HYDRODYNAMIC FACTORS AFFECTING THE RECRUITMENT OF BIVALVE MOLLUSCS IN A TIDALLY DOMINATED ESTUARY

by

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For my parents

who encouraged the different drummer

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Abstract

The physical oceanography of a shallow estuarine system located along the Eastern Shore of Nova Scotia was studied to examine sources and tidal transport of mero- and holoplankton groups. The estuary was highly flushed and characterized the dispersive endmember of the physical retention continuum. Estuarine residence times were found to be much lower than that required for molluscan planktonic development, indicating that larvae tended to be exported from the system. Gastropod larvae exhibited especially large exports from estuary to sea. However, all groups, including bivalve larvae and holoplankton, were consistently transported between estuary and the nearshore zone. Recruitment of benthic organisms to the system is probably dependent on an allochthonous source of larvae.

A laboratory flume was used to examine the transport of burrowed juvenile soft-shell clams (2 weeks post-settlement) when exposed to flow velocities typical of tidal currents measured in the field. Clams resisted erosion until the initiation of sediment transport, after which they were rapidly advected from sections of test substrate. Comparisons between living and dead clams indicated that burrowing behavior was important for maintaining position at velocities below the critical erosion velocity for sediment movement. The ability of low density, shallow-burrowing juvenile bivalves to avoid transport as bedload or resuspended particles is probably minimal during erosional periods.

The effects of juvenile transport on the recruitment patterns of three estuarine bivalves (*Mya arenaria*, *Macoma balthica*, and *Gemma gemma)* were investigated at four sites in the Eel River estuary, Nova Scotia. The sites differed in the magnitude of horizontal current velocity and aerial exposure. Immigration of animals into experimentally defaunated sediments and monthly samples of clam populations over the three year study confirmed that all these species have the ability to recruit through juvenile transport. Transport rates were sufficient to replenish juvenile clams in defaunated plots to control values within days.

Laboratory and field experiments were conducted to compare growth of juvenile clams as a function of aerial exposure. In the laboratory, growth of clams held at different levels of aerial exposure, but supplied with an equal food ration, allowed separation of the physiological effects of emersion from that of reduced feeding. In a second experiment, clams were grown at three exposure levels in the field. Both laboratory and field experiments confirmed a significant reduction in shell growth and tissue weight of clams placed at mid-intertidal exposures in comparison to those continuously immersed.

Abbreviations and symbols

Symbol	Description	Units
a_t	m	Tidal amplitude
A_{yh}	m^2	Cross-sectional channel area
C	ind m^{-3}	Plankton concentration
F	ind m^{-2} d	Bivalve transport rate
G	mm	Growth
GR	mm d^{-1}	Growth rate
h*	m	Calibrated tidal height
h_t	m	Low tide water level
κ	dimensionless	von Karman constant (0 4)
k_s	m	Bed roughness scale
L	m	Tidal excursion length
N	ind	Net plankton transport
ν	m^2 s^{-1}	Kinematic viscosity of seawater
Q	m^3 s^{-1}	Volume transport
Q_P	ind s^{-1}	Plankton transport
Re_*	dimensionless	Bottom roughness Reynolds number
r_t	dimensionless	Tidal exchange ratio
SL	µm, mm	Shell length
T_D	d	Larval development time
T_{Dmin}	d	Minimum larval development time
T_L	d	Larval retention number
T_R	d	Recolonization time
T_{RES}	d	System residence time
T_{Tide}	d	Tidal period
U	m s^{-1}	Horizontal current velocity
U_∞	cm s^{-1}	Free-stream velocity
u_*	cm s^{-1}	Shear velocity
u_{*crit}	cm s^{-1}	Critical shear velocity for bed erosion
U(z)	cm s^{-1}	Depth-dependent horizontal current velocity
V_{FW}	m^3	Freshwater volume
Ω	m^3	Tidal prism
Ω_E	m^3	Ebb tidal prism
Ω_F	m^3	Flood tidal prism
w_s	cm s^{-1}	Partical fall velocity
z	cm	Depth
z_0	cm	Roughness length
z_R	m	Resuspension height
z_t	m	High tide water level

Acknowledgments

This research endeavors to determine if clams really are happy at high tide. To this end, I must thank the people in the Oceanography and Biology departments at Dalhousie University and at the Bedford Institute of Oceanography for making my stay in Canada such a formative experience while in pursuit of the answer. In particular, I thank Terri Sutherland, Rob Marsh, Geoff MacIntyre, and Peter Simard who risked bodily harm by braving the chilling Atlantic fog, midnight flood waters, monstrous marsh mosquitoes, and warm beer to collect larval samples. Carl André, Andrew Bauder, Geoff MacIntyre, Chris Pearse, and Terry Rowell were there to lug the heavy EMOBS across muddy intertidal zones and along tidal channels to my camouflaged study sites. I appreciate the input of Terri Sutherland during phytoplankton field collections in Chapter 1 (sorry about your camera!), as well as for her perceptive insights over the years into the often puzzling human interactions. I especially acknowledge the influence of Carl André, who worked closely on the flume experiments in Chapter 2 during his postdoc at Dal. Mats Lindegarth and Jim Eckman were also contributors to this work, which would have been impossible without the (nearly) flawless flume design and construction carried out by Carl and Bryan Schofield. Thanks to Brian Beal for supplying the *Mya* pediveligers used in Chapter 2, and Regina Marsh for growing phytoplankton cultures used in Chapter 4 and other studies. Paul Hill provided a very constructive review of Chapter 2. To my committee members, Tony Bowen, Barry Hargrave, and Terry Rowell, I thank you for your nonrestrictive guidance and critical review of the manuscripts spawned from this work. I am very appreciative of my supervisor, Jon Grant, for his continued support. Funding for this dissertation was provided through DFO/Subvention grants (1990-1996) and a Dalhousie Graduate Scholarship. Finally, thanks to The Sixteen Men of Tain and their ilk, for inspirational evenings.

Introduction: Recruitment of marine bivalve molluscs

The factors controlling the abundance of marine organisms are of great scientific and practical concern (Committee on Biological Diversity in Marine Systems 1995). On the one hand is the need to interpret the ecological links between marine systems in the face of increasing environmental degradation, and on the other are fisheries management and aquaculture issues. Of the coastal invertebrate groups, bivalve molluscs are perhaps unique in their importance for regulating habitat quality through bentho-pelagic coupling (Officer *et al.* 1982; Newell 1988) while concurrently supporting large and profitable fisheries. Thus, understanding the recruitment of coastal bivalve populations would aid both ecosystem preservation and fisheries management.

The life cycle of most commercially important bivalves consists of a planktonic larval phase, a period of juvenile growth and development, and an adult reproductive stage. Reproduction in broadcast spawning bivalves is initiated by the release of gametes into the water column where fertilization and larval growth occur (Thorson 1950). The bivalve veliger larvae typically remains planktonic for two to six weeks, and the larval phase is the primary mechanism for long distance dispersal. Mature larvae nearing completion of their planktonic development are termed "competent for settlement," and descend to the substrate to initiate searching behavior to find a suitable settlement site. Both active and passive processes are involved in the distribution of competent larvae in the water column (Butman 1986; Roughgarden *et al.* 1991), and choice of settlement site can be strongly selective (Busheck 1988) or more or less passive (Snelgrove *et al.* 1993), depending on species specific factors. "Settlement" occurs with

the irreversible loss of the larval swimming organ (the velum) and is followed by metamorphosis into the juvenile form. Species lacking a larval phase brood their young and release juveniles directly to the substrate.

"Recruitment" of benthic organisms is the measure of changes in abundance at a locale over time scales that are defined by the researcher (Roegner 1991). In this thesis, recruitment encompasses both larval settlement and post-settlement processes such as immigration, emigration, and mortality. This research is concerned with determining the stages (larvae, juveniles, or adults) that contribute to changes in numerical abundance, and with physical mechanisms controlling bivalve dispersal , transport, and growth. Since bivalve species can be relatively long-lived, recruitment to a size threshold (for fisheries applications) or reproductive stage (an ecological definition) may require years.

Biological factors, such as predation, competition, and growth, and physical factors like temperature, salinity, tidal periodicity, and hydrodynamic forces, are capable of influencing population structure during all stages of the bivalve life cycle. Rates of larval settlement and early post-settlement survival are extremely varied in bivalve populations, and reproductive cohorts often fail to reach or survive to maturity at a given site. This can result in local age or size distributions that are composed of only a few year classes (*i.e.* Möller and Rosenberg 1986). The early post-settlement and juvenile periods has not been well studied for many bivalve species despite its importance on later abundance (Rodriguez *et al.* 1994; Roegner & Mann 1995). In general , immature bivalves are more susceptible to mortality events and post-settlement dispersal mechanisms than larger individuals. This may be because juvenile infauna are generally restricted to

surficial sediments which increases the opportunity for mortality by predators or physical disturbance With growth, refuges from predators and disturbance can be achieved by position in the sediment or large size (Zwarts & Wannik 1993) Size also enhances reproductive potential, as large adults contribute numerically more gametes to the reproductive pool than smaller individuals (Ayers 1956, Brousseau 1978) Deciphering the causes of the large variations in recruitment constitutes a major endeavor in biological oceanography (Young 1987)

Recent investigations have focused on coupling physical oceanographic processes with biology to examine factors influencing recruitment (Butman 1986, Farrell *et al.* 1991) A distinction has been made between "recruitment limited" populations, in which changes in population structure at a site are mediated by variations in larval supply, with "recruitment regulated" populations that are maintained through post-settlement survival or migration (Lewin 1986) In most systems, both the magnitude of larval supply and the intensity of juvenile mortality or migration together determine the temporal variations in species abundance

In this thesis, the role of hydrodynamic factors on the regulation of estuarine bivalve populations is examined The physical environment imposes fundamental and measurable limits on the advective transport of larvae to sites (Farrell *et al* 1991, Jonsson *et al* 1991), settlement distributions (Butman 1987, Eckman 1990), and the stability of benthic populations (Matthiessen 1960, Emerson & Grant 1991) The first chapter examines the mechanisms of larval transport in relation to the dominant circulation patterns of a tidally dominated estuary Advection of larvae with estuarine and coastal

water masses is investigated to determine sources of larval supply to estuarine benthic sites. The second chapter summarizes results from a laboratory study of the transport of juvenile clams in boundary-layer flow using a recirculating flume. In this study, the near-bed hydrodynamic forces typical of coastal environments are quantified and their effect on the transport of newly settled clams is determined. In Chapter 3, data from three years of observations are reported to show the recruitment patterns of three estuarine bivalve species in relation to the contributions of larval settlement versus juvenile transport. Sites within the study area differed in aerial exposure, horizontal current velocity, and ice cover. In the final chapter, the growth of clams in relation to aerial exposure and food level was examined. The results of these investigations illustrate the important effects of physical factors on bivalve population dynamics in energetic regimes.

Chapter 1. Advective transport of molluscan larvae through a shallow tidal estuary

1.0 Introduction

The processes affecting dispersal of meroplankton results in large variations in the recruitment of marine benthic organisms in both space and time. Rates of larval supply influences the intensity of settlement (Gaines *et al.* 1985; Farrell *et al.* 1991; Roughgarden *et al.* 1991; Gaines & Bertness 1992; Bertness *et al.* 1992), and fluctuations in settlement and early post-settlement survival are important for structuring subsequent abundance (Connell 1985; McConaugha 1988; Feller *et al.* 1992; Rodriguez *et al.* 1992; Roegner & Mann 1995). On generation time scales, recruitment-limitation can result in the collapse of populations at a site, especially in populations suffering from heavy mortality pressure such as fishing (Hargis & Haven 1986) or disease (Peterson & Summerson 1992), while in other systems retention mechanisms may lead to self-seeding populations (Levin 1983, 1986). Over geological time scales, wide dispersion allows for the colonization of new habitats and contributes to speciation (Scheltema 1975, 1986; Hedgecock 1982).

In estuaries, bivalve molluscs comprise one of the most important ecological and economical groups of organisms, and while juveniles can be very mobile (Chapters 2 and 3), the limited post-settlement migration capabilities of adults has made larval supply critical for determining overall recruitment patterns. One research focus has been the study of retention mechanisms of bivalve larvae in estuaries, often with the implied assumption that export from the system equates with mortality. However, a less often considered alternative is that immigration from external populations contributes to variation

in local year class strength. Import, or reinvasion, of fishes and crustaceans to estuarine habitats has been investigated, but relatively few studies have addressed analogous problems with molluscs (see reviews in Weinstein 1988). Understanding and predicting the sources of larvae and the transport mechanisms supplying larvae to estuarine sites is a critical need for fisheries and habitat management.

Dispersion of larval bivalves results from the interaction of their behavior with physical transport mechanisms. Debate has centered around the relative importance of these two factors for determining larval retention and recruitment intensities (see reviews by Mann 1986a; Stanyck & Feller 1986; Scheltema 1986). It is clear that the instantaneous horizontal position of larvae in an estuary is determined by advective transport (Butman 1986, 1987). Net horizontal swimming velocities of bivalve larvae, averaging less than 10^{-4} m · s^{-1} (Cragg & Gruffydd 1980; Mann 1986b), are insufficient for directed motion in estuarine currents that typically range from 10^{-2} to > 10^{0} m · s^{-1}. Over time scales on the order of a tidal excursion, larvae will be transported as passive particles with the water parcel in which they reside. Extensive landward or seaward displacements often result; for example, transport of veligers in James River (Andrews 1983) or Delaware Bay (Jacobsen 1990; Jacobsen *et al.* 1990) can exceed 11 km per tide, while Tremblay & Sinclair (1988) estimated larval scallop transport in the Bay of Fundy to be 22 to 44 km · d^{-1}.

Over many tidal cycles, behavior can affect horizontal position if larvae can select water column strata of differing velocities. Active retention is hypothesized to occur by vertical migration cued to estuarine circulation, where by interacting with shear zones

such as the benthic boundary layer or the layer of no net motion, larvae can elicit some control over their net position via the resultant residual currents (Pritchard 1953, Bousefield 1955, Butman 1986) Laboratory studies indicate vertical swimming and sinking speeds are adequate to transverse more than 10 m of water within a tidal period (Mileikovsky 1973, Mann 1988), and evidence exists that environmental cues such as salinity (Haskin 1964, Hidu & Haskin 1978, Mann 1988, Mann *et al* 1991), pressure (Bayne 1963, Cragg & Gruffydd 1980, Mann & Wolfe 1983), and light (Bayne 1964a, Hidu & Haskin 1978) can initiate a directed swimming response to enhance the likelihood of retention

However, field surveys suggest that physical processes typical of the systems investigated can disrupt selective behavioral aggregations Rates of vertical mixing, determined by solar, tidal, and meteorological forcing, appear to regulate the ability of larvae to vertically aggregate in both estuaries (Carriker 1951, 1961, Haskin 1964, Boicourt 1982, Seliger *et al* 1982, Andrews 1983, Mann 1988, Tremblay & Sinclair 1990a, but see Raby *et al* 1991) and continental shelf environments (Mann 1986b, Scrope-Howe & Jones 1986, Tremblay & Sinclair 1990b) Physically determined vertical distributions generally predominate under energetic conditions, while active depth regulation can occur when stratification ensues The ability of larvae to control horizontal position thus varies with the vertical stability of the water

Ontogenic changes in larval swimming responses, established from the laboratory and field studies cited above, have important consequences for larval transport and retention While younger bivalve stages tend to remain in the water column and are

subjected to strong horizontal displacement and dispersal, larvae nearing settlement congregate near the bed. In many of the partially mixed estuaries investigated, this behavioral change generally results in seaward advection of immature larvae in surface water, while maturing larvae tend to be transported landward in near-bottom residual flows during presettlement searching behavior. This time-averaged displacement belies the large scale advective transport which is occurring on tidal periodicities. Thus, the question remains whether active behavior is *required* to explain net landward transport (hence retention) against mean seaward flow (*i.e.* Wood & Hargis 1971; Mileikovsky 1973; Haskin 1978) or if landward transport of mature larvae is simply a consequence of presettlement behavior coupled with the residual flow field (Pritchard 1954; de Wolf 1974; Andrews 1981; Seliger *et al.* 1981; Mann 1988; Ruzeki & Hargis 1989). In either case, horizontal dispersion and spatial variation in larval abundance are clearly strongly influenced by physical advection and mixing. "Active" retention of bivalve larvae via vertical migration behavior is only manifested through residual flow patterns.

Given that large-scale transport and mixing are common in most estuaries, larval retention within a system depends on the relative time scales of development in the plankton to the residence time of the estuarine water mass (Ketchum 1954; Ayres 1956; Platt *et al.* 1972; Lewis & Platt 1982). A conceptual comparison of the relevant biological and physical time scales is shown in Fig. 1.1. For any species and set of environmental conditions, a larval retention number $T_L = T_{RES} / T_D min$ can be defined which relates the minimum larval development time, $T_D min$, to the system residence time, T_{RES}. Export tends to dominate if $T_L < 1$, while retention is supported when $T_L > 1$. Many factors

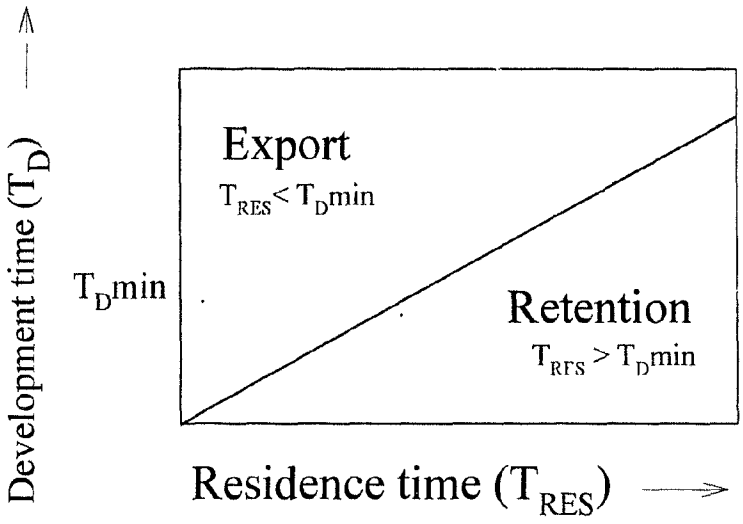

Fig 1 1 Conceptual model of the relation between larval development time T_D and estuarine residence time T_{RES}

potentially regulate T_L Conditions accelerating larval growth, such as improved food resources and optimum salinity and temperature, favor retention (Ketchum 1954) Species-specific differences in development time may underpin community structure, with high retention of species with short planktonic periods resulting in larger or more consistent recruitment events compared to species with a longer life in the plankton (Carriker 1961, Levin 1986) As discussed above, behavioral components modifying susceptibility to transport, such as presettlement activities, may alter retention probabilities during the course of larval development Physical retention can be expected to scale with basin size and topography and vary with tidal range, wind stress, and freshwater input (Fisher *et al.* 1979) Temporal and spatial variation in these factors can make the timing of reproduction important for successful retention. Intuitively, dispersal and loss

from the parental stock is likely in highly flushed systems compared to those estuaries with long residence times.

The objective of the present study was to examine the supply of molluscan larvae to a shallow, tidally-dominated estuary in relation to the physical oceanography of the system. The relatively simple estuary investigated lacked two layer circulation and characterized the dispersive endmember of the physical retention continuum; one would expect recruitment-limitation within such an energetic environment. However, the infaunal clams *Mya arenaria* L. and *Macoma balthica* L., and the mussel *Mytilus edulis* L., which reproduce via planktonic larvae, were extremely abundant in the estuary and distinct recruitment events were measured (Chapter 3). More generally, this research was designed to elucidate mechanisms of larval transport to estuarine sites.

1.2 Materials and Methods

1.2.1 Study Site

The Eel River barrier beach system is located on the Atlantic coast of Nova Scotia, Canada (44° 38' 30" N, 63° 23' 30" E), and forms part of the larger Lawrencetown River estuary (Fig. 1.2). The system typifies many of the small, narrow, and shallow estuaries of large tidal range to depth ratio found in this region.

During the study period, the Eel River estuary consisted of two main sections which contributed to the circulation patterns described below. The lower estuary was a 1.025 km long channel with a surface area of $2.4 \cdot 10^5$ m^2. Depths at low tide varied from intertidal to 0.5 m, and the tidal range was from 0.4 to 1.3 m. Exchange between coastal water and estuary occurred exclusively through a tidal inlet (TI) which entered the larger

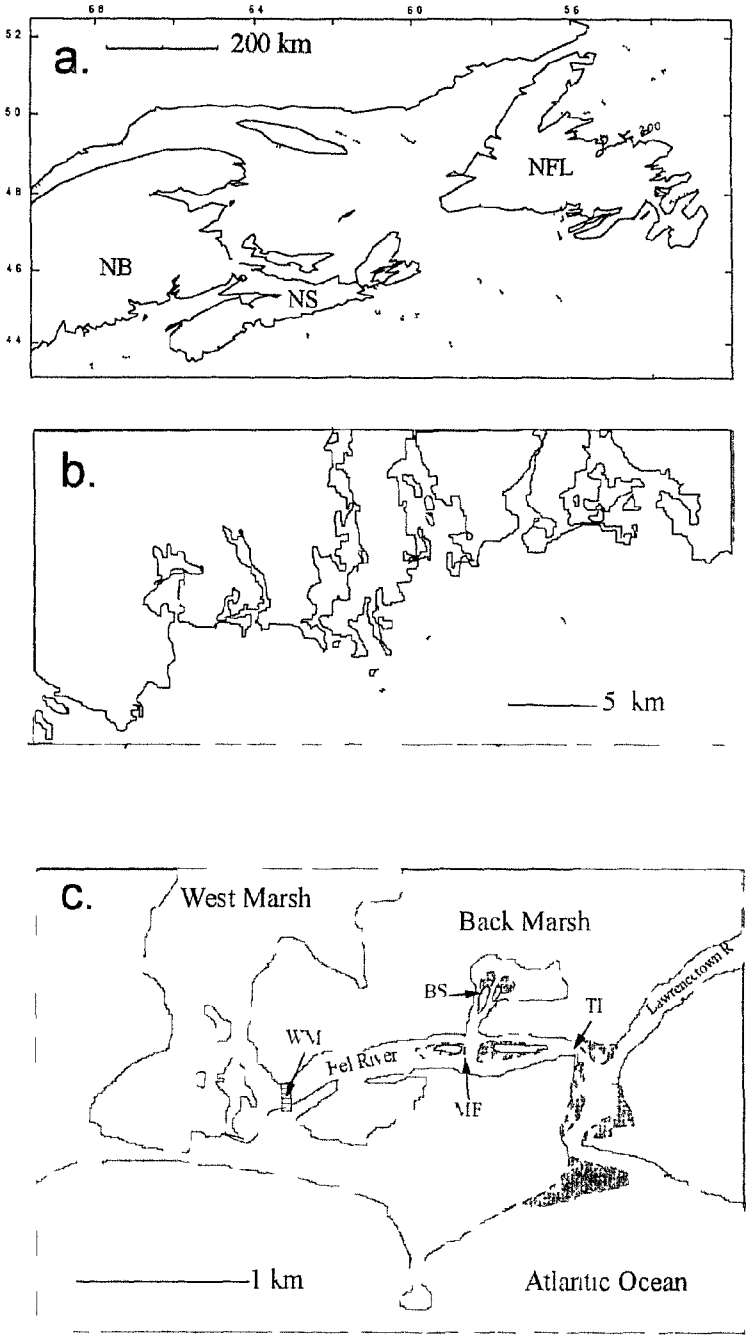

Fig 1 2 Study site *a* Location of Eel River, Nova Scotia NB, New Brunswick, NFL, Newfoundland, NS, Nova Scotia, *b* Eel River-Lawrencetown coastal environment, *c* Eel River estuary Stations TI, Tidal Inlet, ME, Middle Estuary, West Marsh, West Marsh, BS, Benthic Site Arrow at West Marsh points to location of culvert Dark shading indicates intertidal sandflats

Lawrencetown River ~0.6 km from the Atlantic Ocean (Fig. 1.2). This lower estuary region drained a shallow peripheral basin, Back Marsh. The second section was the 9.9 · 10^5 m^2 West Marsh (WM) that connected to the lower estuary by a narrow, 1.5 m wide manmade culvert. The culvert greatly restricted interchange of water between the two sections. Freshwater input was by runoff primarily to West Marsh. The remainder of this study is concerned with the dynamics of the lower estuary from the tidal inlet to the connecting culvert at West Marsh.

The tidal inlet was ~200 m long, and had a cross section composed of a 22 m wide main channel (maximum depth 2.6 m) bounded on the north by a 26 m wide intertidal sandflat. A steep peat bank and *Spartina alterniflora* marsh formed the southern boundary. The channel bottom had a topographically rough, heterogeneous structure composed of boulders, large cobbles, sand ripples, clumps of the mussel *Mytilus edulis*, and patches of seagrass (*Zostera marina*). The relatively straight geometry of the inlet forced predominately bidirectional flows past the sampling site. However high turbulence, standing waves, and mesoscale eddies were often observed, indicating the vertically well-mixed nature of the inlet water.

The seaward end of the lower estuary consisted of flood-delta deposits which graded from high intertidal *Spartina*-dominated islands, through intertidal sandflats, to subtidal channels of sand and *Zostera*. Populations of the bivalves *Mya arenaria* L., *Macoma balthica* L., and *Gemma gemma* Totten exceeded combined densities of 10^5 ind · m^{-2} in the sandflat and channel environments. Landward of the flood-delta deposits, the

mainly subtidal Eel River was characterized by silty sediments dominated by *Zostera,* where the density of bivalves was reduced

The shallow Back Marsh embayment draining into Eel River had a surface area of approximately 0 7 10^5 m^2 The seaward section of the embayment was an anastomosing tidal creek and intertidal sandflat complex (Benthic Site, BS) where a 3 year benthic recruitment study was conducted (Chapter 3), while the landward basin was composed of shallow subtidal *Zostera* beds At BS, the channel was ~100 m long, 15 m wide, and had a low tide depth of 0 4 to 0 6 m at the point of measurements, but widened and shoaled shoreward Both sides of the channel were bordered by steep *Spartina* banks seaward, while the northern bank graded into a 100 m^2 sandflat in the shoreward direction The substratum was composed primarily of homogenous sand intermixed with cobbles and *Mya* shells, and was ~20% vegetated by *Zostera*

1.2.2 Data Collection

The hydrodynamic patterns of the Eel River estuary were investigated over several spatial and temporal scales relevant to larval bivalve transport and retention Time series of tidal elevation were measured on a seasonal time scale and used to calculate volume exchange of the estuary Variation of salinity, temperature, and algal pigment concentration as functions of tidal elevation were made on the estuarine spatial scale (among stations within the estuary) over tidal time periods (5 to 10 h) Finally, plankton abundance, current velocity, salinity, and temperature were collected over 2 to 3 tidal cycles (24 to 36 h) at the Tidal Inlet station, and over 5 to 7 h periods in a tidal creek at the Benthic Site station Plankton samples were taken at 2 to 3 hour intervals Both sites

were characterized by strong, bidirectional flow patterns. These investigations allowed the long-term flushing of the estuary to be compared with variation of larvae over tidal time scales

1.2.2.1 Circulation patterns

Tidal exchange

Water level and temperature records were collected at Benthic Site by continuous pressure-temperature recorder (Vemco, Shad Bay, N.S.) deployments during summer 1994 (6 June to 30 August), which encompassed the expected spawning period of the estuarine bivalves. The relationship between mean tide and temperature at Benthic Site was evaluated by cross-correlation analysis with lags of 0 5 h intervals for 6 h. Tidally-driven exchange was estimated from the tidal exchange ratio, r (Ketchum 1954), which was calculated for each summer tide as

$$r_t = 1 - (h_t / z_{t-1}), \qquad \text{eq 1 1}$$

where h_t is the low tide water level (relative to the bottom) at time t, and z_{t-1} is the previous high tide level. At a given high tide water level, $z_t = h_{t-1} + a_t$, where a_t represents the tidal range and h_{t-1} is the previous low tide water level The exchange ratio describes the proportion of water lost per tide and was used to model larval dispersion (see section 1 2 4 0 below) Estuarine residence times were calculated as

$$T_{res} = T_{tide} / r_t, \qquad \text{eq 1 2}$$

where T_{res} is the residence time (d) and T_{tide} (d) is the tidal period (Geyer & Signell 1992) This technique was expected to give a lower boundary on residence times (Geyer

& Signell 1992) Finally, cross-correlation analysis of paired pressure sensor time series was used to evaluate the attenuation and phase shift of the tidal wave as it propagated from Tidal Inlet to Benthic Site and from Tidal Inlet to West Marsh (Fig 1 2) The data for the cross-correlations were lagged 0 5 h intervals for 6 h

Salinity

An overview of the estuarine circulation was provided during 1992 through 1994 by repeated sampling of selected stations over 6 to 10 h periods The sample locations, shown in Fig 1 2, were Tidal Inlet, a middle estuary site (ME), and West Marsh stations in the main section of the lower estuary and the Benthic Site station in Back Marsh At each station, time series measurements of salinity, temperature, and chlorophyll-*a* (chl-*a*) concentration (methods described below) were made in relation to tidal elevation recorded at Tidal Inlet or Benthic Site The time series were used to evaluate movement of water masses and phytoplankton concentrations

1.2.2.2 Volume transport

Current velocity measurements made at Tidal Inlet and Benthic Site were used to calculate volume transport between the estuary and nearshore zone and within the estuarine creek system, respectively At Tidal Inlet, measurements were acquired over 25 to 27 h periods on 3 dates spanning the expected periods of bivalve spawning in 1994 Instruments were deployed subtidally at depths between 0 15 and 1 0 m below mean low water Horizontal (U) and vertical (Z) water velocities were measured with Marsh-McBurney electromagnetic current meters secured with aluminum poles at positions 0 15 and 0 50 m above the bottom The mean velocity and standard deviation were calculated

for 10 min measurement intervals and logged Pressure and temperature were recorded at 30 min intervals, and salinity values were measured periodically with an electronic conductivity-temperature meter At Benthic Site, the current meters were deployed separately 0 15 m above the bottom. At both sites, the cross-sectional area of the channel was measured by standard surveying techniques

Volume transport of water was calculated with velocity and tidal height data in conjunction with channel topography (Hume & Bell 1993) The instantaneous, integrated cross-sectional volume transport Q (m^3 s^{-1}) was determined at each 10 min interval by multiplying the depth-averaged horizontal velocity U (m s^{-1}) by the cross-sectional channel area A_{yh} (m^2),

$$Q = {}_0\int^h U \; A_{yh}\, dt, \qquad \text{eq 1 3}$$

where A_{yh} varied as a function of tidal elevation h Velocity and transport in this study are positive in the landward direction (import) and negative in the seaward direction (export) The relation A_{yh} (h,t) was determined empirically at Tidal Inlet as a second order regression equation

$$A_{yz} = 13\ 4\ (h^*)^2 + 43\ 3\ (h^*) + 43\ 9 \quad (r^2 = 0\ 998,\ p < 0\ 001,\ n=15), \qquad \text{eq 1 4}$$

and with a linear equation at Benthic Site

$$A_{yz} = 12\ 3\ (h^*) + 7\ 4 \quad (r^2 = 0\ 924,\ p < 0\ 001,\ n=8), \qquad \text{eq 1 5}$$

where h* is the tidal elevation calibrated to the marsh surface The calculations of Q assume that the vertically averaged velocity profiles were horizontally homogeneous (i e $\delta U / \delta y = 0$) (Fisher *et al* 1976) The total volume exchanged during a tidal period, the tidal prism Ω (m^3), was determined by numerical integration for ebb and flood periods as

$$\Omega = {}_0\int^T Q \; dt \qquad \text{eq. 1.6}$$

where T is the duration in seconds of the ebb or flood tide (Fisher *et al.* 1976). The tidal prisms were used to compare the steady state volume balance of the estuary as

$$\Omega_E = \Omega_F + V_{FW} \qquad \text{eq. 1.7}$$

where Ω_E is the ebb tidal prism, Ω_F is the flood tidal prism, and V_{FW} is the volume of freshwater, all in units of m^3 (Fisher *et al.* 1976; Hume & Bell 1993).

1.2.2.3 Plankton transport

Plankton samples were collected with a submersible, battery powered sump pump with an intake rate of ~250 m*L* · s^{-1}. The pump had a rotary impeller that minimized damage to captured organisms. The intake hose was 2.45 cm in diameter, and was fitted with a t-joint positioned 0.15 m above the channel bottom and arranged with openings parallel with the bidirectional channel flow. During a sample series, plankton collections were made at 2 to 3 h intervals, and abundance was estimated with 3 replicate 15 *L* water samples which were filtered through 80 μm screens. Immediately after filtration, the contents of each screen was transferred to a specimen container and preserved with 10% buffered formalin and Rose Bengal. Concurrently, 3 replicate algal pigment samples were collected by filtering 50 to 200 m*L* of water (depending on seston concentration) through Whatman GF/C filters (1.2 μm pore diameter). Pigment samples were maintained in a cooler in the field and transferred to a -20°C freezer on return to the laboratory.

During processing, zooplankton samples were washed in filtered seawater and sorted under a dissection microscope. Organisms were sorted to major taxonomic group:

bivalve, gastropod, and annelid larvae, and calanoid and harpactacoid copepods. The longest dimension of bivalve veligers and resuspended juveniles were measured and the bivalves were categorized by size as immature (< 200 μm) or competent for settlement (> 200 to 300 μm). The large dinoflagellates *Ceratium* spp. were also enumerated. Algal pigments were extracted in acetone after freezing and chl-*a* and phaeopigment concentrations measured in a Turner Designs 10 fluorometer.

The instantaneous tidal transport of zooplankton groups, Q_P (ind · s^{-1}), was calculated for each replicate sample by multiplying plankton concentration C (ind · m^{-3}) by the corresponding instantaneous volume transport Q,

$$Q_P = C \cdot Q, \qquad \text{eq. 1.8}$$

where it is assumed that $\delta U/\delta y = \delta C/\delta z = \delta C/\delta y = 0$. The results are presented as time series. Total transport during a tidal period, N (ind), was determined by

$$N = {}_0\int^T Q_P \, dt, \qquad \text{eq. 1.9}$$

where T is as above. The numerical value was found by digitizing the area under plots of spline-interpolated mean Q_P by elapsed time.

For samples collected without velocity measurements, instantaneous plankton concentrations C (ind · m^{-3}) ± SD were plotted as times series.

1.2.3 Statistical analysis

Principal components analysis (PCA) was employed to investigate relationships in the multivariate data set. The physical variables in the matrix were tidal level, salinity, temperature, and light/dark The biological variables included the concentrations of

bivalve, gastropod, and annelid larvae, calanoid copepods, *Ceratium* spp , and chl-*a* The constituents of the factor groupings were designated by correlation coefficients ≥ 0.5

1.2.4 Retention model

A one-dimensional numerical model was used to estimate larval residence times in the estuary during summer 1994 In theory, the model resembles expressions from Ketchum (1954) and Ayres (1956), where population decreases due to flushing were modeled with an exponential decay function, $n_T = n_0 (r)^T$ These models are based on a constant tidal exchange ratio. In contrast, the model presented here was empirical and employed exchange ratios determined from field data, which allowed for variation in retention due to the spring-neap tidal cycle to be included The model simply computed the abundance n for each time step as $n_t = r_t \; n_{t-1}$, where $r_t = 1 - (h_t / z_{t-1})$ For a given simulation, larval retention was evaluated from a single spawning event, and larvae were assumed to be mixed passively and completely The veligers were subsequently lost to the estuary in proportion to the ebb tidal prism, $z_{t-1} - h_t$, and the concentration retained in the estuary was then diluted by the following flood tide, and so on Results from extreme conditions in the field data were plotted against runs of the exponential model using a range of exchange ratios For both models, larval abundance was standardized to an initial value, $N = n / n_{max}$ and a model simulation was run until larvae were reduced to less than $10^{-5} n_{max}$ Time was standardized to development time to settlement, $T_S = t / T_D$, where T_D was set at 14 d

1.3 Results

1.3.1 Circulation patterns

1.3.1.1 Tidal exchange

Tidal elevation and temperature time series

Tidal elevation during Summer 1994 ranged from < 0 3 to 1.1 m, and water level exhibited clear spring-neap variation indicative of tidal set-up (Fig. 1.3a). Residual water levels could exceed 0 4 m during spring tides Tidal exchange ratios ranged from 0 2 to

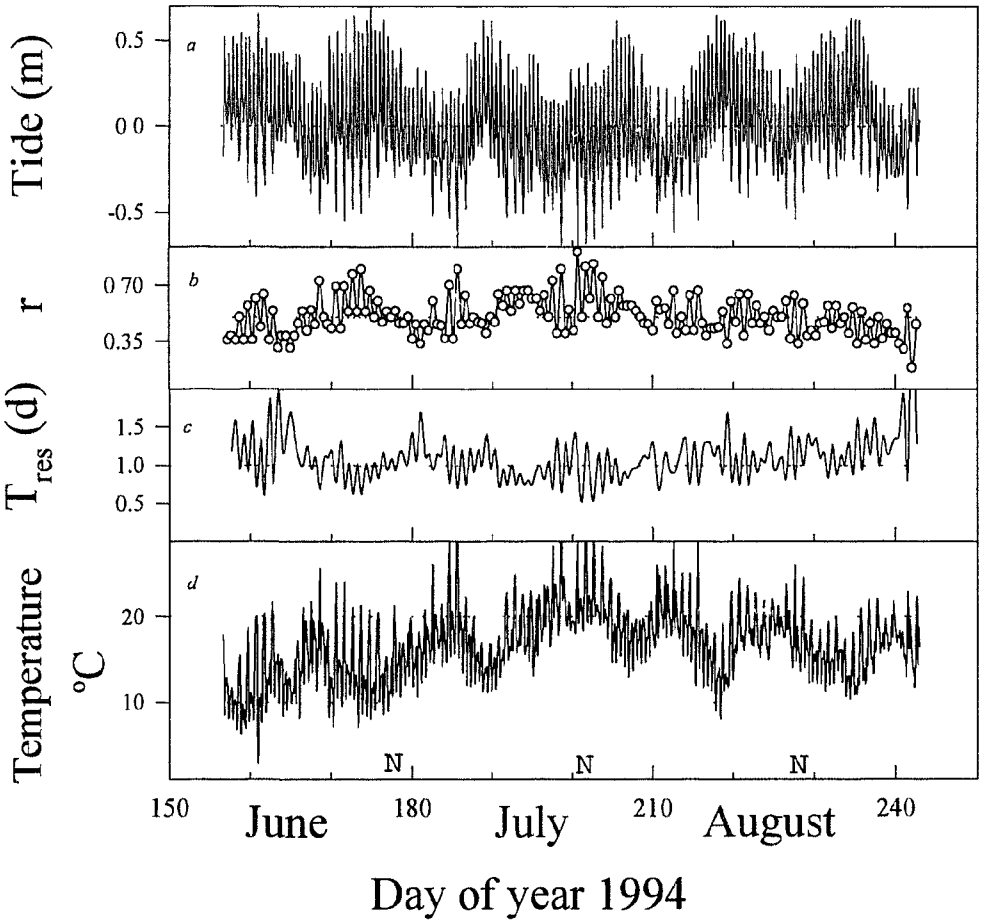

Fig 1 3. Time series of *a.* mean tidal height, *b.* mean exchange ratio, *c.* residence times; and *d.* temperature for the summer of 1994. N designates sample periods at the tidal inlet

0.9 with on average 50.7% (± 12.3% SD) of the water being replaced per tide, indicating the estuary was well ventilated (Fig. 1.3b). The exchange values shown illustrate the temporal variation caused by tidal inequality and the spring-neap cycle. High exchange was maximized during periods of lower low water. Residence times T_{res} were < 2 d throughout the summer (Fig. 1.3c).

Temperature varied on tidal, diurnal, lunar, and seasonal periodicities (Fig. 1.3d). Rapid heating of estuarine water occurred when low tide corresponded with days of high insolation, while cooler seawater temperatures prevailed during flood. This commonly resulted in temperature fluctuations in excess of 10°C in < 1 hr during the day, while the temperature variation between ebb and flood was generally ~5°C at night. The diurnal signal was weaker but flood water was clearly discernible from ebb water by temperature alone. Cross-correlation analysis demonstrated a negative correlation (r^2 =-0.757, $p < 0.001$) between mean water level and temperature at lags of 0 h.

Paired pressure sensor deployments

There was a high coherence between the time series of water level between Tidal Inlet and Benthic Site stations at lags of 0.5 to 1.0 h (correlation coefficients of 0.871 to 0.862), indicating the rapid propagation of the tidal wave from the inlet to the benthic site (Fig. 1.4a). However, attenuation in elevation was generally observed. Additionally, variation in the mean water level between Tidal Inlet and Benthic Site during ebb periods indicated the occasional incomplete draining of Back Marsh relative to the main estuary. The storage of water in Back Marsh, or tidal set-up, was normally limited to a single tidal period and can be observed as diurnal variation in Figs. 1.3 and 1.4a. In contrast, there

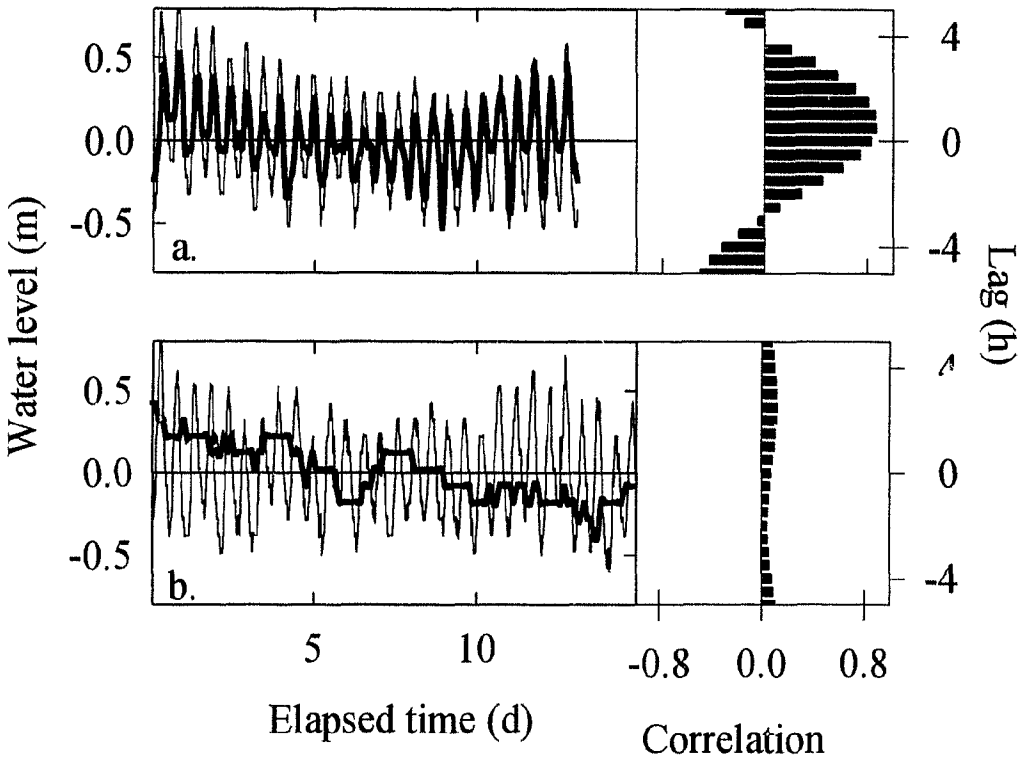

Fig. 1.4. Paired pressure sensor readings (left) and correlation coefficients (right) for *a*, Tidal Inlet (thin line) versus Benthic Site (bold line) and *b*, Tidal inlet (thin line) and West Marsh (bold line). The tidal signal was attenuated at West Marsh.

was little coherence in the tidal time series between Tidal Inlet and West Marsh over the 2 wk measurement period (Fig. 1.4b). Tidal signals were generally < 0.2 m in elevation and 3 to 4 hr out of phase with the tide at Tidal Inlet. Fluctuations in water levels in West Marsh appeared to reflect patterns of freshwater drainage.

1.3.1.2 Salinity

The horizontal distribution of salinity and chl-*a* are presented as time series from stations Tidal Inlet, Middle Estuary, West Marsh, and Benthic Site during 1992 (Fig. 1.5a-c) and 1993 (Fig. 1.5d-e), along with the tidal record from Tidal Inlet. For each

year, the series of 3 plots trace 6 to 10 h sampling periods separated by 2 to 3 wks. All plots show early flood through early ebb tide except plot *a*, which traces the middle of ebb through early flood. A strong horizontal salinity gradient was generally evident, although there was considerable variation in the freshwater input on weekly and yearly scales. Horizontal salinity gradients of up to 20 were observed between West Marsh and Tidal Inlet, while vertical variation in salinity was limited by shallow depth and turbulent flow. These time series illustrate tidal flushing of the lower estuary, variation in the penetration of saline water to West Marsh between tides, and export of autochthonous algal blooms from West Marsh to the nearshore.

Fig. 1.5a illustrates typical ebb tide conditions. Fresher water draining from West Marsh reached the Middle Estuary station, while water exiting from the estuary at Tidal Inlet remained slightly more saline. This was due to mixing with water from Benthic Marsh which had a small terrestrial drainage basin and consequently maintained higher salinity. During flood tide, salinity was raised to coastal values at all lower stations, while salinity at West Marsh remained unchanged during the sample period illustrated in Fig. 1.5a.

In contrast, penetration of coastal water to West Marsh was periodic, reflecting variation in tidal height and freshwater volume. Fig. 1.5b and c show examples of salinity intrusion during flood tides in 1992 and suggest a link between tidal height and salinity penetration. Similar flood tide examples are shown for sample periods in 1993 (Fig. 1.5 d to f) to indicate the tidal excursion length L rarely extended to West Marsh. Maximum salinity signals at West Marsh always lagged the initiation of flood by 2 to 3 h and

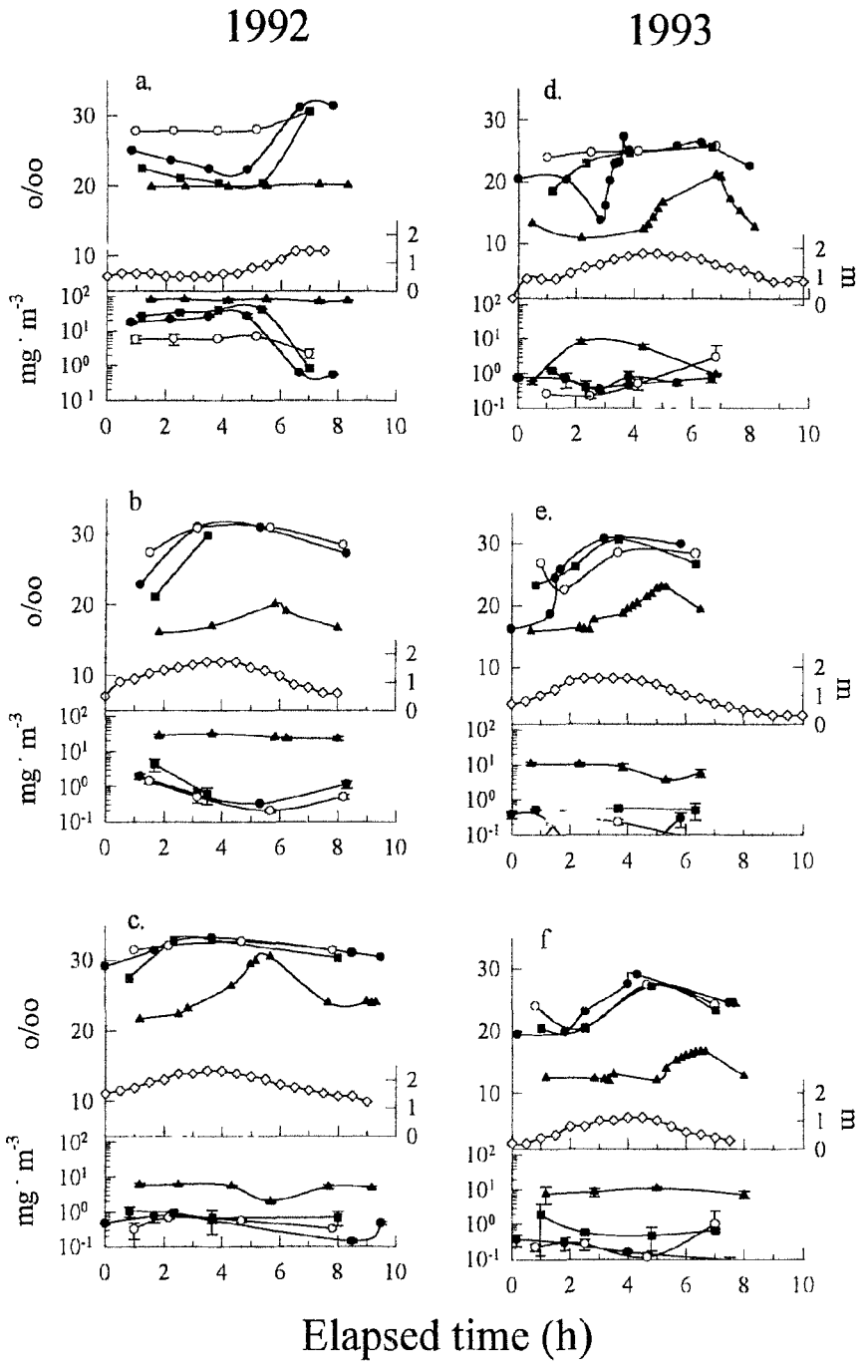

Fig. 1.5. Time series of salinity (upper panels) and chlorophyll-*a* concentrations (lower panels) measured at estuarine stations Tidal Inlet (●), Middle Estuary (■), West Marsh (▲), and Benthic Site (O), with tidal height measured at Tidal Inlet (middle panels). *a.* 4 September 1992; *b.* 17 September 1992; *c.* 5 October 1992; *d.* 9 June 1993; *e.* 25 June 1993; *f.* 9 July 1993.

water appeared to be ebbing from Tidal Inlet while flooding at West Marsh. Thus, portions of water from West Marsh could exit the estuary in a single ebb tide but the area between Tidal Inlet and West Marsh lacked complete tidal exchange. Lower stations were rapidly flushed by the tide.

An intense algal bloom originating in West Marsh during Autumn 1992 seved as a tracer for freshwater and estuarine mixing processes During the ebb tide illustrated in Fig 1.5a, chlorophyll-*a* concentrations, exceeding 80 mg m^{-3} at West Marsh, decreased during the transit seaward due to mixing (and perhaps benthic grazing or settling). A relatively large amount of algae was exported from the estuary (~30 mg chl-*a* m^{-3}). Pigment concentrations were greatly reduced in the flooding water (< 2 mg chl-*a* m^{-3}), and the bloom was not evident at the Benthic Site. Subsequent sampling periods in 1992 indicated a decrease in algal concentrations (Fig. 1.5 b and c), and levels remained moderate in West Marsh during the 1993 periods shown in Fig. 1 5d to f. Note that pigment concentrations generally dipped during salinity maxima at West Marsh

1.3.2 Transport

1.3.2.1 Volume transport at the tidal inlet

At the tidal inlet (Fig 1.6a), time series of salinity, temperature, and velocity had strong coherence with tidal stage and exhibited consistent trends between sample dates. The time series for volume transport closely followed velocity but was modified by the smaller cross-sectional areas during ebb. The following description for 27 June 1994 illustrated in Fig. 1 6 summarizes the observed patterns

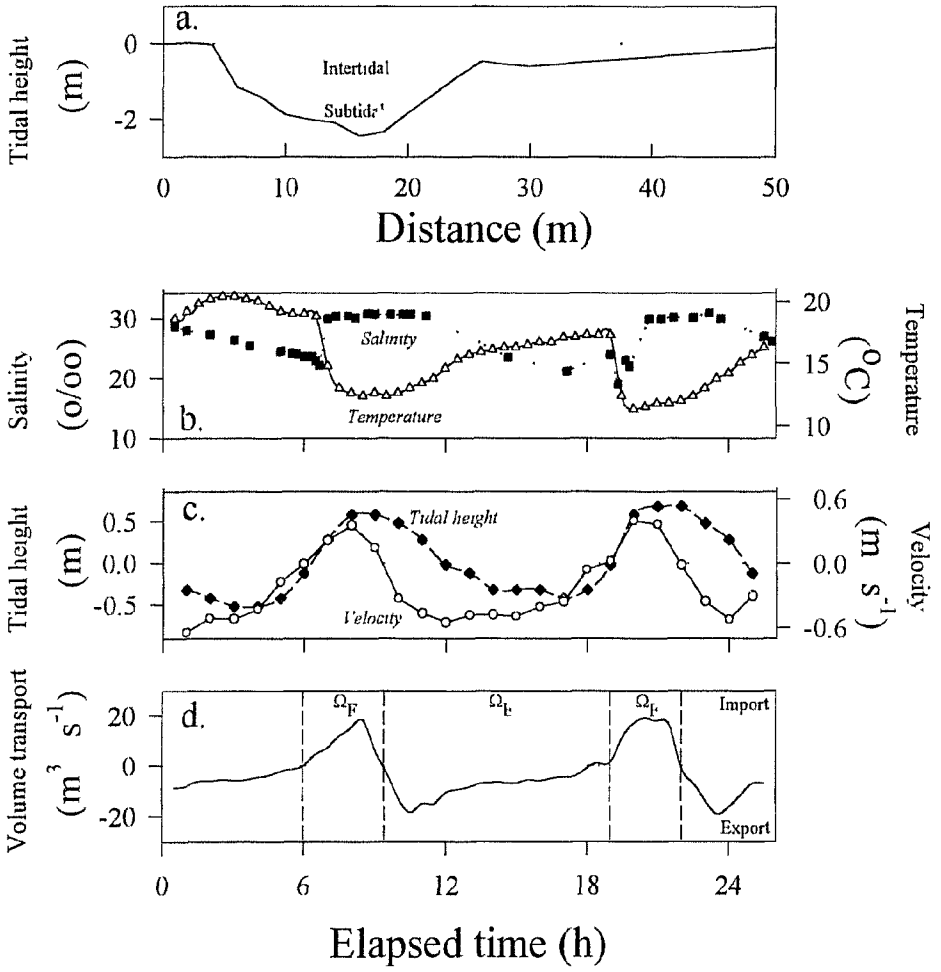

Fig 1 6 Measured and derived physical variables at the tidal inlet. *a.* Channel cross-sectional area as a function of tidal height *b* Time series of salinity (■) and temperature (Δ). *c.* Time series of mean tidal height (◆) and velocity (O). *d.* Time series of volume transport. Ω_F, flood tidal prism; Ω_E, ebb tidal prism. For velocity and volume transport, positive values indicate import into estuary and negative values denote export.

Flood currents lagged 1 to 2 h past the beginning of rising water until equalization of pressure gradient forces between rising flood water and ebbing estuarine water (Fig. 1.6). With increasing tidal height, the ebb velocity steadily declined and usually changed direction with a slack water period of < 15 min. Temperature during ebb

generally remained constant and salinity generally decreased (but see below) until the commencement of flood water, when there was a rapid rise in salinity and drop in temperature to coastal values (Fig 1 6b) Occasionally the salinity and temperature traces exhibited characteristics of tidal trapping (Fisher *et al* 1976), which indicated horizontal mixing with water originating from the Lawrencetown River (Fig 1 6b) The flooding coastal water entered the estuary as a progressive wave in excess of ~0 1 m s^{-1} and completely mixed with and/or displaced the ebbing estuarine water (Fig 1 6c) During this period, salinity fluctuations could exceed 20 o/oo h^{-1}, and temperatures decline more than 15°C (Fig 1 6b) After the passage of the flood tide front, salinity and temperature remained at coastal values while the flood velocity steadily increased to a maximum of 0 5 to 0 6 m s^{-1} Total flood period lasted 3 5 to 5 hours, and peak discharge coincided with maximum velocities Calculated flood tidal prisms Ω_F ranged from 0 46 to 1 43 10^7 m^3 (Table 1 1)

At the end of flood current velocity steadily declined to 0 and again reversed with a only a short period of slack water (Fig 1 6c) The salinity trace during the initial ebb period of high discharge remained at coastal values, indicating the exit of undiluted seawater from the previous flood tide Subsequently, salinity declined and temperature increased as water of mixed salinity flushed from the estuary The ebbing currents maximized 1 to 2 h past flood and remained relatively constant at 0 6 to 0 7 m s^{-1} for the next 4 to 6 h until the next flood period However, discharge peaked near the beginning of ebb and declined with decreasing cross-sectional channel area (Fig 1 6c) The ebb period was generally 1 5 times longer than the flood, and total discharge during ebb was 1 5 to 2

times the flood tidal prism (Fig. 1.6d; Table 1.1). During both ebb and flood, water in the channel was well mixed.

1.3.2.2 Plankton transport at the tidal inlet

There were large differences in plankton transport through the tidal inlet between ebb and flood tides, among dates sampled, and among taxonomic groups. In June, gastropod larvae were found in relatively low abundance with import and export being approximately equal at 1.5 to 2.3 · 10^8 ind · Ω^{-1} (Fig. 1.7, Table 1.1). Over the two tidal periods sampled in June, there was a net import of 1.4 10^8 ind. In contrast, the July and August samples exhibited large exports from estuary to nearshore with total N ranging from 0.2 to 20.0 · 10^6 ind · Ω_E^{-1}, while import rates remained at June levels. Net export was 2.8 10^9 ind over the two tidal periods sampled in July and 1.7 · 10^9 during August. Transport peaked several hours into ebb in waters of estuarine salinity. Clearly, in the latter months the estuary was a source of gastropod larvae and export greatly exceeded import.

Bivalve transport was 1 to 2 orders of magnitude less than that of gastropods (2.8 · 10^6 to 8 9 · 10^7 ind · Ω^{-1}), and veligers were in relatively high abundance in the June and July samples compared to August (Fig. 1.8, Table 1.1). Import exceeded export in 4 of 6 tidal cycles. A net import was measured during each of the three sample dates, but there was no consistent pattern relative to larval size. Overall, 58 to > 99% of the bivalves in a tidal prism were immature larvae < 200 μm in length (Table 1.1). The size structure of the flood and ebb larval populations changed in 3 of 6 tidal periods. During one flood-ebb pair in June, proportionally more large veligers remained in the estuary, while in July

Table 1.1. Total transport of molluscan larvae and *Ceratium* per tidal prism for each of 3 sample dates in 1994. Bivalve larvae are divided by size into immature (< 200 μm) and competent (> 200 μm) groups. Σ designates net transport over the tidal cycles shown, with positive numbers indicating import and negative export from the estuary. Estimated abundance of the two size factions does not sum to total abundance due to variations in the spline-interpolated areas.

		Bivalves (x 10^7 ind.)			Gastropods (x 10^9 ind)	*Ceratium* (x 10^9 ind)	Tidal Pris (10^5 m^3)
Date	**Tide**	**< 200 μm**	**> 0 μm**	**Total**			
27 June	Flood1	3.22	2.21	5.43	0.15	1.72	1.16
	Ebb1	-2.87	-0.57	-3.44	-0.19	-0.74	2.64
	Flood2	5.77	1.28	6.51	0.23	4.22	1.57
	Ebb2	-0.66	-0.15	-0.74	-0.05	-0.79	1.44
	Σ	5.46	2.77	7 74	0.14	4.41	-1.36
21 July	Flood1	8.45	0.71	8.88	0.15	0.34	1.18
	Ebb1	-2.57	-0.86	-3.11	-2.05	-0.11	2.78
	Flood2	1.85	$<10^1$	1.89	0.11	0.03	0.87
	Ebb2	-1.95	$-<10^4$	-1.94	-1.03	-0.03	1.68
	Σ	5.78	-0.15	5.83	-2.82	0 25	-2.41
17 Aug	Flood1	1.51	0.36	1.78	0.04	2.19	0.94
	Ebb1	-0.72	-0.11	-0.94	-1.64	-1.33	2.44
	Flood2	0.17	0.02	0.28	0.11	0.87	0.53
	Ebb2	-0.25	-0.18	-0.43	-0.24	-0.25	1.75
	Σ	0.71	0.09	0.71	-1.74	1.47	-2.73

and August, the ebb waters were enriched in the > 200 μm group in 3 of 4 cases. Proportional size differences between flood and ebb were slight during the other flood-ebb pairs (Table 1.1). The time series of larval transport in relation to the corresponding volume discharge show that while larvae were imported throughout the flood period, the majority of exported larvae were found in the high salinity water, and were rarely observed in the mixed estuarine water. The nearshore zone was thus a source of bivalve larvae for the estuary.

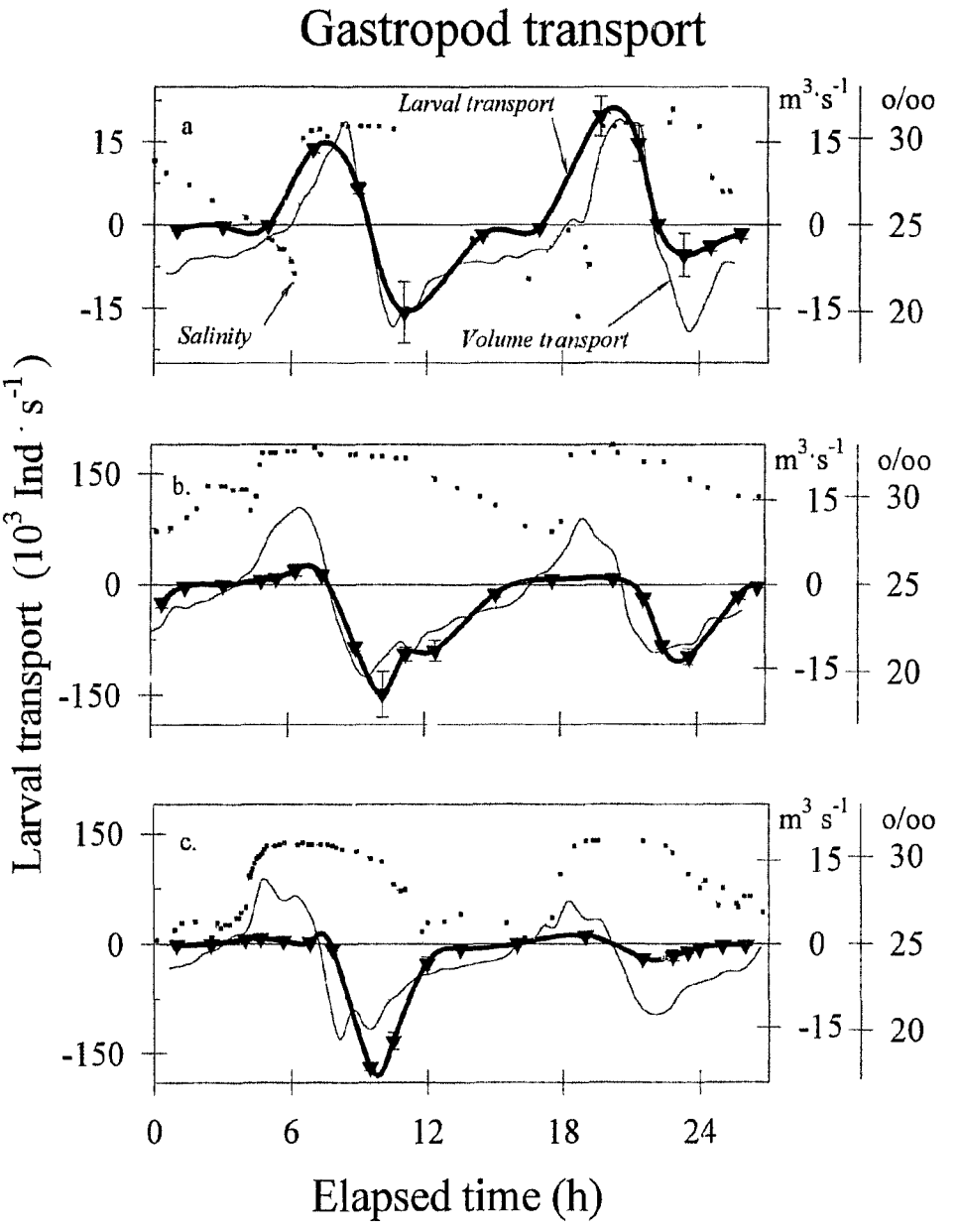

Fig. 1.7. Time series of gastropod larvae transport (ind s^{-1} ± SD, ▼) with salinity (o/oo, ▪) and volume transport (m^3 s^{-1}, thin solid line) at the tidal inlet for 3 dates in 1994 *a.* June; *b.* July; *c.* August.

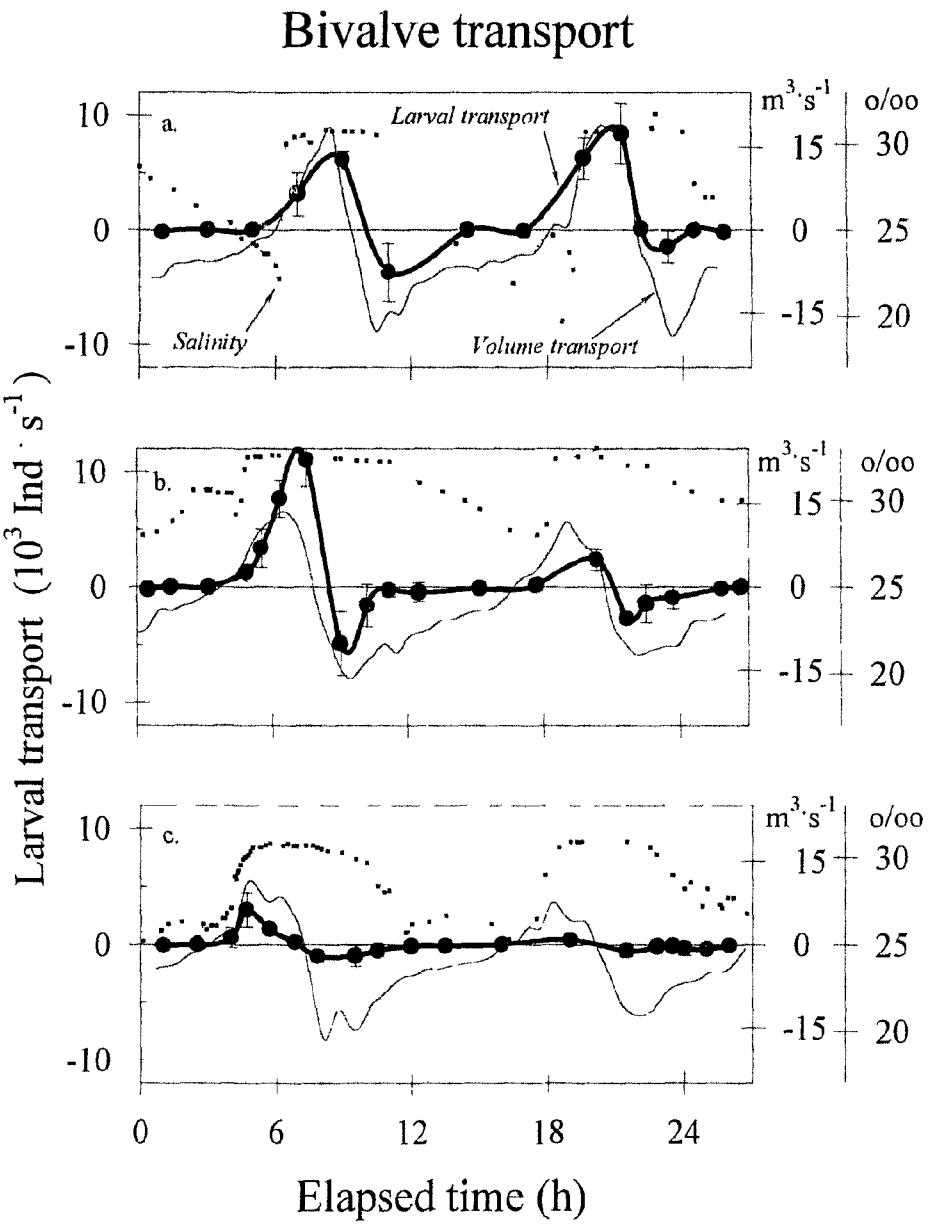

Fig. 1.8. Time series of bivalve larvae transport (ind · s^{-1} ± SD, ●) with salinity (o/oo, ▪) and volume transport ($m^3 \cdot s^{-1}$, thin solid line) at the tidal inlet for 3 dates in 1994. *a.* June; *b.* July; *c.* August.

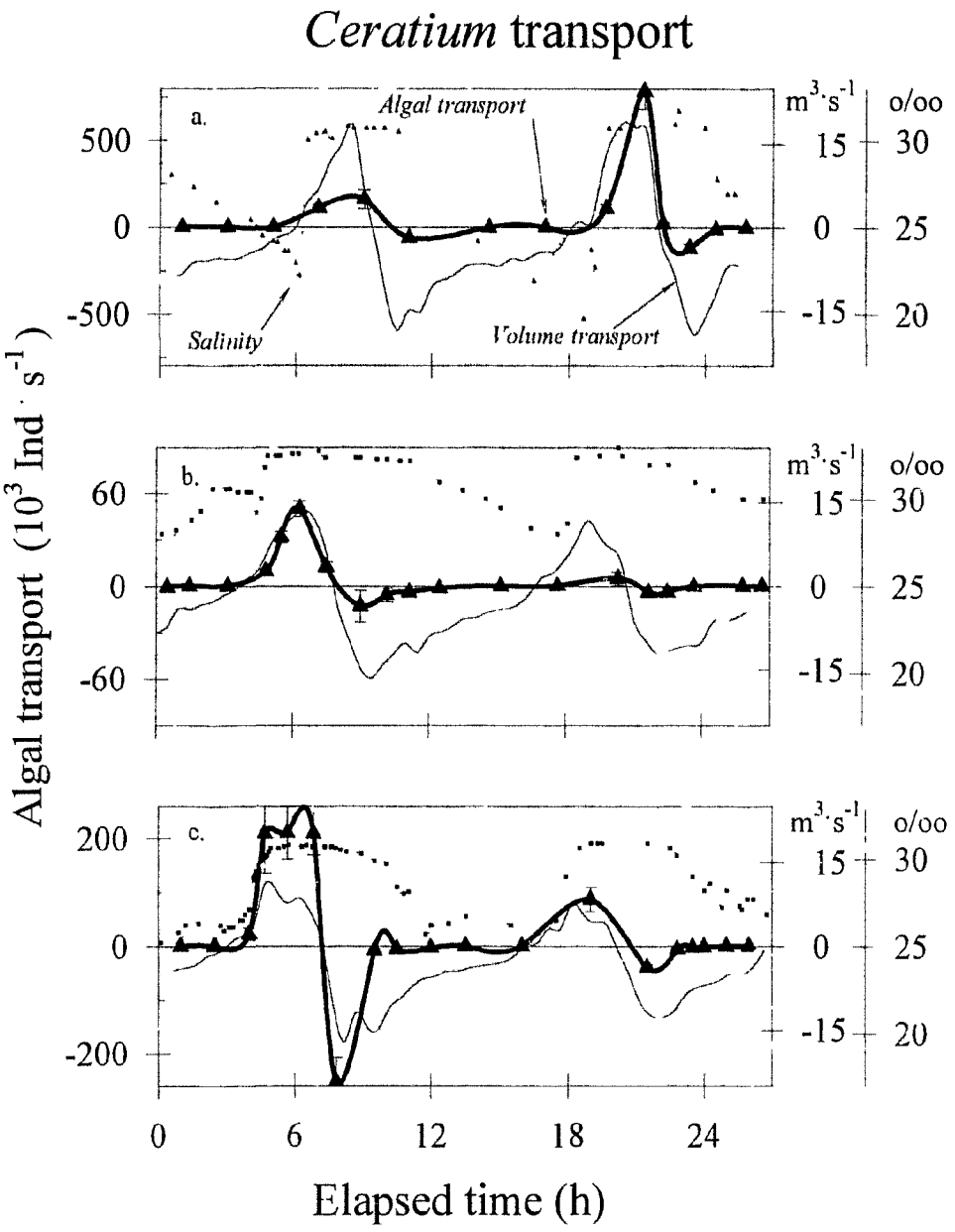

Fig. 1.9

. Time series of the dinoflagellate *Ceratium* spp. transport (ind · s^{-1} ± SD, ▲) with salinity (o/oo, ▪) and volume transport ($m^3 \cdot s^{-1}$, thin solid line) at the tidal inlet for 3

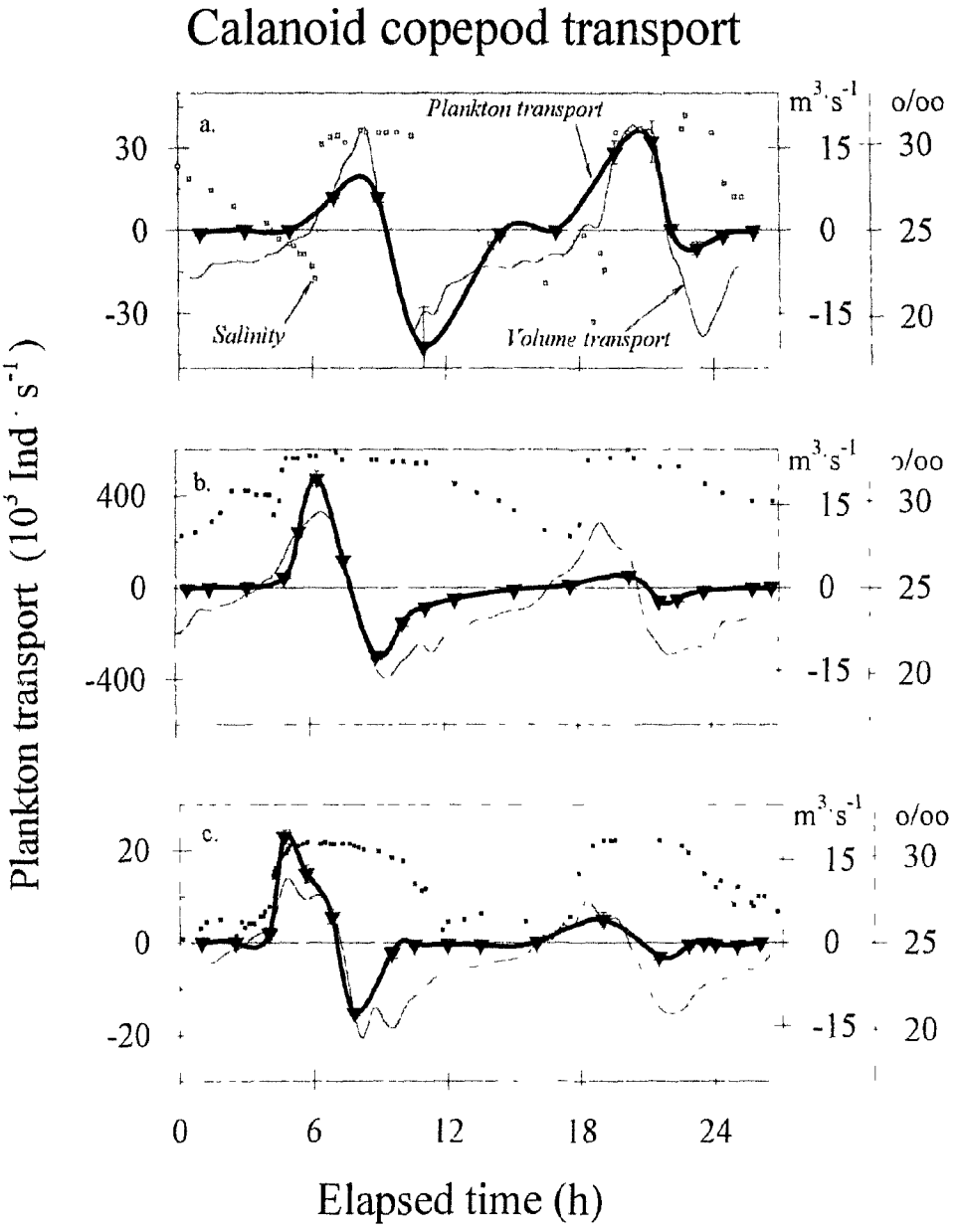

Fig. 1.10. Time series of calanoid copepod transport (ind · s^{-1} ± SD, ▲) with salinity (o/oo, ▪) and volume transport (m^3 · s^{-1}, thin solid line) at the tidal inlet for 3 dates in 1994. *a.* June; *b.* July; *c.* August.

The transport of the large euhaline dinoflagellate *Ceratium* spp., assumed to reflect coastal input, is presented for comparison (Fig. 1.9, Table 1.1). Although abundance varied more widely among sample dates, the transport pattern resembled that of bivalve larvae. Algal cells were imported in high numbers (10^8 to 10^9 ind $\cdot \Omega^{-1}$), and many of the imported individuals were not exported during the next ebb. Net retention occurred during 5 of 6 flood-ebb pairs sampled. Few *Ceratium* were exported in the mixed water mass. Similar results were found for calanoid copepods (Fig. 1.10). Copepods were associated with high salinity water, and abundances dropped off rapidly in the estuarine water mass.

Fig. 1.11 shows the results of time series collected without velocity measurements during a 36 h period beginning 4 August 1993. As indicated by the range of values in the salinity trace, this was a period of high freshwater flushing. Larval mollusc and dinoflagellate concentration patterns (ind $\cdot$ m^{-3}) were found to be consistent with the 1994 results, with peaks of bivalves and *Ceratium* occurring during flood tide and gastropods exhibiting a strong export signal. The export of chl-*a* in the estuarine water near the end of ebb indicates a trophic link of estuarine-derived material with the nearshore. The chl-*a* signal had little relation with dinoflagellate abundance.

1.3.2.3 Volume transport at the benthic site

Measurements made at Benthic Site allowed the transport of plankton within the estuary to be evaluated. Fig. 1.12 shows typical time series of water level and volume transport (Fig. 1.12a), and salinity and temperature (Fig. 1.12b), with transport of bivalve and gastropod veligers (Fig. 1.12c) and *Ceratium* and chlorophyll-*a* flux (Fig. 1.12d) in

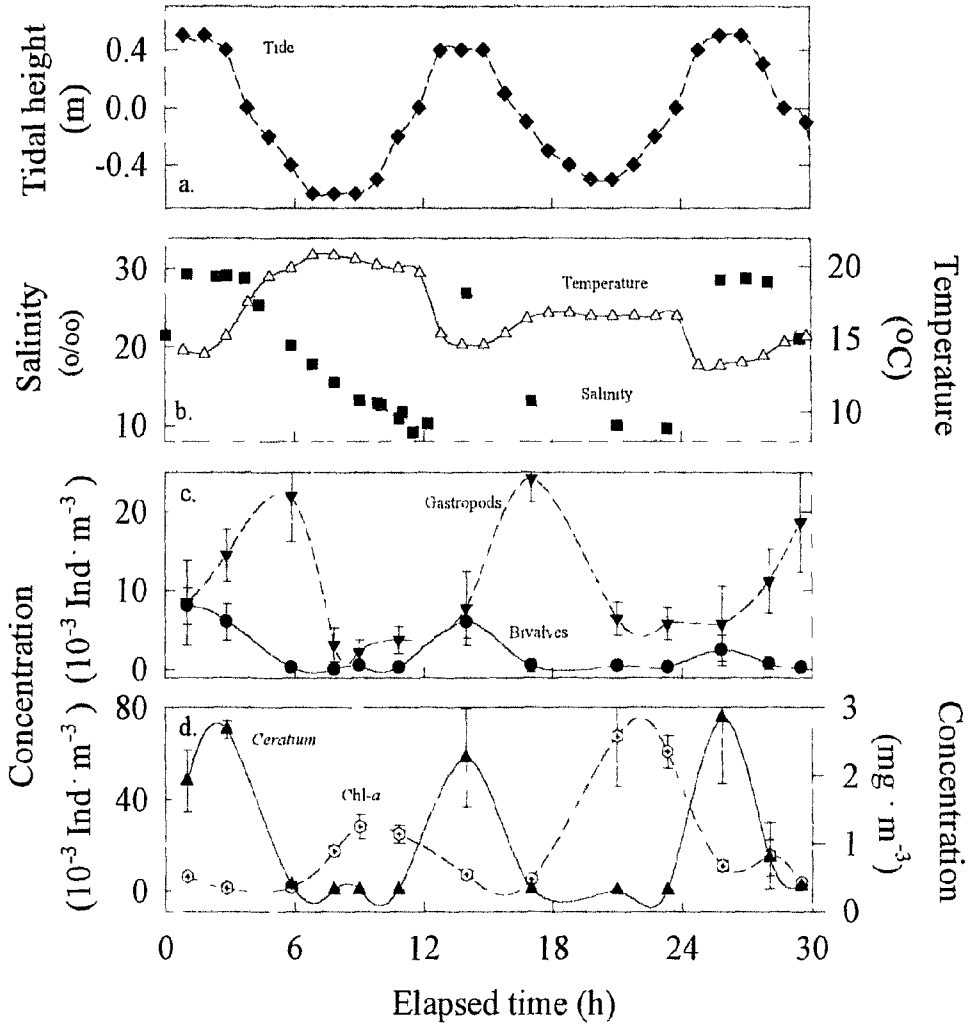

Fig. 1.11. Time series of *a.* mean tide (m); *b* salinity (o/oo, ■) and temperature (°C, Δ); *c.* gastropod (▼) and bivalve (●) larval concentrations (ind m^{-3} ± SD); and *d. Ceratium* (ind · m^{-3} ± SD, ▲) and chlorophyll-*a* (mg m^{-3} ± SD, ⊗) concentrations at the tidal inlet during 4 to 5 August 1993.

the Benthic Site tidal creek. This 5 h period on 30 June 1994 encompassed the end of ebb through most of the subsequent flood. Volume transport during ebb flow was greatly reduced due to the small cross-sectional channel area, and the ebbing water was characterized by constant, high temperature and gradually rising salinity (Fig. 1.12a and b).

The change in direction of volume transport from ebb to flood coincided closely with the rise in water level. The tide increased 0.20 m in height with little variation in salinity or temperature, after which there was a precipitous drop in salinity while temperature remained constant. This $3 \cdot 10^3$ m^3 volume of water originated in the Eel River main channel, and is further evidence of horizontal mixing due to tidal trapping (Fisher *et al.* 1976). The rapid salinity rise and temperature decrease which followed the low salinity water demonstrate the penetration of coastal water to Benthic Site as a relatively unmixed water mass.

1.3.2.4 Plankton transport at the benthic site

The abundance of molluscs and dinoflagellates remained low throughout ebb water and into early flood (Fig. 1.12c and d). A pulse of gastropods moved through the creek 1 h after flood in the tidaly trapped water identified above. There was a concurrent peak in chlorophyll-*a*, but continued low numbers of bivalve veligers or dinoflagellates until the intrusion of the nearshore water, when bivalve transport reached ~$4.0 \cdot 10^3$ ind $\cdot$ s^{-1} and *Ceratium* transport exeeded $3.0 \cdot 10^4$ ind $\cdot$ s^{-1}. Gastropods maintained a transport rate of about $1.0 \cdot 10^3$ ind $\cdot$ s^{-1} during flood. Thus, there was a clear import of bivalves and dinoflagellates to the benthic site in the high salinity flood water, but no evidence of organisms exiting the system during the previous ebb period. Gastropod larvae first appeared in water originating in the Eel River, and were subsequently imported to Benthic Site with coastal water. Further examples of temporal variation of mollusc larvae in tidal creeks are shown in Figs. 1.13 and 1.14, which again demonstrate the prevalence of bivalves with flood water and gastropods with ebb.

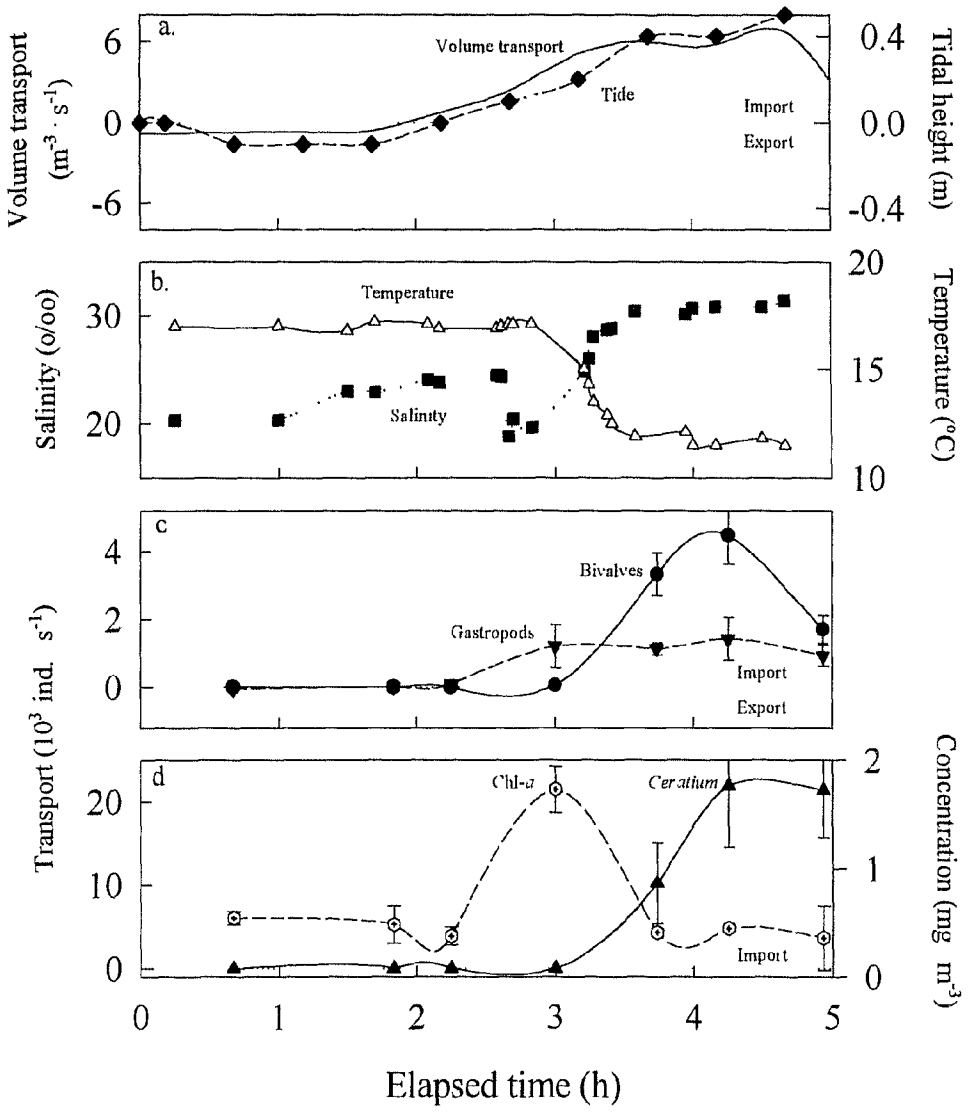

Fig. 1.12. Time series of *a.* mean tide (◆) and volume transport (solid line); *b.* salinity (o/oo, ■) and temperature (°C, Δ), *c.* gastropod (▼) and bivalve (●) larval transport (ind · s^{-1} ± SD); and *d. Ceratium* transport (ind s^{-1} ± SD, ▲) and chlorophyll-*a* concentration (mg · m^{-3} ± SD, ⊗) at the benthic site during 27 June 1994.

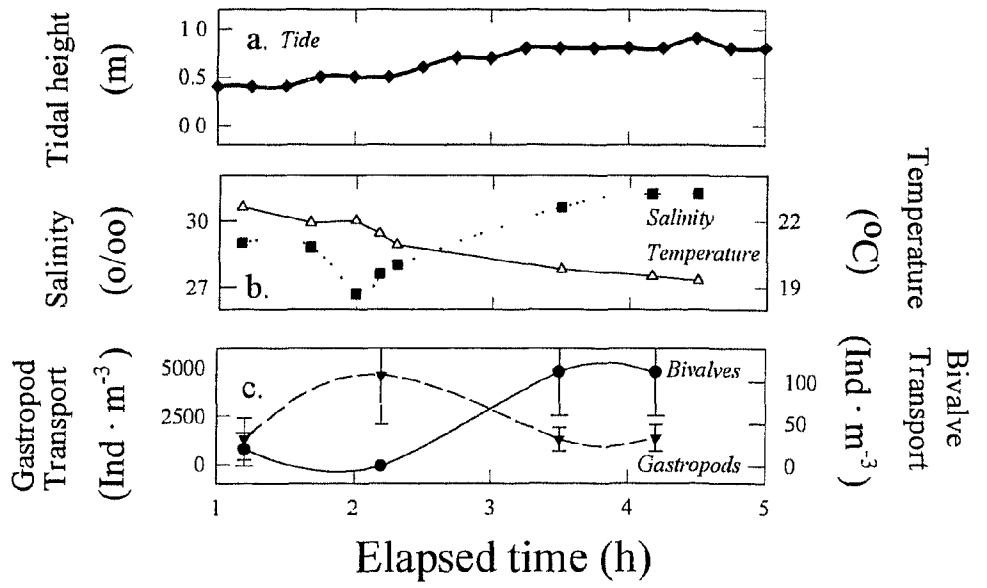

Fig. 1.13 Time series of *a.* mean tide (◆); *b.* salinity (o/oo, ■) and temperature (°C, Δ); *c.* gastropod (▼) and bivalve (●) larval concentrations (ind · m^{-3} ± SD) at the benthic site during 5 September 1993.

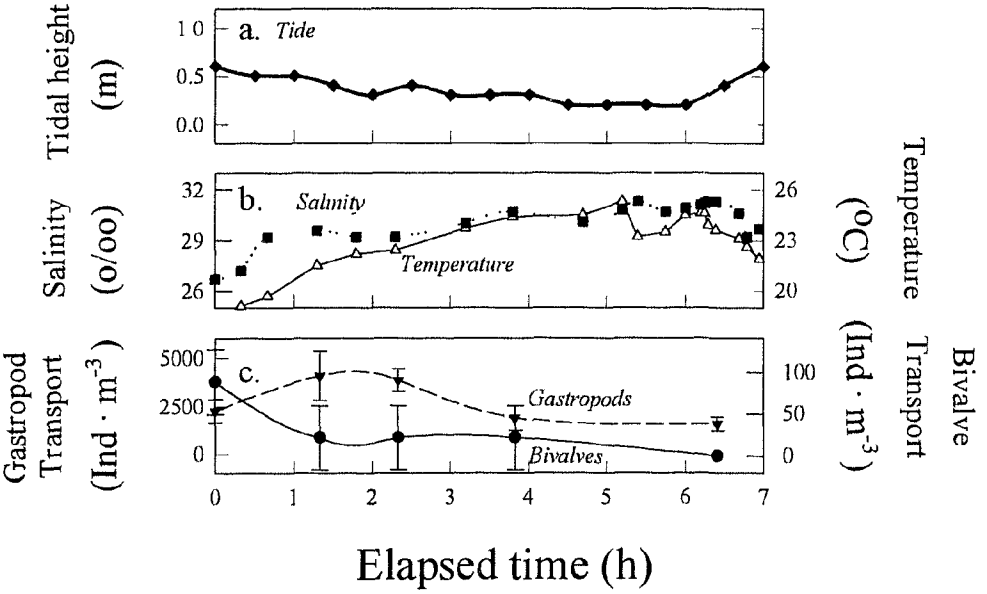

Fig. 1.14. Time series of *a.* mean tide (◆); *b.* salinity (o/oo, ■) and temperature (°C, Δ); *c.* gastropod (▼) and bivalve (●) larval concentrations (ind · m^{-3} ± SD) at the benthic site during 7 September 1993.

1.3.3 Statistical analysis

Table 1.2 lists the component loadings of the physical and biological variables comprising each of the first four factors of the principal components analysis, which together accounted for 75.26% of the variance in the data set. For each factor in Table 1 2, the boxes enclose those variables with component loadings ≥ 0.5. Factor 1 consists of positive correlation between tide, salinity, and the abundance of bivalves, calanoids, and *Ceratium*, while showing a negative correlation with chl-*a*. This factor, explaining 29.6% of the variance, comprises the oceanic group Factor 2, with 18.4% of the variance, is composed of positive correlation between Chl-*a*, annelid larvae, and copepods, and a negative relation with salinity, suggesting an estuarine influence. Factor 3 consists of a link between annelid and gastropod larvae and darkness. Factor 4, comprises just under 10% of the variance and is represented solely by temperature Fig. 1.12 shows factor loading plots for Factor 1 vs Factor 2 (top), and Factor 1 versus Factor 3 (bottom) Both plots clearly reveal the oceanic group, while the estuarine components appear more diffuse.

Table 1.2 Component loadings for principal components analysis

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Mean Tide	0.77	0.11	-0 07	-0.2
Ceratium	0.75	0.38	0.11	-0.02
Bivalves	0.67	0.26	0.01	0.28
Calanoids	0.64	0.51	0.07	0.39
Salinity	0.56	-0 61	-0 19	0.23
Chlorophyll-a	-0.54	0.72	0.05	0.07
Annelids	-0 27	0.62	-0.52	-0.04
Light/Dark	0.06	-0.09	0.85	0.01
Gastropods	-0 09	-0 26	-0.75	0.39
Temperature	-0 48	-0.04	0.37	0.71
% Variance	**29.64**	**18.36**	**17.45**	**9.83**

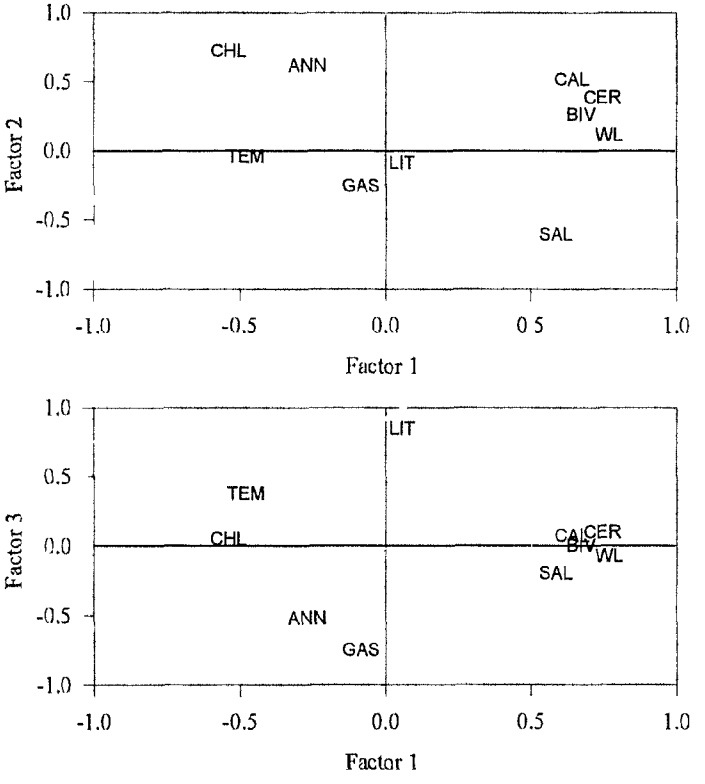

Fig. 1.15. Factor plots for the first three factors of the principal components analysis. See Table 1.2 for factor groupings. ANN, annelid larvae; BIV, bivalve larvae; CAL, calanoid copepods; CER, *Ceratium*; CHL, Chl-*a*; GAS, gastropod larvae; LIT, light/dark; SAL, salinity; TEM, temperature; WL, mean tide.

1.3.4 Tidal exchange model

Fig 1 16 shows larval abundance N as a function of development time for two simulated spawning events Larval concentrations exhibited exponential decline, and in both cases export to concentrations less than 10^{-5} N_{max} occurred before the completion of larval development The index for larval settlement, $T_S = t/T_D$ was consistently less than 0 5, indicating most larvae were flushed from the system within 1 week During periods of high exchange, a single ebb tide could remove up to 70% of the larvae present Maximum retention occurred near the neap tidal cycle, but observed variation in the spring-neap amplitudes or tidal set-up was not sufficient for autochthonous development to

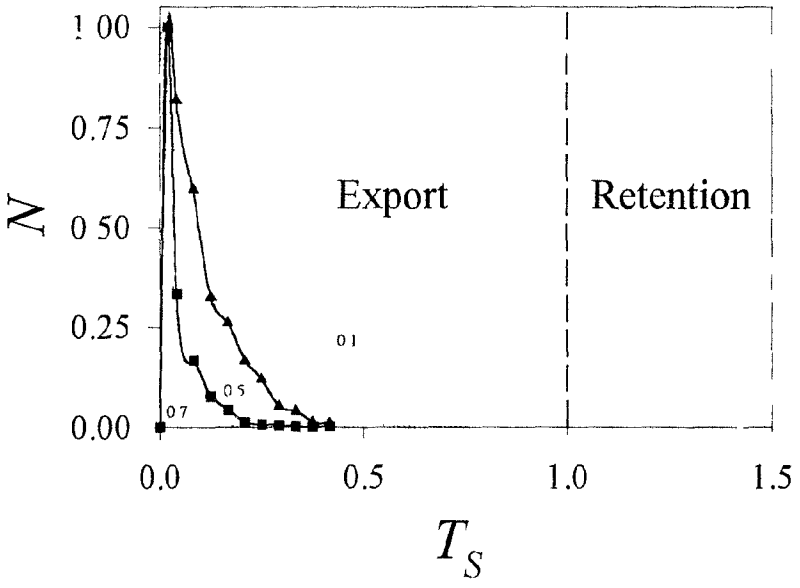

Fig 1 16 Modeled retention of larvae at extreme neap (▲) and spring (■) tide conditions during summer 1994 compared with the exponential model $N_t = N_o r^T$ (dotted line), where numbers designate exchange ratios, r *N*, relative concentration remaining, T_S, larval retention number (t/T_D) Retention is expected when $T_S \geq 1$

occur. However, short term retention on the order of days can be important for settlement of mature larvae imported from the nearshore zone. High passive loss of larvae is thus expected in well mixed, well flushed environments. The exponential model of Ketchum (1954) used by Ayres (1956) reproduced the shape of the loss curve with reasonable accuracy but consistently overestimated retention.

1.4 Discussion

There is a growing understanding of the processes controlling the recruitment of benthic marine organisms. On micro- and mesoscales, relations between hydrography, settlement behavior, and early post-settlement mortality and transport help explain zonation and patchiness of organisms within an environment (Butman 1986, 1987; Grassle *et al.* 1992; Snelgrove *et al.* 1993). But on the large scale, passive transport of larvae by physical processes directly regulates larval supply to sites (Roughgarden *et al.* 1991; Farrell *et al.* 1991). In this study, the Eel River estuary was observed to have large exchanges of materials, including mollusc larvae, with the nearshore zone at tidal periodicities. This suggests that embayments of similar geometry will also be strongly influenced by coastal processes and that exchange and especially import of larval forms must be considered in order to understand the population dynamics of estuarine invertebrates.

1.4.1 Estuarine circulation patterns

In the Eel River, the supply of plankton was controlled by advective processes. The dominant circulation patterns were mainly due to the interaction of barotropic forces with basin topography. Despite strong horizontal density gradients, tidal current mixing and shallow depth prevented the development of vertical density gradients which could

influence the horizontal flow field. Salinity time series indicated the tidal excursion length L ranged between the Middle Estuary and West Marsh stations. A typical flood tide completely replaced water in this $7.5 \cdot 10^4$ m^2 area and forced the estuarine water mass back towards West Marsh. During high tidal amplitudes and/or low freshwater input, the seawater penetrated to the culvert at West Marsh but normally a mixed region of high horizontal salinity gradient (greater than 15 o/oo in ~ 500 m) developed between Middle Estuary and West Marsh. The volume of water flooding through the culvert into West Marsh rarely exceeded 10% of Ω_F, due to physical constriction and the short 2 to 3 h duration of flood tide at West Marsh. In contrast, during ebb, first the recently imported coastal water, then the mixed estuarine water, and finally fresher water from West Marsh flushed from the estuary. The amount of West Marsh water exiting apparently varied with freshwater input and length of the ebb period, but up to $1.1 \cdot 10^5$ m^3 could exit the culvert during a 9 h ebb. Thus, the seaward half of the lower estuary (where clam populations were most abundant) was well flushed by every tide and experienced wide salinity and temperature fluctuations. On ebb, the mixed water between West Marsh and Middle Estuary stations and water exiting the culvert first drained seawards, where some portion was exported, while the remainder mixed with flooding waters and was redirected landward, giving rise to variable retention times in this water mass. Without the restrained drainage from West Marsh, a much larger area of the Eel River would be emersed at low tide. On average ~50% of the water in the estuary was exchanged every tide, and residence times ranged between 0.5 and 2 d (Fig. 1.3).

The Back Marsh embayment containing the Benthic Site station had a low drainage area and generally maintained higher salinity than at Middle Estuary. Coastal water rapidly replaced ebbing water during flood, but the high salinity water was usually preceded by a tidally trapped slug from the Eel River with a volume of ~$3.0 \cdot 10^4$ m^3. This process was an important mechanism for material exchange between Back Marsh and Eel River (Fig. 1.13), and indeed a larger scale occurrence of the same phenomenon was noted between Eel River and Lawrencetown River (Fig. 1.5) It is interesting that systems such as Back Marsh and Eel River which were so closely connected physically maintained such disparate water masses. Set up by the tide was responsible for the retention of relatively large volumes of water in Back Marsh; however, the retention time was normally only a single tidal period (Fig. 1 4a).

1.4.2 Plankton transport through the Eel River estuary

Large numbers of mollusc veligers were imported into the estuary during each flood tide (Table 1.1; Figs 1 7, 1 8, and 1 11) In 1994, between 10^6 and 10^8 bivalve and 10^7 and 10^9 gastropod larvae entered the estuary per Ω_F, indicating average larval concentrations in the nearshore between 10^1 and 10^4 ind m^{-3}. The range of these values are typical of shelf and coastal studies (*i e* Harding *et al* 1986, Mann 1986b, Scrope-Howe & Jones 1986; Tremblay & Sinclair 1988; 1990a, b; Raby *et al.* 1993) There were also large inputs of the dinoflagellate *Ceratium* spp. (Fig. 1 9) as well as holoplanktonic crustaceans such as calanoid copepods (Fig 1 10), with the coastal water Meroplankonic echinoderm plutei, annelid larvae, and crustacean nauplii and zoea were

consistently found in varying abundance. Advected plankton penetrated well into the estuary during a typical tidal excursion.

During ebb, there was extensive export of material from estuary to sea. In July and August, 10^9 gastropods were transported to the nearshore in a single ebb tide (Fig. 1.7). These veligers were abundant in estuarine water and peak transport occurred in water of mixed salinity, indicating their estuarine origin. Similarly, chl-*a* derived from autochthonous algal blooms in West Marsh was exported to the coastal water (Figs. 1.5 and 1.11). Principal components analysis demonstrated that both chl-*a* and gastropods were negatively correlated with salinity (Table 1.2, Fig. 1.15). In contrast, the time series for bivalve larvae, *Ceratium*, and calanoid copepods show peak export generally coincided with peak ebb volume transport, which occurred within 1.5 h of the change in tide. This water was invariably of high salinity, indicating its coastal origin, and demonstrating the passive export of organisms which had entered on a previous flood tide. Relatively few of these organisms were found in the mixed water mass, as confirmed by Figs. 1.7 to 1.11 and the factor groupings in the PCA table (Table 1.2).

The estuary had net imports of gastropods in June, and bivalves and *Ceratium* during all sample periods. Cumulative imports during the 2 tidal periods measured on each sample date revealed the quantity of organisms remaining in the estuary was similar to the maximum tidal transport of that date (Table 1.1). Tidal set-up and the resultant increase in residence times suggest that passive storage of water may explain the observed retention (Fig. 1.17). However, settlement or mortality within the estuary cannot be excluded. It is necessary to have longer time series to completely elucidate net

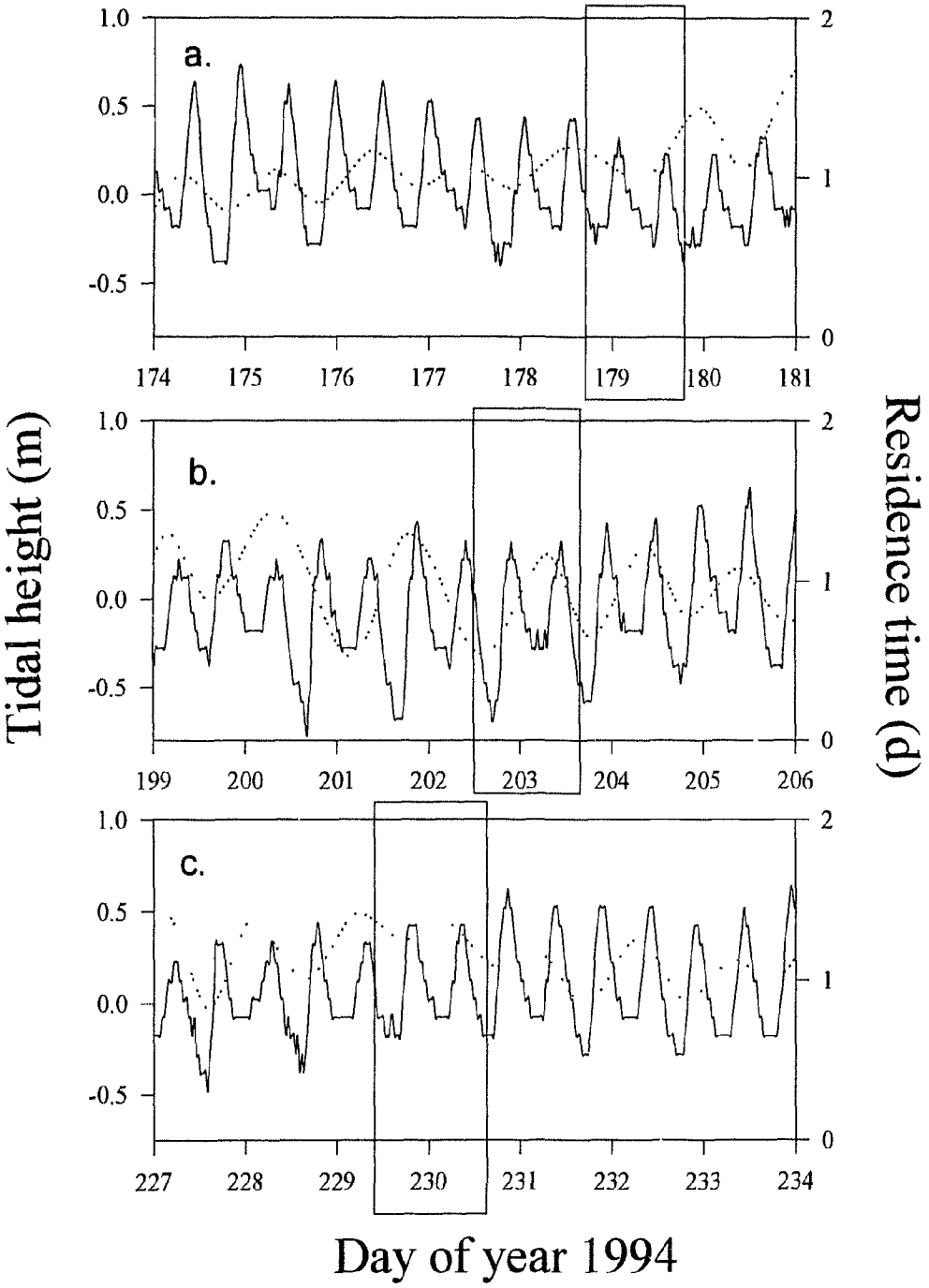

Fig. 1.17. Tidal curves (solid lines) and residence times (dotted lines) surrounding sample periods during June (top); July (middle); and August (bottom). Boxes enclose periods of plankton collection.

exchanges In contrast, gastropod export in July and August was 10 to 100 times greater than the import quantities.

1.4.3 Physical and behavioral factors affecting retention

The physics of the Eel River circulation imposed constraints on larval swimming behavior At the tidal inlet, current meters recorded free-stream velocities greater than 0 15 m s^{-1} for the majority of the sampling period, with maximum velocities above 0 6 m s^{-1}. These rates certainly exceeded the ability of larvae to actively control horizontal position through vertical migration (Butman 1986; Jonsson *et al.* 1991, Grassle *et al.* 1993) Likewise, during flood in the main tidal channels and tidal creeks, near-bottom flows less than 0.15 m s^{1} occurred only for a short period during the beginning and end of the flood period, and maximum currents peaked at ~0 30 m s^{-1} At both the inlet and within the estuary, vertical velocities ranged between 10^{3} and 10^{-1} m s^{1} (varying with tidal stage) indicating relatively strong vertical mixing. Strong shear in near-bottom flow resulted in erosion of bottom sediments (Chapter 2 and 3). While embedded in such turbulent flow, horizontal transport would be inevitable. Larval vertical swimming velocities range from 0 5 to 2 3 10^{3} m s^{-1}, depending on stage of development (Mann 1986b) At a free-stream velocity of 0 3 m s^{-1}, a straight-hinge larvae vertically migrating at 0 5 10^{-3} m s^{-1} would travel 600 m during a 1 m ascent Faster sinking rates enable a greater control over vertical position, but in the energetic lower estuary the turbulent eddies and vertical mixing generated at the measured flow velocities and shallow depths would tend to disrupt depth regulation by vertical migration Thus, during flood, larvae would travel

significant distances into the estuary as passive particles before directed swimming could affect horizontal position.

In contrast, the reduced currents in the basins suggest that larvae transported into the shallow subtidal portions of Back Marsh or between the Middle Estuary and West Marsh stations would likely encounter a flow field allowing for directed vertical swimming to influence position. The benthos of the basins was dominated by extensive beds of *Zostera marina*, in which larvae could find refuge from eroding currents, and movement into the boundary layer might reduce transport (Eckman 1983). While a large portion of this water was exchanged every few tidal periods, short term retention in these areas was physically possible.

Ebb velocities within the estuary varied widely, and if entrained into a tidal creek, larval transport distance would depend on stage of the ebb tide At Benthic Site, the initial ebb flow had velocities of ~0.2 $m \cdot s^{-1}$, and due to the high water level it was during this period that most volume transport occurred. Subsequently, the channel water level drained to between 0.1 and 0.3 m and velocities reduced to between 0.01 and 0.10 $m \cdot s^{-1}$ for more than 5 h. In this low velocity shallow water, larvae would have the opportunity to maneuver, but in the free-stream position they could nevertheless traverse completely through the Back Marsh creek system (>900 m) and into the higher flows of the Eel River during this period. Ebb velocities in the Eel River consistently exceeded 0.3 $m \cdot s^{-1}$, and larvae would once again be subjected to passive transport. Once near the inlet, ebb velocities increased to ~0 6 $m \cdot s^{-1}$, and larvae would have no opportunity for behavioral regulation of position.

Export through the tidal inlet appears to result in a loss of planktonic organisms to the estuarine system, except for those residing in the tidally trapped volume. The salinity signal clearly shows that the estuarine plume was dispersed and coastal water comprised most of the flood volume. It is surmised that the plume is advected away, and the plankters entering the estuary are mainly new immigrants. The difference between the fluxes of gastropod larvae and chl-*a* between ebb and subsequent flood prisms supports this contention. The physical oceanography of the Eel River system thus precludes autochthonous recruitment of bivalves with long meroplanktonic development.

It is noteworthy that the large export signal measured for gastropods was not observed for bivalves, despite the similarity in locomotor abilities and physical attributes (i.e. density) of the veliger forms. This is surprising given the high biomass of reproductively active bivalves within the estuary which have the potential for a large larval production. The location of the dense beds of *Mya arenaria* and *Mytilus edulis* in the lower estuary makes any chance of larval retention dependent on spawning during flood tide. Flushing would promptly export embryos and trochophores originating from these sites during ebb flow Larvae spawned during flood would be advected into Back Marsh or the middle estuary, where various degrees of mixing and passive retention could occur. However, the subsequent ebb flow would tend to remove much of the water and presumably the passively distributed embryos and trochophores with it. Indeed, as discussed in the introduction, the larval behavior required to remain in the system normally is not observed before larvae are nearing settlement size (previous citations). In fact, the

behavioral tendency of young larvae for upward swimming, which may serve to limit predation from benthic organisms, increases the probability of export.

Differences in reproductive modes and the sampling periodicity likely explains the discrepancy between the abundance of larval bivalves and gastropods. The numerically dominant gastropod in the estuary was the prosobranch *Hydrobia minuta* (Totten), which lays attached eggs that hatch after ~1 wk into a free-swimming veliger larvae (Barnes 1988). Variation in egg laying and hatching contribute to a relatively long period of larval presence. In contrast, the bivalves within the system *Mya*, *Macoma*, and *Mytilus* are broadcast spawners with planktonic development times of 2 to 5 wks. A synchronous bivalve reproductive effort and rapid exportation of the weakly swimming early larval forms within the relatively coarse 3 wk sampling intervals likely explains the different export signals. It thus appears that most larvae spawned within the Eel River would be removed within a few tidal periods.

In summary, larvae transported in the tidal channels of the lower Eel River estuary would have little chance of controlling their horizontal position. Settling into near-bottom flow would reduce the transport rate, but the ability to remain at or the near the benthos is unlikely given the high velocities and associated shear. Additionally, the entire section within a tidal excursion was completely flushed by swiftly moving flood and ebb water, and residence within this area is not likely. In the basins and during part of the ebb cycle in the tidal creeks, velocities were reduced enough to permit behavioral modification of position, but the physical residence times of water appear limited to time scales on the order of a few days. Thus, physical retention of larvae is not likely over the

(minimum) 2 wk larval development period. The system is probably dependent on the import of larvae which are physiologically capable to settle, and which can commence settlement behavior when introduced to estuarine sites.

The results of this study strongly support the hypothesis that immigration of larvae can contribute to estuarine recruitment patterns. Further, the Eel River estuary functioned as both a supply of larvae and chl-*a* to the nearshore, as well as a sink for allochthonously produced organisms. The generality of larval exchange can be found in both modeling and studies from other field sites. Ketchum (1954) and Ayres (1956) used mathematical models employing the tidal exchange ratio to predict planktonic retention and concluded import was necessary in well flushed systems. Carriker (1951) examined oyster *Crassostrea virginica* and clam *Mercenaria mercenaria* larval dynamics in the highly flushed Home Pond, in Gardiners Bay, NY. Relatively high concentrations (>1.3 · 10^4 ind · m^{-3}) of oyster larvae were endogenously produced, but were rapidly reduced by tidal flushing, and few larvae developed to maturity *in situ*. Ebbed water reportedly dispersed quickly in the nearshore (depending on wind stress), thus transporting propagules to Long Island Sound. Concentrations up to 1.2 10^4 ind · m^{-3} were imported through the tidal inlet, and it was concluded that recruitment depended on allothchonous transport. Larval *Mercenaria* were also passively transported, but because development time was only 7 d, clams had a greater likelihood for retention.

In the larger Little Egg Harbor, N.J., Carriker (1961) found export of *Mercenaria* to be dependent on proximity to the tidal inlet. Vertically well mixed conditions with coastal salinity values and high temperature typlified the study period, and tidal exchange

ratios varied from 0.2 at neap to 0.4 at spring tides. Individual cohorts of clam larvae were identified and followed, and swarms of newly spawned veligers initially maintained definable patches, but horizontal dispersion eventually resulted in more uniform distributions. Spawning events and larval retention were maximal during neap tides, while complete loss of cohorts occurred during high flushing events Large horizontal gradients in larval concentration were also noted, with the highest abundance in central lower bay (> 6 7 10^5 ind $\cdot$ m^3), and low concentrations near the inlet.

Christy & Stancyk (1982) computed net larval fluxes over 25 h periods through a tidal inlet in South Carolina They found a high larval exchange between estuary and nearshore, but few net fluxes differed significantly from zero over a given sample period Bivalve larvae had a net export in only 1 month (July), during which time export was greater during neap (1 4 10^{10} ind) than spring (1 1 $\cdot$ 10^{10} ind) tide samples There were net imports in all other months, ranging from 4 0 10^7 (Nov) to 4 7 10^9 (May) ind tide^{-1} Net gastropod transport varied more (8 0 $\cdot$ 10^5 to 2 9 10^9 ind tide^{-1}) and export dominated in 3 of 8 sample periods In all cases, net transport varied inconsistently with tidal stage, and although behavior was invoked to explain these findings, the 153 µm mesh size used undersampled the abundance of smaller mollusc larvae.

Carlson *et al.* (1984) measured large concentrations (> 2.4 10^4 ind m^3) of straight hinge (immature) larvae entering a Maine coastal embayment during flood, and the depleted abundances of veligers and phytoplankton exiting during ebb flow was attributed to benthic grazers Booth & Sephton (1993) monitored oyster larvae (*Crassostrea*) abundance and the physical oceanography of Caraquet Bay, New

Brunswick, Canada. They found patchy distributions and rapid changes of all larval size classes with time, until a strong intrusive event emanating from the adjacent Baie de Chaleurs flushed the larvae from the estuary. A week later, larvae reentered the system at settlement size. Detailed vertical and horizontal sampling revealed no evidence of retention or diurnal vertical migration. The results of these studies are evidence for the large scale advection of larvae and demonstrate that immigration can constitute an important source of larval supply to estuarine sites.

1.5 Conclusions

This study demonstrated that, in the Eel River, mollusc larvae and other plankton are routinely transported between the estuary and ocean. High flushing and a relatively long planktonic phase indicates that retention in the estuary throughout planktonic development is limited in such small scale coastal systems. Additionally, the relatively high import values suggest the existence of a nearshore larval pool that is probably supplied from local estuaries and coastal embayments. Thus larvae exported from an estuary are not necessarily lost to the larger system. Obviously, efforts to manage commercially important bivalve stocks such as *Mya arenaria* must acknowledge that populations within such estuaries exist as linked systems.

It is probable that benthic populations in other tidally dominated systems also exhibit a pattern of recruitment dependent upon allochthonous larval input. However, the fate of a particular cohort exported from a site and mechanisms for reinvasion to an estuary presently remain speculative, as it is difficult to achieve the concurrent physical and biological measurements necessary to track transport processes (but see Harding *et al.*

1986; Raby *et al.* 1994). Clearly, processes influencing the residence time of the coastal waters and delivery of larvae to inlet mouths will impact variation in recruitment (Hatchey 1937, 1955; Petrie & Drinkwater 1978). Longshore transport, tides, and wind events during the crucial planktotrophic period will be the main determinants of the coastal distributions of larvae, while larval behavior may play an important role moderating ingress into estuaries. Physical and biologcial variables in the nearshore zone must be more extensively sampled in order to improve our understanding of estuarine recruitment.

Chapter 2. Transport of recently settled soft-shell clams in laboratory flume flow

2.1 Introduction

The recruitment of many marine benthic invertebrates begins with a dispersive larval phase in the plankton, and is followed by a benthic phase which is initiated during settlement and progresses through juvenile development to the adult form and habitat There has been much focus on the processes affecting larval settlement patterns in order to explain and predict variations in species distributions and abundance (see reviews by Butman 1987, Rodriguez *et al* 1993) For sedentary epibenthic organisms attaching to hard substrates (*e g* macroalgae, barnacles, oysters, serpulid polychaetes, corals), larval supply (Roughgarden *et al* 1991, Gross *et al* 1992), settlement and metamorphic cues (Chia & Rice 1978), hydrodynamics (Mullineaux & Butman 1991, Gross *et al* 1992) and mortality (Keough & Downes 1982, Connell 1985) are among the factors investigated to elucidate recruitment patterns These studies and many others have made clear the integrated variables which control settlement distributions However, implicit in these studies of attached epibenthic organisms is the importance of the larval settlement site on later survival, the irreversibility of site selection after metamorphosis onto hard substrates profoundly influences post-settlement mortality rates Relocation cannot be used to respond to site-specific variations in food supply and acquisition, predator prevalence, competitive interactions, or physical stresses such as siltation, desiccation, and freezing Because of this dependence of survival on site, relating settlement intensities to abundance of later stages is a reasonable approach (with caveats) for understanding distribution patterns on hard substrata

Recruitment to soft-bottom environments is influenced by processes similar to those affecting recruitment to hard bottoms (Woodin 1986, 1991; Butman 1986, 1987; Butman *et al.* 1988). However, in contrast to hard substrate areas, macroinfauna such as polychaetes and bivalves, while more-or-less sedentary as adults, have mobile juvenile phases and can undergo active and/or passive redistribution from the site of larval settlement. Wind and tide-induced hydrodynamic forces have been shown to alter demographic parameters of the benthos, and recolonization experiments have demonstrated the importance of transported juveniles or adults on recruitment (Santos & Simon 1980; Grant 1981; Thrush & Roper 1988; Frid 1989). Meiofauna are also susceptible to current-induced movement and may recruit predominately as adults (Palmer 1988). Post-settlement transport enables a switch from nursery areas into the adult zone for such species as the bivalve *Macoma balthica* (L.) (Beukema 1978) and the polychaete *Arenicola marina* (L.) (Reise 1985). The relevance of juvenile transport to recruitment dynamics has only begun to be investigated for most marine communities, but it can be appreciated that where transport rates are high, settlement may have little bearing on later abundance (Woodin 1991). These complex recruitment patterns involve interactions between behavior and physical forces, and may act to free organisms from the constraints imposed by direct settlement into the adult habitat as in many hard substrate communities.

For bivalve molluscs, transport of juveniles can involve both voluntary and passive mechanisms which operate over varying length and time scales. On the smallest scale, surface crawling or sub-surface burrowing abilities of most juvenile (and many

adult) soft-sediment bivalves are limited to a range $\leq$ *ca* 1 m $\cdot$ d^{-1} (Smith 1955; Ahn *et al.* 1993; Richardson *et al.* 1993). Deposit-feeding bivalves especially may be required to shift position to locate food resources, but the daily excursions during these feeding transits also appear small (Brafield & Newell 1961). Larger scale movements are dependent on the prevailing hydrodynamic regime. Even in species adapted for escape swimming (*i.e.* pectinids and razor clams), currents greatly influence the extent of horizontal transport (Dadswell & Weihs 1990, Manuel & Dadswell 1991). More extensive spatial movements in the range of < 1 to perhaps 10^3 m over temporal scales of minutes to hours (Beukema & de Vlas 1989) to possibly days per excursion can occur from resuspension and the subsequent passive transport of juveniles via byssal drifting. This behaviorally-mediated ability to migrate occurs in a variety of bivalve genera (Sigurdsson *et al.* 1976) and has major ramifications in the recruitment of the tellinid *Macoma balthica* (Beukema & de Vlas 1989; Armonies & Hellwig-Armonies 1992), the mussel *Mytilus edulis* (L.) (Bayne 1964, Lane *et al.* 1985), and probably other species (Möller 1986; Martel & Chia 1991; Armonies 1992; Beaumont & Barnes 1992; Cummings *et al.* 1993). Finally, passive transport as bedload or resuspended particles during episodic wind events (Matthiessen 1960; Emerson & Grant 1991) as well as during higher frequency tidal cycles (Williams & Porter 1971) can also significantly affect infaunal bivalve abundance at intermediate distances of 1 to 10^2 m and periods of 0.5 to 3 d. Thus, many bivalves undergo a prolonged juvenile recruitment phase which may encompass kilometers of horizontal distance and weeks or more of cumulative travel time before reaching the relatively sedentary adult phase.

The purpose of this experiment was to investigate the ability of recently settled soft-shell clams (*Mya arenaria* L.) to be transported by simulated tidal currents. As adults, *M. arenaria* are deeply burrowing suspension-feeding bivalves found in a wide range of current regimes and sediment types (Newell & Hidu 1986). Burial depth is a positive function of size (Zwarts & Wanink 1989), and while older individuals are sedentary, juveniles < 15 mm actively crawl on the surface and burrow but are confined to the upper sediment column because of their relatively short siphons (Medcof 1950). Newly settled juveniles are found both on the substrate surface as well as byssally attached to objects on the bed (Hidu & Newell 1989). Passive transport of juveniles >1 to 15 mm shell length (SL) has been demonstrated in the field (Smith 1955; Matthiessen 1960; Emerson & Grant 1991), but not quantified with measurements of flow velocities or shear stresses. In this experiment we examined the transport of recently settled *M. arenaria* (2 wk post-settlement; 240 to 290 µm SL) in a recirculating flume. Free-stream velocities ranged from still water to 35 cm · s-1 (shear velocities, u_*, up to 1.75 cm s^{-1}), simulating a shallow, tidally dominated clam habitat in Nova Scotia, Canada. The low-density, surface-dwelling juveniles used are the most susceptible benthic stage to erosion and transport, and allowed for a determination of the flow conditions expected to affect settlement distributions. The objective of this investigation was to quantify the hydrodynamic transport of recently settled clams.

2.2 Materials and methods

2.2.1 Rearing of animals

Week-old *Mya arenaria* larvae were acquired from the Beals Island shellfish hatchery in Maine, USA in June 1993, and were maintained in 30 L plastic containers at Dalhousie University, Halifax, Canada. The larvae were fed a mixture of *Isochrysis galbana* and *Chaetoceros muelleri gracilis* and kept at a temperature of 19 °C Settlement and metamorphosis commenced when the animals were 12 to 15 d old. The juveniles were kept on an 80 μm Nitex mesh supplied with 5 μm filtered running seawater and fed every second day as above The experiments were conducted from 21 to 30 July 1993, *i.e.* about 1 month from fertilization and two weeks after settlement

2.2.2 Burial time

The burrowing behavior of juvenile *Mya arenaria* was studied in still water Petri dishes were filled with filtered seawater and 175 μm median diameter quarry sand, which was pre-conditioned for 48 h in 5 μm filtered running seawater Juveniles ranging in size between 240 and 270 μm SL were placed individually on the sediment surface with the aid of a Pasteur pipette. The burrowing behavior of 14 individuals was examined under a dissecting microscope at 25 X by noting the time elapsed for (1) the initiation of digging, (2) posterior margin becoming flush with the sediment surface, and (3) complete burial

2.2.3 Flume experiments

The experiments on transport of juvenile *Mya arenaria* were performed in a recirculating flume at Dalhousie University The flume channel is formed by an acrylic

container, 50 cm high, 50 cm wide and 732 cm long. Recirculating water is driven by a propeller powered by a variable speed DC motor which is inserted into a 37 cm diameter PVC pipe that forms the conduit for return flow (cf. Vogel 1981). The PVC pipe feeds into a head box that opens into the flume channel via a rectangular opening of the same dimensions. This minimizes jet effects at the entrance to the flume, and a collimator, located 20 cm downstream the entrance (10 cm long, with cells of 0.64 cm diameter), dampens cross-stream circulation. The working section includes a sediment box (40 cm long, 15 cm deep) and is located 525 to 565 cm downstream of the water entrance. At this distance, the boundary layer was fully developed in our experiments.

Flow in each experiment was characterized by measuring horizontal velocity at 9 vertical positions (1 to 3 mm apart) with a hot film anemometer (Dantec Type 55 M 01) equipped with a "hot film 180" conical probe. Average speeds and standard deviations were calculated from 2 min measurements at each height. Water depth in the flume during the experiments was 8 cm; temperature was 19.5 to 20.5 °C.

Boundary shear velocities, u_*, were calculated from the logarithmic section of the velocity profiles by fitting velocity measurements to the "law of the wall" (*e.g.* Jumars & Nowell 1984):

$$U(z) = (u_* / \kappa) \ln (z / z_0) \qquad \text{eq. 2.1}$$

where $U(z)$ = mean downstream velocity at height z above the bottom; z_0 = roughness length; and κ = von Karman's constant (0.4). Estimates of u_* were also used to calculate the bottom roughness Reynolds number, Re_*:

$$Re_* = u_* k_s / \nu \qquad \text{eq. 2.2}$$

where k_s = the physical roughness scale of the bed (here the median grain size of sediments, 175 μm), and ν = kinematic viscosity of seawater A summary of the flow characteristics is presented in Table 2 1

Table 2 1 Flow conditions in the flume boundary-layer U_z free-stream velocity, u_* boundary shear velocity, Re_* roughness Reynolds number, z_0 roughness length, Rouse Rouse number, SD standard deviation, nd not determined Values for the 16 3 and 28 6 cm s^{-1} treatments were computed from both sets of flume experiments, while measurements for the 35 0 cm s^{-1} treatment were restricted to 2 profiles during a single replicate run

$U_z \pm$ SD (cm s^{-1})	$u_* \pm$ SD (cm s^{-1})	$Re_* \pm$SD	$z_0 \pm$ SD (cm)	Rouse± SD		n
				clams	sand	
6 6±0 20	0 62±0 04	1 09±0 07	0 021±0 007	1 41±0 22	3 27±0 78	3
16 3±0 73	1 03±0 09	1 79±0 15	0 006±0 004	0 85±0 14	1 96±0 48	3
28 6±1 00	1 62±0 19	2 80±0 35	0 004±0 002	0 54±0 10	1 25±0 32	7
35 0±1 30	1 75±nd	3 05±nd	0 002±nd	0 50±nd	1 16±nd	1

2.2.4 Experimental setup

The flume sediment box was filled with conditioned 175 μm quarry and that was kept level with a thin layer of identical sediment deposited onto the flume floor On the sediment surface we gently placed 3 vertical cylinders 10 cm high and 2 6 cm in diameter The cylinders were located 6 5 cm apart in a row perpendicular to the flow direction Fifty juvenile *Mya arenaria* (240 to 290 μm SL) were added to each of the cylinders and, based on the still water experiments, were allowed a 5 min acclimation period to burrow (see results) After acclimation we removed the cylinders and gradually increased the flow up to the desired velocity, which was maintained for 50 min The flow was then turned off, and the areas where the juveniles had been deposited were sampled by

inserting wider cylinders (7.0 cm diameter) down into the sediment centered on the same locations as the thinner cylinders. The sediment (and animals) within the cylinders was then siphoned off, collected on a 80 μm sieve, and preserved in a formalin-Rose Bengal solution. Prior to enumeration, the animals were extracted from the sediment by resuspension, and the supernatant containing most of the juveniles was decanted and collected on a 63 μm sieve. The material on the sieve was examined under a dissecting microscope at 12 X magnification. The sand in the sediment box was replaced prior to each new run.

2.2.5 Treatments

To simulate the flow regime on a shallow soft bottom over a tidal cycle we exposed juvenile *Mya arenaria* to the following free-stream velocities, U_∞: 0, 7, 16, 29 and 35 cm $\cdot$ s^{-1}. For each flow speed there were three replicate runs which were randomized over the course of the experiment. We used a nested analysis of variance with runs nested within flow to test for differences in numbers of remaining *M. arenaria* among flow regimes. To investigate the importance of burrowing behavior on post-settlement transport, we conducted a second flume experiment using both live and newly killed *Mya arenaria*. The treated animals were killed by submersing them for a few minutes in a 4% formalin-seawater solution. The experimental procedure described above was repeated at only two flow-speeds, U_∞: 16 and 29 cm $\cdot$ s^{-1}, and two replicate runs. The results were analyzed using ANOVA with condition (live vs dead) and flow speed as main orthogonal factors, and experimental runs nested within both condition and speed.

Prior to the analyses of variance for both sets of flume experiments we examined the homoscedasticity among treatment variances using Cochran's test; no departure from

homoscedasticity was found ($p > 0.05$). Treatment means were compared using the Student-Newman-Keuls procedure with $\alpha = 0.05$.

2.2.6 Fall velocities

Fall velocities of live and killed *Mya arenaria* and sediment grains, were measured in a settling chamber (12.5 cm high, 5.5 cm long and 7.5 cm wide) submersed in a constant temperature bath. Individual clams and grains were released 1 cm below the water surface and their decent recorded using a horizontally mounted video camera (Pulnix TM-7 EX) equipped with a macro lens. Measurements were made on 19 individuals from each of the 3 groups, and analyzed using the image analysis program OPTIMAS. Fall velocities (w) were used to calculate a Rouse parameter ($w / \kappa u_*$) for each experiment (Table 2.1). The Rouse parameter defines the likelihood of particle motion in a shear flow and its tendency to transport as either bedload or suspended load.

2.3 Results

2.3.1 Burial time

In still water juvenile *Mya arenaria* started to burrow almost immediately (13 ± 7 s; mean ± SD) after release on the sediment surface. The animals were flush with sediment within 2 min (83 ± 68 s) and were completely burrowed after 5 min (169 ± 136 s).

2.3.2 Transport in flume

In the still water treatment greater than 90 % of the juvenile *Mya arenaria* were recovered (Fig. 2.1). In the flowing water conditions, there was no difference in the level of recovery which occurred at flow speeds up to 16 cm $\cdot$ s^{-1} ($p > 0.05$), while at U_∞ = 29 cm $\cdot$ s^{-1} the percentage of remaining *M. arenaria* was reduced to 65 % ($p < 0.05$). At

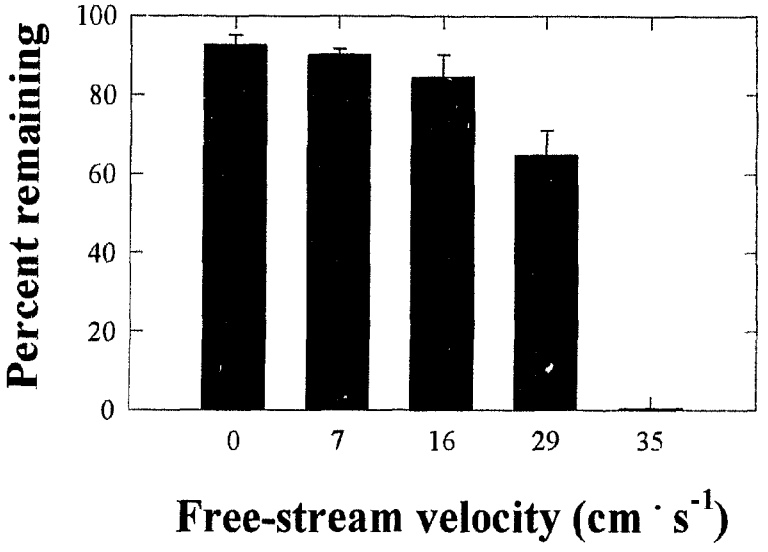

Fig. 2.1. Mean percent (± SE) of *Mya arenaria* juveniles remaining in the sediment at various free-stream velocities. Virtually all clams were removed at the highest velocity.

the highest flow speed, $U_\infty = 35$ cm · s^{-1} transport was complete and virtually no *M. arenaria* remained in the sediment (Fig. 2.1; Table 2.2).

Table 2.2. Two-factor nested ANOVA comparing transport of juvenile *Mya arenaria* exposed to 5 different flows

Source	df	SS	MS	F	p	Error term
Flow	4	53484	13371	1740.1	< 0.001	Run
Run(Flow)	10	767	77	0.5	0.89	Residual
Residual	30	4794	160			

The increased erosion of juveniles at the higher flow speeds coincided with the initiation of bulk sediment movement. At 7 cm · s^{-1} organic flocculates occasionally

moved over the bed, but the sediment was undisturbed, and at 16 cm · s^{-1} single sand grains started to roll over the sediment surface, although there was insignificant overall movement. In contrast, at 29 cm · s^{-1} grains were saltating over the bed, and at 35 cm · s^{-1} there was extensive bedload transport. At the two highest velocities the flow caused a deformation of the bed and ripples were formed. At 29 cm · s^{-1}, straight transverse ripples measuring 1 to 3 mm in height and 70 to 90 mm in length occurred, while at 35 cm · s^{-1} 3-dimensional linguoid ripples developed. These ripples had a mean amplitude of 13.4 mm and ranged in length from 60 to 100 mm.

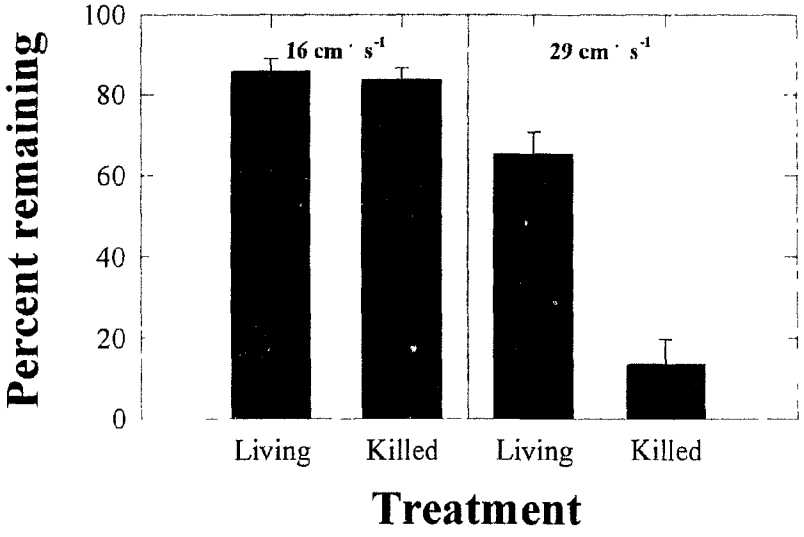

Figure 2.2. A comparison of the effect of clam burial on retention (mean % ± SE) in sediments. Dead clams lying on the sediment surface were eroded at current velocities which did not transport burrowed clams.

In the experiment with newly killed animals there was a significant interaction between condition (live vs dead) and flow speed (Fig. 2.2; Table 2.3). At 16 cm · s^{-1}, little erosion occurred, and there was no difference between the recovery of live and dead

animals. At 29 cm · s^{-1}, live clams were eroded to the same degree as in the first experiment (Figs. 2.1 and 2.2), while the killed animals were almost completely removed from the test section.

Table 2.3. Three-factor nested ANOVA comparing transport of live and newly killed juvenile *Mya arenaria* exposed to 2 different flows. L/D, Live versus dead factor.

Source	df	SS	MS	F	p	Error term
Live vs Dead	1	4324	4324	13.1	0.022	Run
Flow	1	12386	12386	37.6	0.004	Run
L/D * Flow	1	3712	3712	11.3	0.028	Run
Run (L/D * Flow)	4	1317	329	4.0	0.021	Residual
Residual	16	1327	83			

2.3.3 Fall velocities

Live and dead *Mya arenaria* had equal fall velocities, 3.5 ± 0.5 and 3.5 ± 0.7 mm · s^{-1} (mean ± SD) respectively, whereas the sediment grains fell with more than twice the velocity, 8.1 ± 1.9 mm s^{-1}.

2.4 Discussion

The transport experiments demonstrated that recently settled *Mya arenaria* maintained position in the sediment until the critical shear velocity for ripple formation was exceeded. Clam transport was initiated at a free-stream velocity of about 29 cm · s^{-1} (u_* = 1.6 cm · s^{-1}) and was essentially complete at a velocity of 35 cm · s^{-1}. There was a transition of the bed from low amplitude transverse current ripples to higher amplitude linguoid ripples over this 6 cm · s^{-1} velocity change. At the higher flow there was mobilization of the sediment in the entire test section through both ripple migration and

saltation events, and it was evident that the clams had minimal refuge from transport The bedforms observed at the test velocities correspond well to published empirical results presented in predominance diagrams (i e Allen 1985) It is reasonable to conclude that persistence of small surface-dwelling infauna is related to stability of the sediment

Burrowing by *Mya arenaria* was effective at reducing transport at $u_* \leq$ the critical velocity for ripple generation In the experiment with killed animals, at the higher shear velocity there was a marked drop in the retention of dead clams relative to living clams Observations indicated that living clams rapidly burrowed into the test substrate and had ample time to dig before the initiation of flow, whereas killed individuals remained upon the sediment surface fully exposed to fluid forces Clams lying on the surface would thus erode before clams buried just below the surface Fall velocities of living and killed *M arenaria* were not different, indicating the brief formalin treatment did not alter properties of the clams (such as density) which could have resulted in differential transport Thus the shear velocity affecting bulk sediment movement controlled the initial transport of *M arenaria*

Explanations for the loss of clams at U_z values between 0 and 16 cm s^{-1}, when sediment transport did not occur, include sampling error during retrieval as well as enhanced transport of live individuals which failed to burrow Alternatively the clams may have crawled from the 38 cm^2 test areas This distance (~ 90 body lengths) would have required a sustained crawling velocity of 0 45 mm min^{-1} by a 0 25 mm long juvenile Although this rate is feasible, our observations indicate the clams were more likely to burrow into the sediment than crawl laterally This contention is supported by Ahn *et al*

(1993), who compared the effect of density of the clam *Gemma gemma* (Totten) on the emigration rates of newly settled clams *Mercenaria mercenaria* (L.) from 2.65 cm diameter cores over a 3 d period. Less than 5% of the *M. mercenaria* juveniles moved from the control cores, while competitive interactions apparently induced a higher emigration in treatments with *G. gemma*. However, under field conditions (a subtidal channel), greater overall loss rates were measured (Ahn *et al.* 1993), perhaps due to a higher current regime. Zobrist & Coull (1992) also found low emigration of newly settled *M. mercenaria* in response to meiofaunal densities, and measured burrowing rates in agreement with the values presented here Burrowing behavior is adaptive for stabilization of recently settled bivalves in energetic regimes.

When eroded from the benthos *Mya arenaria* juveniles would be advected downstream as bedload or suspended particles. The type of transport can be estimated by the Rouse number = $w_s / u_* \kappa$, which compares the particle fall velocity w_s to the shear velocity at the bed u_* (κ is von Karman's constant). Ratios in excess of unity (where $u_{*cr} > u_*$) are indicative of bedload transport, while resuspension occurs at Rouse numbers < 1.0 (Wiberg & Smith 1985). Table 2.1 compares the Rouse numbers for clams and sand for the experimental shear velocities. At the U_∞ values where sediment transport was noted, the Rouse number predicts clams would be resuspended while sand grains would move as bedload. Streamwise transport of a single resuspended particle depends on the height of resuspension z_R, the fall velocity w_S, the vertical velocity profile U(z), and the boundary shear velocity u_*. As a very simple prediction of transport potential, the maximum downsteam advection distance for a resuspension event can be calculated as L =

$U_\infty \cdot z_R / w_S$, where a linear vertical velocity gradient is assumed. These potential transport distances are shown in Fig 2.3 for $w_S = 0.35$ cm s^{-1} (the fall velocity of juvenile clams) and a range of U_∞ and z_R values At the higher values of U_∞ and z_R, meter scale transport lengths are indicated for a single resuspension event Over a tidal period or during a storm, repeated incursions into the water column could result in transport distances of 10 to 10^2 m. Crawling excursions over similar time scales produce transport distances several orders of magnitude less than resuspension excursions Newly settled bivalves could thus be rapidly redistributed from the settlement site, and concentrations of transported individuals would be expected in lower energy regimes where $u_* < u_{*cr}$

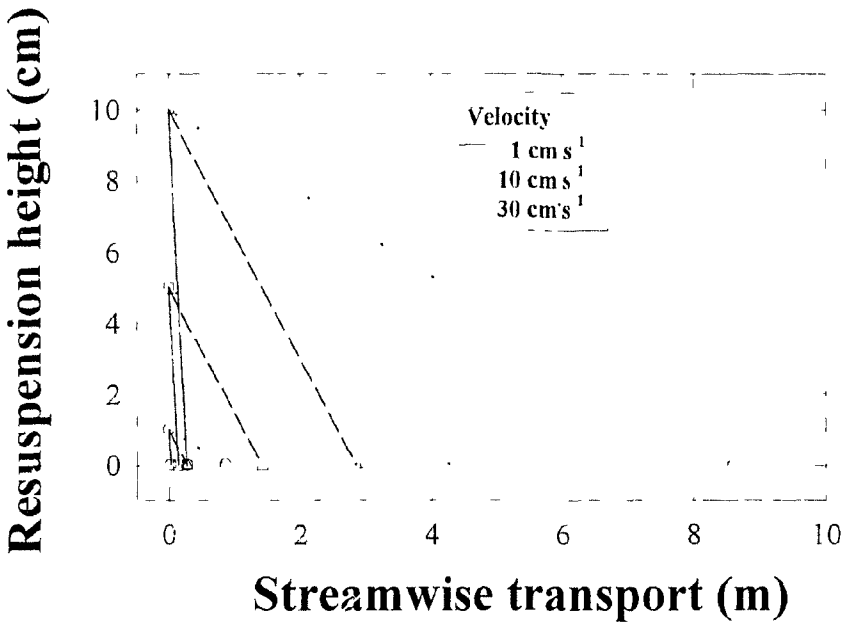

Figure 2 3 Estimated transport distances of resuspended clams as a function of free-stream velocity, U_∞ and resuspension height, z_R For each of 3 resuspension heights, filled symbols o: $z_R = 1$ cm, □: $z_R = 5$ cm, W $z_R = 10$ cm, there are 3 transport distances (open symbols) dependent on free-stream velocity (line type) Lines are not intended to describe trajectories.

Behavioral adaptations other than burrowing can influence the potential for clam transport. *Mya arenaria* up to about 15 mm can augment stabilization in shifting substrates by anchoring with byssal threads (Newell & Hidu 1986). Adhering to immobile objects allows for retention at high flow velocities, and even amalgamating small sediment grains in a net of threads would increase the relative density of the clam and thus tend to reduce erodability. However, we observed no byssal connections to sand grains during the experiments, although clams readily attached to the surfaces of laboratory containers. The recovery process may have disrupted these attachments.

Byssal threads also function to increase lift and resuspension during byssal drifting (Sigurdsson *et al.* 1976), although the anchoring and drift thread types differ, at least in *Mytilus edulis* (Lane *et al.* 1985). Most thread-drifting individuals in field studies have been found to measure between 1 and 3 mm SL (Sigurdsson *et al.* 1976; Möller 1986; Armonies 1992; Cumminngs *et al.* 1993), however Beukema & de Vlas (1989) demonstrated *Macoma balthica* up to 10 mm were capable of resuspension in the laboratory. Transport can occur at near bottom velocities as low as 1 $cm \cdot s^{-1}$ (Sigurdsson *et al.* 1976), well below that necessary for erosion of the bed. Lane *et al.* (1985) estimated byssal lifting in *Mytilus edulis* could result in resuspension heights between 0.5 and 5 m, and enable mussels to reduce their fall velocity to about 1 $mm \cdot s^{-1}$, which would greatly extend the advection distances calculated above. Even without byssal resuspension, behavioral adaptations that bring clams to the surface (*e.g.* Brafield & Newell 1961; Zobrist & Coull 1992; Ahn *et al.* 1993; Cumminngs *et al.* 1993; Richardson *et al.* 1993)

would increase the likelihood for passive transport. Such behaviors of juvenile bivalves may form a general mechanism for redistribution from unfavorable sites.

Our flume experiments were designed to investigate the range of current velocities found in a tidal creek dominated by *Mya arenaria* (Chapter 3). In the flume, smooth-turbulent conditions characterized the bed (prior to sediment transport) at all tested current velocities ($Re_* < 3.5$) (Table 2.1). Such conditions do not accurately mimic the more variable nature of turbulent flows in the field (Butman 1986), especially after the transition of a planar bed to a rippled erosional bed (Allen 1985). The linguoid ripples formed at $U_z = 35$ cm $\cdot$ s^{-1} resulted in flow separation eddies; such hydrodynamic features characteristically develop during the transition between smooth- and rough-turbulent beds and are associated with the disruption of the viscous sublayer (Leeder 1982). Comparison of our erosion data with field conditions are compromised by uncontrolled variables which increase or retard erosion at a given free-stream velocity, and are difficult to apply to our smooth surface of well-sorted, azoic quartz. Sediment binding by biogenic films (Paterson *et al.* 1990), bioturbation (Grant *et al.* 1982; Grant *et al.* 1986; Davis 1993), physical processes such as dewatering and compaction (Anderson 1983), and topographically heterogeneous substrate causing rough-turbulent flow (Nowell & Jumars 1987) all influence sediment transport. However, field measures of sediment transport under ambient flow conditions demonstrate that near shore and intertidal areas commonly experience tide- or wind-induced currents which exceed the critical shear stress of the bed (Williams & Porter 1971; Eckman 1979; Gross & Nowell 1983; Grant *et al.* 1984; Haas & Eisma 1993). In fact, ripples are diagnostic of sediment

transport and indicate areas subjected to erosion events capable of redistributing small infauna

The ecological implications of the hydrodynamic transport of small, surface-dwelling organisms such as recently metamorphosed clams are important Since passive transport can occur immediately following settlement to the benthos, the settlement site may have little bearing on overall recruitment patterns Simple scaling arguments and field measurements indicate that the transported clams can be advected significant distances over a single tide or storm There may be selection advantages in a decoupled recruitment pattern consisting of an initial settlement period, followed by a mobile juvenile phase characterized by frequent transport events, and concluded when a permanent position is achieved Settlement into an area occupied by dense concentrations of adult suspension-feeders or bioturbators has been theorized to induce high mortality of larvae or settlers through both direct and indirect means (Bayne 1964, Woodin 1976, Andre & Rosenberg 1991) In contrast, recruitment into such areas as individuals > 1 mm probably reduces these competitive interactions Such a juvenile transport phase which reduces settler mortality in bivalves is a mechanism which has been hypothesized by Bayne (1964) and Beukema & de Vlas (1989)

The relative importance of post-settlement transport versus larval settlement on infaunal recruitment to a given area is dependent on the hydrodynamic regime Quiescent depositional areas may have high settlement and low export rates, but be subjected to import of varying magnitude from surrounding areas For example, Moller (1986) found settlement to predominate over post-settlement import of *Mya arenaria* in Sweden

Conversely, post-settlement transport can cause pronounced structuring of the population, either by removal of individuals by storms (Emerson & Grant 1991) or migration of individuals into an area which had received low larval settlement (Beukema & de Vlas 1989, Gunther 1991, Armonies & Hellwig-Armonies 1992) High energy areas can limit settlement altogether (Gross *et al* 1992), or alternatively, it may be simply impossible for settlers or small juveniles to remain in energetic regimes, whereas the larger, deeper burrowing clams can withstand erosion in areas with periodically unstable sediment layers Energetic areas may offer benefits such as increased food flux Passive transport rates are periodic on temporal scales dependent on whether the dominant forcing is wind (seasonal to episodic) or tidal (fortnightly), and may be coupled with a behavioral component controlling vertical position in the sediment column (Cummings *et al* 1993) However, even in relatively low energy areas, substantial redistribution of infauna from the settlement site is likely The determination of the physical and behavioral components mediating post-settlement transport phenomenon is important for explaining patchiness and rapidly changing infaunal demographies and for elucidating differences between these effects and other factors such as predation and competition

Chapter 3. Recruitment dynamics of infaunal bivalves in a tidally dominated estuary

3.1 Introduction

Recruitment of molluscs to soft substrate sites can occur by the addition of young of the year (the 0-group) or by immigration of older individuals (Ólafsson *et al.* 1995). A growing body of information is revealing that juvenile transport is widespread in molluscs and other infaunal groups, and can be an important structuring mechanism for populations in the marine intertidal (Baggerman 1959; Matthiessen 1960; Grant 1981; Hagerman & Rieger 1981; Thrush & Roper 1988; Palmer 1988; Emerson & Grant 1991; Woodin 1991), shallow subtidal (Möller 1986; Beukema & de Vlas 1989; Rankin *et al.* 1994), and deepsea (Levin *et al.* 1994) environments. This paper assesses the relative importance of larval settlement to juvenile transport on the population structure of 3 sympatric bivalve species in a tidally dominated estuarine environment in Nova Scotia.

The species investigated were the soft-shell clam *Mya arenaria* (L.), the tellinid *Macoma balthica* (L.), and the venerid gem clam *Gemma gemma* (Totten). *Mya* is a large (up to 110 mm shell length), long-lived, suspension-feeding bivalve which resides deep in the sediment as an adult but is restricted to surficial sediments when small (Kellogg 1900; Medcof 1950). Adult clams are relatively sedentary, while juvenile *Mya* are readily mobile if disturbed. The medium sized *Macoma* (to 30 mm) feeds facultatively on seston or deposits (Brafield & Newell 1961), increases burial depth with shell length (Gilbert 1973, 1978; Zwarts & Wannik 1989), is long lived and capable of

mobility at all sizes. *Gemma* suspension feeds, attains a maximum size of only 5 mm and life span of 2 to 3 years, and remains at or near the sediment-water interface (Sellmer 1967). Both *Mya* and *Macoma* reproduce via planktotrophic larvae which settle at 200 to 250 μm (Pfitzenmeyer 1962; Chanley & Andrews 1971; Günther 1991) while *Gemma* is ovoviviparous and releases juveniles at a size of 350 to 375 μm (Sellmer 1967). At the study site, recruitment of the 0-group occurs in late summer and early autumn in each of the species.

Bivalve abundance at estuarine habitats was monitored with time series of size-frequency distributions. Changes in abundance of populations could be partitioned into increases or declines in the abundance of new recruits and older (larger) individuals. Interpretation of the survey data was augmented by experiments which measured net bivalve transport into defaunated sediment plots. Recruitment processes were investigated at 4 sites that varied by tidal exposure (subtidal, low intertidal, mid-intertidal) and current regime (grading from high to moderate maximum velocities) within a spatial area of $< 10^3$ m^2. The physical environment was characterized by measurements of tidal height, temperature, substrate elevation, and horizontal current velocity. Further, the winters of 1993 and 1994 were severe, and freezing and ice scour was observed to cause mortality of macrofauna at various areas of the intertidal zone. This fortuitous occurrence allowed a comparison between recruitment before and after natural large-scale disturbance.

3.2 Methods

3.2.1 Site description

The study area was a tidal creek and intertidal sandflat complex located at the Benthic Site of the Eel River estuary described in Chapter 1 Four 10 m^2 study plots were established at subtidal creek and intertidal sandflat habitats along gradients of exposure stress and hydrodynamic forcing Water level was measured with pressure-temperature sensors (VEMCO, Shad Bay, N S.) and standardized to surveyed positions to calculate exposure times A low intertidal plot, at the 30 % exposure level, was located near the terminus of the flood tide delta, and a mid-intertidal plot (~50% exposed) was located ~40 m away Two sites were continuously submerged in the tidal creek ~30 m apart The creek channel was 15 m wide and had a low tide depth of 0 4 to 0 6 m at the seaward site (Site A), but widened and shoaled shoreward (Site B) Currents were higher at the seaward station, but other conditions were similar The substratum at all sites was dominated by well sorted, fine sand between 125 and 250 μm in diameter ($\phi = 3$)

3.2.2 Hydrographic characteristics

The hydrodynamic regime at the subtidal sites was characterized by time series of tidal height, temperature, and current velocity Tidal currents were measured with Marsh-McBurney velocity sensors deployed 0 15 m above the bottom and oriented normal to the predominantly bidirectional flow The measured velocities allow comparison of the boundary layer conditions in the field with data acquired from laboratory flume experiments (Chapter 2) Data is presented for measurements made in November 1993 and September 1994 During the 1993 sampling, optical backscatter sensors (OBS) were

arranged vertically at 0.03, 0.10 , and 0.15 m above bottom to estimate the transport of suspended material. Additional time series illustrating variations in salinity, temperature, and chl-*a* with tidal height are presented in Chapter 1. Profiles of the site topography were made by standard surveying techniques in July 1993 and November 1994.

3.2.3 Size-frequency time series

Size-frequency histograms were used to determine recruitment patterns of the 3 dominant infaunal bivalves *Mya*, *Macoma*, and *Gemma*. The population structure was measured on 26 dates at bimonthly to monthly time scales during ice-free periods from June, 1992 to November, 1994. Clams were collected at each of the 4 benthic stations with 3 replicate 0.03 m^2 cores. During sampling, the upper 10 mm of the surface sediment were first scooped from the core and retained. This material was later sieved through a 250 μm mesh in the laboratory to measure the abundance of small bivalves. The remainder of the core was then completely excavated by hand (to avoid shell breakage) and all sediment was sieved *in situ* through a 1 mm mesh. For sampling subtidal plots, the core barrels were long enough to span the water column at low tide (generally 0.2 to 0.4 m) thus preventing surrounding material from flowing into the excavation. The sieved sediment was retained and then added back into the excavation to avoid altering the hydrodynamic regime of the benthos. The defaunated sections of substrate were subsequently used to measure recolonization over specific time intervals as described below. Defaunated plots were labeled with identifying markers.

In the laboratory, bivalves were enumerated by species, and the greatest shell dimension was measured with a dissection microscope or callipers. Abundance over time

was plotted as the mean ± SE. Size-frequency histograms were constructed for each sample date (bar widths of 1 mm for *Mya* and *Macoma*, and 0.5 mm for *Gemma*) to determine recruitment pulses and modal lengths. Changes in the abundance of the different size (age) distributions between consecutive sample dates were used to evaluate the mode of recruitment. Addition of individuals < 1 mm was considered evidence of larvalsettlement, while juvenile transport was identified by increases in abundance of individuals too large to be accounted for by *in situ* growth over the given time period.

Growth rates of *Mya* cohorts were estimated by regressing mean size by time for clam groups separated visually from the size-frequency histograms. These growth rates are not necessarily cohort specific, since clear size-frequency distributions were not usually apparent for all ages of clams. Without clear separation of cohorts, graphical cohort analyses such as the Harding (1959) method are subjective (Grant *et al.* 1985; Grant 1987)

Biomass of *Mya*, expressed as the ash-free dry weight (AFW) of tissue (dried at 70°C for 40 h and ashed at 500°C for 2 h), was determined and related to shell length for each replicate date-station combination using linear regression on log transformed data. The regression equations were then used to estimate mean total biomass (g AFW $\cdot$ m^{-2}) from the size-frequency data.

3.2.4 Transport experiments

Two types of defaunation experiments were used to estimate the contribution of juvenile transport to recruitment. In 1992, the defaunated cores from the regular benthic sampling described above were resampled at the next sample period (2 to 4 weeks) using

a 0.004 m^2 core inserted into the center of the defaunated area (identified from markers). All clams between 1 and 15 mm were enumerated. The small area of the sample cores was increased in 1993 and 1994, when three replicate 0.1 m^2 plots were defaunated and subsequently sampled with 0.03 m^2 cores. The mean transport of bivalves (F, ind. $\cdot$ $m^2 \cdot d^{-1}$) imported to the defaunated regions per sample period was then computed from the replicate cores. Since immigration and emigration can occur simultaneously, these rates expressed net transport. For each species, recolonization (R_T) was defined as the time needed for clams to repopulate the plot to the initial mean bivalve abundance (*Mya* and *Macoma* between 1 and 15 mm) assuming a linear transport rate. Recolonization time was determined as T_R (d) = ind $m^{-2} \cdot (\text{ind} \cdot m^2 \cdot d^{-1})^{-1}$.

3.3 Results

3.3.1 Meteorological conditions

While the winter of 1992 (prior to the initiation of sampling) had normal temperatures, the winters of 1993 and 1994 were extreme. In 1993, ice up to 0.7 m thick completely covered the site from mid-January to the end of March. Restricted water movement led to O_2 depleted water, measured at 53% of saturation just prior to breakup. Ice floes during breakup caused significant mobilization of sediment, especially at the mid-intertidal site. Additionally, in the mid-intertidal, water circulation to the benthos was obstructed, while the low intertidal had continued exchange. In contrast, in 1994 the ice was only ~0.15 m thick, but had frozen directly to the intertidal sediment surface, and all macrofauna down to ~10 % aerial exposure level were observed frozen *in situ*. During breakup, ice floes lifted the upper sediment layers away. Mounds of the rafted

substrate and dead clams were later observed as deposits in the *Spartina* marsh. The effects of ice on the sandflat were similar to descriptions given by Anderson (1983) for a mudflat environment in Maine

3.3.2 Hydrodynamic regime

The general hydrodynamic patterns of the tidal creek are illustrated in Fig. 3.1 for a 7 d period in September 1995. Water levels ranged 0.5 m, and the influence of the neap-spring neap cycle on the mean water level is apparent (Fig. 3.1a). Temperatures changed dramatically with tidal stage and time of day, with a maximum range of 13 °C (Fig. 3.1b). The sharp spikes in temperature at the beginning of flood are indicative of tidal trapping described in Chapter 1 (Fisher *et al.* 1979). Tidal currents were flood dominant but highly asymmetric, and due to topography, were of greater magnitude at subtidal Site A than at subtidal Site B (Fig. 3.1c and d). Maximum flood velocity 0.15 m above the bottom was > 0.3 m s^{-1} and ebb velocity was about 0.2 m $\cdot$ s^{-1} at subtidal Site A, while maximum velocities at Site B were more equal between ebb and flood at about 0.2 m $\cdot$ s^{-1}. These rapid near-bottom flows likely induced shear velocities in excess of the critical value for sediment transport (Chapter 2). Ebb tide was 1.5 to 2 times the duration of flood tide, indicating hydrographic choking.

Figure 3.2 illustrates time series of tidal height, velocity 0.15 m above the bottom, and voltage output from an OBS sensor located 0.03 m above the bottom during 2 to 3 November 1993. Voltage peaks corresponded to velocity maxima, especially during flood tide periods. Although the material being transported past the sensors was not

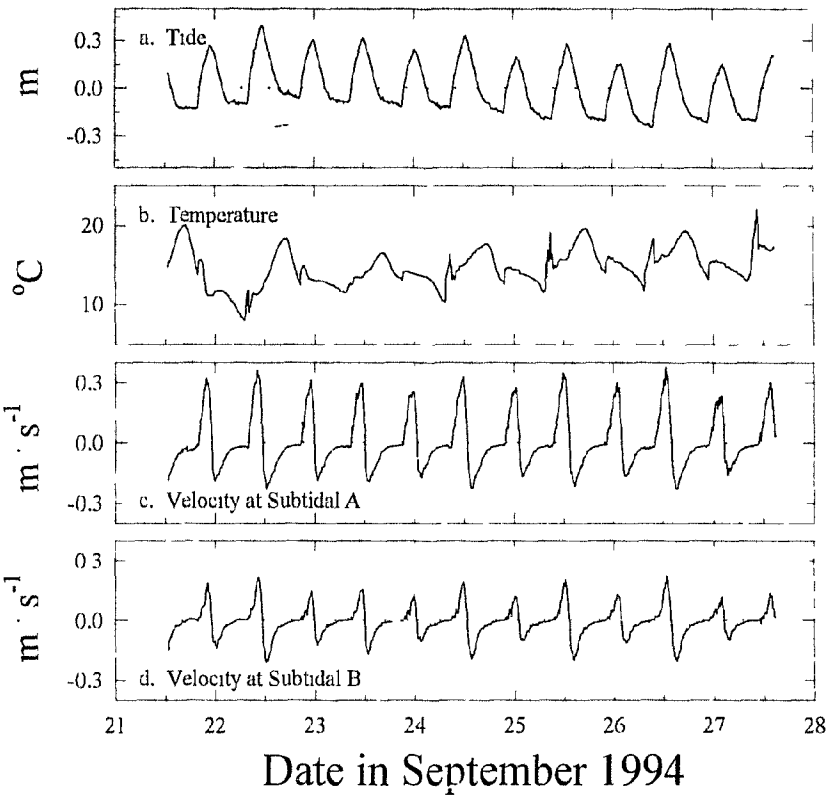

Fig. 3 1. Time series of *a.* mean water level, *b.* temperature; *c.* horizontal current velocity at subtidal Site A, and *d.* horizontal current velocity at subtidal Site B for 6 days in September, 1994 On the figure, date labels begin at 0 h and tick marks indicate 1200 h

sampled, current ripples noted in the channel bottom also suggest that sediment resuspension was occurring.

There was substantial movement of the substrate during the study (evidenced by varied degrees of ripple formation) and significant topographic changes occurred over time. Fig 3.3 compares sediment profile transects scaled to MLW made on 20 July 1993 and 17 November 1994. Sediment was eroded from high energy tidal creek habitats,

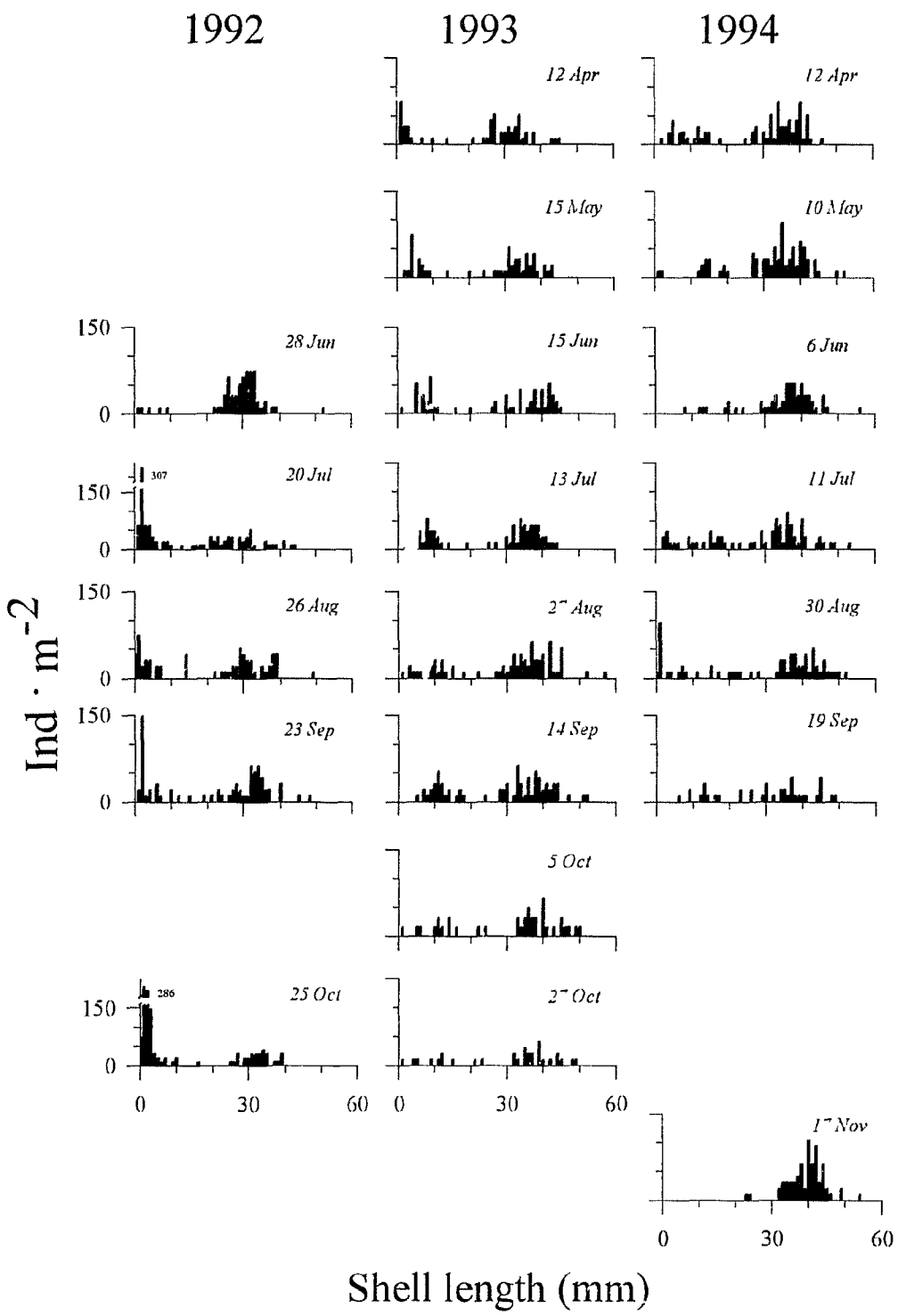

Fig. 3.6. Monthly size-frequency histograms for *Mya* at subtidal Site B. Bar widths are 1.0 mm. Dotted reference line is at 40 mm. ND: Not done.

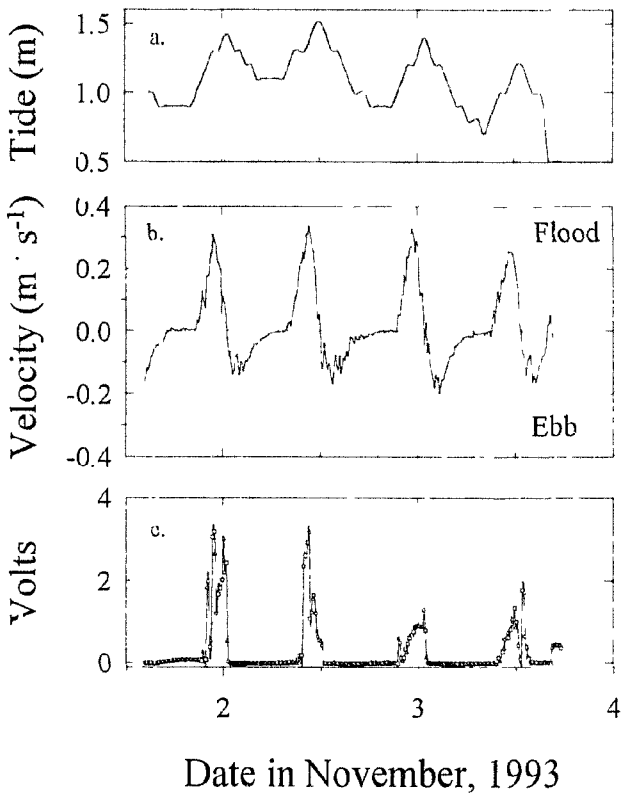

Fig. 3.2. Time series of *a.* mean water level; *b.* horizontal current velocity at subtidal Site A; and *c.* optical backscatter output for 2 days in November, 1993.

while deposition occurred on the intertidal bank. Subtidal creek sites generally were eroded 5 to 10 cm, while intertidal areas experienced an accretion of 1 to 5 cm over the 1.6 year time period. Evidence of the dynamic nature of the site is emphasized by the ~25 m^{-3} lobe of sediment deposited at the low intertidal site (Fig. 3.3 "along berm"). This feature extended 20 m into an area that was previously a subtidal seagrass bed. Current measurements were not made in the intertidal portions of the experimental area, but

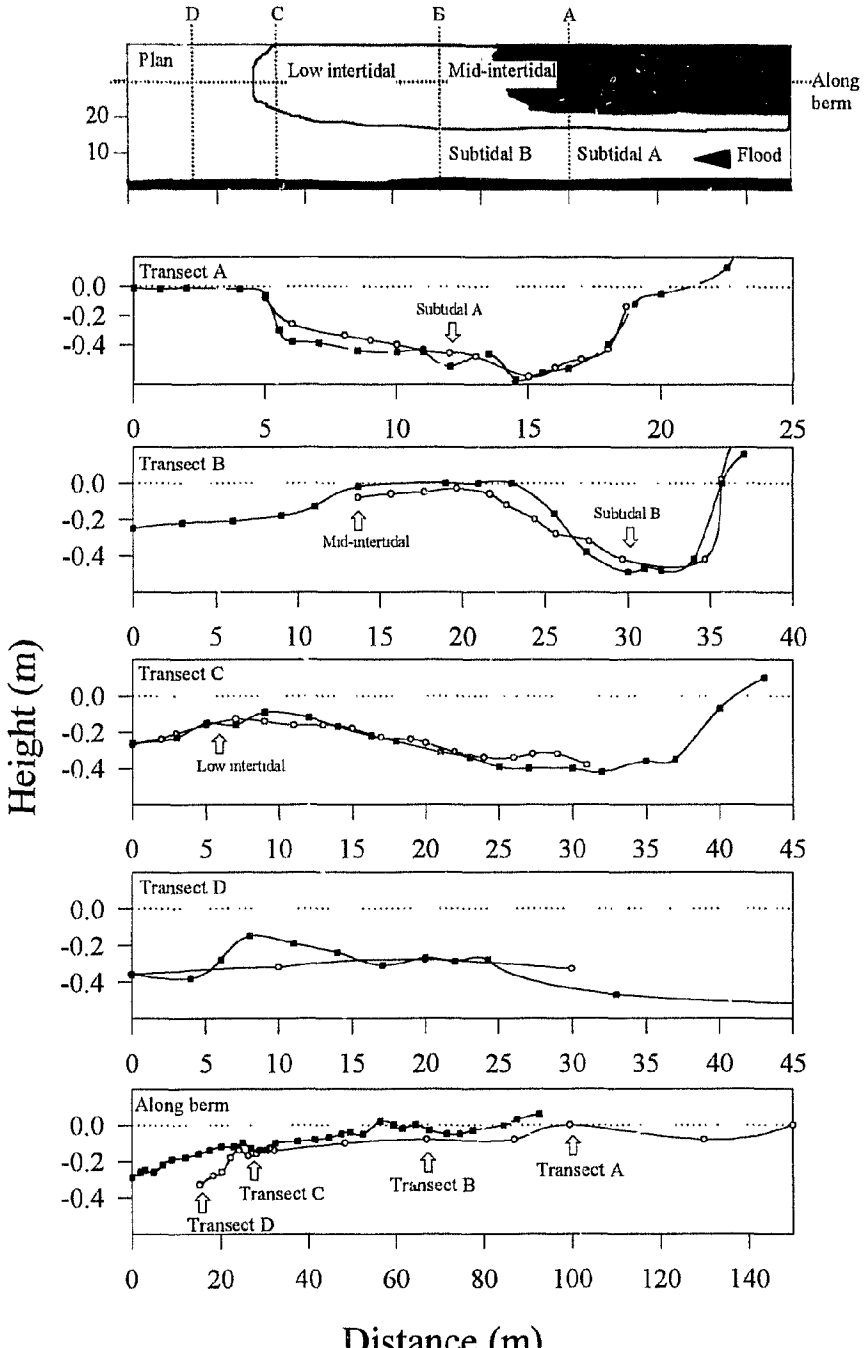

Fig. 3.3. Plan and topography (relative to mean tidal level) of the study site in July 1993 (open circles) and November 1994 (filled squares). In the plan, black is marsh, grey is intertidal sandflat and white is subtidal habitat. Transects A through C profile the intertidal sandflat and the adjacent tidal creek containing experimental plots, while Transect D shows the originally subtidal landward end of the flood-tide delta. "Along berm" is the longitudinal transect (0 is landward) which documents the increase in vertical height and extension of the distal edge of the sandflat. Note scale differences between plots.

the ripple formations there also indicated sediment redistribution over tidal-scale time periods This is in agreement with Leonard *et al.* (1995), who reported a velocity difference of only 0 05 m s^{-1} between tidal currents measured at a height of 0 10 m over subtidal and intertidal sites in a Florida marsh system The Back Marsh habitat can thus be categorized as a moderately high energy, tidally dominated system

3.3.3 Bivalve population structure

The time series of abundance and the corresponding size-frequency histograms illustrate substantial variations in the population structure of the 3 species among sites and over time However, despite annual variations in the magnitude of the 0-group production, recruitment of each species was augmented by juvenile transport The magnitude of the transport suggests clams residing in the upper sediment column constituted a mobile class capable of frequent and rapid translocation

3.3.3.1 ***Mya arenaria***

The recruitment and population structure of *Mya* differed considerably between the subtidal and intertidal sites (Fig 3 4) Subtidal *Mya* populations were bimodally distributed and were composed of relatively immobile, deeply buried adult clams and a more ephemeral number of shallowly residing juveniles < 20 mm (Fig 3 5 and 3 6) Few clams between 10 and 20 mm were ever sampled in the subtidal In contrast, the intertidal populations were highly skewed towards clams smaller than 10 mm, and larger clams, including the 10 to 20 mm size class, were present but more regularly distributed (Fig 3 7 and 3 8)

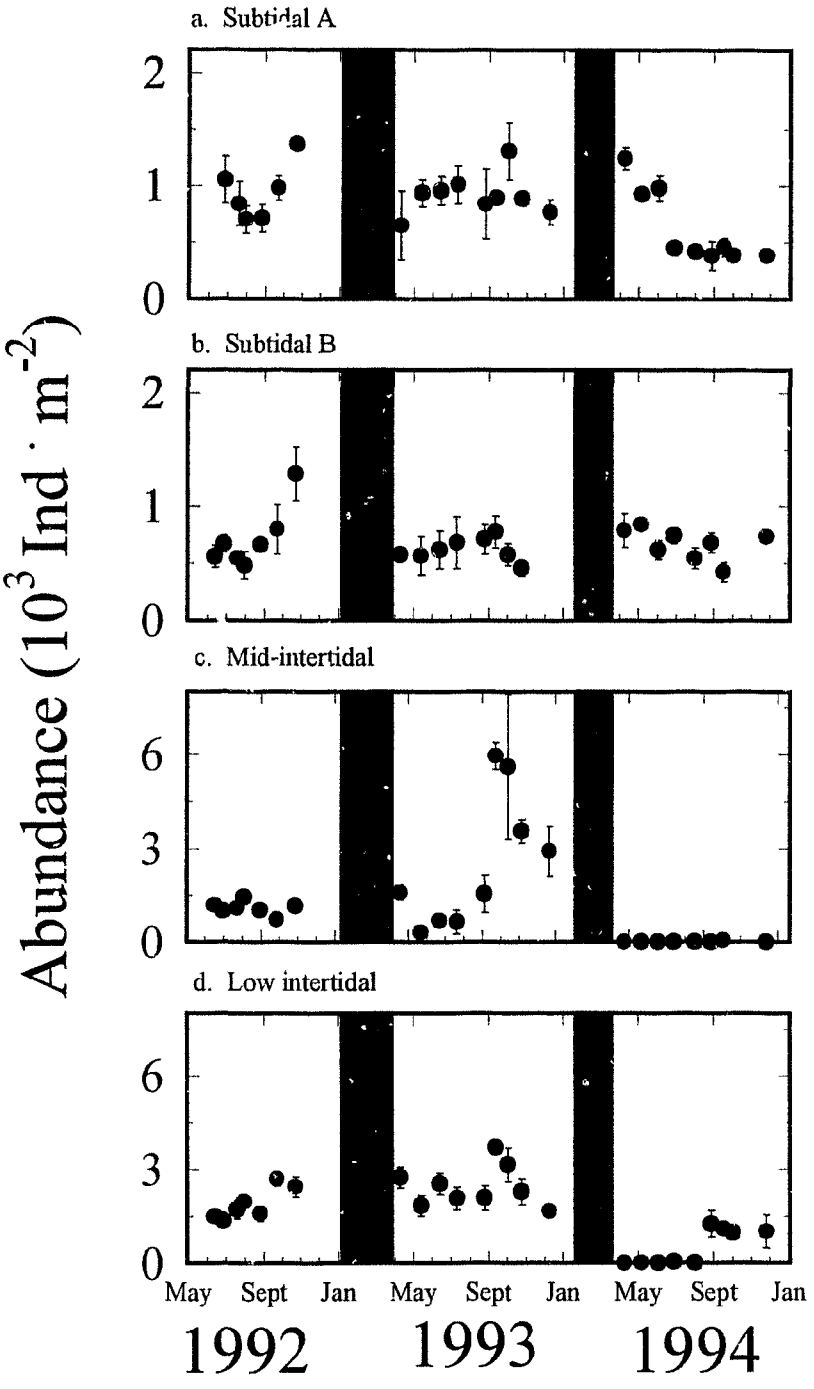

Fig 3 4. Time series of mean *Mya* abundance (± SE) for the 4 experimental sites from June 1992 to November 1994. Shaded areas indicate periods of ice cover.

In the subtidal, abundance of large clams (> 20 mm) remained relatively constant with time until July 1994, when subtidal Site A was impacted by professional clam diggers. Mean abundance was 752.4 ± 41.2 ind · m^{-2} at Site A (1992 to 1993) and 532.5 ± 32.0 ind · m^{-2} at Site B (1992 to 1994) (Fig. 3.4), with a total biomass which ranged seasonally between 100 and 250 g ADW · m^{-2} (Fig. 3.9). During the impact period (probably a single low tide), the abundance of large clams at Site A was reduced from 850 ± 59.9 to 390 ± 9.0 ind. · m^{-2}, with a concomitant ~50% drop in biomass (Figs. 3.4 and 3.9). Aside from this loss, the long-lived populations in the subtidal appeared safe from outside perturbation.

Although the general population structure of large clams was similar at Site A and B, mean size and growth differed (Fig. 3.10). During the 3 year study period, mean size of large clams at Site A increased significantly with time ($p < 0.001$, $r^2 = 0.863$, $n = 24$) at a rate of 0.013 ± 0.001 mm · d^{-1}. From the regression equation Size (mm) = 0.013 * time (d) +32.1 (mm), overall mean growth was 11.3 mm during the 3 year measurement period. Clams at the subtidal Site B, just 30 m away, were slightly smaller and grew slower. The mean growth of large clams was 0.009 ± 0.001 mm · d^{-1} as derived from the regression equation Size (mm) = 0.009 * time (d) + 30.454 (mm) ($p < 0.001$, $r^2 = 0.747$, $n = 23$). The mean size of the clams > 20 mm at Site B increased 7.9 mm during the study period.

Overall abundance of recently settled *Mya* (< 1.0 mm) was low in the subtidal with a maximum abundance of only 78 ind. · m^{-2} (Fig. 3.4 and 3.5). The initial presence of the 0-group cohort was not congruent between sites and years. At Site A, recent

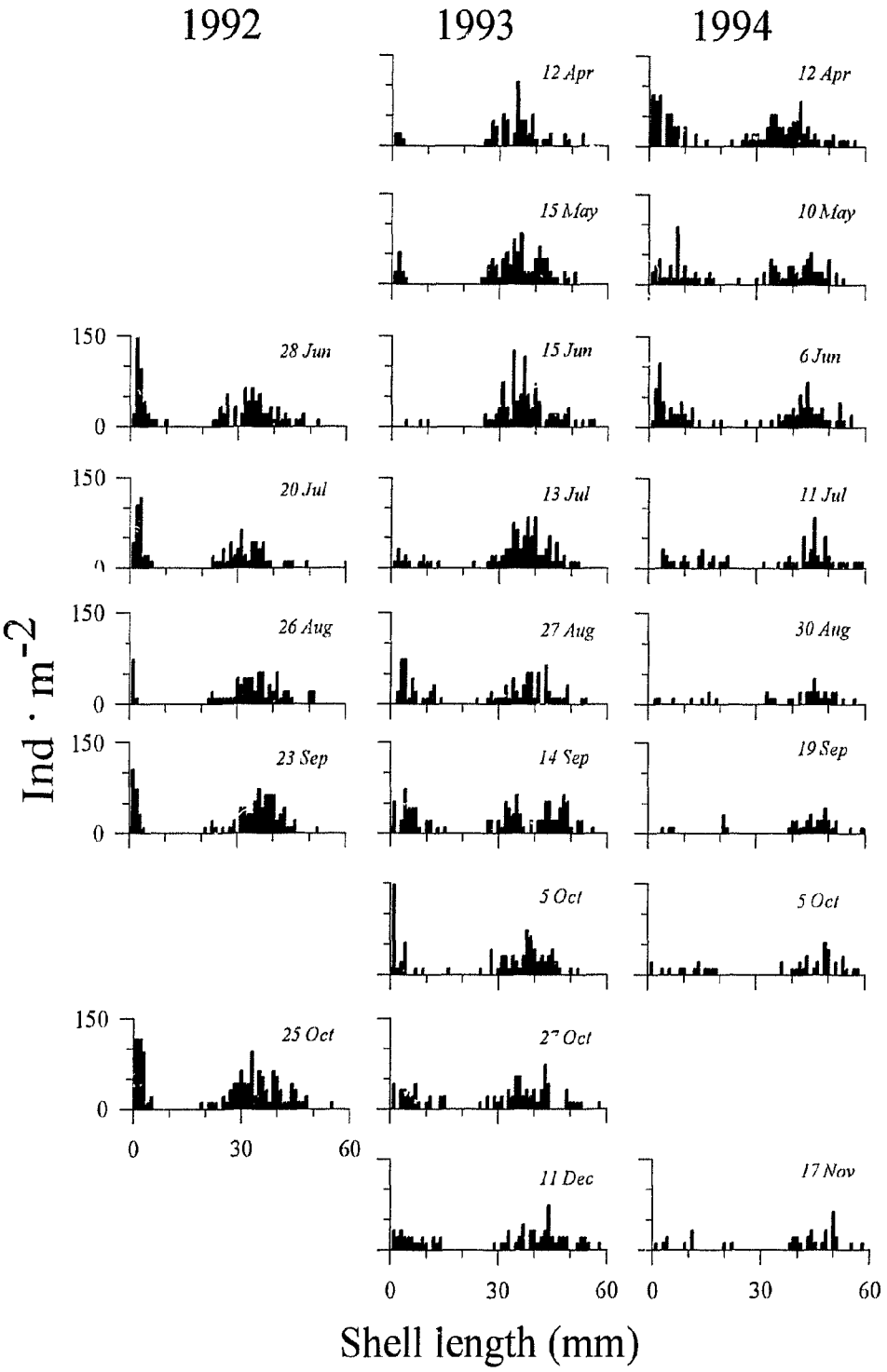

Fig. 3.5. Monthly size-frequency histograms for *Mya* at subtidal Site A Bar widths are 1.0 mm. Dotted reference line is at 40 mm.

settlers were first detected on 23 September in 1992, 14 September in 1993, but were not found in 1994. At subtidal Site B, first detection in 1992 was on 26 August, but there were no recruits in 1993, and only a low abundance on 30 August 1994.

The integrity of juvenile cohorts was generally not maintained over time in the subtidal, and no year class successfully recruited to the subtidal population during the 3 year study. Despite the eventual loss from subtidal plots, the time series of size-frequency distributions illustrate increases in abundance of the 2 to 15 mm size classes consistent with post-settlement transport (Fig. 3.5 and 3.6). By autumn 1992, the 0-group had arrived at both subtidal sites, and abundance of the combined 1991 and 1992 cohorts was 455 ± 47 and 869 ± 184 ind. · m^{-2} (Sites A and B, respectively). Abundance was reduced during winter 1993, but during spring and summer juveniles between 2 and 15 mm recolonized the higher energy Site A (up to 149 ± 86 ind. · m^{-2}). A large import of 1 mm long recent settlers from the 1993 year class was present at Site A on 5 October, but these individuals disappeared during the subsequent 3 weeks. There was no recruitment of the 1993 0-group to Site B, and by the end of autumn, juvenile distributions lacked a strong contribution from the 1993 0-group at either site. The total abundance of the multi-year juvenile cohort present at Site A by the end of 1993 was 191 ± 47 ind. · m^{-2}, of which only about 10% were the 0-group. However, the 1993 cohort increased in abundance to 25 to 50% of the juveniles during spring 1994 at Site A. There was no recruitment of the 1994 0-group. Juveniles at Site A declined in abundance after the disturbance caused by clam diggers (Figs. 3.4 and 3.5). At Site B, juvenile abundance was only ~70 ind. · m^{-2} by 11 July 1994, and a low import of new recruits (75 ind. · m^{-2})

occurred by August, all of which subsequently vanished Thus, by the end of the study, none of the 1991 to 1994 cohorts were present in the subtidal areas

Only the mixed 1991 and 1992 cohorts at Site B in 1993 were identifiable long enough for a growth rate to be estimated (Fig 3 6) This group of clams increased significantly from 3 6 to 11 9 mm in mean length before their disappearance in autumn (size = 0 029 * date- 8 219, $p = 0\ 014$, $r^2 = 0\ 659$, $n = 8$) (Fig 3 10)

In the intertidal zone, *Mya* recruitment patterns were more dynamic due to variations in 0-group abundance, post-settlement transport, and especially the impact of ice (Fig 3 4, 3 7, and 3 8) During winter 1993, there was complete mortality of all organisms at the mid-intertidal site, while clams at the low intertidal were relatively unscathed The following winter, ice froze directly to the sediment surface and freezing caused defaunation of the entire intertidal zone down to about the 10% aerial exposure level Abundance dramatically increased at both intertidal sites during recruitment of the 0-group Addition of recent settlers doubled the low intertidal population in 1992 and 1993 (Fig 3 4) The timing of the arrival of new recruits was extremely predictable at the low intertidal site, and occurred at the end of August of each year (Fig 3 7) Total abundance of recent settlers consistently ranged between 1000 and 1200 ind. m^2 The mid-intertidal site was much more variable, with initial settlers appearing on 23 September in 1992 and 27 August in 1993, while no recruitment occurred to the mid-intertidal in 1994 Abundance of 0-group clams at the mid-intertidal peaked in 1993 at 5318 ± 665 ind m^2, while only about 300 ind m^2 were found in the previous year (Fig 3 8)

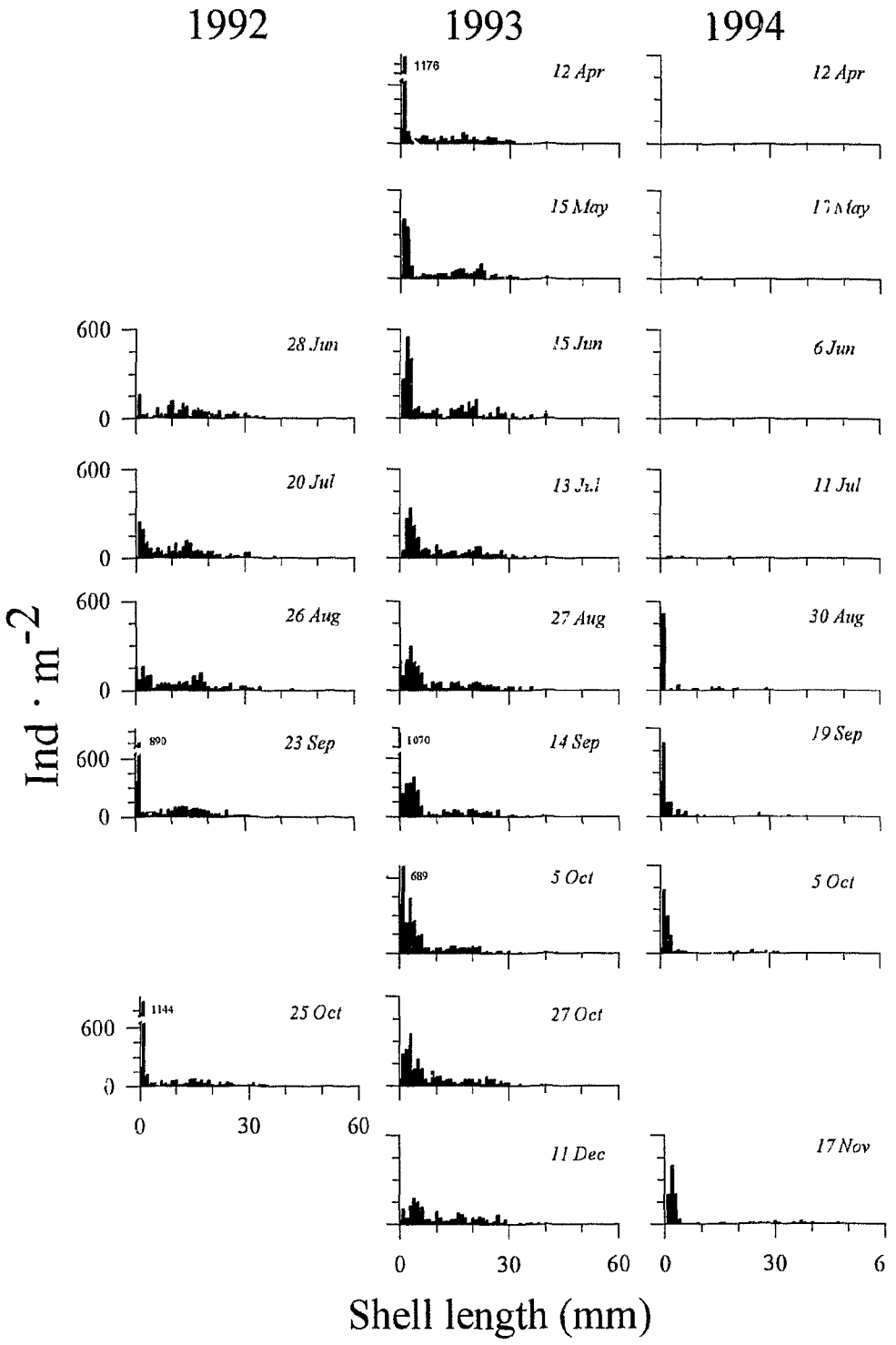

Fig. 3 7 Monthly size-frequency histograms for *Mya* at the low intertidal site Bar widths are 1 0 mm Dotted reference line is at 40 mm

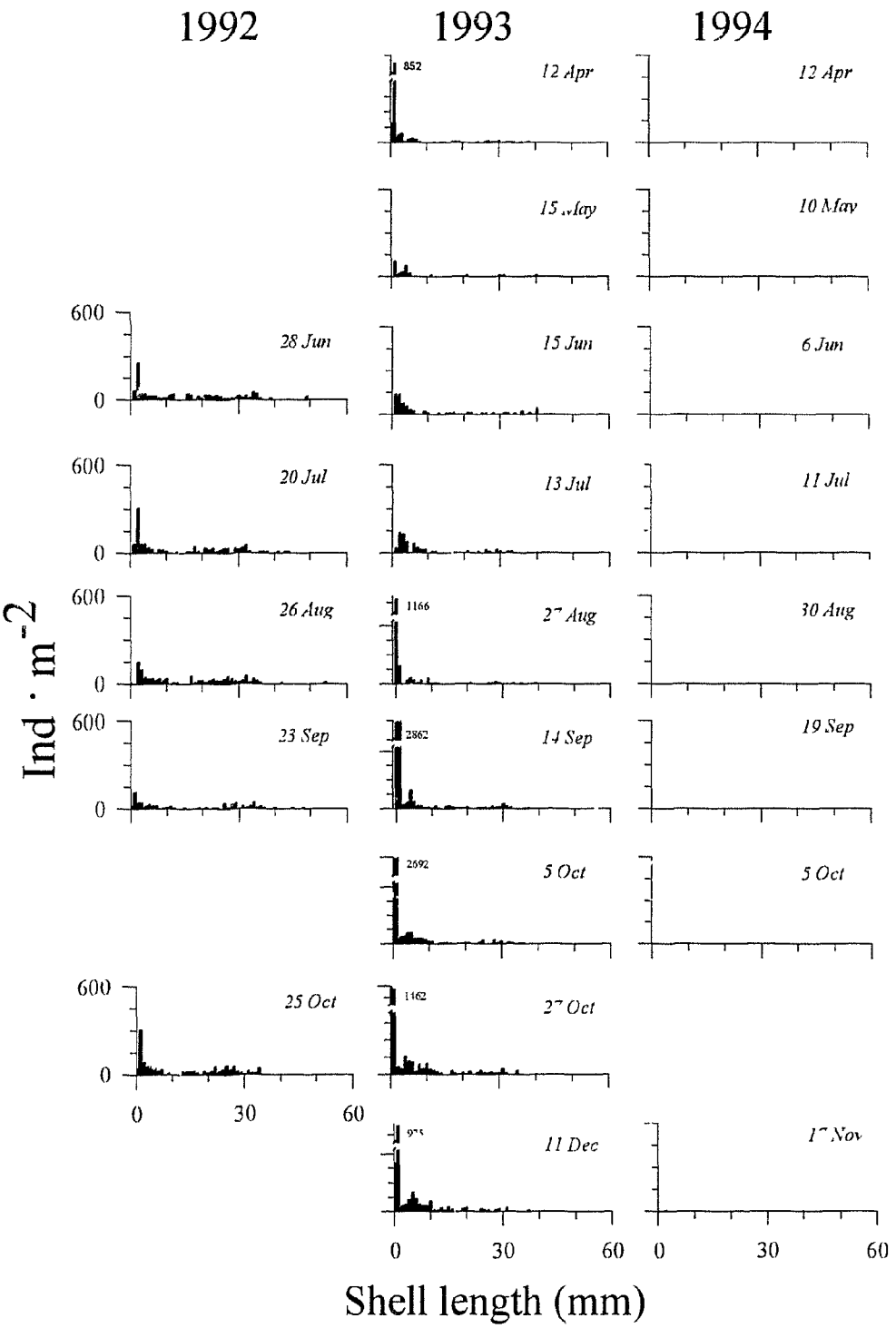

Fig 3 8. Monthly size-frequency histograms for *Mya* at the mid-intertidal site. Bar widths are 1 0 mm Dotted reference line is at 40 mm

Cohorts of recent settlers and juveniles < 3 year old were easily discernible from the size-frequency histograms at both intertidal sites, but differences in growth and survival were apparent. At the mid-intertidal (Fig. 3.8), the *Mya* population was stable during 1992 and showed no trend in change of abundance over time. Total mean abundance was 1086 ± 82 ind. $\cdot m^{-2}$, and growth of all groups was slight. The population was killed during winter 1993, as evidenced by decaying clams found buried *in situ* 3 days after the site was clear of ice in April. The ice cover apparently restricted water flow. However, the 2 to 4 cm of sediment deposited on the previous sandflat surface contained living clams. Transport thus accounted for 100% of the abundance in April. Immigration continued, and by 15 June, ~690 ind. m^{-2} had been transported to the site, mostly in the 2 to 3 mm size classes, although individuals up to 30 mm had also become established. The group of small clams grew to a population mean of 5 mm by 11 December Meanwhile, ~5500 ind $\cdot m^{-2}$ of recent settlers appeared by 5 October, but grew very little by the end of sampling in December. Because of this large import, the 0-group accounted for > 90% of total recruitment by mid-December 1993 All clams were killed by freezing during winter 1994, however, and no subsequent recruitment occurred during the following year.

At the low intertidal site (Fig. 3.7), the evenly distributed populations of clams > 10 mm remained stable in 1992 and 1993 at a mean abundance of 1104 ± 48 ind. $\cdot m^{-2}$. The mean size of clams > 10 mm did not change significantly with time when computed for either the total nondefaunated 1992 to 1993 period ($p = 0.891$, $r^2 = 0.001$, $n = 16$) or during individual years (1992: $p = 0.621$, $r^2 = 0.067$, $n = 6$; 1993: $p = 0.101$, $r^2 = 0.338$,

n = 9). Total biomass in 1992 and 1993 remained between 50 and 75 g ADW m^{-2} (Fig 3 9). Growth in the intertidal was very low. Transport was not easily discernible from the size-frequency histograms, since increases in abundance were concentrated in the < 2 mm faction

There were additions by the 0-group each year in the low intertidal (Fig. 3.7). By 25 October 1992 a maximum abundance of new recruits reached ~1200 ind. m^{-2}. Ice cover during winter 1993 had little effect on the population, and 0-group densities remained at the previous autumn values with no apparent growth These clams clearly overwintered at a very small size The 1992 year class then commenced to grow, and reached a modal length of 3.6 mm by 14 September, when 1070 ind m^{-2} of new recruits arrived at the site This 1993 0-group increased marginally in length, but were largely missing by 27 October. By 11 December 1993, the 0- and 1-group year classes were virtually indistinguishable and had a combined modal length of ~4.0 mm During the 1993, total juvenile abundance decreased from a high of 2452 ± 270 on 5 October to 837 ± 47 ind m^{-2} in December, a 65 9% decline

Mortality eliminated all individuals from the site during winter 1994, and subsequent recruitment occurred from combined addition of both recent settlers and juveniles (Fig. 3 4 and 3 7) However, because the nearest source of migrating clams (the surrounding flats) was eliminated, juvenile transport was low Recently settled recruits were first observed on 30 August at an abundance of 1092 ± 442 ind. m^{-2} (< 1 and 1 mm groups) By this date, small numbers of clams from 5 to 30 mm were also reaching the site (up to 149 ± 9 ind. $\cdot m^{-2}$). The 1994 year class grew to a mean length of only 2 mm

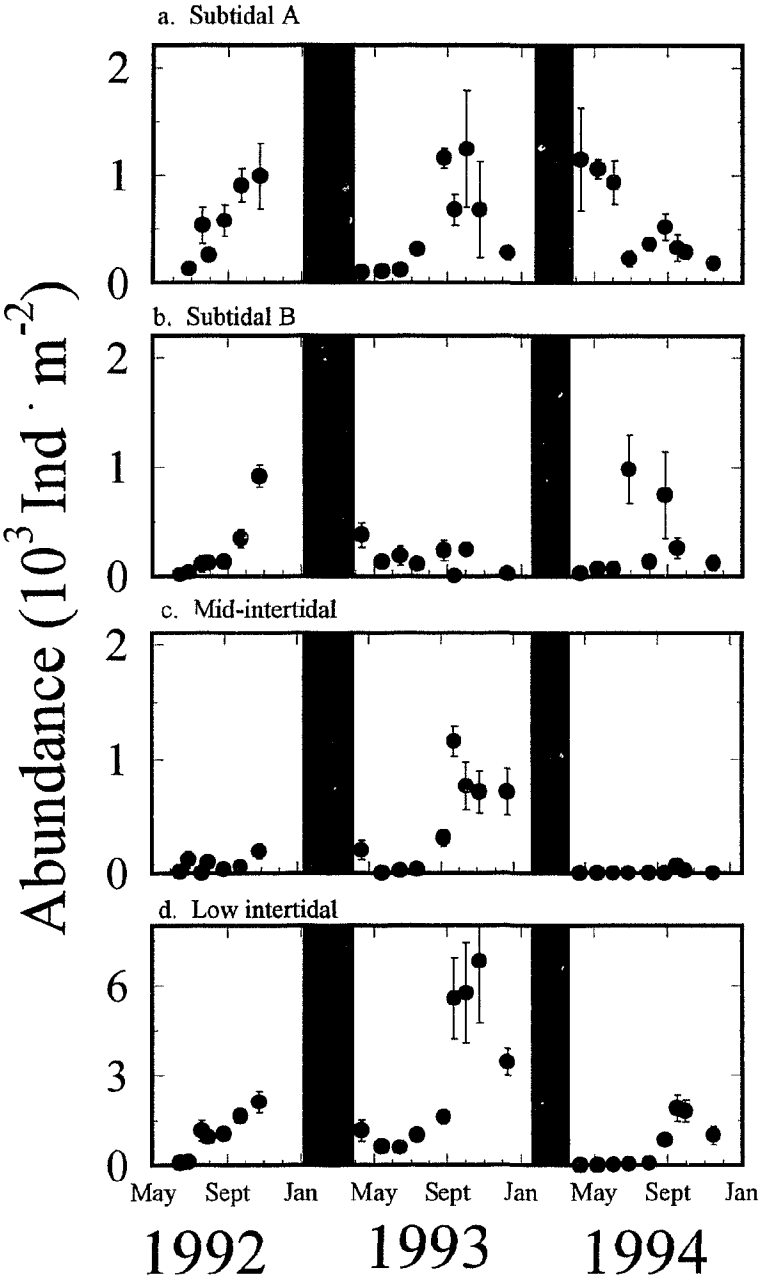

Fig. 3.15. Time series of mean *Gemma* abundance (± SE) for the 4 experimental sites from June 1992 to November 1994. Shaded areas indicate periods of ice cover.

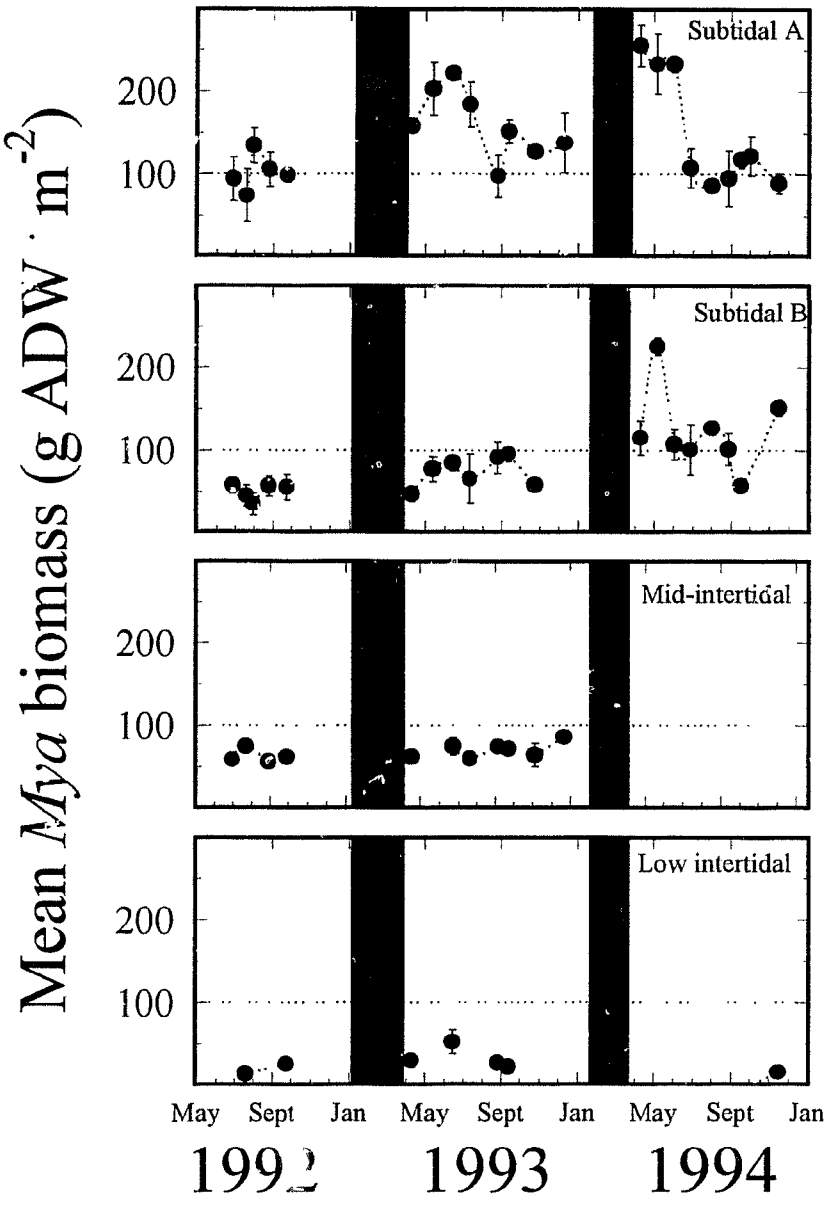

Fig. 3.9. Time series of total mean biomass (± SE) for *Mya* at the 4 experimental sites from June 1992 to November 1994. Shaded areas indicate periods of ice cover.

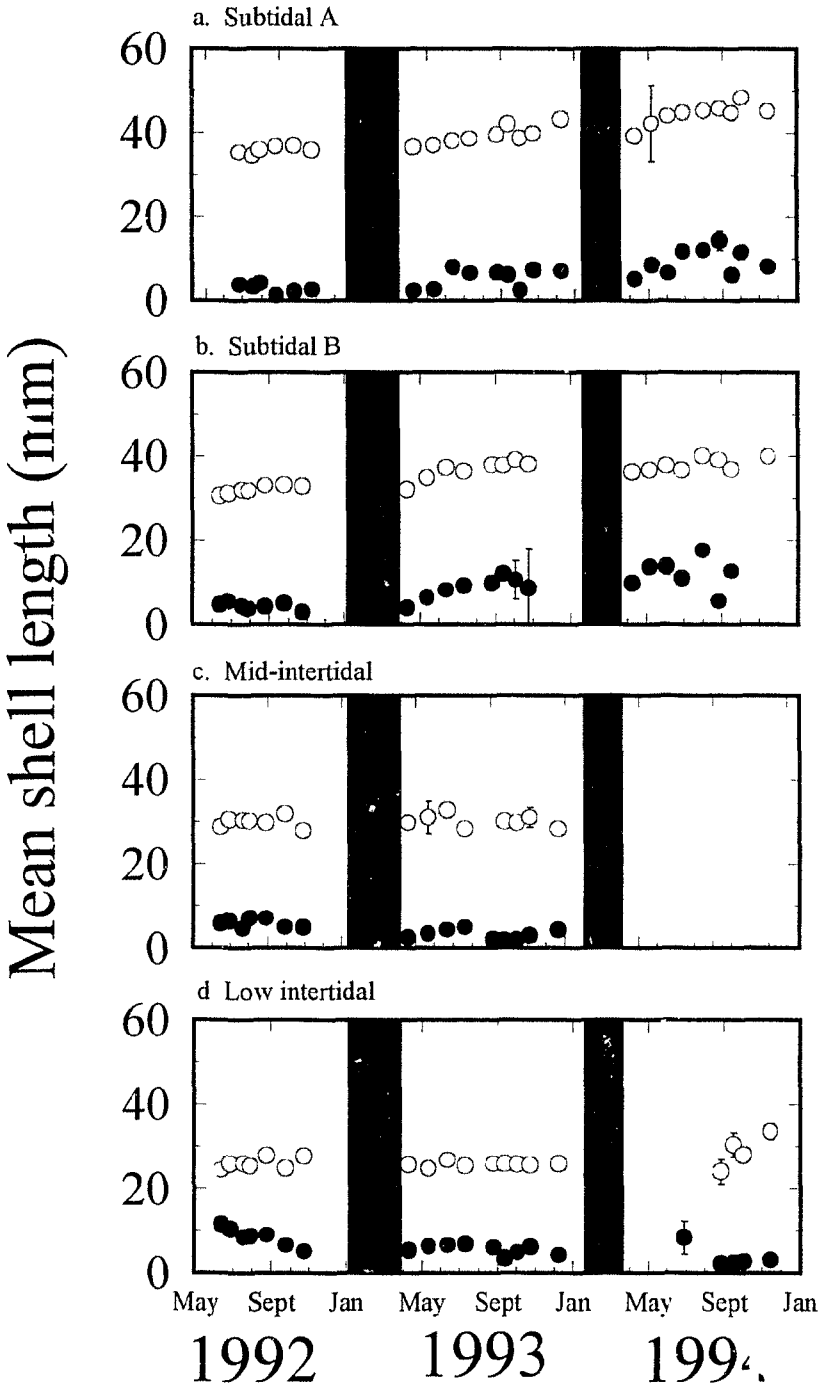

Fig. 3 10 Time series of mean shell length (± SE) for *Mya* at the 4 experimental sites from June 1992 to November 1994. Open circles, clams greater than 20 mm; filled circles clams less than 20 mm. Shaded areas indicate periods of ice cover.

and achieved an abundance of 828 ± 487 ind m^{-2} by 17 November, while the distribution of larger, transported clams was patchy and remained at an abundance of (181 ± 60 ind m^{-2}) Juvenile transport thus accounted for ~18% of total recruitment in 1994, and the low intertidal was the only site where the 1994 cohort survived Total recolonization was 61% of the autumn 1992 population levels, but the percent of large clams shifted from roughly half of the population in 1993 to only ~20 % in 1994

3.3.3.2 ***Macoma balthica***

A clear preference for intertidal sites was observed in *Macoma* (Fig 3 11) Mean abundance was < 50 ind m^{-2} in the subtidal channel at Site A in any year, with few discernible modes in size frequency (data not shown) Site B had about twice the mean abundance but a similar lack of consistent structure to the size-frequency distribution (Fig 3 12) At the mid-intertidal, mean annual *Macoma* abundance increased from 274 ± 36 in 1992 to 613 ± 69 ind m^{-2} in 1993, but significant increases in abundance within years was only found in 1992 (Fig 3 13) In contrast, *Macoma* at the low intertidal had mean total abundance of 1385 ± 72 ind m^{-2} during 1992 and 1993 but abundance tended to decrease over time (Fig 3 14)

Macoma settlers were rare, and most recruitment occurred by post-settlement transport In the subtidal plots, abundance of recently settled clams peaked at only ~50 ind m^{-2} (27 August, Fig 3 12) There was recruitment failure in 1993 and 1994 In the mid-intertidal, abundance of new recruits was < 100 ind m^{-2} and only low levels of 0-group clams recruited in each of 1992 and 1993 Again, no recruitment occurred to the mid-intertidal in 1994 (Fig 3.13) In the low intertidal, clams < 2 mm were present

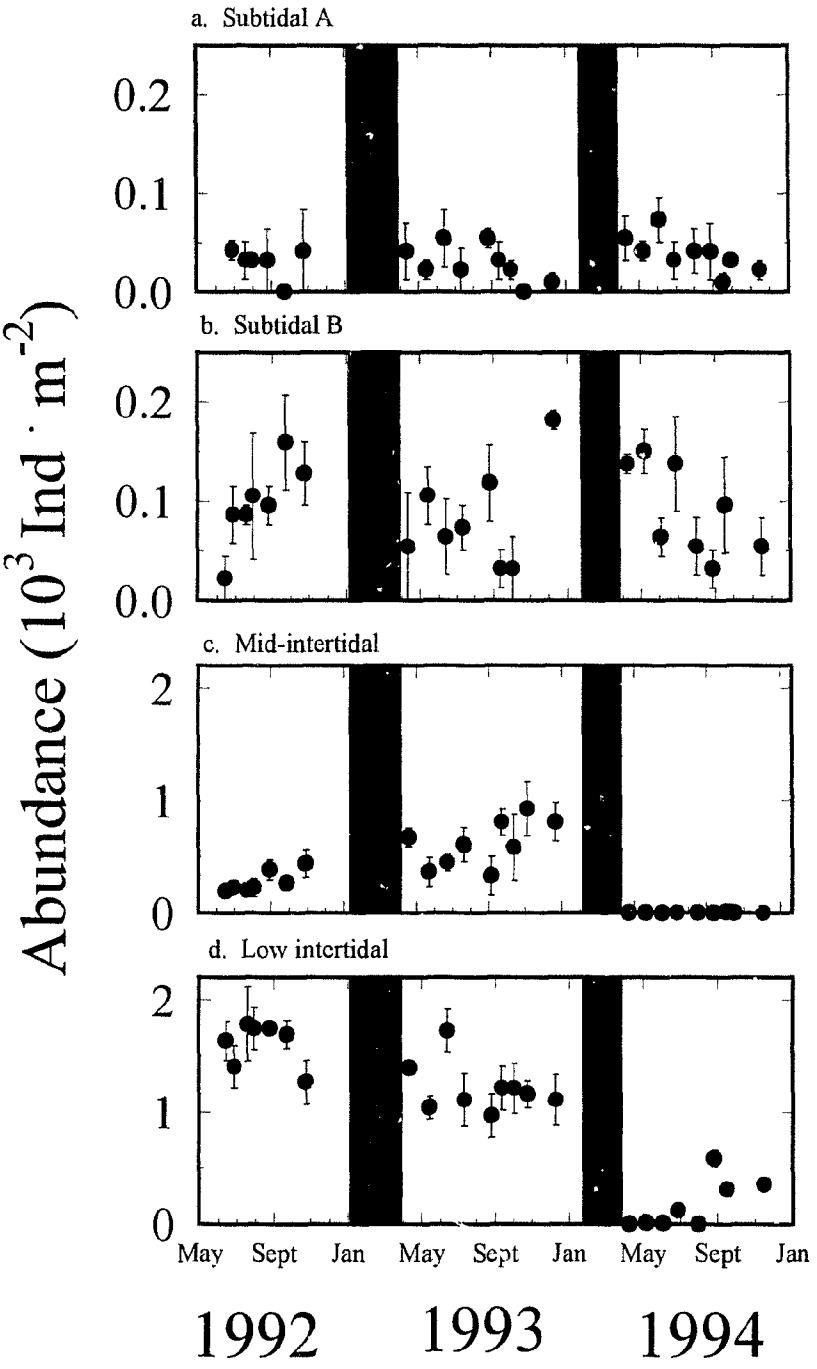

Fig. 3.11 Time series of mean *Macoma* abundance (± SE) for the 4 experimental sites from June 1992 to November 1994. Shaded areas indicate periods of ice cover.

throughout 1992 and 1993. New recruits reached a maximum abundance of only ~100 ind. · m^{-2} in 1992 and 1993, but were very rare in 1994 (Fig. 3.14).

Juvenile transport contributed importantly to the population structure at both intertidal sites. In the mid-intertidal (Fig. 3.13), abundance was low in 1992 until the arrival of new recruits in October ~150 ind. · m^{-2}. The mean population abundance was 436 ± 124, but there was a complete mortality during winter 1993. The distribution in April 1993 (Fig. 3.13) shows that all individuals were transported to the site. The rapidly changing size-frequencies from mid-July through mid-September 1993 are consistent with post-settlement transport. The abundance of 0-group clams was only ~75 ind. · m^{-2} in 1993 with the maximum import occurring in August. Thus, by the end of autumn1993, ~92% of the recruitment to the mid-intertidal site was by post-settlement movement, and all sizes of clams were involved. However, mortality again eliminated the population during winter 1994, and like *Mya, Macoma* failed to recruit to the mid-intertidal site by any means during the following year.

In the low intertidal (Fig. 3.14), the initially unimodal size-frequency distributions in June 1992 became bimodal 3 weeks later with the import of ~650 ind. · m^{-2} of clams 1 to 4 mm in shell length (51.2% of the population). There followed an increasingly negatively skewed distribution as new recruits (~300 ind. · m^{-2} in the < 2 mm faction) arrived at the site. Survival over winter 1993 was good, with a total abundance of 1391 ± 60 ind. · m^{-2} remaining after ice breakup. The modal length of clams < 10 mm increased from 1 mm in April to 3 mm by 13 July 1993, after which the frequency distribution became less clear. About 100 ind. · m^{-2} of 1993 0-group *Macoma* recruits were

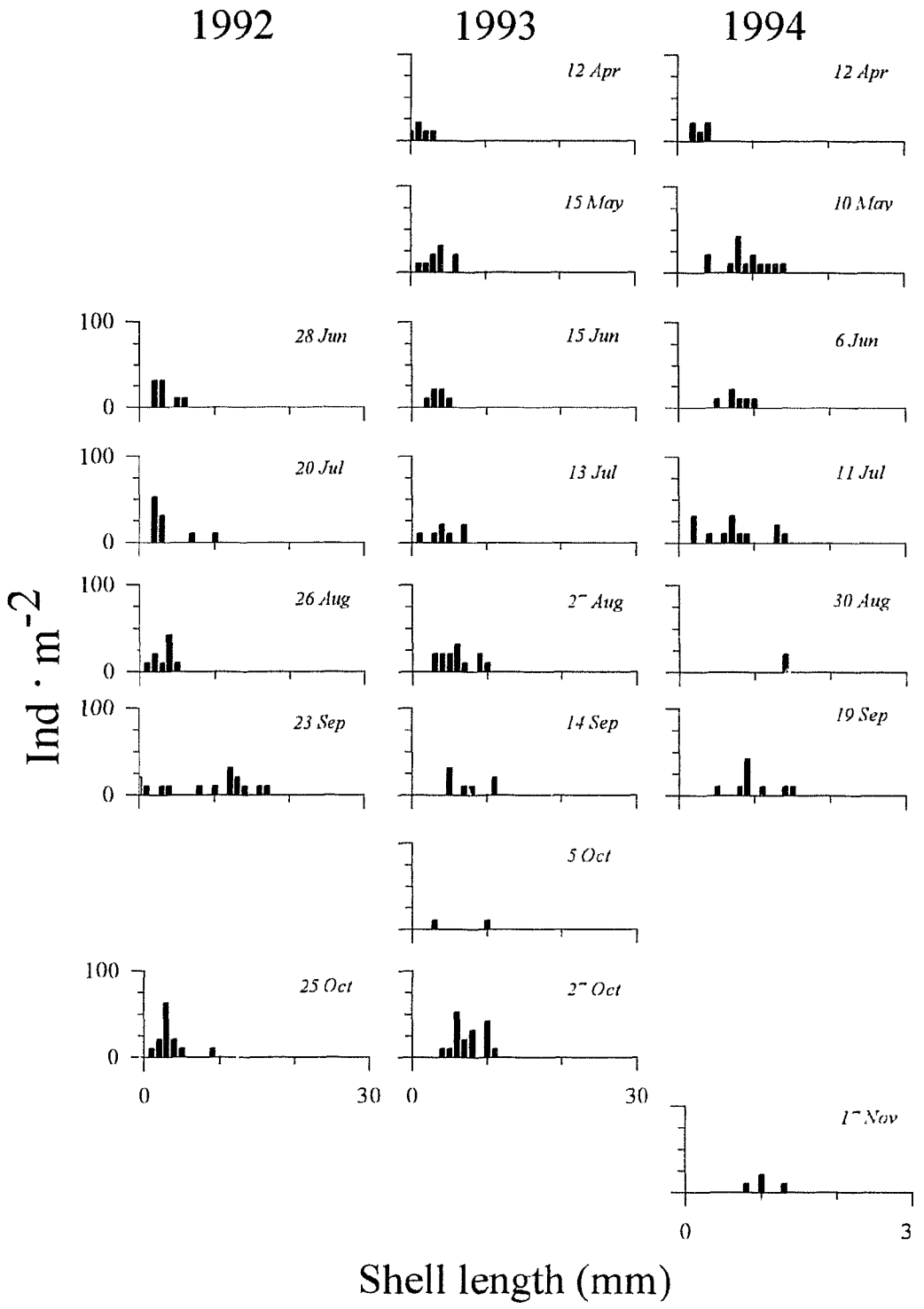

Fig. 3 12. Monthly size-frequency histograms for *Macoma* at subtidal Site B. Bar widths are 1 0 mm. Dotted reference line is at 10 mm.

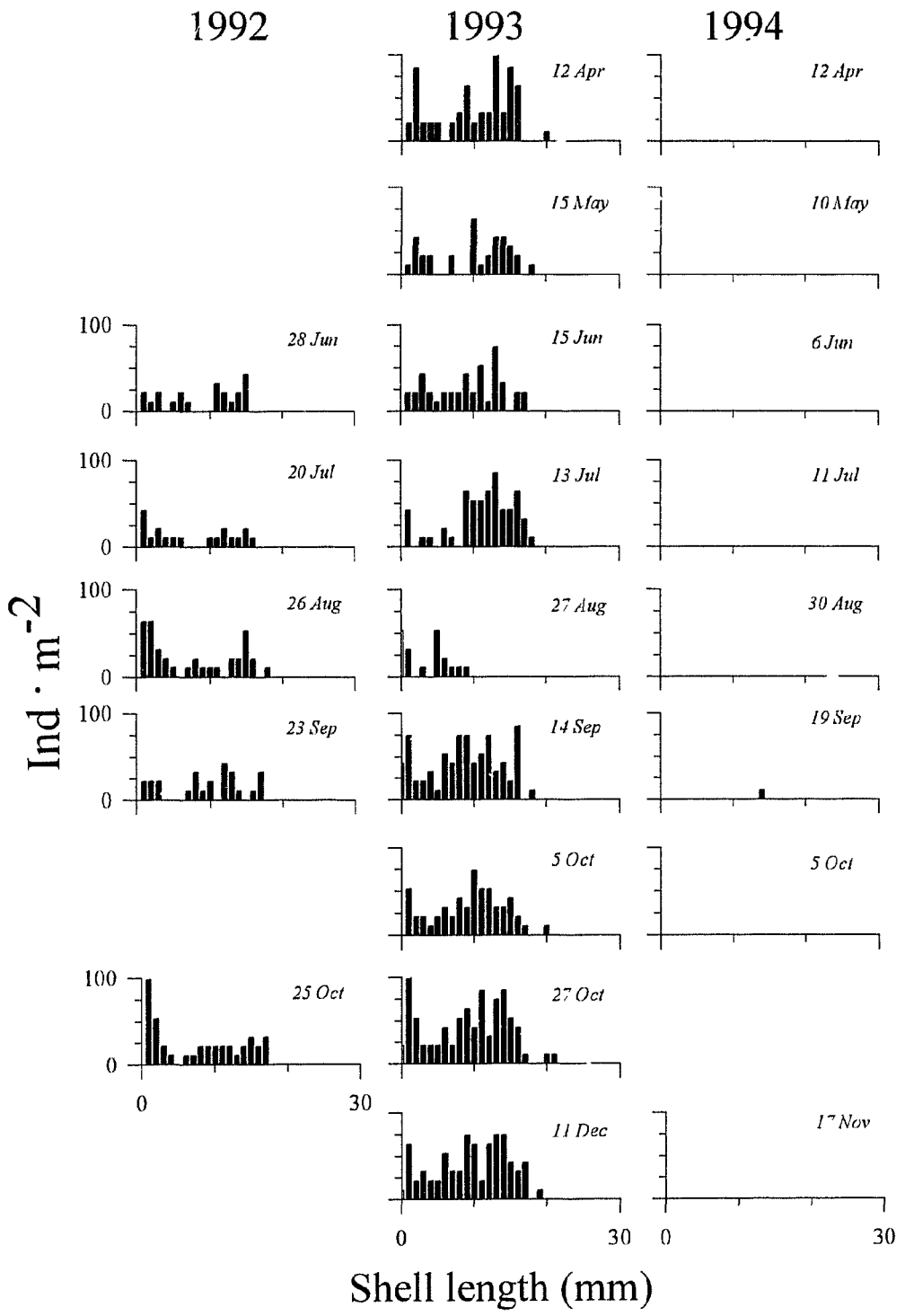

Fig. 3.13. Monthly size-frequency histograms for *Macoma* at the mid-intertidal site Bar widths are 1 0 mm. Dotted reference line is at 10 mm.

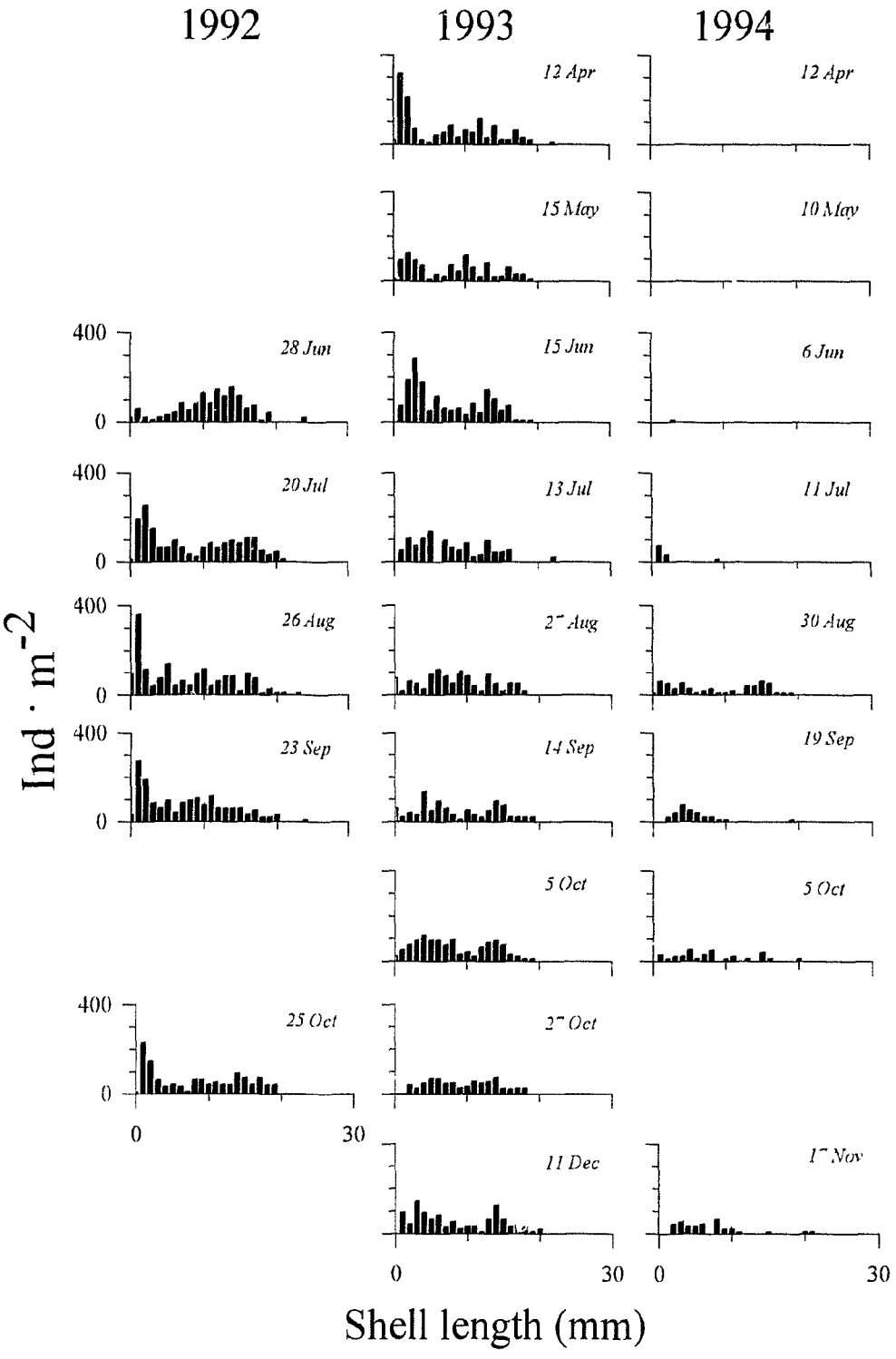

Fig. 3.14. Monthly size-frequency histograms for *Macoma* at the low intertidal site. Bar widths are 1.0 mm. Dotted reference line is at 10 mm

present by September, but these subsequently vanished. By 11 December, a bimodal patterr was reestablished with modal lengths of 3.5 mm for clams < 10 mm and 14.2 mm for clams > 10 mm, respectively. No living clams were found after ice breakup in April 1994. The site remained uninhabited except for a few, variously sized individuals until 30 August when *Macoma* of all size classes were found to have been transported to the site. Three weeks later only a well defined distribution (mode = 4.0 mm) of clams < 10 mm was present, but these later dispersed and by 17 November a population of 350 ± 47 ind. · m^{-2} consisting of most size classes was measured. The 1994 year class also failed to recruit, and the supply of clams to the site was entirely through post-settlement transport. The recolonization abundance was 32% of the previous autumn population, and *Macoma* < 10 mm composed 75% of the recruited clams

3.3.3.3. *Gemma gemma*

Marked fluctuations occurred in abundance and size-frequency distributions of *Gemma* measured at both sub- and intertidal plots in all three years of observation (Fig 3.15 to 3.19). At subtidal Site A, *Gemma* abundance increased from 127 ± 31 in June 1992 to 987 ± 302 ind · m^{-2} by Autumn, and most of the added population consisted of new recruits (Fig 3 16) Abundance was reduced to less than 100 ind. m^{-2} after winter 1993 and remained near this level until 27 August when representatives from all size classes were present at a total abundance of 1156 ± 477 ind. m^{-2}. Seventy-five percent of this increase was by individual gem clams larger than 1 mm. The resultant evenly distributed size-frequency structure of the population was maintained through the rest of the sampling period until total abundance fell abruptly to 277 ± 70 ind m^{-2} between 27

October and 11 December 1993, suggesting size-independent emigration or mortality. There was no strong addition from the 0-group in 1993. After winter 1994, the population expanded to 1146 ± 477 ind. · m^{-2} at Site A and maintained near that abundance with a mean clam size of ~2 mm for the next several months. By 11 July, abundance was reduced to 222 ± 73 ind. · m^{-2}, possibly an indirect effect of clam digging activity. A pulse of new recruits (436 ± 121 ind. · m^{-2}) was present on 30 August, but by the next sample date only 20% of this amount remained, and subsequent samples show reduced abundance of individuals in this cohort. The final abundance was 181 ± 57 ind. · m^{-2}, and the population had a regular size frequency distribution comprised of low numbers of all size classes.

Reduced numbers of *Gemma* occurred at subtidal Site B (Fig. 3.17). Overall abundance was low in 1992 until Autumn, when both new recruits (382 ± 66 ind. · m^{-2}) and larger gem clams (531 ± 41 ind. · m^{-2}) were present. Very few *Gemma* were found at the site during 1993, with numbers ranging between 0 and ~ 400 ind. · m^{-2}. Abundance remained low until the transport of 977 ± 322 ind. · m^{-2} of *Gemma* > 1.5 mm on 11 July, 1994. These clams were largely missing by 30 August, but new recruits with an abundance of ~500 ind. · m^{-2} were present. However, abundance subsequently waned to low levels by the end of Autumn 1994. The subtidal *Gemma* populations thus fluctuated greatly over time in a manner consistent with variations in benthic transport.

The highest population densities of *Gemma* were found at the low intertidal site (Fig. 3.15). Additionally, the size frequency distributions were consistently negatively skewed, reflecting the accumulation of smaller recruits (Fig. 3.18). In 1992, gem clams

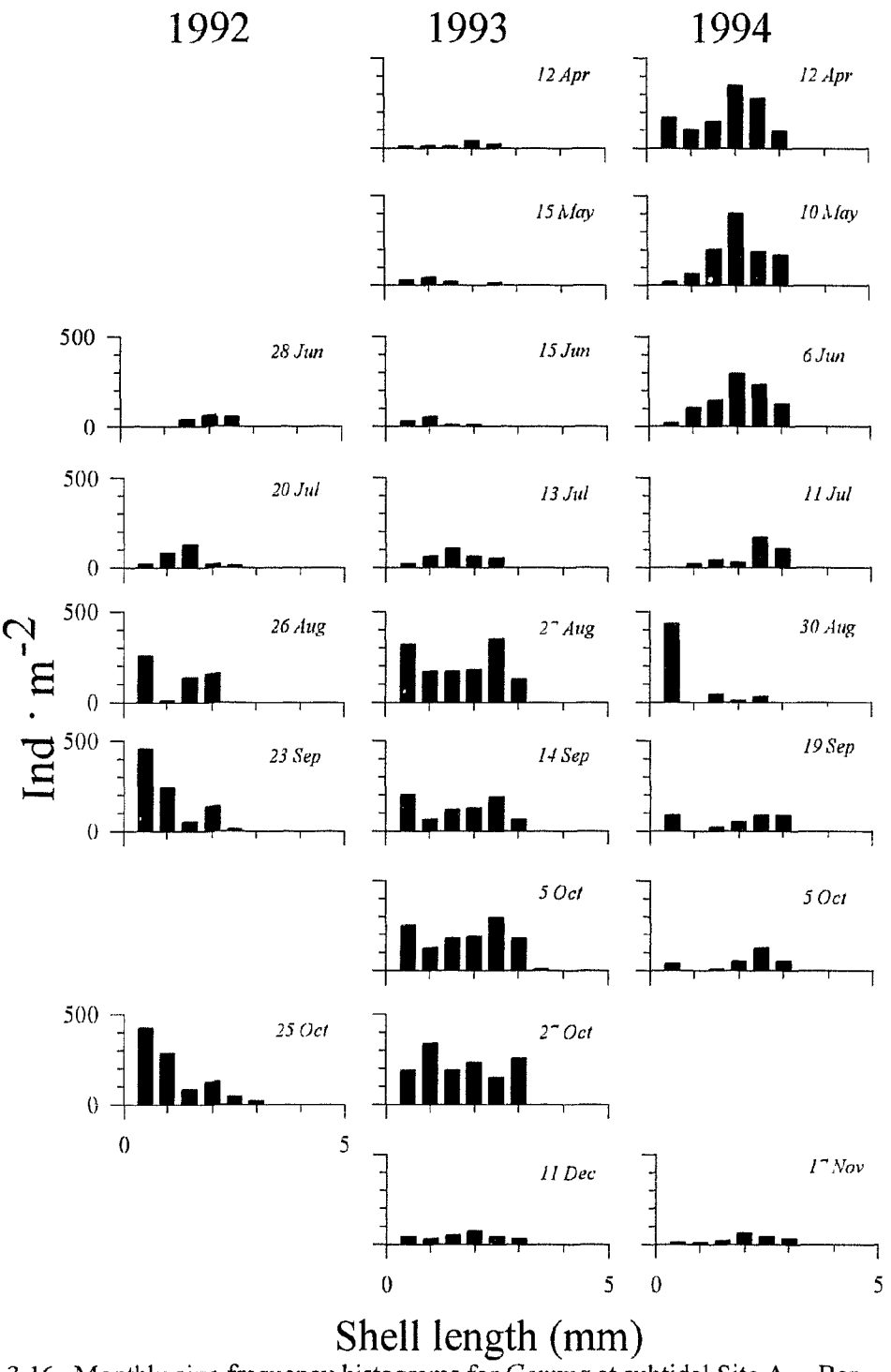

Fig. 3.16. Monthly size-frequency histograms for *Gemma* at subtidal Site A . Bar widths are 0.5 mm.

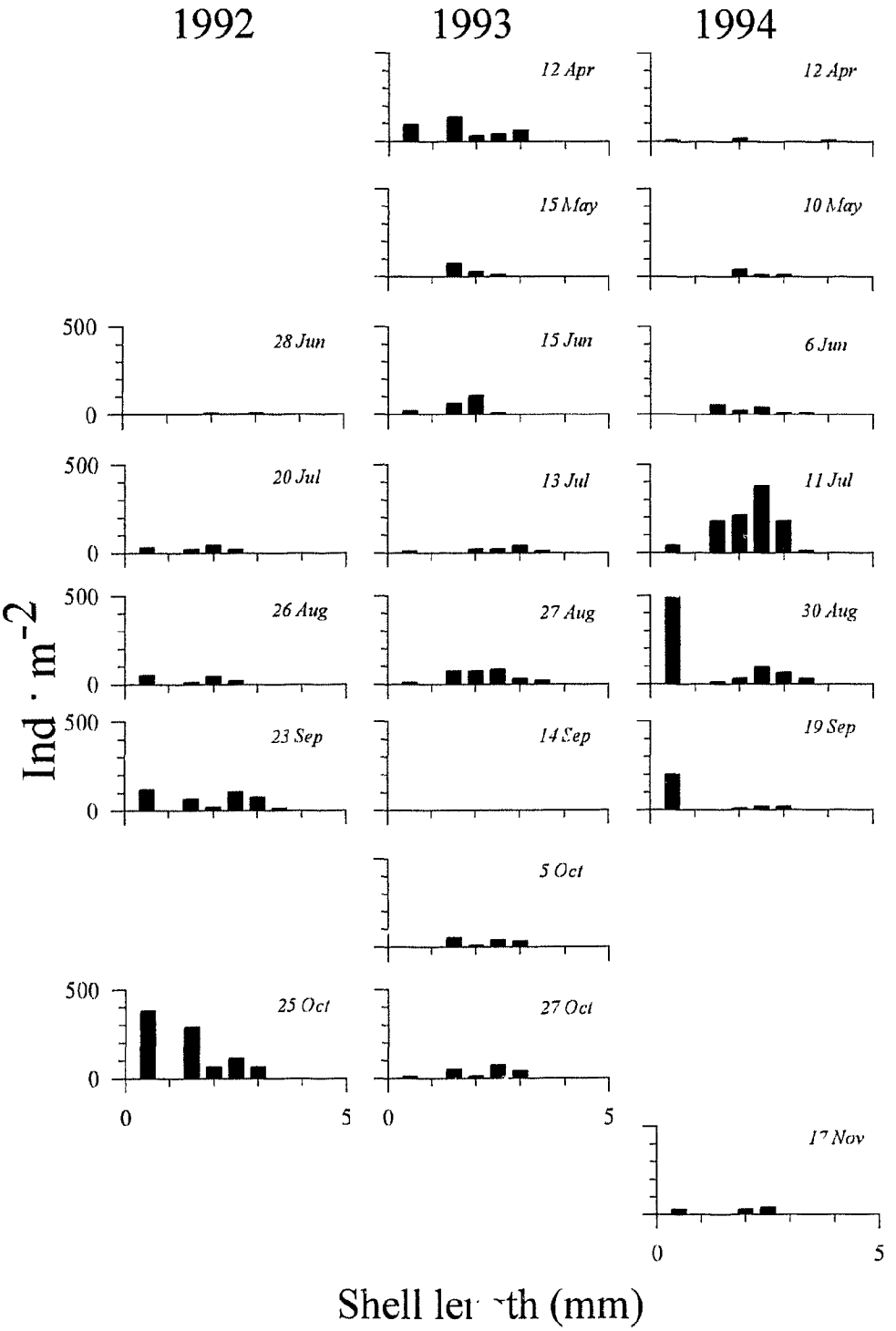

Fig. 3.17. Monthly size-frequency histograms of *Gemma* at subtidal Site B site. Bar widths are 0.5 mm.

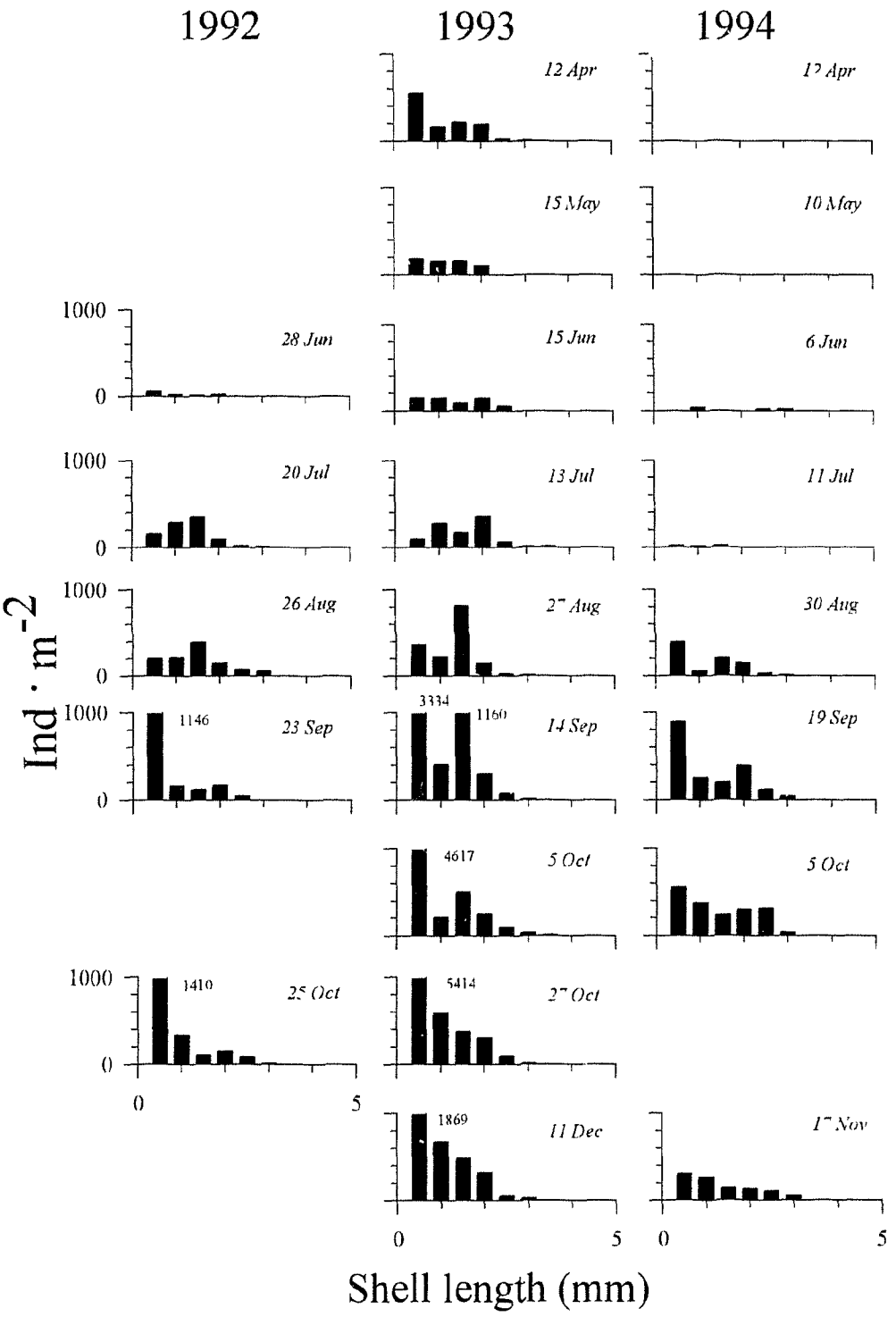

Fig. 3 18. Monthly size-frequency histograms for *Gemma* at the low intertidal site. Bar widths are 0.5 mm.

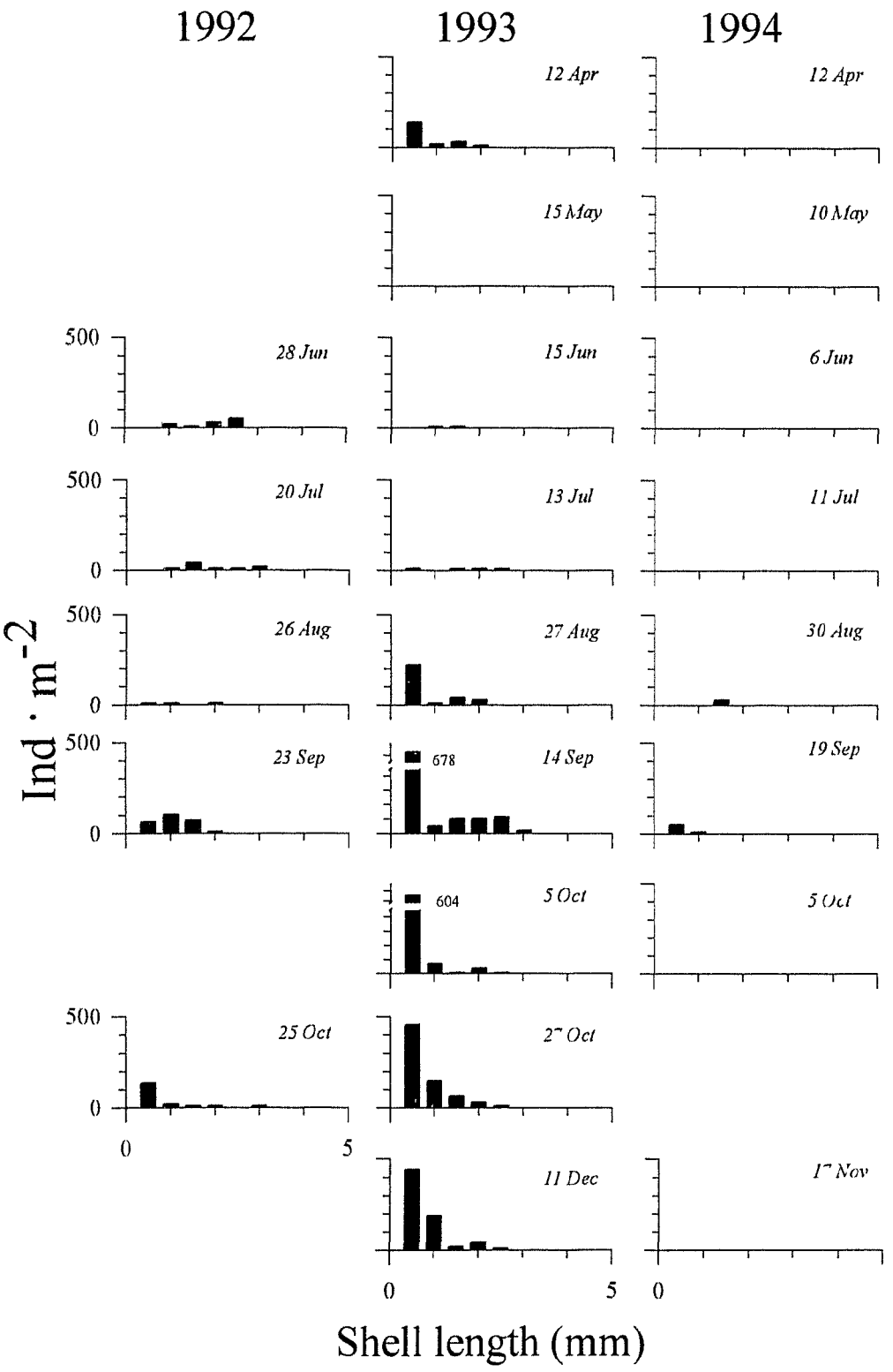

Fig. 3.17. Monthly size-frequency histograms for *Gemma* at subtidal Site B. Bar widths are 0.5 mm.

of all sizes increased significantly from 70 to over 1000 ind. $\cdot$ m^{-2} by August (Table 3.3), and by September new recruits at a abundance of 1146 $\pm$ 248 ind. $\cdot$ m^{-2} populated the site. The size structure remained similar through winter 1993, but the abundance of the 1992 year class decreased during spring 1993, with total numbers remaining less than 600 ind. $\cdot$ m^{-2}. New recruits became very abundant in September 1993 (3334 $\pm$ 551 ind. $\cdot$ m^{-2}) and reached a maximum of 5414 $\pm$ 2038 ind. $\cdot$ m^{-2} by 27 October, thereafter declining to 1869 $\pm$ 286 ind. $\cdot$ m^{-2}. Total abundance in 1993 peaked at 6805 $\pm$ 2057 ind. m^{-2}, but was roughly half that by 11 December. New recruits constituted ~50% of the population. As with the other species, there were no survivors after winter 1994, and recolonization did not occur until 30 August, when a mixed size frequency of 837 $\pm$ 194 ind. $\cdot$ m^{-2} reached the site (53% >1.5 mm). A relatively weak pulse of new recruits (891 $\pm$ 388 ind. m^{-2}) was present on 19 September, but subsequent total abundance declined to < 1000 ind. m^{-2} by the end of Autumn.

The mid-intertidal site supported few *Gemma* in 1992, and abundance was also low in 1993 until August, when ~250 ind. $\cdot$ m^{-2} of new recruits and some larger clams were present (Fig. 3.19). Maximum recruitment occurred in September 1993 (678 $\pm$ 82 ind. $\cdot$ m^{-2} new recruits, 477 $\pm$ 73 ind. $\cdot$ m^{-2} larger clams). No recruitment occurred in 1994.

3.3.4 Transport experiments

Transport of bivalves into defaunated sediments was concentrated at the low intertidal and subtidal plots (Tables 3.1 to 3.5). In 1992, transport was consistently higher at the low intertidal site for all three species (Tables 3.1 to 3.3). A maximum net

transport of 101 ind m^{-2} d^{-1} was found for *Mya*, and 166 ind m^{-2} d^{-1} for *Gemma* Transport to the subtidal sites was intermediate for *Mya* and *Gemma*, ranging between 3 and 73 ind m^{2} d^{-1}, but *Macoma* transport was generally low No species had significant transport to the mid-intertidal site in 1992

The experiment conducted between 15 and 29 July 1993 at subtidal Site A and at the low intertidal site demonstrated the rapid movement of juvenile *Mya* (< 10 mm) and *Macoma* up to 16 mm into 0 10 m^2 defaunated cores (Fig 3 20 and 3 21) The *Gemma* data were unfortunately lost The size-frequency histograms comparing the population of transported bivalves to the population of the resident (control) animals show essentially complete recolonization of the smaller *Mya* and most of the *Macoma* in the subtidal plots (Fig 3 20 and 3 21) In the intertidal, peak *Mya* transport occurred in the 1 to 5 mm size class, with smaller numbers up to 10 mm in length (Fig 3 20) *Macoma* transport was concentrated in the 4 to 7 mm size range, which was slightly larger than the control distribution (Fig 3 21) Transport rates were similar to 1992 values (Table 3 1 and 3 4)

Transport was lower in 1994 following the impact of ice on the intertidal populations (Table 3 5) The reduced transport was probably due to lack of local supply of older individuals, since the surrounding flats were denuded of organisms New recruits comprised the bulk of the transported bivalves All rates were low on 4 August, when the intertidal zone was still largely devoid of macrofauna At the intertidal site, *Mya* abundance peaked at 58 ind m^{2} d^{-1} on 30 August as a result of settlement of the 0-group, but thereafter diminished *Macoma* transport was low but clams nevertheless repopulated the site with a range of size classes by 17 November (Fig 3 14) Mainly 0-group *Gemma* were transported at low levels during August, while an increased import

of all size classes occurred in November (Fig. 3.19). In the subtidal, rates of *Mya* and *Macoma* transport were only 0.3 to 2.3 ind. $\cdot m^{-2} \cdot d^{-1}$ for all periods sampled, reflecting the low abundance of these groups after the disturbance by clam digging activity in July (Fig. 3.5, 3.6, and 3.12). Rates of *Gemma* transport were also low compared to 1992, except for the high transport of new recruits on 30 August (Table 3.5). However, mobility of all sizes was evident in November (Fig. 3.19).

Table 3.1. Transport of *Mya* to 4 benthic sites in 1992. F: Bivalve transport (ind. $\cdot m^{-2} \cdot d^{-1}$) ± SE; R_T: Time (d) for recolonization to resident abundance (clams between 1 and 15 mm).

Date	Subtidal A		Subtidal B		Mid-intertidal		Low Intertidal	
	F	R_T	F	R_T	F	R_T	F	R_T
28 June			11.9±5.9	21.1	11.9±5.9	56.1	101.2±33.1	15.7
9 July	37.9±7.5	4.4	15.1±15.1	5.5	0	–	68.2±34.7	30.5
20 July	22.7±13.1	7.3	30.3±15.5	5.5	0	–	30.3±20.4	49.5
31 July	17.1±7.6	29.3	7.5 ±7.5	22.1	0	–	30.3±20.4	52.3
26 Aug	3.2±3.2	78.1	12.8±8.5	13.1	11.9±5.9	99.1	48.1±19.2	38.3
23 Sep	17.9±13.6	9.3	17.9±8.9	4.7	0	–	50.6±10.7	16.5
25 Oct	2.7±2.7	62.1	16.3±12.3	5.2	8.1±4.7	51.7	34.3±18.8	89.9

Table 3.2. Transport of *Macoma* to 4 benthic sites in 1992. F: Bivalve transport (ind. $\cdot m^{-2} \cdot d^{-1}$) ± SE; R_T: Time (d) for recolonization to resident abundance

Date	Subtidal A		Subtidal B		Mid-intertidal		Low Intertidal	
	F	R_T	F	R_T	F	R_T	F	R_T
28 June			11.9±9.8	9.8	5.9±5.9	34.3	47.6±15.7	8.9
9 July	45.5±2.6	2.3	0	–	0	0	60.6±49.6	8.9
20 July	7.6±7.6	31.1	17.2±7.8	7.7	0	–	45.5±13.1	27.3
31 July	5.7±0.1	20.7	0	–	0	–	37.8±20.0	12.5
26 Aug	3.2±3.2	0	0	–	0	–	44.9±14.0	15.8
23 Sep	0	–	8.9±5.2	13.2	0	–	14.9±10.7	59.8
25 Oct	0	–	5.4±5.3	21.9	0	–	6.0±4.7	58.5

Table 3 3 Transport of *Gemma* to 4 benthic sites in 1992 F Bivalve transport (ind m^{-2} d^{-1}) ± SE, R_T Time (d) for recolonization to resident abundance

Date	Subtidal A		Subtidal B		Mid-intertidal		Low Intertidal	
	F	R_T	F	R_T	F	R_T	F	R_T
28 June			29 7±11.9	0	11.9±11.9	34.3	53.6±37 1	0
9 July	15.2±15 2	0	0±0	–	0	0	106.1±7 8	2 2
20 July	45.5±13 1	4 5	37 8±11.9	3.1	0	–	53.0±27 3	8 1
31 July	73.8±49 7	5 7	7 8±7 8	0	0	–	166.7±132.7	5 6
26 Aug	41 7±3 2	9 8	6 4±3 2	36 8	6 4±6 4	0	76 9±5 6	6 7
23 Sep	23 8±5 6	34 6	11.9±3.0	9.9	8 9±5.2	0	89.3±23 6	14.3
25 Oct	18 8±9 7	31 3	18.8±7.1	6.3	2.7±2.7	0	66.5±12 3	6 4

Table 3 4. Transport of *Mya* and *Macoma* to 2 sites in 1993 F Bivalve transport (ind m^{-2} d^{-1}) ± SE, R_T Time (d) for recolonization to resident abundance

Species	Subtidal A		Low Intertidal	
	F	R_T	F	R_T
Mya	7 4±0 6	19 9	29.1±3 5	42.8
Macoma	1 9±0 5	19 3	17.9±3.3	38.2

Table 3 5 Transport of *Mya*, *Macoma*, and *Gemma* to 2 sites in 1994 F Bivalve transport (ind m^{-2} d^{-1}) ± SE, R_T Time (d) for recolonization to resident abundance

Date	Species	Subtidal A		Low Intertidal	
		F	R_T	F	R_T
4 Aug	*Mya*	0.3±0.3	340	0 3±0 3	–
30 Aug		0 4±0.4	208	56 8±36.9	22 3
5 Oct		0 6±0 3	36	–	–
18 Nov		2.3±1.1	63.5	9 6±6 0	97 3
4 Aug	*Macoma*	1 6±1.6	27.2	0 3±0 3	306.1
30 Aug		0	–	1 7±0 4	357 5
5 Oct		0 3±0.3	0	–	–
18 Nov		0.8±0.4	44.1	4 3±0 9	82 8
4 Aug	*Gemma*	1.6±1 6	231.2	1 3±1 3	51 1
30 Aug		27 8±10 2	19.6	9 4±4 9	93 4
5 Oct		4.6±1.6	0	–	–
18 Nov		8 6±1.8	34.9	21.0±1 8	89.6

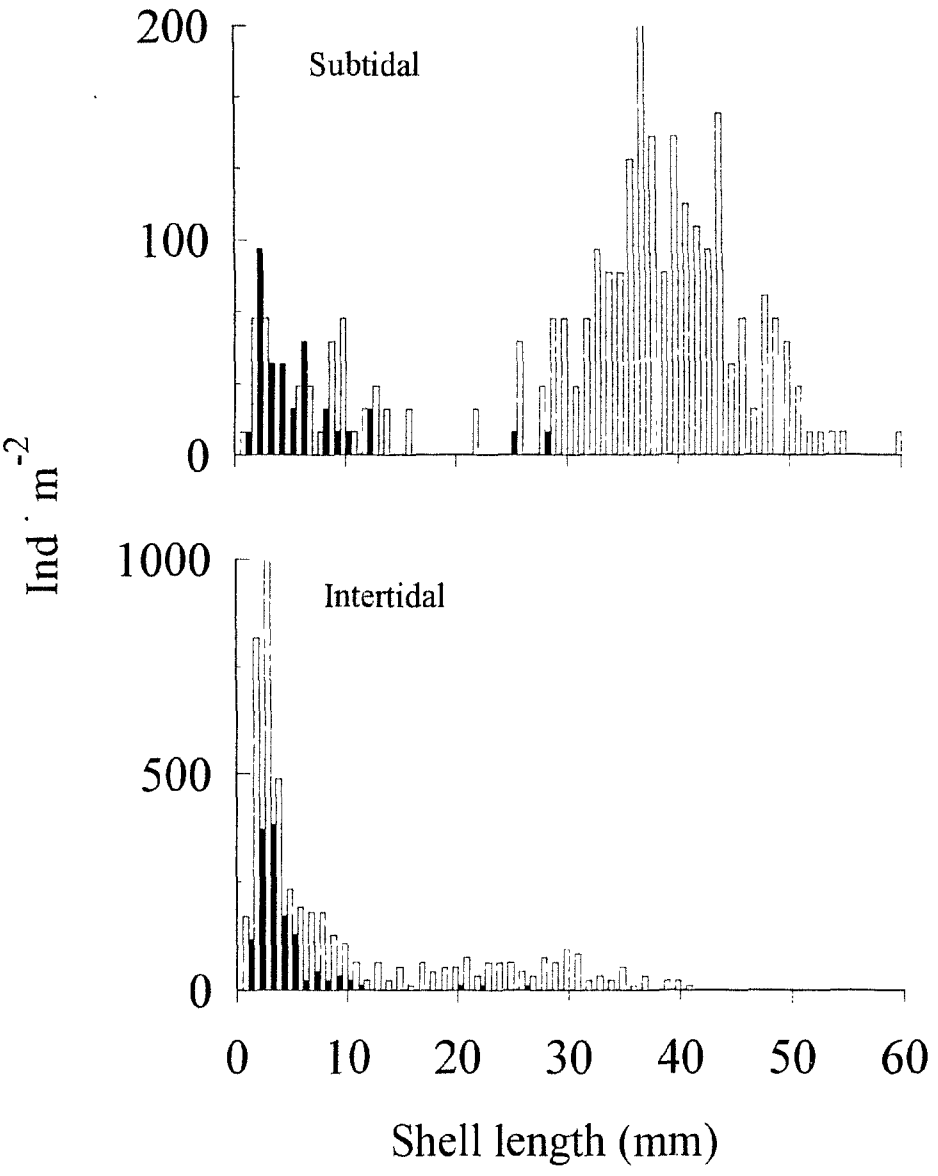

Fig. 3.20. Size-frequency histograms of transported (black bars) versus resident (white bars) *Mya* at subtidal and intertidal sites in 1993. Bar widths are 1.0 mm.

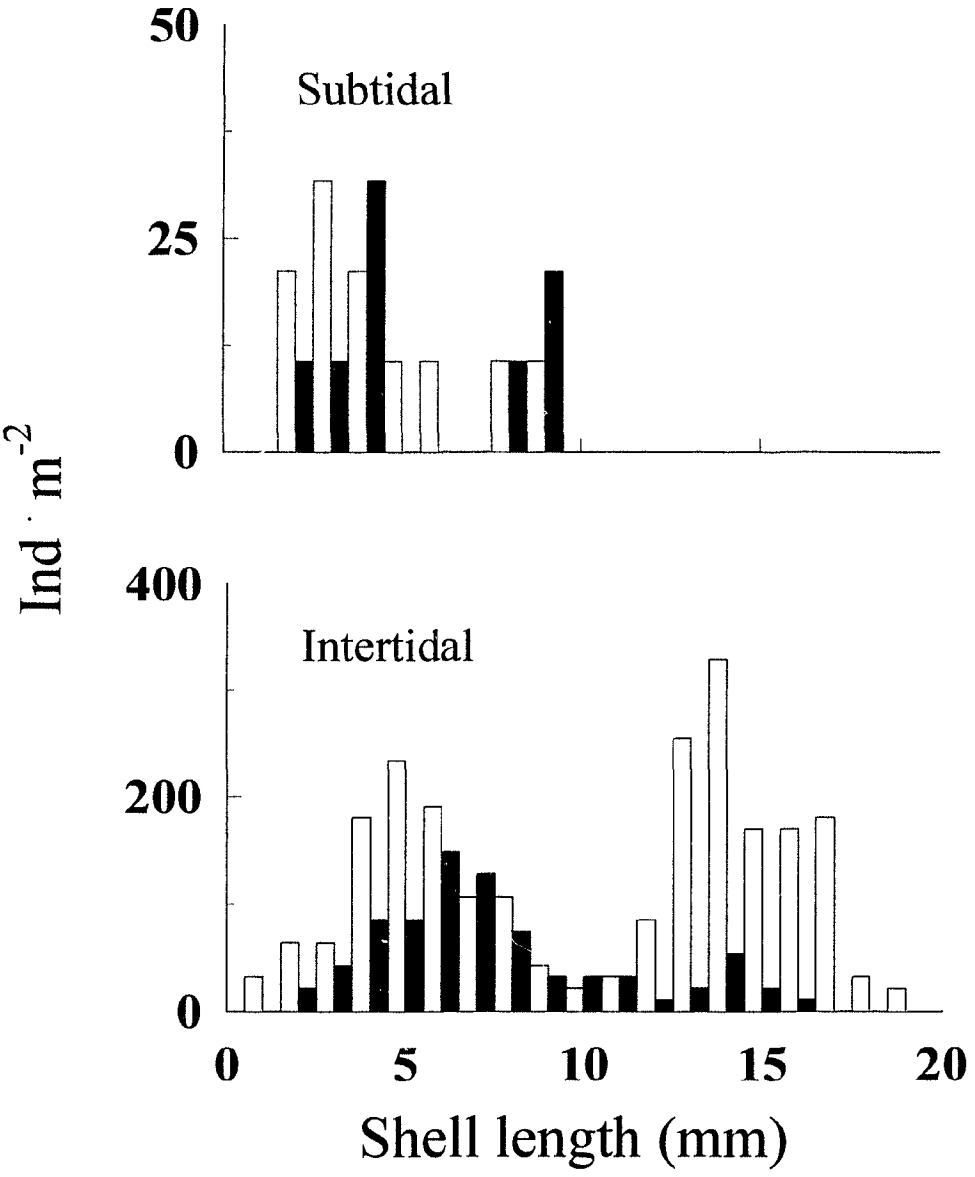

Fig. 3.21. Size-frequency histograms of transported (black bars) versus resident (white bars) *Macoma* at subtidal and intertidal sites in 1993. Bar widths are 1.0 mm.

Based on the transport rate and initial bivalve abundance, clams were capable of rapidly repopulating defaunated areas (Tables 3.2 to 3 6). Subtidal *Mya* juveniles up to ~15 mm and all sizes of *Gemma* could recolonize defaunated areas to background levels in a span of a few days to several weeks *Macoma* densities and transport rates were low in the subtidal and replenishment was patchy In the low intertidal, all bivalve species demonstrated high transport rates at pre-ice scour abundance Despite the high transport, *Mya* and *Macoma* required 2 to 6 weeks to fully recolonize defaunated intertidal sites, mainly due to high resident populations Numbers of *Gemma* increased to background numbers in the span of 2 days and 2 weeks After the ice scour and clam digging disturbance, transport declined and recolonization rate increased dramatically, demonstrating the importance of local immigrant supply on recolonization

3.4 Discussion

This study demonstrates that the bivalves *Mya*, *Macoma*, and *Gemma* recruited to benthic sites through both primary reproduction (the 0-group) and as juvenile or adult immigrants At a given site, the relative importance of recent settlers versus transport of larger individuals varied due to differences in the physical regime, the magnitude of the annual 0-group production, and in the supply of potential migrants Because of high erosion potential for small clams (especially settlers), the location of the settlement site cannot be definitely addressed with the sampling periodicity employed However, it is clear that a significant transport of clams occurred into the experimental sites. Immigration was unequivocally demonstrated by defaunation experiments and by increases in the abundance of juvenile clams in size-frequency histograms At the given sampling

periods, *in situ* growth cannot account for the observed increases in juvenile abundance. Decreases in abundance may be explained by alternative (but not mutually exclusive) possibilities of export and mortality. The results show that in tidally energetic sites such as the Back Marsh system, organisms in the upper layers of the sediment column can be transported on relatively short time scales. Thus, while the magnitude of primary recruitment sets upper limits on overall abundance within a system, juvenile redistribution can be rapid and extensive, and allow for a continuation of habitat selection by infauna.

3.4.1 Larval settlement

At Back Marsh, new recruits of *Mya* and *Gemma* entered the population each year, with the first appearance of the 0-group occurring in late August or September. This is in agreement with other sites along the Eastern Shore of Nova Scotia (Burke and Mann 1974; Witherspoon 1984; Emerson and Grant 1991). Both species exhibited maximum abundance of new recruits in 1993. In contrast, *Macoma* settlers were rare, and were relatively abundant only in 1992 at the low intertidal site. Interannual variation in bivalve settlement is the norm for most areas investigated (*i.e.* Beukema 1982; Möller & Rosenberg 1983; Möller 1986; Feller *et al.* 1992; Beukema *et al.* 1993), and at Back Marsh variation in the species with planktotrophic larvae likely reflects oceanographic processes controlling the supply of competent larvae from the nearshore zone (Chapter 1).

The abundance of recently settled bivalves in this study was lower than maximum values recorded elsewhere. *Mya* settlement densities of 10^4 to 10^5 ind. $\cdot$ m^{-2} are known (Möller & Rosenberg 1983; Möller 1986; André & Rosenberg 1991; Emerson & Grant

1991, Gunther 1992), but settlement densities in the range 10^1 to 10^3 ind m^{-2} measured in this study agree with values reported by Pfitzenmeyer (1962) in Chesapeake Bay, Brousseau (1978) in New England, Beukema (1982) in the Wadden Sea, and Winter & Grey (1985) in Sweden Similarly variable abundance of new recruits have been recorded for *Macoma* (i e Beukema 1982, Gunther 1991, Armonies 1994) and *Gemma* (Sellmer 1967, Green & Hobson 1970), with the numbers from Back Marsh generally being comparatively low However, neglecting the post-disturbance period in 1994, the total abundance of bivalves (all individuals) remained remarkably high over time and fluctuated around 1 5 and 2 5 10^4 ind m^{-2} for subtidal and 5 0 to 9 0 10^4 ind m^{-2} for intertidal plots Aside from disturbance events, this environment obviously supported large numbers (and biomass) of bivalves

3.4.2 Magnitude of transport

All 3 bivalve species immigrated to each of the sites, as demonstrated by the changing size-frequency histograms and the transport experiments In 1992 and 1993, net transport into defaunated subtidal plots was rapid enough to replenish the population of similarly sized individuals in the span of a few days to several months (Tables 3 1 to 3 4, Figs 3 20 and 3 21) Overall transport was higher in the intertidal areas, but the replenishment time was often lower because of the large density of resident clams Lower recolonization rates in 1994 can be attributed to winter mortality of juveniles in the surrounding area

Mya transport measured in this study were in the range of the summer conditions found by Emerson (1991) and Emerson & Grant (1991), but far below the maximum

transport of 2600 ind. $\cdot m^{-1} \cdot d^{-1}$ they measured during storm events. Mean size of the clams captured by sediment traps was 9 mm (Emerson 1991), which was larger than the 1 to 6 mm range found to comprise most immigrants in Back Marsh (Fig. 3.20). This probably reflects differences in the size structure of the populations at Eastern Passage and Back Marsh. Matthiessen (1960) also suggested that storms caused redistribution of *Mya* (2 to 15 mm), while data on transport of clams into sediment trays in Maine presented by Smith (1955) yields recolonization rates comparable to those reported in Tables 3.2 to 3.6.

In contrast, movement of *Macoma* at Back Marsh greatly exceeded that found at Eastern Passage (Emerson 1991). Armonies (1994) calculated maximum turnover rates on the order of 1 d for migrating *Macoma* in the Wadden Sea, and Bonsdorf (1984) documented rapid recolonization of larger sized *Macoma* to subtidal populations following dredging disturbance. The Back Marsh *Macoma* population likewise recruited mainly as juveniles and adults. The ability of virtually all sizes of *Macoma* to be transported via resuspension or as bedload allows for rapid changes in population structure. At Back Marsh, *Gemma* was also able to rapidly recolonize defaunated sediments, at rates in the range of those inferred from data in Rankin *et al.* (1994) and Committo *et al.* (1995). Again, the entire size range of population was mobile. Even with the net transport measured here, it is clear that over a time scale of weeks, the populations of small bivalves were in flux.

Dramatic transport was observed in the intertidal as a result of winter mortality. Clams were eliminated from the mid-intertidal site in both 1993 and 1994, and all

bivalves found on April 1993 (Figs. 3.8, 3.14, and 3.19) were transported to the mid-intertidal site along with 2 to 5 cm of sediment which covered the previous intertidal surface. Included in the transported population was a high abundance (~1200) of 1 mm long overwintered *Mya*. The mass sediment movement was associated with the break up of ice cover and transport of ice floes (Anderson 1983). Subsequent *Macoma* abundance appeared related to this initial influx, but by 27 August *Mya* and *Gemma* had a net increase of both new recruits and larger juveniles. For *Macoma* and *Gemma*, all size classes were present and recruitment was effected completely through transport. In contrast, the large import of the 0-group accounted for the majority of total *Mya* abundance (Figs. 3.8, 3.14, and 3.19).

Recruitment to the low intertidal in 1994 illustrates the importance of migrant source on benthic abundance (Figs. 3.7, 3.13, and 3.18). Transport into defaunated plots was only a fraction of the 1992 and 1993 rates when the surrounding intertidal flats were devoid of clams after winter mortality (Tables 3.5 to 3.9). As Fig. 3.7 shows, while there was scattered import of larger clams, the majority of the *Mya* recolonizing the site in 1994 were from the 0-group. In contrast, import of the *Macoma* 0-group was small, and transport occurred in all size classes up to 20 mm. *Gemma* recruited to the site as both new recruits plus older individuals. Committo *et al.* (1995) demonstrated differences in the transport of *Gemma* between summer and winter which also reflects differing resident densities. The source of migrant clams in 1994 was likely the surrounding subtidal zones.

3.4.3 Mechanisms of juvenile transport

While the effect of storms on infauna can be profound (Matthiessen 1960, Emerson & Grant 1991), Back Marsh is protected from wind events, and the primary forcing on the benthos is through tidal currents In these predicable flows, passive transport as bedload or active transport through byssal drifting are both mechanisms enabling the rapid redistribution of juvenile bivalves Based on flume experiments (Chapter 2), velocities measured in the boundary layer of the subtidal creek were sufficient to mobilize sediment and excavate and transport clams Flume data indicates that at a shear velocity U_* value of 1.6 cm s^{-1} (current velocities of 0 3 m s^{-1}), the Rouse number ($w / U_* \kappa$) predicts clams with fall velocities w up to ~0 6 cm s^{-1} would be resuspended Given that 2 to 4 mm *Mya* sink at 6 3 cm s^{-1} (Matthiessen 1961), it is likely that most clams > 1 mm were transported as bedload However, recently settled larvae and small juveniles would be rapidly resuspended and translocated Rankin *et al.* (1994) estimated shear velocities > 0 9 cm s^{-1} caused transport of *Gemma* < 1 2 mm in Massachusetts, and similarly concluded that bedload transport predominated in clam redistibution The abundance of new recruits in the subtidal channel is thus likely controlled in part by erosion and transport by high velocity currents In the low intertidal, there was a concentration of small bivalves, with maximal combined abundance of about 10^5 ind m^{-2} in 1993 The majority of these individuals were < 10 mm and are thus relegated to the surficial sediment layers Transects of the site showed an erosion of tidal creek sites and an accumulation of sediments in the intertidal zone (Fig 3 3) During the later half of the study period, more than 25 m^3 of sediment was accreted in the low intertidal site, presumably as a

consequence of a reduction of velocity shear as the flood tidal currents entered Back Marsh from the tidal creek The high abundance of bivalves of both 0-group and juvenile clams found in this deposit likely reflects hydrodynamic sorting (Matthiessen 1960)

Any discussion of bivalve transport must consider behavior The simplest way for bivalves to avoid transport is to remain burrowed In flows less than the critical shear velocity for sediment transport, U_{*crit}, a buried clam would obviously not experience shearing flow Juveniles may thus resist transport by downward movement, and exposure to fluid forces depends on the relative rates of erosion and burrowing In contrast, active emergence to the surface greatly enhances the probability of transport (Prezant & Chazemwat 1984, Sörlin 1988, Cummings *et al* 1993)

3.4.4 Growth

Growth rate is of critical importance for the stabilization of clams in shifting sediments, since growth allows for deeper burial During this study, growth of new *Mya* recruits was minimal, and 0-group clams rarely exceeded 1 mm by winter Growth during the following summer was also relatively slow In the low intertidal, the 1992 cohort grew to a mode of only 4 mm (range 3 to 6 mm) by December 1993, yielding a maximum growth rate of ~0 02 mm d^{-1} The 1993 cohort vanished from the site before appreciable growth, while the 1994 cohort grew at 0 03 to 0 04 mm d^{-1} from the end of August to mid-November 1993 There were few obvious modes of size-frequency for larger clams, and there was no significant change in the mean size of clams > 10 mm over time at either intertidal site (Fig 3 10) Much of the population remained in the surficial sediments for at least 2 to 3 years In the subtidal plots, juvenile distributions

were not coherent enough to compute growth rates, except for juveniles at subtidal Site B in 1992 (which grew at ~0.03 mm · d^{-1}). Growth of larger clams was 0.009 to 0.013 mm · d^{-1} when calculated over the entire 3 year period, while during individual years growth rates ranged from 0.011 to 0.025 mm · d^{-1}.

3.4.5 Recruitment dynamics

The relative contribution of larval settlement to juvenile transport on bivalve recruitment patterns varied by species and site, and was strongly affected by abiotic and anthropogenic disturbance. By the end of the 3 year study, there was no significant recruitment to the subtidal plots by any species. A portion of the net decline in abundance and biomass was due to clam digging activity. However, absence of *Mya* between 10 and 20 mm suggests recruitment to the subtidal population had not occurred during the last 5 to 6 years. The inability of the small clams to recruit to subtidal areas is likely a function of post-settlement transport. The stable adult *Mya* populations in the subtidal, composed of no more than 1 to 3 annual cohorts, may have been recruited during a period of reduced hydrodynamic forces. These populations of large clams were buried below the level of normal erosion events and survived both severe winters. An examination of annual growth rings suggested most of the large individuals were > 7 years old and normally grew 2 to 4 mm · yr^{-1}, which agrees with the growth regressions determined from Fig. 3.10. Biomass estimates in the subtidal were very large compared to similar infauna assemblages (*i.e.* Burke & Mann 1974; Möller & Rosenberg 1983; Zwarts 1991; Beukema *et al.* 1993; Zwarts & Wannik 1993), due to the high numbers of large clams (Fig. 3.9). Clams in the creek environment thus had the capacity for a large annual

reproductive effort. However, the lack of recruitment to the population makes this population vulnerable to clam digging activities.

In the intertidal area, recruitment patterns for *Gemma* and *Macoma* depended on juvenile and adult transport. *Macoma* primary recruitment was negligible, and all sizes of *Macoma* and *Gemma* were able to colonize defaunated areas. New recruits were relatively more important for the population dynamics of *Mya*, especially after the widespread 1994 defaunation event. Before winter mortality, the intertidal population was concentrated in young, small clams, but was composed of multiple year classes. Growth was low, and the small clams remained vulnerable to physical disturbance. The severe winters of 1993 and 1994 resulted in the complete elimination of the intertidal populations representing 5 to 7 annual *Mya* cohorts. In the low intertidal in 1994, *Mya* recolonization was ~80% by the 0-group and ~20% by larger juveniles. However, given the relatively rapid recolonization rates, it is likely transport also delivered many of the recently settled clams to the site. Thus, for all 3 species, juvenile transport was an important mechanism structuring the populations. Of course, since the supply of immigrants is dependent on past reproductive events, larval settlement ultimately controls the abundance of planktotrophic species to a system over long time scales. Redistribution allows for microscale habitat selection to occur.

3.5 Conclusions

All 3 species investigated in this study have mobile benthic stages. Small short-lived ovoviviparous infauna such as *Gemma* are prone to movement throughout their life. Juvenile transport is essential for their dispersal and the thick, globular shell of *Gemma*

may be an adaptation to resist abrasion during translocation. *Macoma* has adapted for widespread post-settlement dispersal with the evolution of a thin, light shell and ability to produce a drifting thread that allows for resuspension and long distance migrations (Lane et al. 1985). The larger and longer lived *Mya* burrows deeply for protection, and when >20 mm is relatively resistant to all but extraordinary erosion events. However, the juveniles are readily transported and the length of the vulnerable stage is dependent on growth. In Back Marsh, this may be as long as 4 years. Clearly, recruitment of infaunal bivalves is a process that includes both larval and post-larval components.

Finally, given the ability of hydrodynamic forces to redistribute infauna, care must be taken in interpreting abundance and size-frequency data. Rapid declines in the abundance of small members of the population do not necessarily indicate mortality has occurred, as is often supposed. Likewise, it is easy to misinterpret changes in the abundance of a size class as growth rather than transport, especially in conjunction with biases inherent in graphical methods of cohort analysis (Brousseau 1978; Grant 1985; Grant *et al.* 1987). In fact, given the rapidity of transport and the behavioral responses which facilitate movement in bivalves, understanding recruitment dynamics in soft sediments necessitates accounting for post-settlement transport mechanisms. The small individuals restricted to the mobile upper layers cannot be assigned as "recruited" to a single place when they can be translocated significant distances in a few tides. Studies of population dynamics must entertain the hypothesis that faunal transport structures size-frequency distributions, in conjunction with alternative hypothesis such as variations of larval

supply and predation. At a minimum, the frequency and magnitude of hydrodynamic stresses to the substrate should be evaluated for the potential to transport fauna.

Chapter 4. The effect of aerial exposure on the growth of juvenile soft-shell clams *Mya arenaria* (L.)

4.1 Introduction

The classical intertidal zonation paradigm predicts that the upper limit of species distribution is determined by stresses incurred during periods of aerial exposure (Connell 1985; Peterson & Black 1988). These stresses affect the energy balance of intertidal organisms (Newell 1980; Bieras *et al.* 1995). A fundamental requirement for survival is that energy acquisition equal basal metabolic expenditures when integrated over some time interval. At the other extreme, maximal increases in somatic and reproductive biomass occur with the greatest positive energy balance, known as the scope for growth (SFG). Organisms exist within these extremes and generally have a SFG less than the potential maximum due to factors which limit energy acquisition or increase metabolic costs. The results of a decreased SFG include reductions in growth rate (Shick *et al.* 1988) and fecundity (Suchanek 1981).

For bivalve molluscs, aerial exposure induces several energy balance problems that can reduce net energy levels relative to animals with longer immersion periods (see McMahon 1988 for a review). The foremost constraint is the reduction of ingested ration when feeding ceases during emersion, especially for suspension-feeders where particle capture is not possible during exposure (Wanink & Zwarts 1993). Differences in the length of feeding time due to level of aerial exposure can result in differences in growth (*i.e.*, Peterson & Black 1988). Another constraint is the lower efficiency of anaerobic versus aerobic respiratory pathways that occurs during valve closure (Shick *et al.* 1988). Valve closure is a response to limit desiccation and/or predation (McMahon 1988), but

the resultant anaerobiosis yields a lower energetic output than does aerobic oxidation (Widdows & Shick 1985). The resultant oxygen debt and associated elevation of metabolic rate upon re-immersion also consume resources (Widdows *et al.* 1978; Ellington 1983; Widdows & Shick 1985). Finally, desiccation and thermal shock are physical stresses which may require energy expenditures for tissue repair or increase mortality. All of these stresses can limit the distribution and/or growth of bivalves and other intertidal organisms.

To compensate, intertidal bivalves have evolved a variety of responses to aerial exposure. These energy-saving adaptations include a reduction of metabolic activity during emersion (Widdows & Shick 1985), the evolution of more efficient anaerobic pathways of metabolism (de Zwaan & Wijman 1976), and, in some species, aerial respiration (air gaping) (Widdows *et al.* 1978; Newell 1980; McMahon 1988). Additionally, many authors have demonstrated the ability of organisms to acclimate or acclimatize to intertidal conditions (Kennedy & Mihurshy 1972; Newell & Bayne 1973; Anderson 1978; Newell & Branch 1980; Wilson & Elkaim 1991; Beiras *et al.* 1994). Acclimation can affect rates of physiological processes orspecific metabolic pathways, thus allowing for adjustments to the allocation of resources (Newell & Bayne 1973; Demers & Guderley 1994). Of course, there are also species which have evolved an increased tolerance to emersion stresses which allows for life high on the shore (i.e. Widdows *et al.* 1978; Ellington 1983; Nicchitta & Ellington 1983; Wilson & Elkaim 1991; Demers & Guderley 1994). Generally, low shore bivalve species tend to withstand exposure by reducing metabolic rate and undergoing anaerobic metabolism (McMahon 1988). In contrast, many

upper shore species air gape and must balance the competing factors of desiccation and anaerobiosis (McMahon 1988; Shick *et al.* 1988). The costs of exposure on SFG generally increase with the duration of emersion (Ellington 1983).

Previous field and laboratory studies of epifaunal and free-living bivalves usually reported trends for reduced growth with increasing aerial exposure. Roegner & Mann (1995) reviewed the literature for various oyster species worldwide and generally found lower growth rates above the mean low water level relative to subtidal levels, while both positive and negative growth effects were reported at shorter exposures. Mussels have long been a subject of growth studies. For example, Seed (1969) considered feeding restrictions to be responsible for the decreasing growth with increased emergence in blue mussels (*Mytilus edulis* L.). Aldrich & Crowley (1986) determined that mean weight-based condition indices of *M. edulis* in Ireland were nearly 4 times greater in suspended versus intertidal culture, and about twice as large as mussels in subtidal bottom culture. In the White Sea, shell growth of *M. edulis* was 2 to 5 times greater in suspended culture compared to growth near the mid-intertidal level (Sukhotin & Maximovich 1994).

Similarly, with the semi-infaunal ribbed mussel (*Geukensia demissa* Dillwyn), Hardwick-Witman (1985) in New Hampshire and Stiven & Gardener (1992) in North Carolina showed increasing shell growth with increasing submergence in intertidal marsh habitats, and Franz (1993) demonstrated decreasing size and weight at age and decreasing shell and tissue growth rate with increasing exposure in Jamaica Bay, NY. Lin (1989) showed reduced growth of *G. demissa* with increasing emersion at the marsh edge, while differential food availability was postulated to explain conflicting results

between 2 sites at high intertidal edge and interior locales. New Zealand green-lipped mussels (*Perna canaliculus* Gmelin) grown in suspended culture had twice the shell length of intertidal mussels after 18 months (Hickman 1979). Griffiths (1981) measured significantly less growth in the mid-intertidal zone than in the low intertidal for the mussel *Choromytilus meridionalis* (Kr.) in South Africa, despite extensive post-settlement migrations of juvenile mussels from low intertidal settlement sites to locations higher on the shore.

Gillmor (1982) examined the responses of 6 bivalve species to aerial exposure in field and laboratory experiments in Maine and showed linear decreases in growth rate with increasing exposure for subtidal or low intertidal species (*Modiolis modiolis* L., *Argopecten* (=*Aequipecten*) *irradians* Lamark, and *Ostrea edulis* L.). However, in exception to the previous results, enhanced growth (relative to subtidal treatments) was reported for intertidally grown American oysters (*Crassostrea virginica* Gmelin) and blue and ribbed mussels (Gillmor 1982).

For infaunal bivalves, field surveys have reported both positive and negative relations between growth and emersion. Jensen (1992) found that growth rate declined with increasing exposure in cockles (*Cerastoderma edule* L.) in the Danish Wadden Sea. Density-dependent factors were implicated for growth below "expected" decreases set by exposure Wanink & Zwarts (1993) summarized 3 years of size-frequency data for 5 species of bivalves (*C. edule*, *Macoma balthica* L., *Mya arenaria* L., *Mytilus edulis*, and *Scrobicularia plana* Da Costa) in the Dutch Wadden Sea and found negative relations between exposure and growth. Suspension feeders were determined to be more affected by

exposure than detritivores. Harvey & Vincent (1990) surveyed intertidal populations of *M. balthica* in the St. Lawrence Estuary and reported greater overall shell length and biomass values at low (25% emersed) versus mid-intertidal (47% emersed) locales, although the spring initiation of growth often occurred 1 to 2 weeks earlier at the upper level. Due to adversely high temperatures, a shorter total growth period occurred in the mid intertidal zone, and a negative SFG was indicated for large individuals during summer (Harvey & Vincent 1990). Likewise, Vincent *et al.* (1994) found increased growth of *M. balthica* with increased immersion in the same area. Bachelet (1990), in contrast, reported higher growth and different size-frequency distributions of *M. balthica* in the high intertidal rather than at MLW, these results were attributed to adverse physical factors lower on the shore. Similarly, distributions of *M. balthica* in the Bay of Fundy were thought by Cranford *et al.* (1985) to be restricted to middle to upper intertidal areas by higher energy hydrodynamic conditions in the subtidal region.

One difficulty with inferring the importance of a given factor from population surveys is the lack of experimental controls for the synergistic effects of exposure. However, experimental studies evaluating growth and survival of infaunal bivalves in relation to intertidal zonation are relatively rare. Newcombe (1935) attributed lower food availability to be responsible for the inverse relationship of tidal elevation and growth in experimental plots of soft-shell clams (*Mya arenaria*) in the Bay of Fundy. Eldridge *et al.* (1979) and Eversol *et al.* (1990) found non-significant trends of reduced growth in low intertidal versus subtidal plantings of juvenile quahogs *Mercenaria mercenaria* L in South Carolina. Peterson & Black (1987, 1988) demonstrated clear growth reductions at

relatively low exposures (~25% emersed) compared to subtidal animals for 4 of 5 species of infaunal suspension-feeders tested in Australia. A reduction of food available for the intertidal bivalves was postulated to be reducing growth to levels higher than predicted from exposure alone (Peterson & Black 1987, 1988, 1991)

Although food limitation is commonly invoked to explain growth reductions along the tidal gradient (i.e. Newcombe 1935; Peterson & Black 1987, 1988, 1991; Lin 1989; Jensen 1992), and differential energy acquisition can certainly contribute to differential growth, growth rate is actually the response of organisms to the entire suite of emersion stresses. The individual costs of these stresses on growth have not been well documented in the laboratory and are not easily testable in the field. In this paper, the effect of emersion time on bivalve growth was examined. In laboratory experiments, growth of *Mya arenaria* was compared at different aerial exposures but equal food rations in excess of metabolic needs. In a second experiment, applicability of the laboratory results was evaluated by measuring growth at 3 exposure levels in the field. In both cases, juvenile clams were used to avoid the partitioning of resources into gonadal material. The response to exposure was evaluated as changes in both shell length (SL) and ash-free dry weight (ADW).

4.2 Methods

4.2.1 Laboratory experiments

The response of clam growth to emersion was examined by feeding groups of experimental animals equal rations while controlling the exposure/immersion and temperature cycles. Aerial exposure and microalgal food supply to experimental growth units

were manipulated with a system of electronic solenoid drain valves activated by 24 h timers. Each experimental unit consisted of a 7 L plastic container within which floated a plastic fish breeding tank ("growth chamber"). The growth chambers held a 15 mm thick layer of medium-grain quarry sand (95% of the particles were 0.125 to 0.250 mm) into which a group of marked clams burrowed. The chamber had perforated walls which allowed exchange of flow-through water with the plastic container. Air and water temperatures were maintained at constant values (~15°C). The clams were thus afforded relatively benign conditions of substrate, temperature (except see below), and relative humidity to reduce non-emersion related stresses (i.e. Pamatmat 1983).

Each test container was connected to a drain solenoid valve which allowed the water level of the container, and hence the position of the floating growth chamber, to be controlled. Filtered seawater at 15°C and ambient salinity (30 to 31) was continuously pumped into the test containers from a mixing reservoir at a rate of about 2 m$L \cdot s^{-1}$. During exposure, the growth chamber rested on the bottom of the drained container, and input water exited through the open drain valve. At the initiation of an immersion period, the drain valve closed and the test container began filling with seawater. The growth chamber containing the clams was first submerged and then floated up with the rising water level within the container. When the container was filled, water exited from overflow ports yielding a water exchange rate of about 1 h.

During exposure periods, the drain solenoid valves switched open and the water exited the test containers at a rate > 4 m$L \cdot s^{-1}$. As the water level descended, the floating chambers gradually settled to the bottom of the containers, allowing water in the

substrate to drain and effecting aerial exposure. Thus, for the intertidal treatments, when the solenoid valves were open the test containers drained in 0.3 to 0.5 h, simulating low tide, and when the valves were closed water filled the containers and immersed the clams.

The feeding period was controlled by a solenoid valve connected to the algal reservoir, and the addition of microalgal food (*Isochrysis galbana, Chaetoceros gracilis,* and/or *Thalassiosira pseudonana*) was set to commence 0.5 h after the beginning of immersion and terminate 1.5 h prior to exposure. Thus, algae were supplied only after all treatments were immersed, which insured that clams in each treatment received an equal opportunity to feed. Strong aeration enhanced mixing between chamber and container, and algal delivery to the test chambers was estimated periodically with *in vivo* fluorescence.

Clam growth was compared at 4 exposure treatments. A subtidal treatment was continuously immersed (ST). There were two 25% exposed low intertidal treatments, one at ambient 15°C air conditions (LIT-A), and another in which the substrate temperature was elevated with an incandescent lamp to between 23 and 25°C during exposure (LIT-H). Finally, there was a mid-intertidal, 45% exposure to ambient air temperature (MIT). The standardized 14°C air and 15°C water temperatures were designed to establish stable environmental conditions for clam growth with minimal temperature stress for the intertidal treatments, while the treatment with elevated substrate temperature reflected observed field temperatures caused by solar insolation on intertidal sediments (Roegner, pers. obs.). To verify the exposure effects, the temperature of the upper few mm of

sediment was continuously measured with thermocouples and recorded to an interfaced computer system. Input water and air temperatures were similarly recorded; ambient air temperature was maintained 1 to 2°C lower than the water temperature to enable exposure periods to be distinguished on the temperature time series.

Juvenile *Mya arenaria* were collected from the low intertidal zone of the Eel River, Lawrencetown, Nova Scotia Preceding an experiment, the clams were held subtidally in a 10 ppt alizarin red and seawater solution for 15 d at 15°C to mark the initial shell length (Hidu & Hanks 1967). Every 3 d, the stain solution was changed and the clams were fed 3*L* of mixed algae culture. At the end of the staining period, the clams were graded into two size classes by shell length (SL): "small" (mean = 3.2 ± 0.06 mm SE) and "large" (6.5 ± 0 13 mm). Both size classes were randomly allocated to 5 groups of 25 small and 15 large clams · treatment^{-1}. One group was retained for initial tissue weight measurements, and each of the remaining four groups was delegated to an exposure treatment.

During the growth period, each experimental container received 4 $L \cdot d^{-1}$ of microalgae at initial densities (in the algal reservoir) of 1.5 to 2.0 · 10^6 cells · mL^{-1} This supply resulted in potential rations in excess of 10^8 cells clam^{-1} d^{-1}. Food concentrations in the growth chambers ranged between 20 and 30 µg Chl · L^{-1} during feeding, a ration that is clearly above metabolic requirements. Algae was supplied for 4.5 h per 12 h cycle.

The experiment was run for 28 d, and length measurements were made after 14 d as well as at the termination of the experiment. The whole (including shell) dry weight

(55°C for 100 h) and the ash-free dry weight (ADW) (500°C for 2 h) of each clam were determined at the end of the experiment.

4.2.2 Field experiment

Two hundred *Mya arenaria* of initial SL 13.5 mm (± 1.17 SE) were marked on the shell with fluorescent spray paint and divided into 5 groups of 40 individuals. One group was immediately sacrificed for tissue weight determination as described above, and a second group was placed in the laboratory under minimal food conditions (< 0.01 μg Chl-$a \cdot L^{-1}$). The other 3 groups were planted in 0.10 m^2 plots in a sandflat in the Eel River. Each plot was defaunated of macrofauna to 20 cm by sieving the sediment through a 500 μm mesh. The exposure levels were 50% (mid-intertidal), 20% (low intertidal), and subtidal (at a depth of ~30 cm at low tide). The plots were horizontally separated by 3 to 8 m along a tidal creek-flood tide delta system dominated by dense beds of *M. arenaria*. Tidal heights and water temperatures were measured at 10 min intervals with a Sealog pressure-temperature recorder (VEMCO, Shad Bay, NS) located in the creek adjacent to the subtidal treatment. The experimental period extended for 26 d (10 May to 6 June). At the conclusion of the experiment, clams were recovered from the plots by sieving the sediment through a 1 mm mesh. Shell length and ash-free dry weight were determined as above.

4.2.3 Analysis

Recording the initial shell length of clams stained with alizarin red or spray paint allowed for individual growth rates to be computed. Growth G (mm) was evaluated as

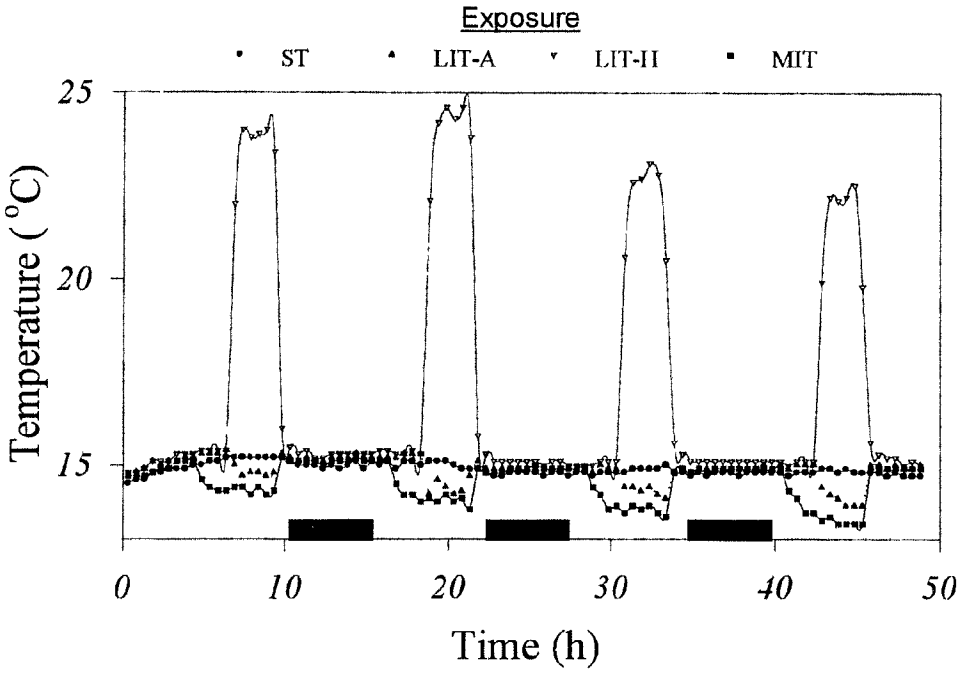

Fig. 4.1. Surface sediment temperature time series during simulated tidal cycles. The temperature traces are analog for periods of exposure or immersion. Treatments: ST, Subtidal, LIT-A, low intertidal ambient temperature; LIT-H, low intertidal high temperature; MIT, mid-intertidal Black bars designate feeding periods

the linear increase in SL (final - initial SL) measured with an ocular micrometer, and daily growth rates (*GR*, mm · d^{-1}) were calculated by dividing individual growth by the measurement period. Standardized growth (*GR* / initial length) was used for statistical tests with the field experiment due to the larger range of initial lengths. Single factor analyses of variance (ANOVA) and Tukey HSD tests were employed to compare growth rate and tissue weight values by treatment for each sample date, after Bartlett's HOV tests revealed no significant deviations from homogeneity in variance. For both experiments, AFW was compared among exposure levels and initial values.

4.3 Results

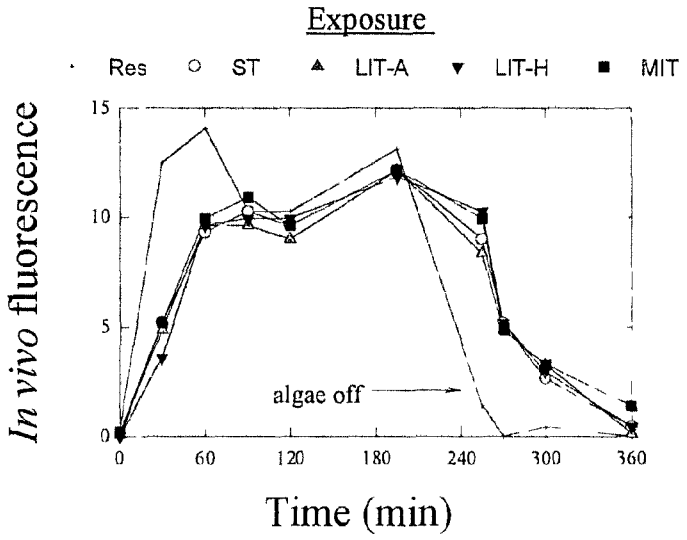

Fig 4 2 Time series of *in vivo* fluorescence (volts) in the mixing reservoir and growth chambers during a feeding period. "Algae off" indicates closure of algal supply solenoid valve. Treatments: Res, mixing reservoir, ST, Subtidal; LIT-A, low intertidal ambient temperature; LIT-H, low intertidal high temperature; MIT,

4.3.1 Laboratory Experiment

The experimental apparatus resulted in well controlled exposure and feeding regimes. Figure 4.1 depicts surface sediment temperature traces for the 4 treatments over a 50 h period The figure clearly distinguishes among exposure periods for the 4 treatments Feeding times are indicated by solid blocks Figure 4.2 is an example of an *in vivo* fluorescence time series demonstrating the equal availability of food to the clams during a feeding period.

While most clams had relatively rapid shell growth at all treatment levels, 6% of the small 3.2 mm and 25% of the larger, 6 5 mm clams exhibited no growth even though overall mortality was less than 5%. Considering the benign laboratory conditions, these

clams were removed from further analysis. Aerial exposure exerted a negative effect on the addition of new shell material (Table 4.1; Fig. 4.3). ANOVA and Tukey HSD results indicated significant treatment effects for each size class of clams tested after both 14 and 28 d (Table 4.2). For the large clams, shell growth at subtidal and low intertidal heated treatments were significantly greater than growth at the mid-intertidal treatment on either date. Growth of large clams was significantly lower at the low intertidal ambient treatment than at the subtidal level. Between low intertidal levels, higher temperature

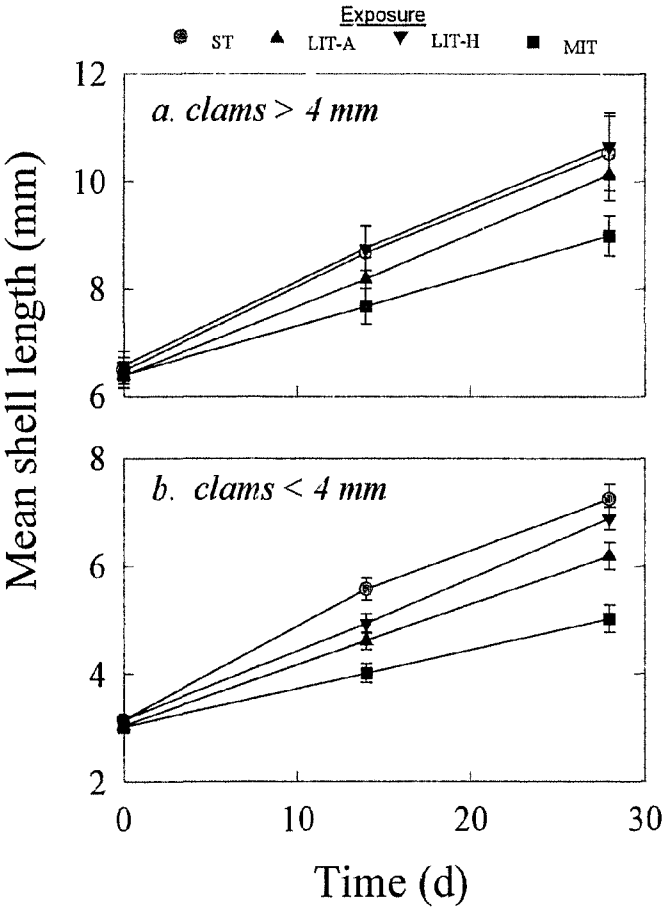

Fig. 4.3. Mean shell length (± SE) per exposure treatment after 14 and 28 d for *a*, large and *b*, small clams in the laboratory experiment. Treatments: ST, subtidal; LIT-A, low intertidal ambient temperature; LIT-H, low intertidal high temperature; MIT, mid-intertidal.

increased growth of large clams relative to ambient conditions at week 2 but not week 4. After 28 d, SL of large clams had increased 1.6 to 1.8-fold at subtidal and low exposures compared to a 1.4-fold increase at the mid-intertidal.

Table 4.1. Summary of mean growth rate (± SE), relative increase in SL (final SL/ initial SL), and relative increase in ADW (final weight/initial weight) for laboratory (Lab) and field experiments. Exp, Experiment; ST, Subtidal; LIT-A, Low intertidal (20 % exposed) at ambient temperature; LIT-H, Low intertidal (20 % exposed) at high temperature; MIT, Mid-intertidal (45 % exposed) at ambient temperature; LAB, Laboratory subtidal conditions.

Exp	Mean initial size (mm)	Time (d)	Treatment	Growth rate ($mm \cdot d^{-1}$)	Relative SL	Relative ADW
Lab	6.5	14	ST	0.219 ± 0.014	1.5	-
			LIT-A	0.143 ± 0.015	1.3	-
			LIT-H	0.215 ± 0.017	1.4	-
			MIT	0.127 ± 0.011	1.2	-
	6.5	28	ST	0.184 ± 0 024	1.8	4.2
			LIT-A	0.141 ± 0.022	1.6	2.8
			LIT-H	0.196 ± 0.012	1.8	4.2
			MIT	0.110 ± 0.017	1.4	2.5
	3.2	14	ST	0.182 ± 0.014	1.7	-
			LIT-A	0.127 ± 0.011	1.5	-
			LIT-H	0.147 ± 0.009	1.7	-
			MIT	0.083 ± 0.010	1.3	-
	3.2	28	ST	0.154 ± 0.018	2.3	3.9
			LIT-A	0.127 ± 0.016	2	2.7
			LIT-H	0.145 ± 0.012	2.1	3.2
			MIT	0.084 ± 0.015	1.6	1.8
Field	13.5	26	ST	0.029 ± 0.003	1.04	1.1
			LIT	0.029 ± 0.006	1.02	1.2
			MIT	0.004 ± 0.001	0.97	1.1
			LAB	0.006 ± 0.001	0.92	1.1

For small clams, shell growth was significantly less at the mid-intertidal level than at any other treatment. Shell growth was greater at the subtidal level than at the low intertidal ambient, but not different from the low intertidal heated treatment. No difference in growth was detected between either low intertidal treatment (Table 4.2). These results were consistent for both sample dates. Small clams more than doubled in length at the subtidal and low intertidal treatments after 28 d, while clams at the mid-intertidal level were only 73% larger. However, it should be noted that clams grew relatively well even at the long exposure treatment (Table 4.1).

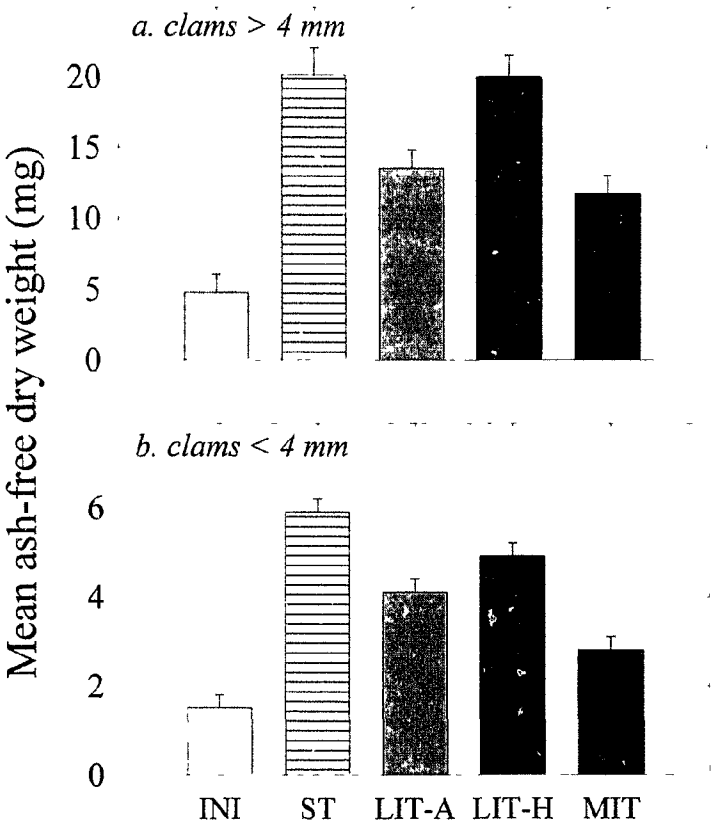

Fig. 4.4. Mean ash-free dry weight (± SE) per exposure treatment after 28 d for *a.* large and *b.* small clams in the laboratory experiment. Treatments: INI, initial; ST, subtidal; LIT-A, low intertidal ambient temperature; LIT-H, low intertidal high temperature; MIT, mid-intertidal.

Mean initial tissue weight was 4 7 ± 0 35 mg ADW for large and 1.5 ± 0.05 mg ADW for small clams. Weight increased between 1.8 and 4 2 times the initial value in 28 d (Table 4.1; Fig 4 4). Significant treatment effects of exposure on clam biomass were detected for both size classes of clams (Table 4.3). Tukey HSD post-hoc comparison revealed that all treatment group means were significantly different from the initial mean clam tissue weight, indicating positive tissue growth for both size classes at all exposure levels. For large clams, the ADW of clams grown at subtidal and low intertidal heated treatments was significantly greater than that of clams at the low intertidal ambient and mid-intertidal treatments For small clams, the results for ADW were the same as for shell length (Table 4 3, Fig 4 4)

Table 4.2. ANOVA table for mean shell growth by treatment for the laboratory experiment. For the Tukey HSD comparisons, lines denote treatments which are not significantly different at $\alpha = 0.05$. Time· Days Treatments: 1 = subtidal, 2 = low intertidal ambient temperature, 3 = low intertidal high temperature, 4 = mid-intertidal

Initial SL = 6 5 mm

Time	Source	df	SS	MS	F	p	Tukey
14	Treatment	3	16 4	5 47	10 7	<0 001	1 3 2 4
	Error	45	22 9	0.51			
28	Treatment	3	6.4	15.47	9 3	<0.001	3 1 2 4
	Error	50	83 1	1 66			—

Initial SL = 3 2 mm

Time	Source	df	SS	MS	F	p	Tukey
14	Treatment	3	23.1	7.69	13 9	<0.001	1 3 2 4
	Error	89	49.4	0.55			—
28	Treatment	3	52.5	17.52	15.8	<0.001	1 3 2 4
	Error	90	99 7	1 11			—

Table 4.3. ANOVA table for mean ADW by treatment for the laboratory experiment. For the Tukey HSD comparisons, lines denote treatments which are not significantly different at $\alpha = 0.05$. Size: Initial shell length. Treatments: 0 = initial, 1 = subtidal, 2 = low intertidal ambient temperature, 3 = low intertidal high temperature, 4 = mid-intertidal.

Size	Source	df	SS	MS	F	p	Tukey
> 4.0	Treatment	4	1935.1	438.8	18.4	<0.001	1 3 2 4 0
	Error	57	1520.1	26.7			
< 4.0	Treatment	3	284.2	71.1	33.9	<0.001	1 3 2 4 0
	Error	114	238.6	2.1			

4.3.2 Field experiment

Figure 4.5 shows the water level and temperature fluctuations during the 26 d field experiment. Salinity values for this period ranged from about 20 to 31o/oo, and water temperatures ranged between 3 and 24°C. Of the 40 clams · treatment^{-1} initially planted, 90 and 92.5% were recovered from the subtidal and mid-intertidal plots, respectively, while only 40% of the low intertidal treatment clams were located. This probably reflects the less stable nature of the substrate in this area (a ripple zone), where clams could be transported with eroding sediment (Chapter 2 and 3).

There was significantly greater shell growth in the subtidal and low intertidal treatments compared with the mid-intertidal or laboratory-held treatments (Fig. 4.6a; Table 4.4). While clams lower on the shore increased an average of 0.8 mm in SL, the mean length of mid-intertidal clams was not significantly different from the initial mean size. However, the only significant gain in biomass occurred in the low intertidal treatment. (Table 4.4, Fig. 4. 6b).

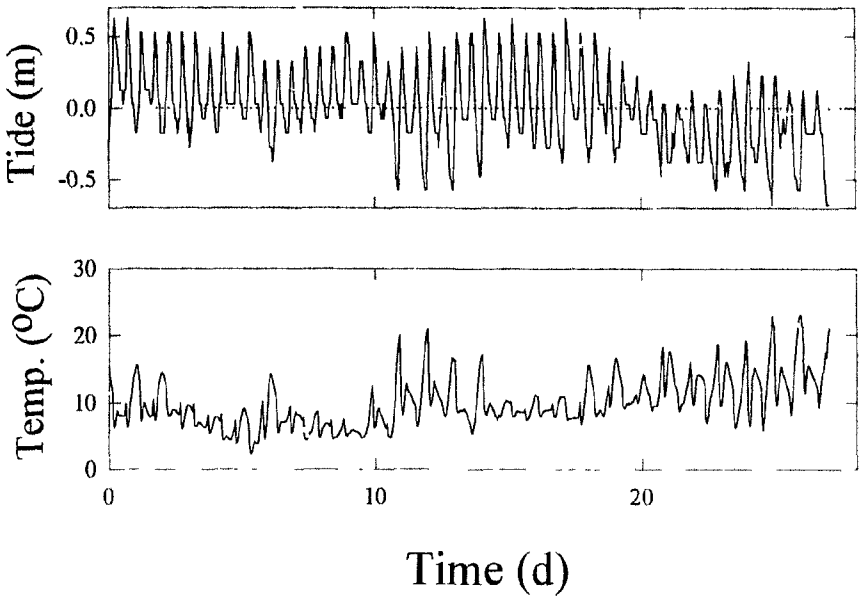

Fig. 4.5. Time series of mean water level (m) and temperature (°C) recorded during the 26 d field experiment.

Table 4.4. ANOVA tables for mean shell growth (SL) and ash-free dry weight (ADW) by treatment for the field experiment. For the Tukey HSD comparisons, lines denote treatments which are not significantly different at $\alpha = 0.05$. Treatments: 0 = initial, 1 = subtidal, 2 = low intertidal, 3 = mid-intertidal, 4 = laboratory.

Variable	Source	df	SS	MS	F	p	Tukey
SL	Treatment	3	13.6	4.5	29.1	<0.001	2 1 3 4
	Error	124	19.3	0.2			
ADW	Treatment	4	342.8	85.7	2.6	0.036	2 1 3 4 0
	Error	160	5183.7	32.4			

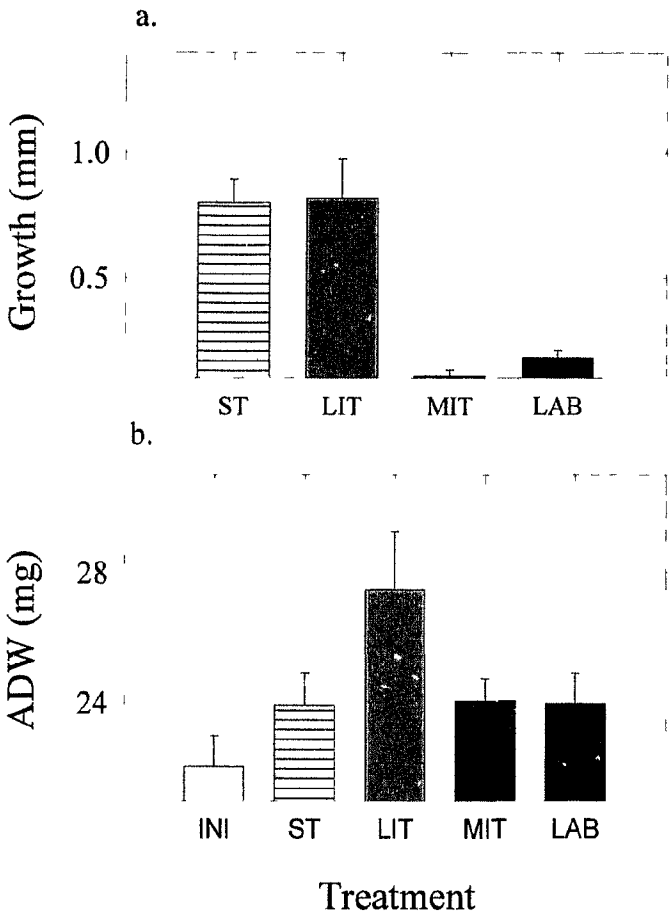

Fig. 4.6. *a.* Mean shell length (± SE) and *b.* mean ash-free dry weight (± SE) per exposure treatment after 26 d in the field experiment. Treatments: INI, initial; ST, subtidal; LIT, low intertidal; MIT, mid-intertidal; LAB, laboratory.

4.4 Discussion

The laboratory and field experiments reported here confirm a significant reduction of both shell and tissue growth of juvenile clams *Mya arenaria* placed at mid-interti exposures versus those continuously immersed. The laboratory experiments demonstrate a cost associated with location in the intertidal habitat beyond that of a simple reduction in feeding time. Even at high ration, the metabolic response to long exposure in these

exposure in these clams resulted in a lower growth rate, despite stable environmental conditions. The reduction of growth in the mid-intertidal was exacerbated in the field study, where shell growth was curtailed relative to lower on the shore. Shorter exposures had a more variable affect. In nature, decreased growth with increasing exposure is likely due to both increased metabolic expenditures as well as reduced food acquisition.

Despite high ration and mild exposure effects in the laboratory, clams at the 45% exposed level were only ~60% as long and about half the weight of subtidally grown clams after 28 d. Short exposure (25%) at ambient conditions resulted in biomass values which were only 67 to 69% of the subtidal treatment. Shell growth at the low intertidal ambient level was intermediate between growth at subtidal and mid-intertidal for small clams, but exhibited no difference for large clams after 28 d. While positive shell and tissue growth occurred at all treatment levels, the reduced SFG in the intertidal treatments suggests that exposure affected the energy balance of these clams, either through a lower assimilation efficiency or an increased metabolic demand. The long siphons of *Mya* have limited surface area for diffusive exchange and probably preclude aerial respiration. The exposure-related reduction in SFG could be due to O_2 debt (Ellington 1983), a high digestive or other metabolic expenditure while exposed (Widdows & Shick 1985), or inefficiencies in processing ingested ration while exposed.

Conversely, it was somewhat surprising to find that elevating the sediment temperatures during exposure had beneficial effects on clam growth, as this treatment was intended to invoke an additional stress typical of the intertidal habitat. Temperature has well known effects on metabolism, and variation in SFG as a function of temperature is

dependent on ration (Kennedy & Mihursky 1972). For example, Stickney (1964) found increasing growth of subtidally grown *Mya arenaria* with increasing water temperature (6, 12, and 20°C), and concluded augmented food could greatly enhance laboratory growth over natural clam populations in Maine. However, an increased metabolic rate effected by high temperature will induce starvation with insufficient food resources (Kennedy & Mihursky 1972; Harvey & Vincent 1990). Hummel (1985) found laboratory growth of continuously immersed, suspension-feeding *Macoma balthica* was negative at < 1.3 mg carbon $\cdot L^{-1}$, and clams required a daily maintenance ration of 1.3% algal wet weight to bivalve dry weight. In the present study, the heated exposure treatment was expected to induce a growth reduction relative to ambient conditions at a given food ration. However, animals at the short exposure heated level were never significantly different in length or weight compared to the subtidal treatment. We speculate that high ration compensated for potential negative effects of increased temperature at these short exposures.

Clam growth during the field experiment was less than that observed in the laboratory experiment. Ash-free dry weight exhibited a significant (but marginal) increase over initial values in only one treatment comparison (low intertidal versus initial). Shell growth was also small, although significant increases were found at the subtidal and low intertidal stations relative to the clams grown at the mid-intertidal station or in the laboratory. These field results are in general agreement with the laboratory findings but illustrate the more varied factors influencing growth in the field. For example, Fig. 4.5 shows the varied exposure and thermal regimes experienced by clams during the field

experiment. Additionally, food resources during this period were relatively low (1 to 2 μg Chl-$a \cdot L^{-1}$) and growth at all stations was apparently food limited compared with the augmented feeding of the controlled laboratory experiment.

The maximum mean growth rate of juvenile *Mya arenaria* in the laboratory study was 0.22 mm $\cdot$ d^{-1}, which is rapid compared to the highest values of ~0.16 mm $\cdot$ d^{-1} measured by Stickney (1964) for similarly sized clams. His experiments on subtidal growth in relation to food concentration and clam density found the highest relative growth at mean daily rations of the order of 10^6 to 10^7 cell $\cdot$ $clam^{-1}$ $\cdot$ d^{-1}. In this study, the maximum potential rations were about 10^8 cells $\cdot$ $clam^{-1}$ $\cdot$ d^{-1}, but the actual ingested ration, although not quantified, was probably much less. *In vivo* fluorescence measurements and observations of the clams during feeding periods indicated that the clams were unable to deplete the water in the test containers of seston (Fig. 4.3). Importantly, the experimental clams were well supplied with food, and growth differences cannot therefore be attributed to differential food supply.

While food limitation can certainly reduce SFG in intertidal clam populations, variation in temperature, desiccation stress, and exposure time as a result of tidal fluctuations, as well as physiological adaptations to exposure, have important implications for the metabolism and SFG of intertidal organisms. Energy expenditures due to intertidal stresses can be expected to exacerbate the diminished SFG caused by a reduction in feeding time. De Zwaan & Wijsman (1976) measured decreasing ATP levels over time during valve closure in *Mytilus edulis*, and concluded mussels were not completely dormant during exposure. Boyden (1972) demonstrated metabolic activity in *Cerastoderma edule*

during emersion, and Shick *et al.* (1988) concluded there was an energetic cost to digestion and/or absorption during exposure in both *M. edulis* and *C. edule*. Ellington (1983) found the magnitude of the O_2 debt increased non-linearly with increasing exposure period, and Pedersen (1992) measured large metabolic outputs in *Mya arenaria* during expected low tide periods. Other energy expenditures in the intertidal zone may be a response to predators, such as the increase in mean depth with exposure reported in *Mercenaria mercenaria* by Roberts *et al.* (1989). These energy expenditures can reduce the SFG in excess of losses "expected" from reduced feeding alone (Peterson & Black 1987, 1988, 1991; Lin 1989; Jensen 1992).

Growth rate and the related burial depth are crucial factors affecting survival of juvenile infaunal bivalves. Increased burial depth reduces the likelihood of erosion (Chapter 2), and sediment buffers clams from environmental fluctuations such as temperature (McMahon & Wilson 1981) and water loss (Deaton 1992). Additionally, in *Mya arenaria*, there is a strong relation between size, burial depth, and predation intensity from crabs (Blundon & Kennedy 1982; Skilleter 1994) and birds (Zwarts & Wannik 1989, 1993; Zwarts 1991; Piesrsma *et al.* 1993). Due to the protection afforded by the sediments, factors which limit growth (and thus minimize burial depth) will tend to increase the probability of predation. For example, using data from Wanink & Zwarts (1993), the regression equation relating burial depth (mm) to size (SL, in mm) for *M. arenaria* was determined as

$$\text{Depth} = -0.01815 \cdot SL^2 - 2.17 \cdot SL + 4.238 \quad (P < 0.0001, r^2 = 0.982).$$

Then, using the growth rate values for low intertidal and mid-intertidal clams from the laboratory study, the time-dependent depths of burial were calculated. As a measure of predation intensity, the 30 mm size refuge from knot (*Calidris canutus*) predation given in Piersma *et al.* (1993) was employed. The results indicate that clams in the mid-intertidal habitat would spend twice the time in the "harvestable fraction" (Piersma *et al.* 1993) of this bird predator compared to individuals lower on the shore. Thus, stresses incurred in the intertidal zone that reduce growth rate are likely to increase predation rates.

In conclusion, population surveys, field experiments, and laboratory results indicate that increasing exposure to air leads to suboptimal growth for both in- and epifaunal bivalves. The growth reductions are a result of both a metabolic cost of emersion as well as a reduction in feeding time. The negative physiological effects of emersion appear ration dependent, and at high ration growth can occur even at long exposures. Short exposures to air may have limited negative effects, while elevated temperature during emersion was found to increase growth, perhaps by enhancing the digestion and/or processing of ingested ration. At longer emersion times, an increasing portion of the assimilated energy will be required for reoxidation of anaerobic metabolites and other costs of exposure. During periods of high environmental stress and low food, starvation will occur. Thus, in aquaculture ventures, judicious placement of bivalves along the exposure gradient can be used to balance growth with culture maintenance activities and predation control.

Conclusion

Hydrodynamic forces shaped bivalve populations in the Eel River estuary by controlling larval supply, redistributing juveniles, and affecting growth. The population dynamics of bivalves in the Eel River is thus structured in part by tidal currents. Given the widespread occurrence of this estuarine saltmarsh habitat the associated physical regime, hydrodynamic structuring of populations is likely to determine the recruitment process of many organisms in soft sediment ecosystems.

A major result of this study was the measurement of large exchanges of larvae between the estuary and coastal ocean. It is clear that for species with planktonic reproductive modes, the production of self-seeding benthic populations depends on the time scale of water exchange of the system compared to the time necessary for the completion of planktonic development. In the Eel River and similar small-scale coastal estuaries, it is unlikely that many of the endogenously produced larvae remain in the system long enough to complete development. In contrast, relatively large numbers of bivalve larvae were found to be imported into the estuary from the nearshore zone during flood tide. The important ramification is that larvae exported from estuaries may form a pool of potential recruits for the whole coastal system, not just the estuary of origin.

However, the reliance on the supply of larvae from the coastal zone suggests that recruitment limitation (low larval supply) has the potential to be a strong determinant of annual year class strength in estuaries like the Eel River. During this study, relatively large amounts of bivalve larvae were found to be exchanged between estuary and sea on most of the tidal periods sampled, suggesting that larvae were retained near shore. But

during other years and certainly over other seasons, the advection of coastal water offshore has the real capability of removing potential settlers from access to estuarine sites. Much of the interannual variability in recruitment might thus be caused by large-scale advective processes which concentrate or disperse larvae from coastal sites. How specifically coastal oceanography and larval behavior interact to mediate larval reinvasion to estuaries needs to be addressed with future studies in order to more fully understand and predict the recruitment process.

At the benthic site, a combination of hydrodynamic structuring and stochastic mortality events determined bivalve abundance. These factors resulted in strong variation in bivalve population structure within small spatial and temporal scales. Tidal fluctuations and current velocities limited the location of settlement, and juvenile transport was responsible for the accumulation of bivalves in depositional locations. In fact, benthic transport was the primary mode of recruitment for *Gemma gemma* and *Macoma balthica*. Laboratory flume experiments demonstrated that erosion and transport of small, surface-dwelling clams was likely at flow velocities typical of the field site. The hydrodynamic regime thus resulted in a time-varying abundance of juvenile bivalves in the high velocity channels and a congregation of animals in the low intertidal zone. This basic pattern was severely altered by ice related mortality which obliterated intertidal populations. Thus, both recruitment limitation and recruitment regulation of the bivalve populations were caused by physical factors.

The structure of the subtidal and intertidal populations of *Mya arenaria* are noteworthy at the benthic site of the Eel River. The subtidal population was dominated by a

high density of adult clams. This population remained stable even through the harsh winters, grew slowly, and probably made a major contribution to larval production. However, recruitment to the population was minimal, and the population is therefore highly threatened by clamming events. Once eliminated, recovery of the population will be difficult given then the rapid tidal currents. The intertidal population, on the other hand, was also very dense but had a size-frequency distribution skewed towards juveniles. Further, the clams grew slowly in the intertidal and remained restricted to the surficial layers for several years. Laboratory and field experiments of growth in relation to tidal inundation suggests that the low growth in the intertidal zone was due to emersion stress and reduced feeding times. Small size and the resultant shallow burial depth will effect transport probability as well as predation potential.

The exploitation of soft-shell clams in Eel River (part of a provincial park), and indeed throughout Nova Scotia, occurs unregulated and unabated. All too commonly, overfishing has led to recruitment failure and population decline. As documented in Chapter 3, the effect of clam digging activity on vulnerable populations can be extreme; one need only visit a commercially harvested clam flat to realize the ecological damage which accompanies clam digging. Clam populations are presently in decline throughout the region, and an integrated management of the resource must be implemented to reduce the chance of catastrophic population collapse. Ecosystem enhancement and aquaculture are plausible and desirable options compared to unregulated harvesting, but require thoughtful analysis of cost effectiveness on a site to site basis. Any effective bivalve management plan will have to be based on an understanding of the links of recruitment to

estuarine and coastal processes. The effects of hydrodynamic factors on larval supply and post-settlement transport explain much of the variability in the recruitment of bivalves in coastal estuaries.

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