially but identically deployed spat bags raises some concern. In our past studies of bay scallop recruitment (Ambrose et al. 1992, Peterson and Summerson 1992), settlement onto spat bags and recruitment into natural seagrass habitat at that same site were rather well correlated. Breakdown of this correlation can occur through numerous potential processes, including especially differing rates of post-settlement mortality. We offer no explanation for the breakdown of this relationship in our data; however, the test of recruitment is achieved through a more powerful design than the test of settlement with 2 not just 1 treatment sites. High temporal variability in settlement of bay scallops at the Emerald Isle site makes testing of effects of transplantation on settlement difficult. The absence of a match between settlement onto spat collector bags and recruitment into natural seagrass habitat prevents us from confirming that the enhanced scallop recruitment after transplantation of adults into Bogue Sound was a consequence of enhancement in the abundance of larval bay scallops. There is, therefore, a possibility that we achieved the right prediction about the consequences of spawner transplants for the wrong reason (Dayton 1973).

Collection of physical data along with data on settlement and recruitment of scallops along a transect in the Intracoastal Waterway provides insight into the question of whether bay scallops are indeed recruitment-limited within estuarine basins and thus whether the success of our transplants in promoting recruitment was indeed a consequence of enhancing larval abundances. The total absence of any vertical stratification in water temperature or salinity at any of the three sites at any time during the tidal cycle shows that flow in this channel can be viewed simply as one-dimensional plug flow. The water column was fully mixed at this time of year. Calculations of net water transport at each site reveal that our easternmost transplant site in 1992 lies essentially at the hydrographic center of Bogue

Sound. There was no detectable net transport of water in either direction in the along-channel axis. This observation justifies our isolation of the Dog Island site from the treatment sites in western Bogue Sound because it lies outside the region directly forced by tidal excursion from Bogue Inlet and in the region affected by Beaufort Inlet at the eastern end of Bogue Sound.

The 1992 pattern of greatest settlement of bay scallops onto spat collectors at the end of the transect closest to Bogue Inlet (Fig. 10) may imply that the bay scallop larvae come from a source at that end of the gradient, either because they develop offshore or in higher-salinity waters closest to the inlet. Alternatively, this pattern observed in 1992 may reflect the consequences of a net transport of the water mass containing the developing scallop larvae westward in Bogue Sound. Our physical data do not allow discrimination between these two alternative explanations. This spatial pattern of settlement in 1992 is consistent in either case with the hypothesis that western Bogue Sound is sufficiently isolated hydrographically from the closest bay scallop population in Back Sound on the time scales of relevance to larval duration (5-12 days: Castagna and Duggan 1971, Castagna 1975) that it is appropriate to manage the fishery by hydrographic subpopulations and not as a metapopulation. See the suggestions of Orensanz (1986) for management of another scallop population, which similarly integrate an understanding of site-specific ecology into management.

Although the limited deployment of spat collectors in western Bogue Sound in 1993 failed to reveal any trend in settlement with distance eastward, the virtual absence of recruitment of scallops to the site at Dog Island near the middle of Bogue Sound was repeated in each year. Thus, the spatial information on bay scallop recruitment in Bogue Sound on a larger scale consistent with the range of tidal excursion implies that the population is recruitment-limited as areas become hydrographically separated from concentrations of adult spawners. This spatial relationship thus is consistent with our interpretation that the spawner transplant was indeed successful in enhancing recruitment of bay scallops in both 1992 and 1993 in western Bogue Sound because of its effectiveness in enhancing larval abundance, even though the breakdown of our usual relationship between settlement data on spat collectors and recruitment data from natural seagrass beds prevented us from unequivocal establishment of the mechanism by which the transplants succeeded.

The success of this restoration of bay scallops and its low cost suggest that the technique of transplanting pre-spawning adult scallops might be applied elsewhere within the bay scallop's biogeographic range where populations of this species have disappeared. Wherever the seagrass habitat seems adequate and where historical data show abundant bay scallops, it would be appropriate for shellfisheries managers to consider application of this technique. This may require long-distance interstate transport of bay scallops, requiring transport times in excess of the 4-6 hours that we tested, so additional trials of methods to minimize mortality of this physiologically sensitive species would be required. Furthermore, we did not conduct tests of just what the most effective density should be to insure maximal fertilization of scallop eggs. As suggested by Levitan et al. (1992) for some sea urchins, achieving adult densities sufficient to produce fertilization for this external fertilizer may be the most important process that can limit successive recruitment. We simply do not know. In addition, there are unanswered questions about whether longer-distance transport would induce or inhibit natural spawning, thereby defeating their purpose. Despite the continuing uncertainties that justify further research, results of our test of the effectiveness of adult transplantation at promoting restoration of a bay scallop population are sufficiently encouraging that this technique should be attempted in other degraded ecosystems, such as perhaps Barnegat Bay and Little Egg Harbor in New Jersey, Chincoteague Bay in Virginia, and several lagoons on Florida's west coast. Detection of recruitment limitation has importance not only to basic scientists interested in how natural populations function but also to applied scientists charged with management or restoration.

Acknowledgements. We appreciate the field and laboratory assistance provided by J. Allen, T. Andacht, G. Bath, J.E. Byers, E. Conklin, C. Donahue, W. Ellington, W. Falls, A. Gallagher, G. Grissom, A.R. Hall, J.T. Ham, N. Hendricks, R. Herbert, P. Hunt, K. Lally, L. Kellogg, B. Konar, M. Krause, H. Lenihan, G. McQuilkin, N. McCall, F. Micheli, S. Micheli, E. Orlando, E. Oberdoerster, J. Reisenweber, D. Rittschof, G.W. Safrit, Jr., E. Seeber, P. Wyrick. We thank W.R. Geyer and L. Rosenfeld for helpful discussions of physical dynamics. Financial support came from the North Carolina General Assembly through the Cooperative Institute of Fisheries Oceanography and from the U.S. Environmental Protection Agency in its Near Coastal Waters Program through the University of North Carolina's Water Resources Research Institute on behalf of the Albemarle/Pamlico Estuarine Study.

LITERATURE CITED

Ambrose, W.G. Jr, Peterson, C.H., Summerson, H.C., Lin, J. (1992). Experimental tests of factors affecting recruitment of bay scallops (Argopecten irradians) to spat collectors. Aquaculture 108: 67-86

Belding, D.L. (1910). A report upon the scallop fishery of Massachusetts. Commonwealth of Massachusetts, Boston

Butman, C.A. (1987). Larval settlement of soft-sediment invertebrates: the spatial scales of patterns explained by active habitat selection and the emerging role of hydrodynamic processes. Oceanogr. mar. Biol. A. Rev. 25: 113-165

Castagna, M. (1975). Culture of the bay scallop, Argopecten irradians, in Virginia. Mar. Fish. Rev. 37: 19-24

Castagna, M. Duggan, W. (1971). Rearing the bay scallop Argopecten irradians. Proc. natl Shellfish. Ass. 61: 80-85

Day, R.W., and G.P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59: 433-463.

Dayton, P.K. (1973). Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. Am. Nat. 107: 662-670

Doherty, P., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral reef fish. Science 263: 935-939.

Doherty, P.J., Williams, D. McB. (1988). The replenishment of coral reef fish populations. Oceanogr. mar. Biol. A. Rev. 26: 487-551

Duggan, W.P. (1973). Growth and survival of the bay scallop, Argopecten irradians, at various locations in the water column and at various densities. Proc. natl Shellfis. Assoc. 63: 68-71

Eckman, J.E. (1987). The role of eelgrass hydrodynamics in recruitment, growth and survival of Argopecten irradians (L.) and Anomia simplex (D'Orbigny). J. exp. mar. Biol. Ecol. 106: 165-191

Eggleston, D.B., Lipcius, R.M., Hines, A.H. (1992). Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Mar. Ecol. Prog. Ser. 85: 55-68

Gaines, S., Roughgarden, J. (1985). Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc. natl Acad. Sci. U.S.A. 82: 3707-3711

Gutsell, J.S. (1930). Natural history of the bay scallop. Bull. U.S. Bur. Fish. 46:569-632

Irlandi, E.A. 1994. Large- and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon-nipping on an infaunal bivalve. Oecologia 98: 176-183.

Jordan, W.R., III, M.E. Gilpin, and J.D. Aber. 1990. Restoration ecology: a synthetic approach to ecological research. Cambridge Univ. Press, New York.

Levitan, D.R., Sewell, M.A., Chia, F. (1992). How distribution and abundance influence fertilization success in the sea urchin Strongylocentrotus franciscanus. Ecology 73: 248-254

Mercaldo, R.S., Rhodes, E.W. (1982). Influence of reduced salinity on the Atlantic bay scallop Argopecten irradians (Lamarck) at various temperatures. J. Shellfish. Res. 2: 177-181

Orensanz, J.M. (1986). Size, environment, and density: the regulation of a scallop stock and its management implications. Can. Spec. Publ. Fis. Aquat. Sci. 92: 195-227

Peterson, C.H. (1990). On the role of ecological experimentation in resource management: managing fisheries through mechanistic understanding of predator feeding behaviour. In: Hughes, R.N. (ed.) Behavioural mechanisms of food selection. Springer-Verlag, Berlin, p. 821-846

Peterson, C.H., Summerson, H.C., Fegley, S.R., Prescott, R.C. (1989). Timing, intensity and sources of autumn mortality of adult bay scallops Argopecten irradians concentricus Say. J. exp. mar. Biol. Ecol. 127: 121-140

Peterson, C.H., Summerson, H.C. (1992). Basin-scale coherence of population dynamics of an explited marine invertebrate, the bay scallop: implications of recruitment limitation. Mar. Ecol. Prog. Ser. 90: 257-272

Sammarco, P.W., Andrews, J.C. (1989). The HELIX experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. Limnol. Oceanogr. 34: 896-912

Summerson, H.C., Peterson, C.H. (1990). Recruitment failure of the bay scallop, Argopecten irradians concentricus, during the first red tide, Ptychodiscus brevis, outbreak recorded in North Carolina. Estuaries 13: 322-331

Tester, P.A., Stumpf, R.P., Vukovich, F.M., Fowler, P.K., Turner, J.T. (1991). An expatriate red tide bloom: transport, distribution, and persistence. Limnol Oceanogr. 36: 1053-1061

Tettelbach, S.T., Wenczel, P. (1993). Reseeding efforts and the status of bay scallop populations in New York following the occurrence of "brown tide" algal blooms. J. Shellfish Res. 12: in press

Tettelbach, S.T., Auster, P.J., Rhodes, E.W., Widman, J.C. (1985). A mass mortality of northern bay scallops, Argopecten irradians irradians, following a severe spring rainstorm. Veliger 27: 381-385

Underwood, A.J., Denley, E.J. (1984). Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong, D.R. Jr., Simberloff, D., Abele, L.G., Thistle, A.B. (eds.) Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, p. 151-180

Underwood, A.J., and Fairweather, P.G. 1989. Supply-side ecology and benthic marine assemblages. Trends Ecol. Evol. 4: 16-20.

Walters, C.J. (1986). Adaptive management of renewable resources. Macmillan, New York

FIGURE LEGENDS

Fig. 1. Map of study area showing the 4 receiver sites for transplants in 1992 (GP for Guthrie Point, GC for Goose Creek, SC for Saunders Creek, and EI for Emerald Isle) and the 4 receiver sites for 1993 transplants (C for Wood Island, BI for Bean Island, PI for Piney Island, and EI for Emerald Isle), the locations of spat collectors in 1992 and 1993, the sites where scallop recruit and adult abundance was estimated by suction dredge sampling in 1992 and 1993, and the 3 sites chosen for measurement of vertical profiles in physical parameters (M#42, M#36, and M#28). BR refers to the Emerald Isle bridge site and LI to the Long Island site, two of the locations receiving scallop spat collectors in 1993.

Fig. 2. Results of hourly measurements of oxygen concentration in the sound (control) and in 5-gal plastic buckets of 300 scallops at each of 3 flow treatments (top), stacked over results of hourly measurements of temperature of the water in the sound and in the air during this experiment (bottom).

Fig. 3. Average plus SE (n =2) percent mortality of adult bay scallops after 6 hr under each of 5 alternative sets of holding conditions. Letters over each bar indicate those treatment means that differ significantly at $p = 0.05$ in Duncan's test, conducted after a one factor ANOVA showed a significant effect of holding treatment.

Fig. 4. Average plus SE (n =2) percent mortality of adult bay scallops when held for varying lengths of time out of water inside insolated plastic coolers (top), stacked over results of measurements of water temperature in the sound at the site from which the scallops were collected and inside the coolers at intervals during the experiment (bottom).

Fig. 5. Average (+ SE; n = 10, 36 in 1992; n = 15, 13, 40 in 1993) abundance of adult bay scallops at the donor site of Oscar Shoal in Back Sound from summer until early December in each of the two years when scallops were taken for transplantation into western Bogue Sound. Only an estimated 1.5 percent in 1992 and 2.4 percent in 1993 of available adult scallops were removed for the transplants, as reflected in the lack of a detectable drop in scallop abundance immediately after removal of scallops in 1993. The * symbol indicates the estimated density of adult bay scallops remaining at the donor site after transplants were completed.

Fig. 6. Temporal changes in average (+ SE; n = 16-24) density of

adult bay scallops within the 1,200 m^2 transplant site and in a perimeter area of the same size surrounding each transplant site for each of the four receiver sites in 1992. See Fig. 1 for specific locations of these receiver sites.

Fig. 7. Average (+ SE; n = 8-20) abundance of settled bay scallops per spat collector bag in two years before (without) transplants and in two years after (with) transplants in one treatment location in western Bogue Sound (EI for Emerald Isle) and in two control locations (BB for Banks Bay and YS for Yellow Shoal) where no transplants occurred.

Fig. 8. Average (+ SE; n = 35-61) density of newly recruited bay scallops in natural seagrass beds as measured in early December after cessation of recruitment in each of two years before (without) transplants and in each of two years after (with) transplants in two treatment locations in western Bogue Sound (EI and SP), in two control locations in other sounds where no transplants occurred (BB and YS), and in one location in central Bogue Sound outside the influence of tidal forcing from Bogue Inlet (DI).

Fig. 9. Average (+ SE; n = 20-61) density of adult bay scallops in the same samples described for Fig. 8. Replication is lower for some adult data sets because any sample that fell within any part of the inner or outer perimeter of one of the 4 specific transplant sites was excluded from our estimate of adult density to avoid bias from inclusion of imported adult scallops.

Fig. 10. Average (+ SE; n = 15-20) numbers of settled bay scallops per spat collector bag (top), assessed at the end of October, and average (= SE; n = 20-40) density of recruited bay scallops in natural seagrass beds, assessed in early December, at sites arranged along a transect from behind Bogue Inlet eastward into Bogue Sound. See map in Fig. 1 for specific locations.

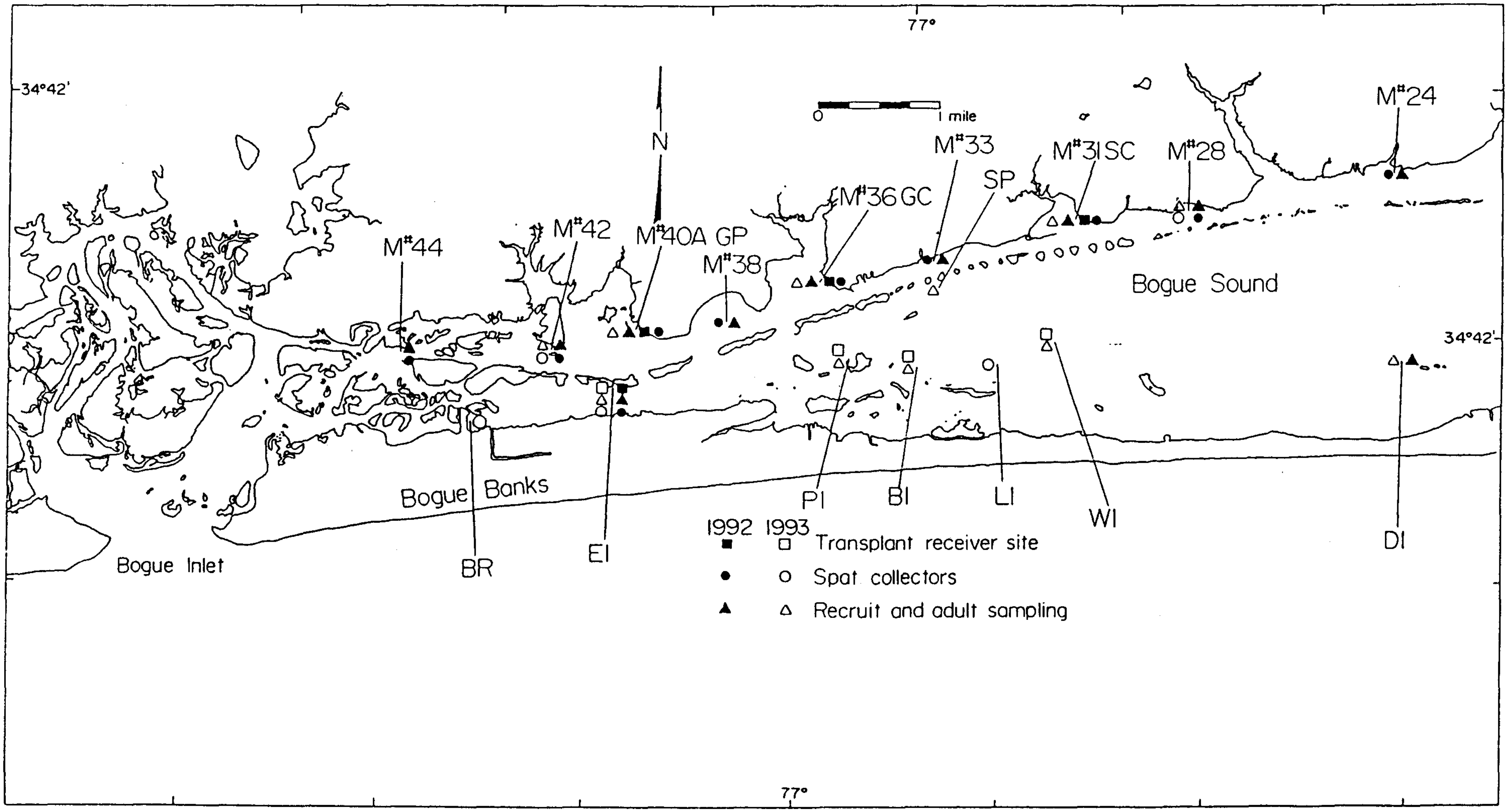
Fig. 11. Time series of continuous water level measurements made from an instrument mooring at the Goose Creek transplant site in autumn 1992. See Fig. 1 for location of Goose Creek.

Fig. 12. Vertical profiles of current velocity in 2 dimensions, temperature, and salinity made near slack high conditions and near maximum ebb conditions at the Marker #28 site in the Intracoastal Waterway.

Fig. 13. Vertical profiles for Marker #36, analogous to Fig. 12.

Fig. 14. Vertical profiles for Marker #42, analogous to Fig. 12.

Fig. 15. Total water flux during a complete tidal cycle through the channel of the Intracoastal Waterway computed from vertical velocity profiles and cross-channel bathymetry at each of 3 sites in western Bogue Sound. See Fig. 1 for the locations of these sites.



77°
34°42'
0
1 mile
N
M#24
M#33
M#31SC
M#28
SP
M#36GC
M#42
M#40A GP
M#38
M#44
Bogue Sound
34°42'
Bogue Banks
Bogue Inlet
BR
EI
PI
BI
LI
WI
DI
1992 1993
■ □ Transplant receiver site
● ○ Spat collectors
▲ △ Recruit and adult sampling
77°

Fig 1

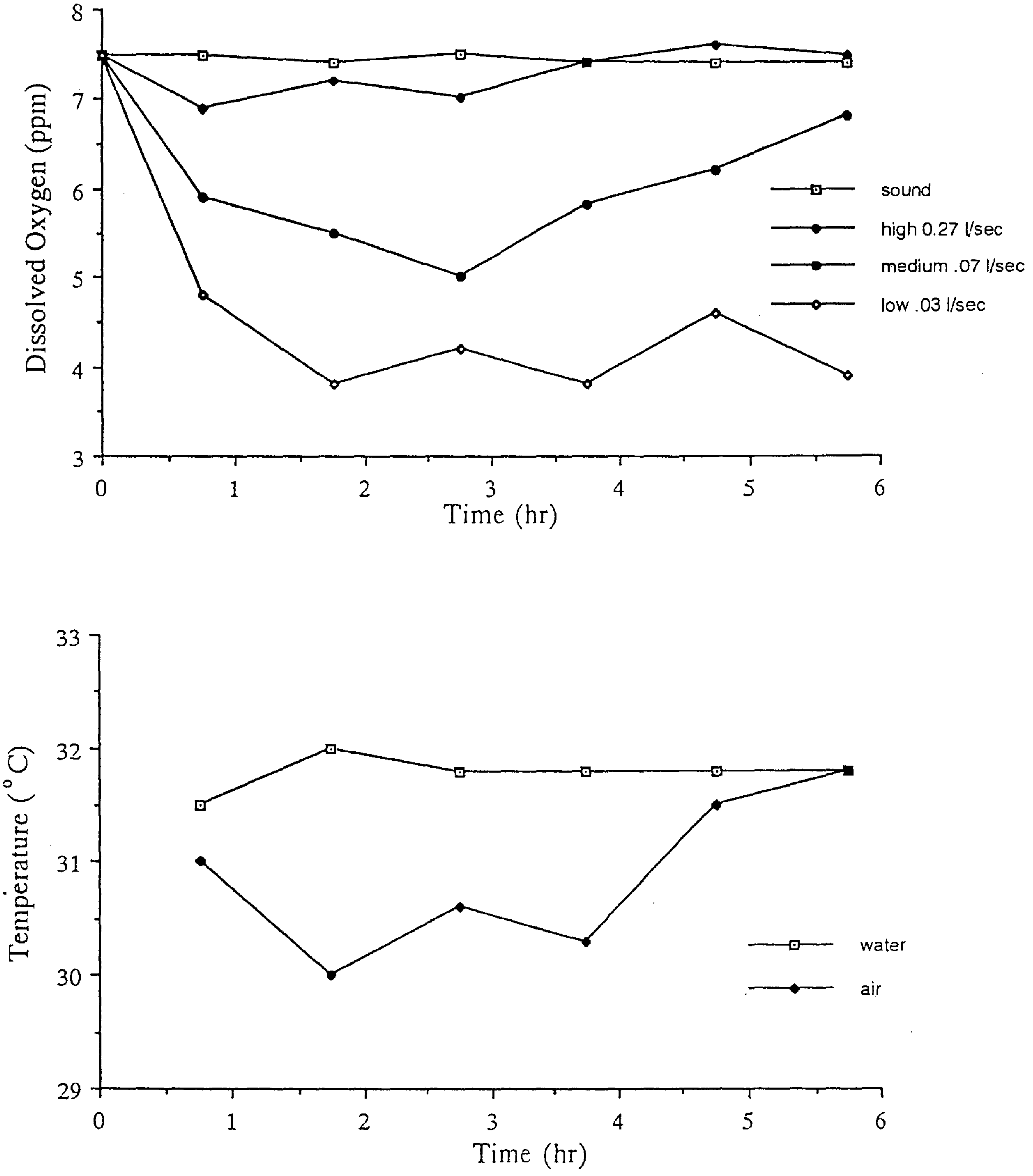
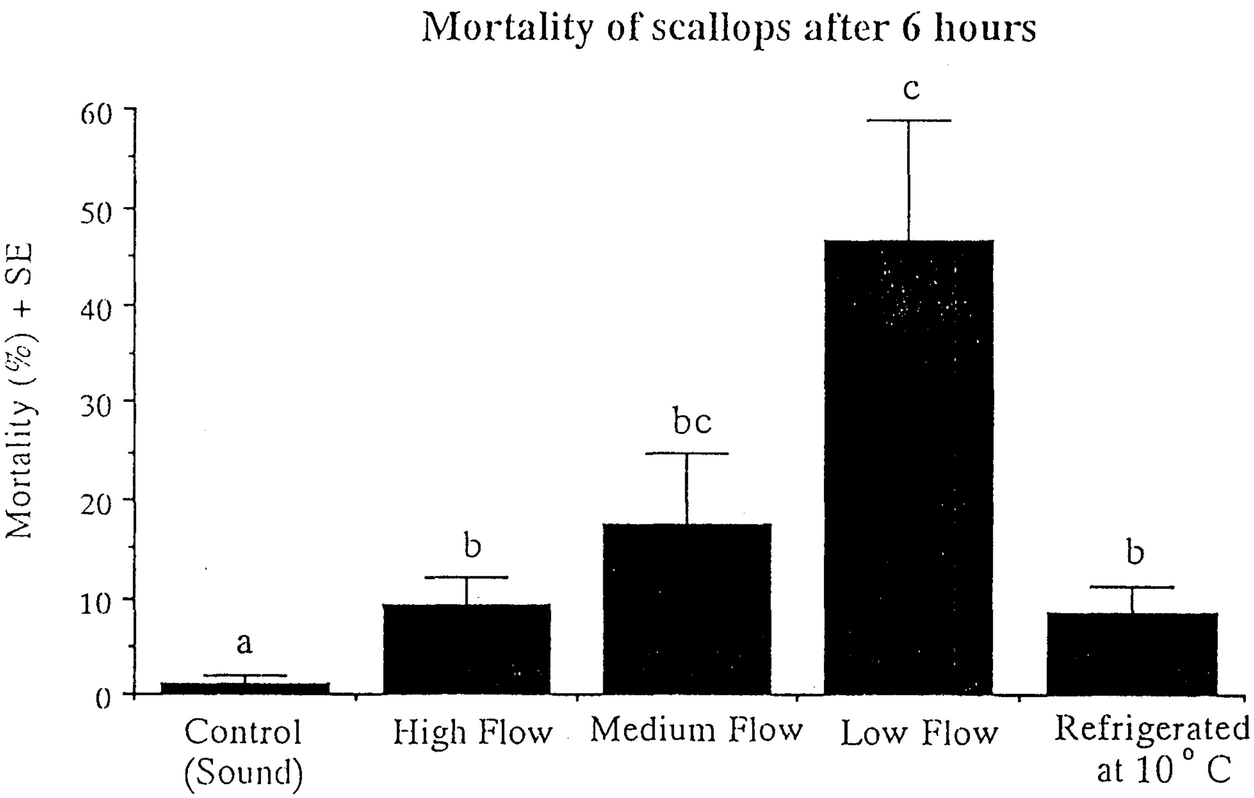

Dissolved Oxygen (ppm)
8
7
6
5
4
3
0
1
2
3
4
5
6
Time (hr)
sound
high 0.27 l/sec
medium .07 l/sec
low .03 l/sec
Temperature (°C)
33
32
31
30
29
0
1
2
3
4
5
6
Time (hr)
water
air

Fig 2



Mortality of scallops after 6 hours
Mortality (%) + SE
60
50
40
30
20
10
0
a
b
bc
c
b
Control (Sound)
High Flow
Medium Flow
Low Flow
Refrigerated at 10 ° C

Fig 3

Scallops stored in coolers

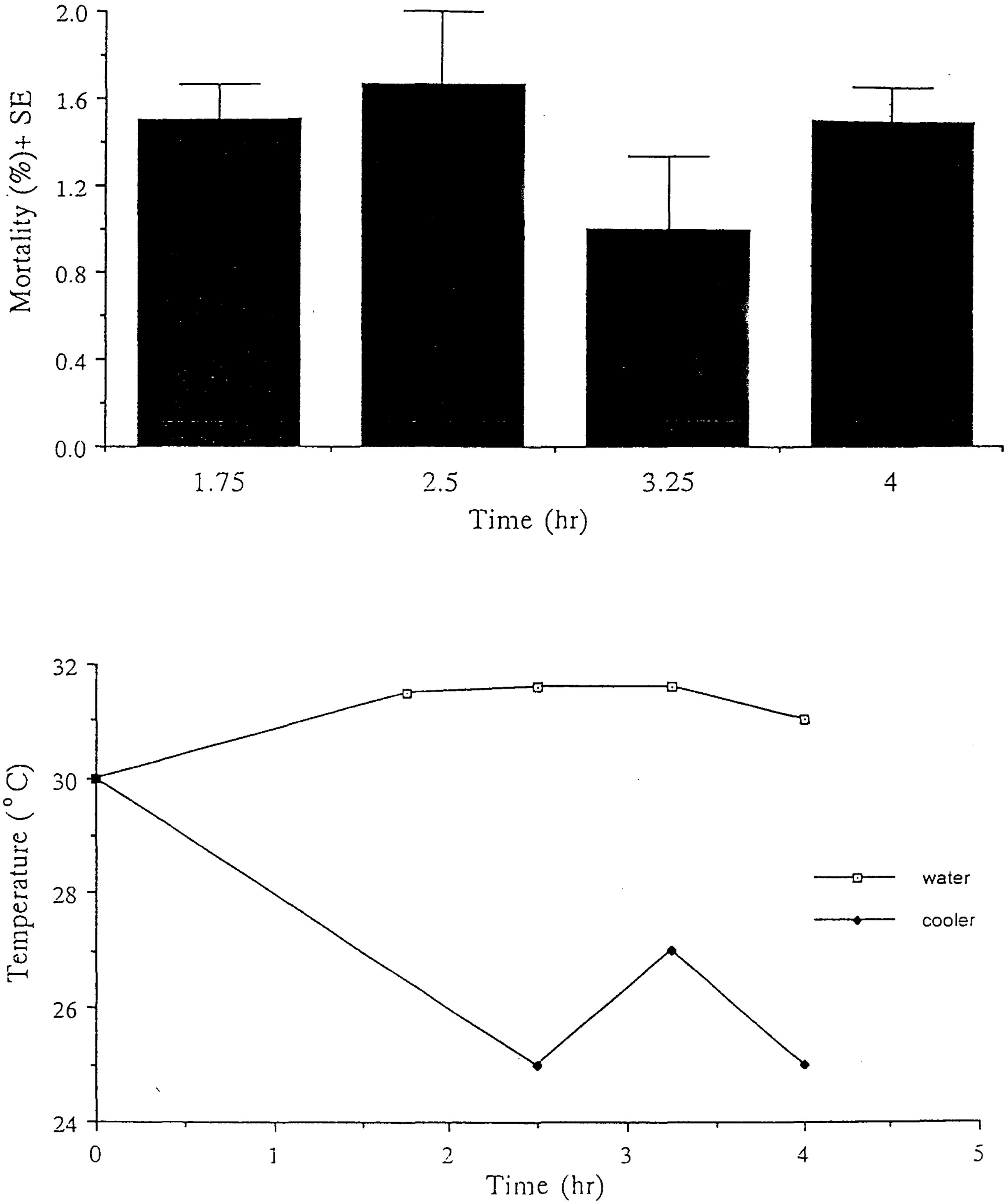


Fig 4

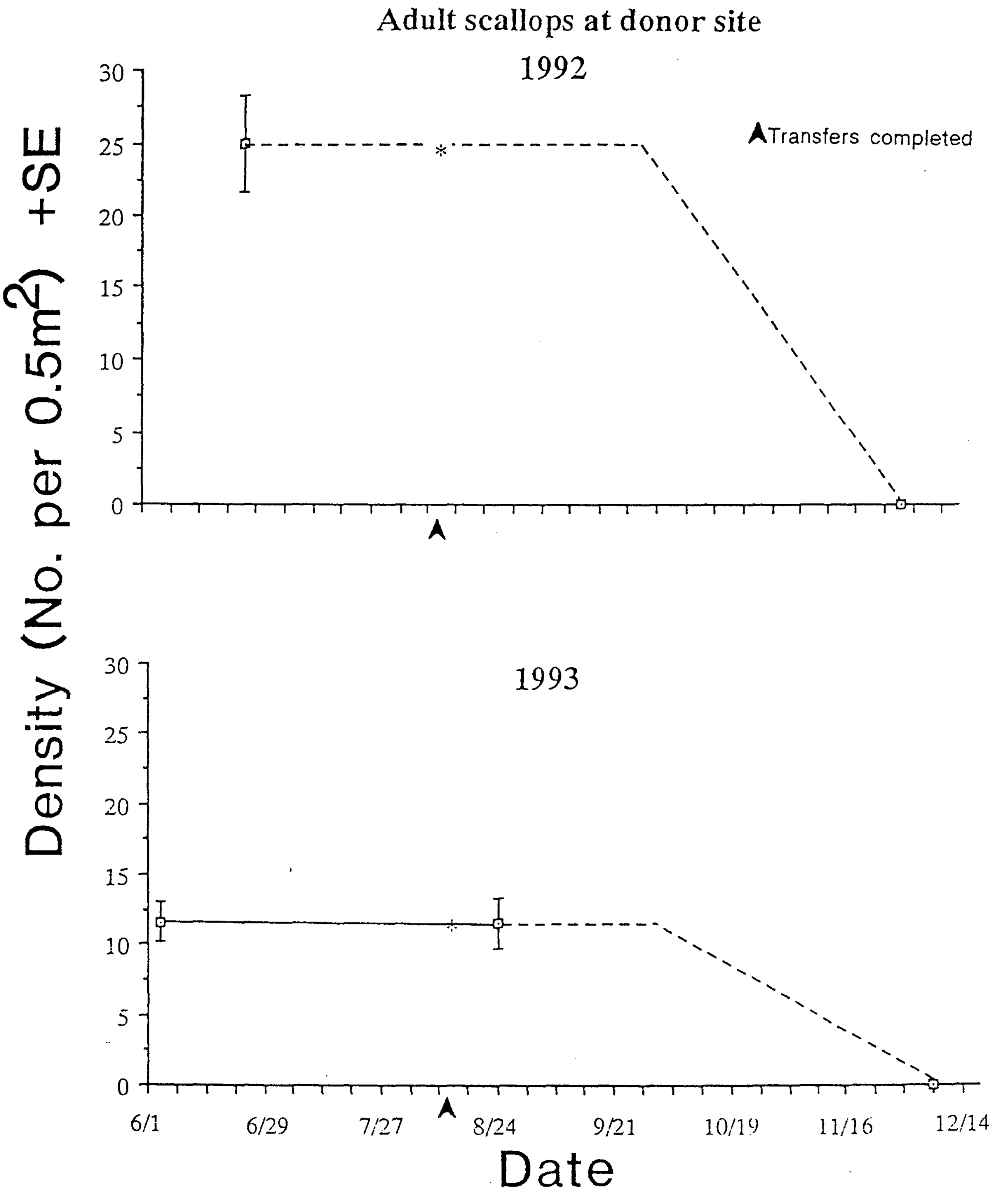
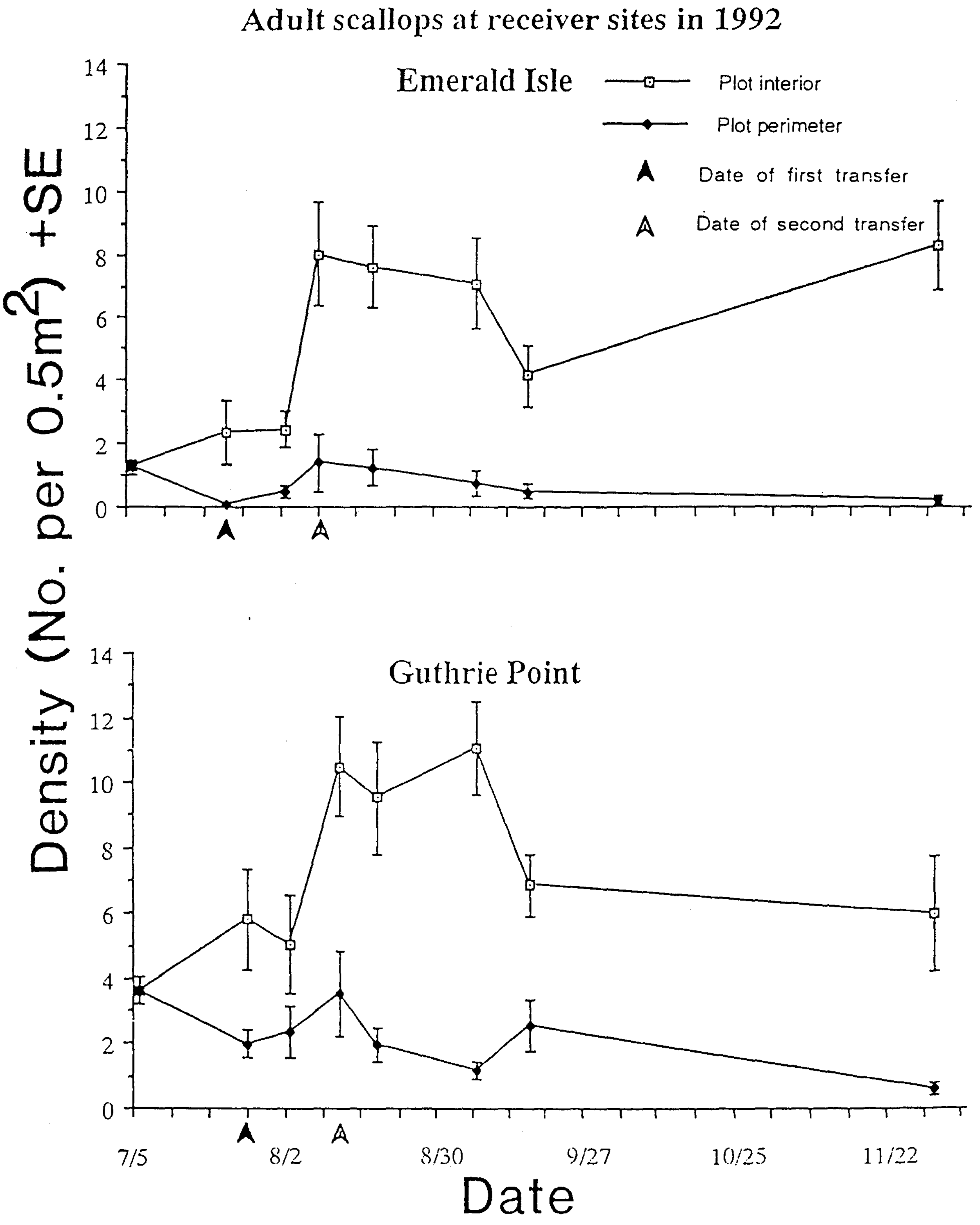

Adult scallops at donor site
1992
Transfers completed
1993
Density (No. per 0.5m2) +SE
30
25
20
15
10
5
0
6/1
6/29
7/27
8/24
9/21
10/19
11/16
12/14
Date

Fig 5



Adult scallops at receiver sites in 1992

Fig 6 A

Adult scallops at receiver sites in 1992

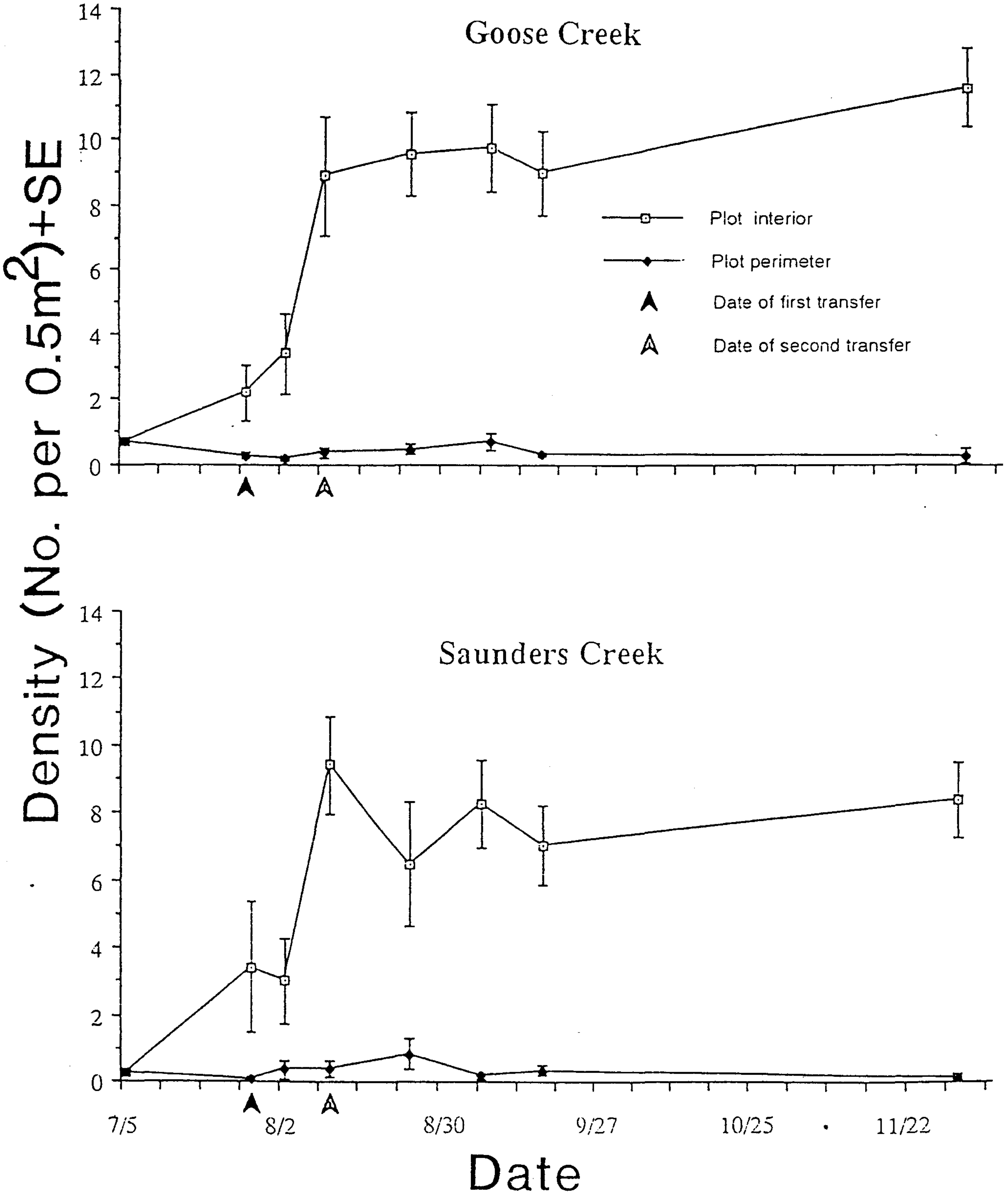


Fig 6B

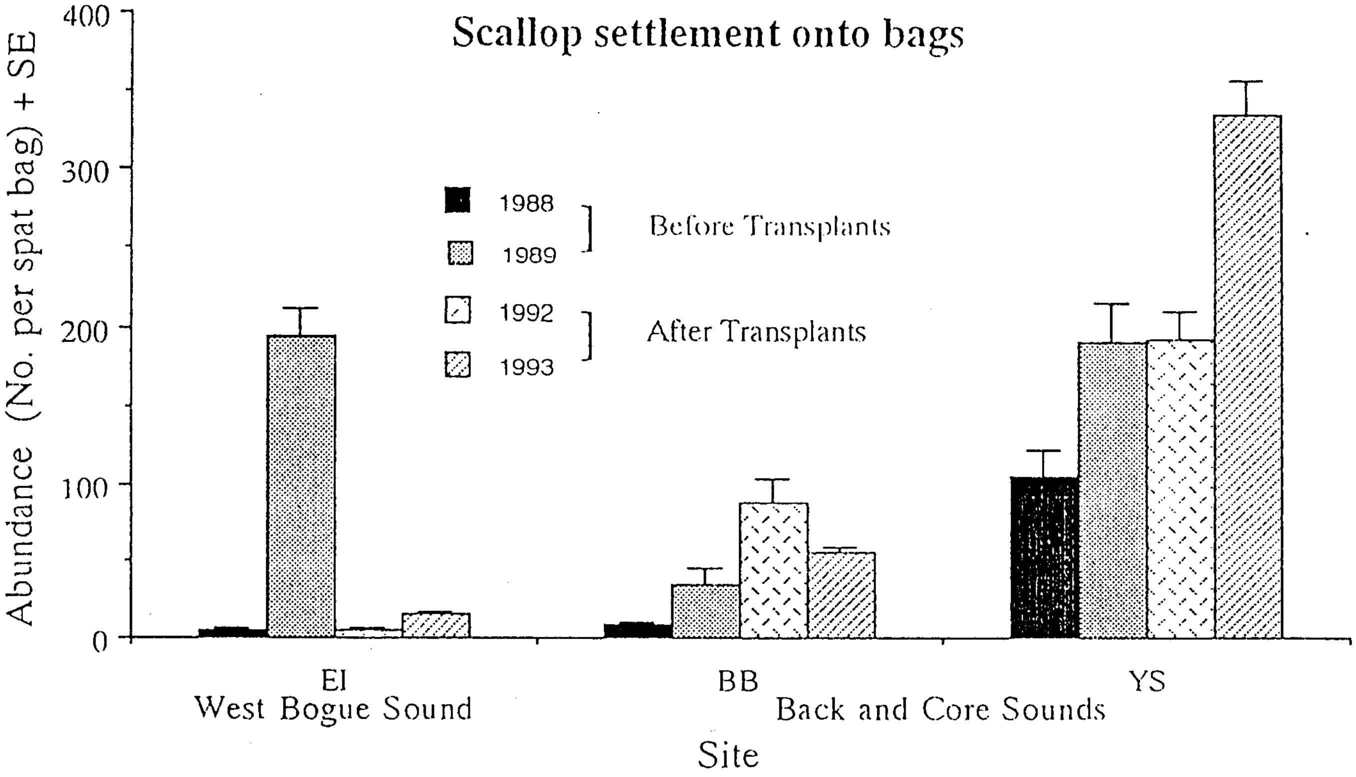

Scallop settlement onto bags
Abundance (No. per spat bag) + SE
400
300
200
100
0
1988
1989
Before Transplants
1992
1993
After Transplants
EI
West Bogue Sound
BB
Back and Core Sounds
YS
Site

Fig 7

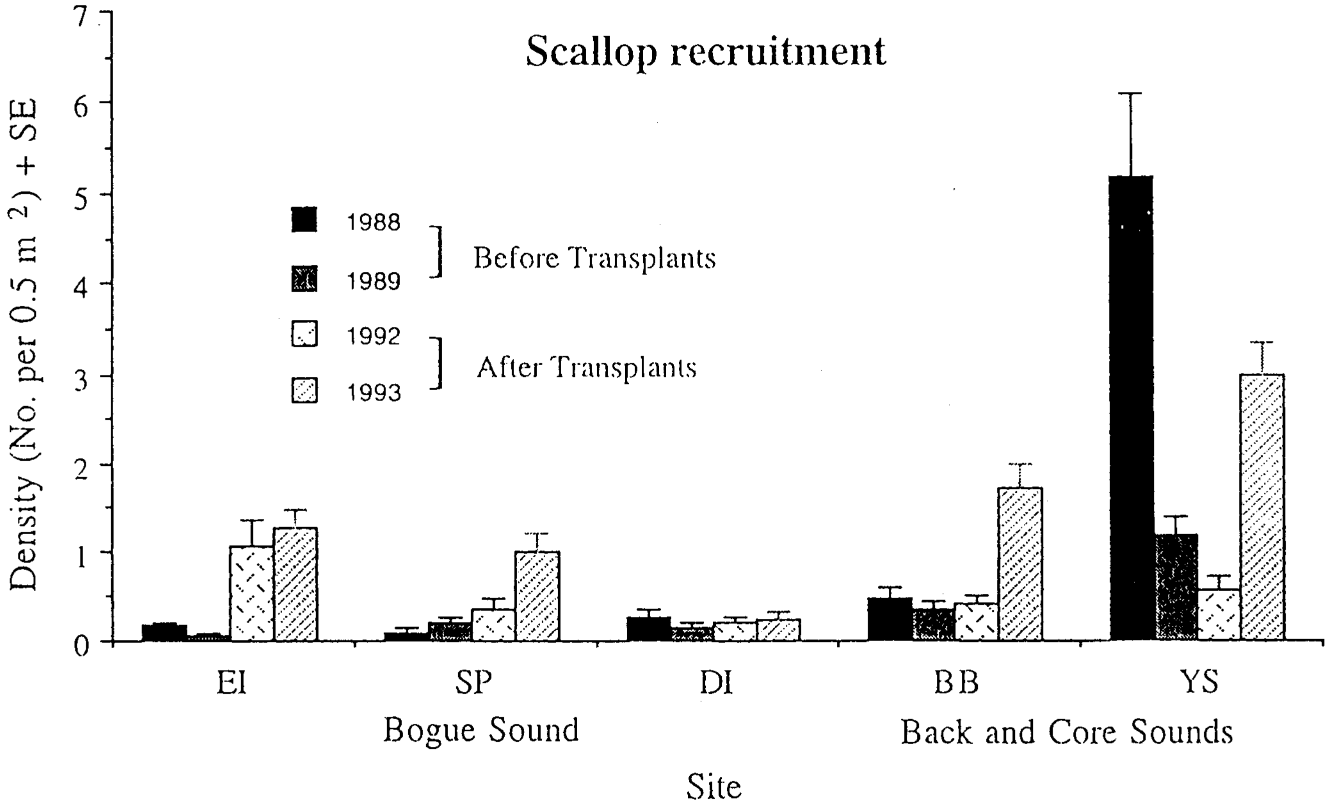

Scallop recruitment
Density (No. per 0.5 m 2) + SE
0
1
2
3
4
5
6
7
1988
1989
Before Transplants
1992
1993
After Transplants
EI
SP
DI
BB
YS
Bogue Sound
Back and Core Sounds
Site

Fig 8

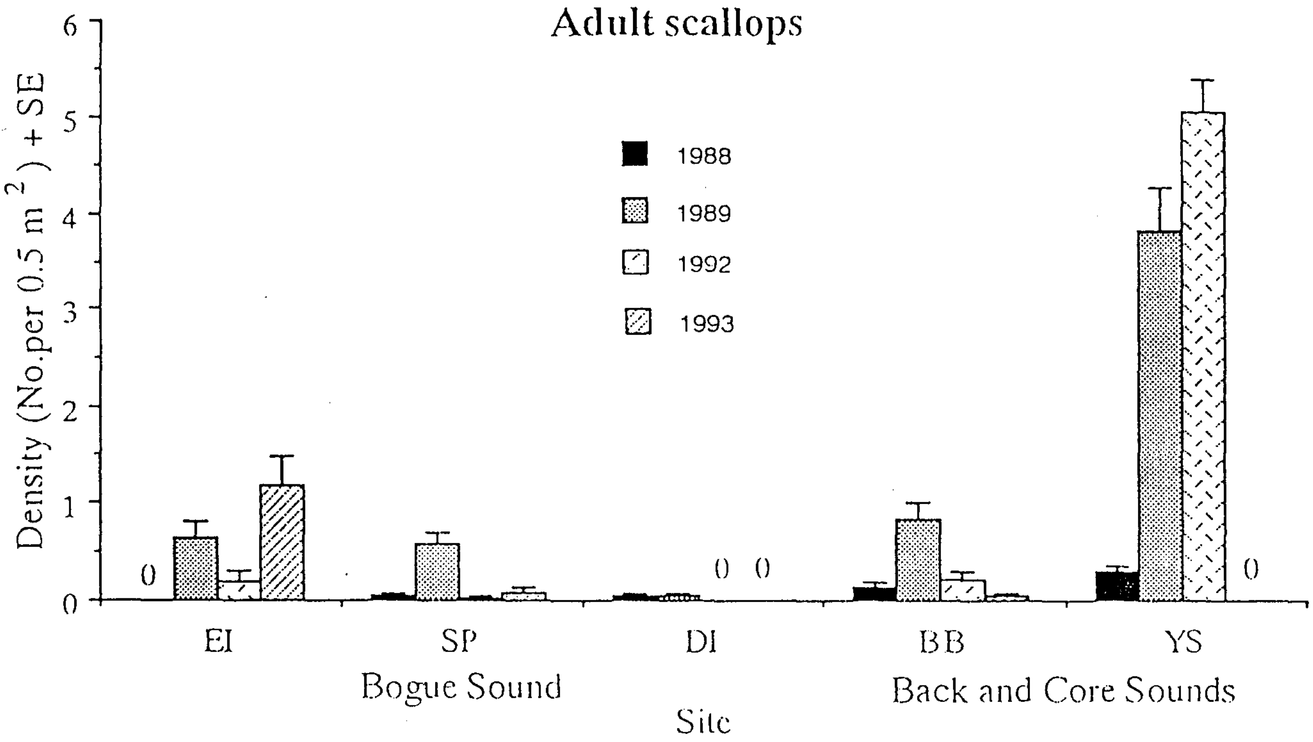

Adult scallops
Density (No.per 0.5 m 2) + SE
0
1
2
3
4
5
6
1988
1989
1992
1993
0
0 0
0
EI
SP
DI
BB
YS
Bogue Sound
Back and Core Sounds
Site

Fig 9

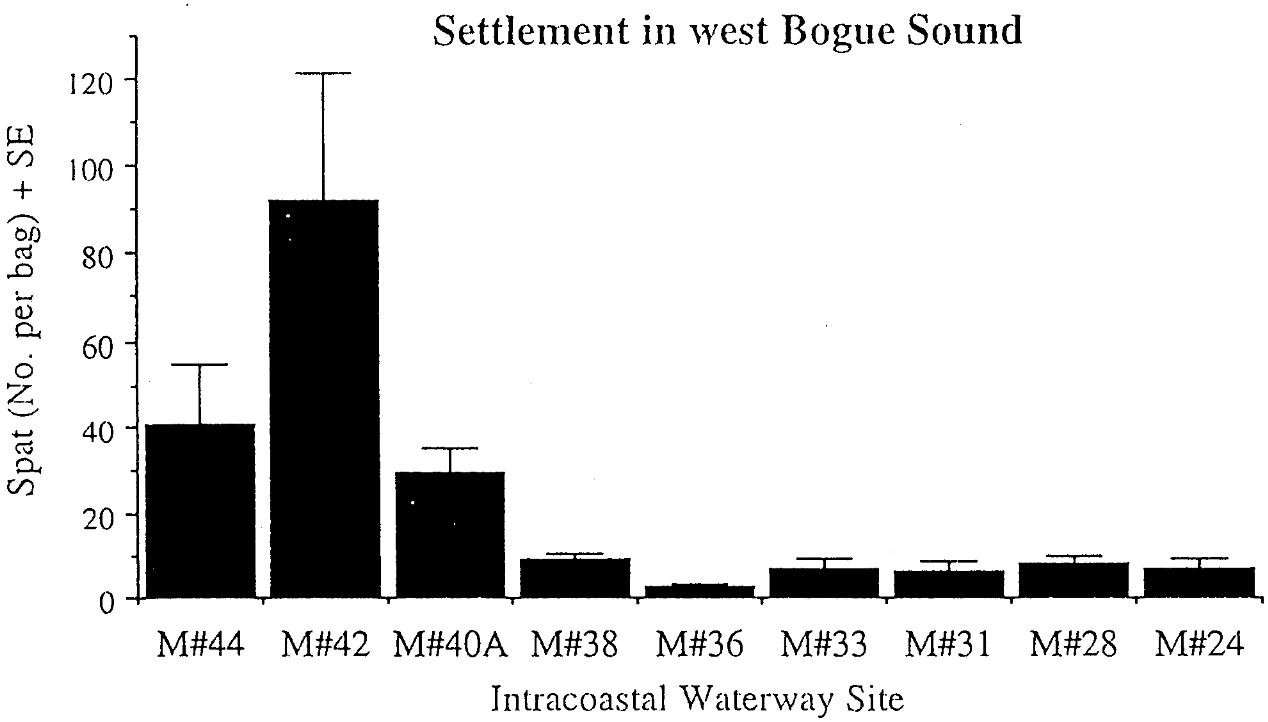

Settlement in west Bogue Sound
Spat (No. per bag) + SE
120
100
80
60
40
20
0
M#44
M#42
M#40A
M#38
M#36
M#33
M#31
M#28
M#24
Intracoastal Waterway Site

Fig 10B

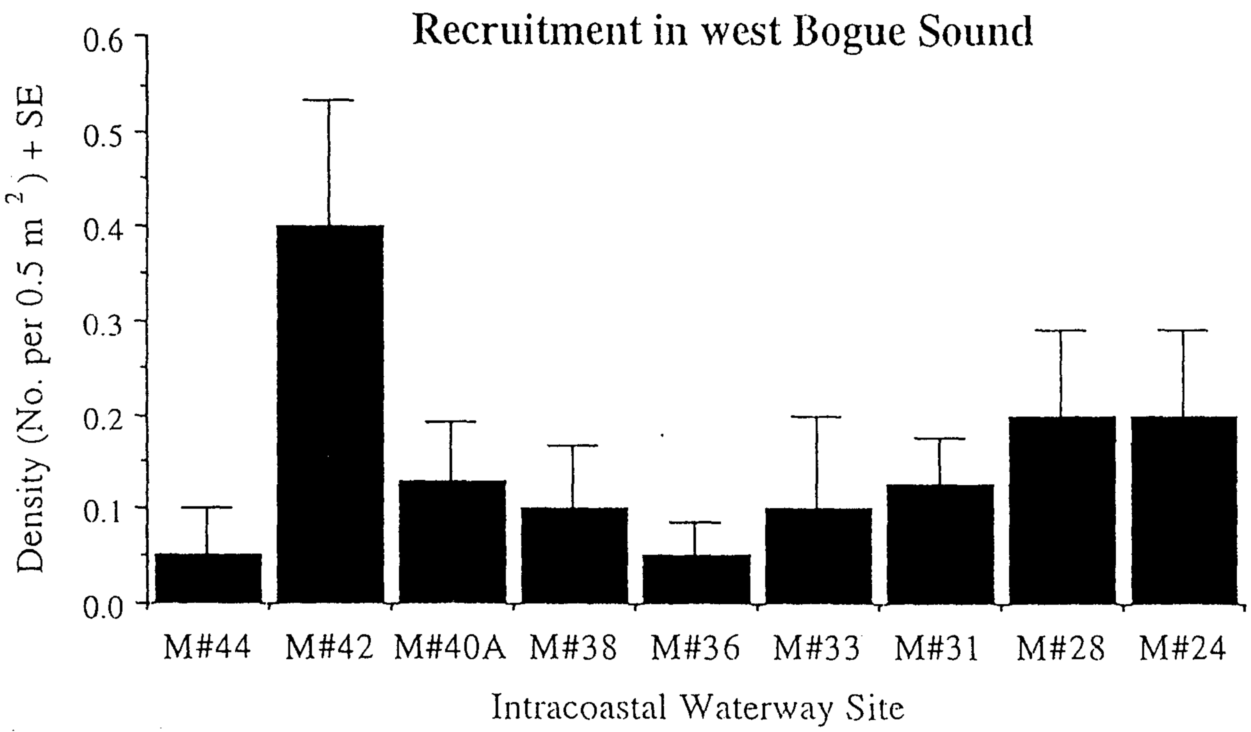

Recruitment in west Bogue Sound
Density (No. per 0.5 m ^{2}) + SE
0.0
0.1
0.2
0.3
0.4
0.5
0.6
M#44
M#42
M#40A
M#38
M#36
M#33
M#31
M#28
M#24
Intracoastal Waterway Site

Fig 10B

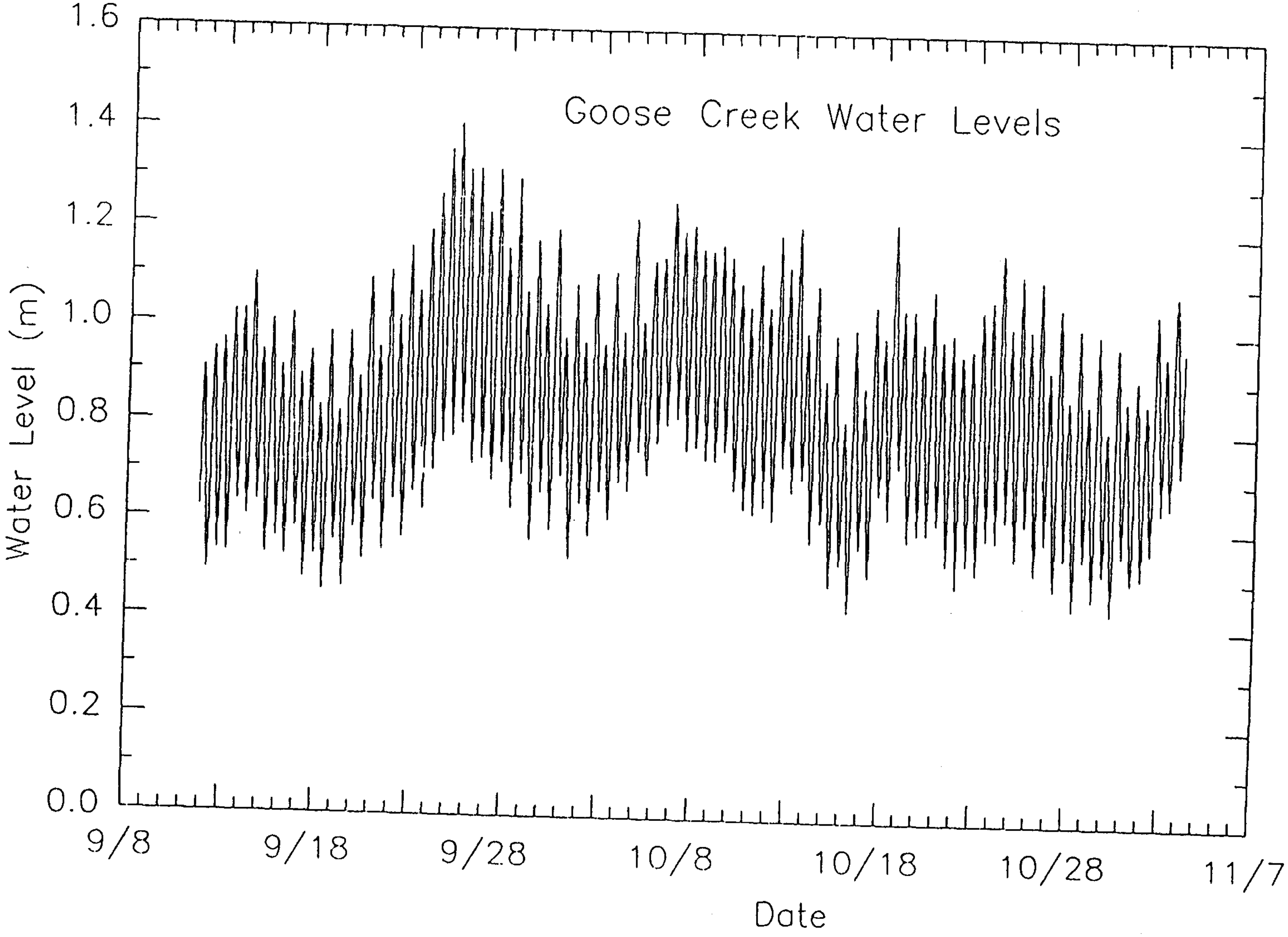
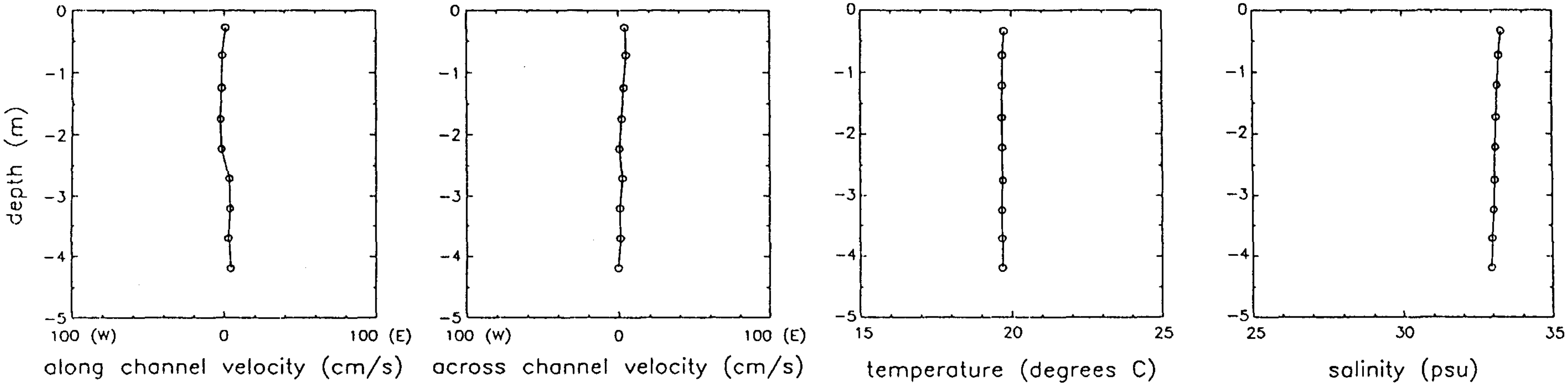

Goose Creek Water Levels
Water Level (m)
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
9/8
9/18
9/28
10/8
10/18
10/28
11/7
Date

Fig 11

MARKER 28 10/12/92 11:00 am



10/12/92 3:00 pm

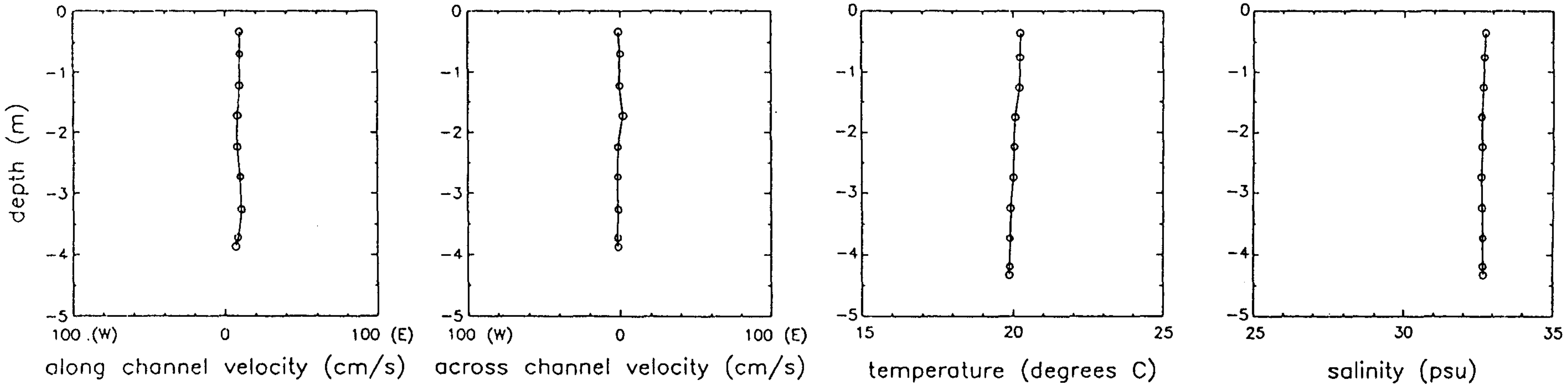


Fig 12

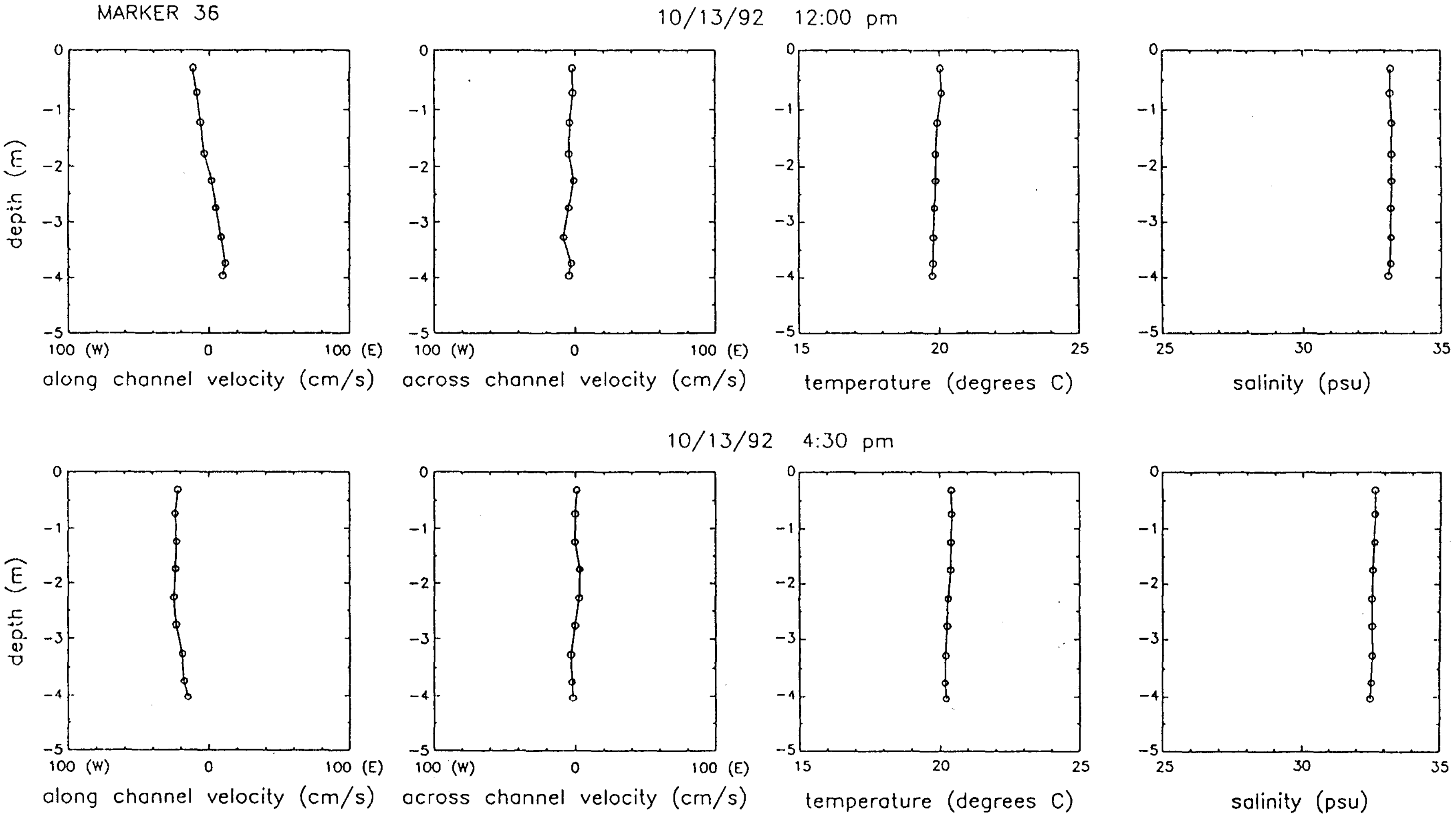
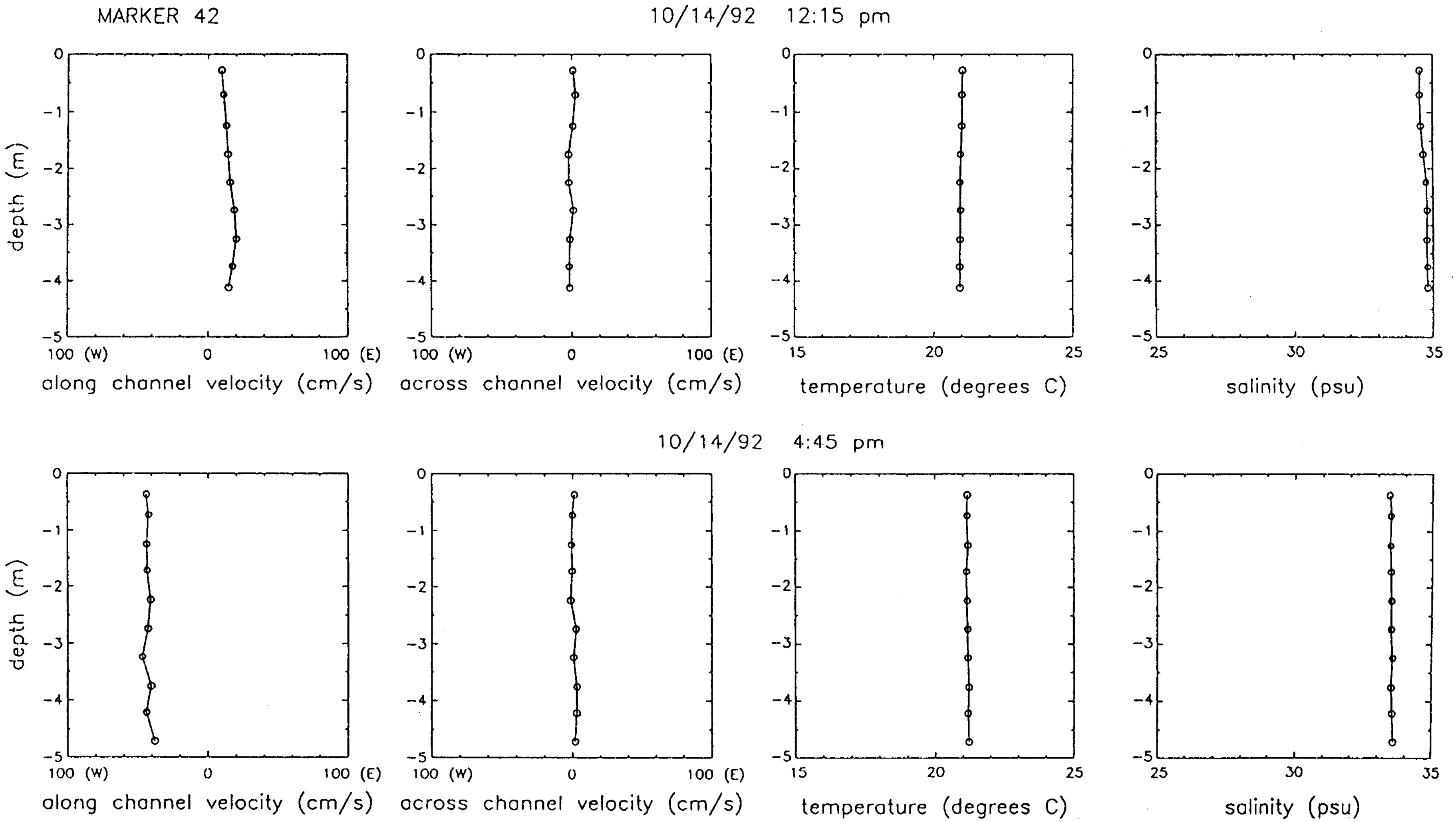

MARKER 36
10/13/92 12:00 pm
depth (m)
0
-1
-2
-3
-4
-5
100 (W)
0
100 (E)
along channel velocity (cm/s)
across channel velocity (cm/s)
15
20
25
temperature (degrees C)
25
30
35
salinity (psu)
10/13/92 4:30 pm
depth (m)
along channel velocity (cm/s)
across channel velocity (cm/s)
temperature (degrees C)
salinity (psu)

Fig 13


MARKER 42

10/14/92 12:15 pm

10/14/92 4:45 pm

Fig 14

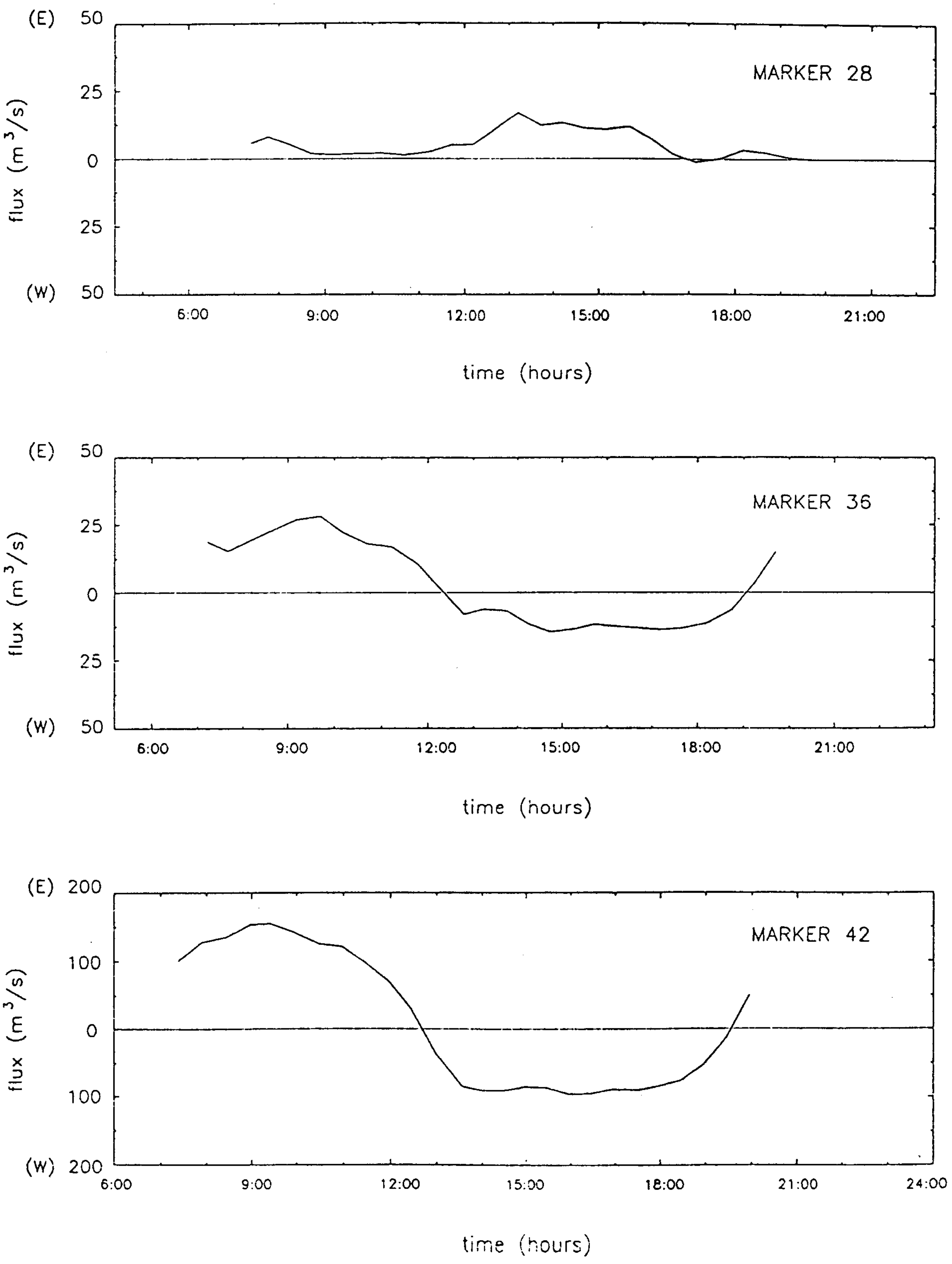

MARKER 28
(E) 50
25
0
25
(W) 50
flux (m³/s)
6:00
9:00
12:00
15:00
18:00
21:00
time (hours)
MARKER 36
(E) 50
25
0
25
(W) 50
flux (m³/s)
6:00
9:00
12:00
15:00
18:00
21:00
time (hours)
MARKER 42
(E) 200
100
0
100
(W) 200
flux (m³/s)
6:00
9:00
12:00
15:00
18:00
21:00
24:00
time (hours)

Fig 15

Table 1. Results of ANOVA testing whether recruitment of bay scallops, as measured by counting juveniles in suction dredge samples in December, varied with site, year, or their interaction. Tests were conducted on 4th root-transformed counts, which homogenized variances in Cochran's test at $\alpha = 0.05$. Significance (*** - $p<0.0001$) comes from 2-factor ANOVA with site and year as fixed, crossed factors: df (degrees of freedom); MS (mean square error); F (variance ratio tested).

Source of variation	df	MS	F	sig
Site (S)	3	9.15	33	***
Year (Y)	3	10.45	38	***
S x Y interaction	9	1.58	5.7	***
Error	753	0.28		

Table 2. Bay scallop recruitment as estimated by suction dredging in December. Temporal patterns of recovery after the 1987-88 red tide outbreak in western Bogue Sound, where adult spawner transplants were conducted in both 1992 and 1993, as compared to two control sites where no transplants took place.

Parameter	Western Bogue Sound		Back and Core Sounds	
	Emerald Isle	Salter Path	Banks Bay	Yellow Shoal
Average density of recruits in 1988 and 1989 (0.5m^{-2})	0.11	0.15	0.43	3.17
Average density of recruits in 1992 and 1993 (0.5m^{-2})	1.16	0.68	1.08	1.79
Average change in recruit density from 1988, 1989 to 1992, 1993	+955%	+353%	+151%	- 44%
	+654%		+ 54%	

Table 3. Results of ANOVA testing whether adult bay scallop densities, as measured by counting adults in suction dredge samples in December, varied with site, year, or their interaction. Tests were conducted on 4th root-transformed counts, which homogenized variances in Cochran's test at $\alpha = 0.05$. Significance (*** - $p<0.0001$) comes from 2-factor ANOVA with site and year as fixed, crossed factors; df (degrees of freedom); MS (mean square error); F (variance ratio tested).

Source of variation	df	MS	F	sig
Site (S)	3	12.6	73	***
Year (Y)	3	10.6	61	***
S x Y interaction	9	5.14	30	***
Error	714			

Table 4. Bay scallop recovery in adult density as measured by suction dredge in December. Transplants of spawners were made into western Bogue Sound in 1992 with adults from that spawn appearing in December 1993 data.

Parameter	Western Bogue Sound		Back and Core Sounds	
	Emerald Isle	Salter Path	Banks Bay	Yellow Shoal
Average adult density in 1988, 1989, 1992 (0.5 m^{-2})	0.28	0.22	0.40	3.06
Average adult density in 1993 (0.5 m^{-2})	1.18	0.08	0.05	0.00
Average change in adult density from 1988, 1989 and 1992 to 1993	+321%	- 71%	- 88%	-100%
	+125%		- 92%	