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Seasonal effects of intraspecific density and predator exclusion along a shore-level gradient on survival and growth of juveniles of the soft-shell clam, *Mya arenaria* L., in Maine, USA

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Abstract

   The relative roles that predation and competition play in regulating populations of infaunal marine bivalves in soft-bottom systems are strikingly different. Exploitative competition for food typically occurs at elevated densities, but crowding rarely results in mortality and competitive exclusion. Predation by decapods, gastropods, and, sometimes asteroids, is more important in controlling patterns of distribution and abundance. Most field tests leading to this synthesis have been conducted between 35°N and 35°S and/or with bivalves in the families Veneridae and Tellinidae. To test the robustness of these ecological processes at another geographic setting (45°N) using a species from another family within the suspension-feeding guild (Myidae), we performed a short-term field manipulation at an intertidal mud flat in eastern Maine, USA. We followed survival and growth of 10,080 juveniles (12.4-mm shell length (SL)) of the soft-shell clam, *Mya arenaria* L., in field enclosures with and without predator-deterrent netting at three densities (330, 660 and 1320 m^{-2}) along a tidal gradient over four sampling intervals from April to December 1996. We used a generalized completely randomized block design to assess variation in these dependent variables within a given tidal height (high, mid, and low) on a particular date.

   Mortality varied seasonally, peaking (13.6%) between August and September when seawater temperatures were warmest. No significant mortality occurred after September, when mean ($\pm 95\%$ CI) percent survival pooled over all treatments was $72.9 \pm 8.5\%$. Netting (6.4-mm aperture) effectively excluded predators along the tidal gradient as overall mean clam survival,

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independent of tidal position, was $88.7 \pm 4.1\%$ in protected units (plastic plant pots with area $= 181$ cm^2), but decreased from upper and mid tide levels ($82.9 \pm 6.1\%$) to lower on the shore ($66.3 \pm 9.7\%$) in unprotected units. Density-dependent mortality resulted in reduced survival (-4.6%) in clams stocked at the two highest levels ($P < 0.001$); however, numbers of dead clams with undamaged valves provided little evidence that this effect was due to starvation. Incremental growth also varied seasonally with greatest amounts of shell added during June–August at all tidal levels. Shell growth stopped or slowed significantly after September at all tidal positions. Mean SL increased with decreasing tidal height (December sizes: high $= 20.6 \pm 2.9$ mm, mid $= 24.1 \pm 1.0$ mm; low $= 28.2 \pm 1.2$ mm); however, submergence time alone failed to explain completely these differences. Density-dependent growth was detected once (August–September). Animals at the two highest densities experienced a growth depression of ca. 7%. We conclude predation, rather than competition, is more important in regulating populations of soft-shell clams in this intertidal location. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

A fundamental goal of many ecological field investigations is to discover the processes that generate specific distribution and abundance patterns of a species or population. Two basic, but interdependent, approaches have evolved in efforts to study infaunal bivalve populations in soft sediments. The first one is a descriptive approach that measures spatial and/or temporal trends of distribution and abundance, or, mortality, fecundity or recruitment schedules by repeated sampling of a population (Commito, 1982; Harvey and Vincent, 1989; Jensen, 1992; Kalyagina, 1994; Hewitt et al., 1997; Weinberg, 1998; Strasser et al., 1999). These descriptive efforts are essential because they focus attention on how life-history strategies are correlated with biotic and abiotic factors in a particular environment or habitat. This class of investigation typically generates testable hypotheses, but can only make inferences about particular mechanisms. The second is an experimental approach that measures one or more response variables (e.g., growth, survival, reproductive effort) after manipulating factors such as size, age, diet or density of individuals (Peterson, 1982a; Boulding and Hay, 1984; Peterson and Black, 1993; Montaudouin and Bachelet, 1996; Thrush et al., 1997a; Whitlatch et al., 1997; Zaklan and Ydenberg, 1997), some aspect of the organism's habitat (Irlandi, 1994), or predator access (Walker, 1985; Peterson 1982b; Peitso et al., 1994; Richards et al., 1999). These types of investigations generally provide information about why patterns exist, how they are maintained, or what is responsible for their dynamic nature.

We are interested in how intraspecific density and predation interact to regulate intertidal infaunal marine bivalve populations along shore level gradients. Numerous manipulative field experiments have focused on density-dependent growth, survival, movement, or recruitment of bivalves (Peterson, 1985; Ólafsson, 1986; Peterson and Beal, 1989; Whitlatch et al., 1997; Fernandez et al., 1999), the effects of excluding predators on clam growth and/or survival (Marelli and Arnold, 1990; Cummings et al., 1997; Smith and Langdon, 1998; Masski and Guillou, 1999; Richards et al., 1999;

Nakaoka, 2000), or the interactive effects of intraspecific density and predator exclusion or inclusion (Peterson, 1982a,b; Skilleter and Peterson, 1994). Largely limited to venerid or tellinid species, these trials have demonstrated the relative importance of predation in limiting bivalve populations and that crowding produces measurable reductions in growth (presumably due to competition for limited supply of phytoplankton) and recruitment, but not survival (but see Peterson and Black, 1993; Summerson et al., 1995; Cigarria and Fernandez, 1998). Other experimental studies have examined how intraspecific competition affects bivalve growth and/or survival along tidal elevations (Peterson and Black, 1987; Vincent et al., 1989; Montaudouin and Bachelet, 1996). Survival of infaunal suspension-feeding clams in these studies was not influenced by either tidal elevation or intraspecific density, but animals typically added shell and somatic tissue faster at lower shore elevations where immersion times are longer and, presumably, feeding time is longer per tidal cycle compared to higher elevations. We are unaware of any field study that has investigated the factorial effects on survival and growth of intraspecific clam density, tidal elevation, and predator exclusion and how these variables interact through time.

In Maine, USA, the soft-shell clam, *Mya arenaria* L., is a ubiquitous, iteroparous, year-round infaunal resident of intertidal soft-bottoms and extends from the upper shore to the lowest level exposed on spring tides (Hanks, 1963). Shallow subtidal populations exist, at least in eastern Maine (B. Beal, personal observation), but their abundance and distribution has yet to be quantified. High densities of 0- and 1-year class individuals concentrate near the upper shore of most low energy mud flats (Dow and Wallace, 1961; Matthiessen, 1963; B. Beal, personal observation; but see Emerson and Grant, 1991 for a counterexample on a high-energy sand flat). Whether this is the result of hydrodynamic factors, post-settlement mortality events, density-dependent migration, or other reasons are unknown. In addition, individuals that occur at lower shore levels tend to be larger and grow faster than conspecifics of similar age at or near the upper shore (B. Beal, personal observation). Mortality of young individuals (< 12-mm shell length, SL) during the first 5 years is estimated to be 96.5% year^{-1}, and, after attaining an SL > 30 mm, *Mya* reaches a size refuge from the naticid snail, *Euspira heros* (Say) (Commito, 1982), and a spatial refuge in burial depth from decapods and other predators (Blundon and Kennedy, 1982; Lipcius and Hines, 1986). Green crabs, *Carcinus maenas* (L.), are another major predator that limits the growth of clam populations in Maine (Ropes, 1968). The range extension of this non-native, portunid crab into eastern Maine waters during the 1950s has been correlated with historic declines of commercial catches of *Mya* during the period between 1950 and 1970 (Wallace, 1997).

The work presented here attempts to integrate previous field trials with *M. arenaria* and extend our understanding of mechanisms regulating in situ bivalve populations by explaining observed patterns of growth and mortality along a shore-level gradient. We manipulated the intraspecific density of hatchery-reared individuals of *Mya* within protected and unprotected experimental units at each of three tidal levels at an intertidal flat in eastern Maine and used a generalized randomized complete block design (Underwood, 1997) to assess the importance of spatial and temporal variability associated with each of these three factors. We used cultured juveniles of *Mya* for five reasons. First, hatchery-reared animals have been shown to model the behavior (survival

and growth characteristics) of similarly sized wild individuals (Beal and Vencile, in press). Second, animals may be obtained in sufficient quantities and within a narrow size range for large-scale manipulative studies. Third, once added to sediments, cultured individuals develop a unique mark so that they are easily distinguished from wild clams (Beal et al., 1999). Fourth, small clams are more susceptible to mortality agents and generally grow faster than large clams allowing treatment effects to be detected more easily. Fifth, recent commercial landings of soft-shell clams along Maine's coast, and, particularly, eastern Maine, have declined to historically low levels (Wallace, 1997). Coastal communities have begun efforts to enhance intertidal wild stocks with cultured juveniles (Beal, 1994). Results from experimental field manipulations, as opposed to correlative studies, have the potential to provide local stewards and fisheries managers greater insights about which factor(s) are important in regulating populations and can be used to design and test new management strategies on larger temporal or spatial scales (Botsford et al., 1997; Lenihan and Micheli, 2000).

2. Methods

2.1. Study site

The study was conducted between 6 April and 10 December 1996 at three intertidal heights (high [0.5 m], mid [0.0 m], and low [−0.5 m] measured in relation to mean sea level) on the northern (inner) side of Flake Point Bar (FPB; Lat. 44°36′48″N, 67°33′43″W), at the mouth of Mason's Bay located 9.7 km north of Jonesport, ME, USA. Surficial sediment grain size at FPB was more coarse and variable in the high intertidal (mean $\Phi \pm s = 1.91 \pm 0.15$; $n = 2$) compared to the low ($4.87 \pm 0.02\Phi$; $n = 2$) where sediments were more homogeneous and muddy. Although sediment samples were not taken near the mid intertidal, qualitatively, grain size and texture were similar to those measured near the low (B. Beal, personal observation). Linear distance from the shore to the low intertidal was approximately 300 m with a gradual slope (ca. 0.25°) from upper to lower tidal heights. Distance from the shore to the high intertidal was approximately 50 m while the distance was 150 m from the high to the mid and 100 m from the mid to the low intertidal. FPB experiences semidiurnal tides with mean tidal range of 3.8 m at high tide at the mid intertidal (0.0 m). This depth ranges from 3.5 to 4.6 m on neap and spring tides, respectively. Further information on hydrographic features of FPB can be found in Congleton et al. (1999). Seawater temperature varied at the site from a low of 5 °C on 9 April and 9 December to 16 °C on 6 September 1996. Seawater temperatures from early August to late September, measured at nearby Beals Island Regional Shellfish Hatchery (BIRSH), Beals, ME (44°31′21″N, 67°36′38″W) ranged from 13 to 16 °C (Beal, unpublished).

2.2. Experimental animals, experimental units, and treatments

To examine interactive effects of intraspecific density and predation intensity along a tidal gradient on growth and survival of *M. arenaria*, we used overwintered (Beal et al.,

1995), hatchery-reared juveniles (mean SL $\pm$ 95% CI = 12.4 $\pm$ 0.31 mm, $n = 191$, range = 8.6–20.8 mm) produced during 1995 at BIRSH. This narrow range of clam sizes essentially removes any size-related bias from analyses of experimental effects.

Clam individuals ($N = 10{,}080$) were added to ambient sediments within 15.2 cm (diameter) $\times$ 15.2 cm (depth) plastic plant pots (experimental units; forced into the sediments to a depth of ca. 15 cm; $A = 0.018$ m^2) at one of three stocking densities (6, 12, or 24 individuals unit^{-1} representing approximate stocking densities of 330, 660, and 1320 m^{-2}). Animals were planted 1 cm below the sediment surface within each experimental unit. The lowest density is similar to mean ambient density of > 1-year-old wild individuals reported by Commito (1982) from a nearby intertidal flat in eastern Maine (Federal Harbor, Lubec: 44°51′21″N, 67°04′42″W) from 1977 to 1979. Experimental units were arrayed equally at each tidal height.

Clams in one-half of the units at each tidal height were protected from large, epibenthic predators using a flexible piece of plastic netting (6.4-mm aperture; 40.5 g m^{-2}; InterNet, N. Minneapolis, MN). Netting completely covered the top of each unit and overlapped the sides such that the four corners of each piece met at the bottom of the unit. Two rubber bands placed around the netting near the middle of the experimental units helped secure the netting to the pot. This arrangement also reduced the chances of large infaunal predators (e.g., *E. heros*, *E. triseriata* [Say], and *C. maenas*) gaining entrance by burrowing between the netting and the unit. Each protected experimental unit was positioned in situ so that a 0.2-cm lip protruded above the sediment surface. Netting in direct contact with sediments can reduce clam growth by interfering with siphonal activity at the sediment/water interface and/or create localized anoxic conditions (Beal, 1994). To avoid these problems, each piece of netting was pulled vertically ca. 4 cm above the rim of each experimental unit. Netting was rigid enough to remain in this position during the entire experiment.

The other one-half of the experimental units allowed predator access, but were designed to minimize emigration from the units by the cultured clams and migration of small, wild clams into the units (Beal, 1994). This was accomplished by affixing a piece of 6.4-mm (aperture) flexible netting (10 (wide) $\times$ 35 cm (long)) around the circumference of each unit using two rubber bands so that when positioned in the sediments (as described above) the netting protruded approximately 4 cm above the rim of each unit. We refer to these corral-like experimental units as unprotected, or open, enclosures (sensu Peterson and Beal, 1989).

2.3. Field design and sampling procedures

From 6 to 9 April 1996, 240 experimental units were established at each tidal height at FPB ($N = 720$). Experimental units were grouped in blocks of 12 pots each (two replicates of each of the six treatment combinations of intraspecific density [three levels] and predator exclusion [two levels]) comprising a 2×6 matrix with 1-m spacing between rows and columns. Treatments were assigned randomly to positions within each block. Twenty blocks were arrayed randomly at each tidal height in an approximate 2×10 matrix with 10-m spacing between each block. This field design was a general-

ized randomized complete block design (GRCBD; sensu Neter et al., 1990). Unlike randomized complete block designs (i.e., $n = 1$ within each block), the GRCBD allows one to test whether the main and interactive effects of the factorial treatments differ spatially (i.e., from block-to-block within a particular tidal height on a given sampling date) (Underwood, 1997).

To assess temporal effects of the treatments on clam survival and growth, we sampled five blocks (destructively and without replacement) chosen randomly from each tidal height on four pre-determined dates: 5 June, 6 August, 26 September, and 8–10 December 1996. The dates encompass the time that approximately 99% of shell growth occurs in eastern Maine (Beal, 1994) and were chosen specifically to test a priori hypotheses. We predict that $< 20\%$ of shell growth occurs between April and June, 60–70% between April and August, 90–95% between April and September, and $> 95\%$ between April and early December. Because sampling dates were chosen before the experiment was initiated, we considered this source of variation as a fixed effect in all analyses (see below). On each sampling date, experimental units ($N = 180$) were transported to the University of Maine at Machias where the contents of each were washed through a 1-mm sieve. Living and dead clams from each unit were enumerated and measured (SL to the nearest 0.1 mm using Vernier calipers). Dead clams were divided into three categories based on shell damage: (1) undamaged valves, (2) crushed or chipped valves typical of crustacean predation, and (3) drilled with one or more countersunk holes in a valve typical of naticid gastropod predation. In addition, number of clams missing per unit was assessed. We were able to distinguish cultured vs. wild clam juveniles because each hatchery-reared clam had a distinctive mark (line) on both valves that separated new shell growth (white) from the darker umbo portion of each valve associated with its initial size at the time of field planting (Beal et al., 1999). Live predators (green crabs and moon snails) within an experimental unit at the time of sampling were also enumerated and measured to the nearest 0.1 mm using Vernier calipers (*C. maenas*: greatest carapace width CW; *Euspira* spp.: distance between spire and apex). During the experimental interval, we observed no commercial or recreational harvesting of soft-shell clams at the study site, which was closed by the Town of Jonesport to the taking of shellfish for conservation purposes (G. Feeney, selectman, Jonesport, ME, personal communication).

2.4. Tidal inundation measurements

Time of tidal inundation during a 12-h cycle was measured for selected blocks at each tidal height during a neap (26 June 1996; $+ 0.33$ m) and spring (3 July 1996; $- 0.71$ m) tide.

2.5. Statistical analyses

Data for mean percent survival per experimental unit were transformed using the arcsine (angular) transformation (Sokal and Rohlf, 1995) to homogenize variances (Cochran's test [$P > 0.05$]; Winer et al., 1991) before employing univariate analysis of

variance (ANOVA). Treatment effects on clam growth used mean final SL per experimental unit since mean initial length was similar across all 720 experimental units in April 1996 ($P > 0.05$). The growth data required no transformation to meet assumptions of ANOVA. The linear model for the survival and growth data contained both fixed (sampling date, tidal height, netting, intraspecific density) and random (block) factors. The four fixed factors are orthogonal to each other (yielding 15 sources of variation) and the block factor is nested within the combination of sampling date and tidal height (yielding four sources of variation; see Appendix A for the mean square estimates for each of the 19 sources of variation associated with the linear model).

We used a priori, single degree-of-freedom contrasts to examine hypotheses concerning the three main factors with more than 2 *df* (i.e., sampling date, tidal height, and intraspecific density) based on results from previous work in Maine (Beal, 1994), the Canadian Maritimes (Newcombe, 1935) and Massachusetts (Brousseau, 1978, 1979; Chalfoun et al., 1994).

2.5.1. Sampling date

Specific intervals were chosen based on shell growth and survival estimates from Beal (1994), who observed that approximately 20% of annual growth of cultured juveniles of *Mya* occurred between April and June and from September to December while nearly 60% occurred between June and August at two intertidal flats in eastern Maine. Similar seasonal shell growth was observed by Newcombe (1935) in nearby St. Andrews, New Brunswick. In addition, survival varied seasonally with highest mortality of cultured juveniles of *Mya* varying directly with warmest seawater temperatures (Beal, 1994; Brousseau, 1978):

Contrast (1): June vs. mean of the three remaining sampling dates (August, September, and December)

tests whether mean SL and percent survival from April to June differs from the mean of the three other periods (i.e., April to August; April to September; April to December). We predict this contrast to be highly significant for both dependent variables. Between April and June, relatively slow shell growth should occur due to limited amounts of phytoplankton in the water column (Townsend and Cammen, 1988) and relatively cool water temperatures. Survival is related directly to predator activity (Commito, 1982; Brousseau, 1978); therefore, mortality should be relatively low during this first interval compared with rates later in the year since most vertebrate and invertebrate predators increase their foraging activities as seawater and air temperatures increase.

Contrast (2): August vs. mean of the two remaining sampling dates (September and December)

also should be significant for both dependent variables as the period from early August to mid-September is the period of time when seawater temperatures are warmest.

Additional shell growth should occur during this period (Newcombe, 1935; Beal, 1994), and, greatest rate of mortality due to predators should occur (Brousseau, 1978).

Contrast (3): September vs. December

should not be significant for either variable as minimal growth should occur during the period between mid-September and early December (Newcombe, 1935; Beal, 1994) and mortality rates after September should be low due to lowering seawater temperatures and decreased predator activity.

2.5.2. Tidal height

Newcombe (1935) determined the rate of growth of 2-year-old soft-shell clams (18.4 mm SL) varied inversely with shore level. Beal (1994) observed shell growth of cultured *Mya* (SL = 6–8 mm) was slower and survival higher when animals were planted at mid tide level compared with lower tidal levels in eastern Maine.

Contrast (4): High vs. mean of mid and low intertidal

should be highly significant for both dependent variables. Final mean SL should be significantly greater for clams at the lower vs. upper shore due to differences in emersion (Roseberry et al., 1991), and, therefore feeding times (e.g., Peterson and Black, 1987). Also, predicted disparities in final mean lengths between these shore levels may be due to physiological differences relating to metabolic activity (Anderson, 1978; Lewis and Cerrato, 1997). Survival should vary inversely with tidal height. Clams placed at mid and lower intertidal levels should suffer higher rates of mortality than animals living near the upper shore because waterborne predators such as crustaceans, gastropods, and benthic fish are more numerous and/or effective than predators that appear only when the tidal flat is exposed such as land mammals and birds (B. Beal, personal observation).

Contrast (5): Mid vs. low intertidal

also should be significant for both dependent variables for the reasons given in contrast (4).

2.5.3. Stocking density

Beal (1994) observed significant negative effects of increasing intraspecific density of hatchery-reared juveniles of *Mya* (> 10 mm SL) on survival, but not growth:

Contrast (6): 330 m^{-2} vs. 660 and 1320 m^{-2}

should reveal significant (negative) crowding effects on survival (low-density refuge) but not shell growth.

Contrast (7): 660 vs. 1320 m^{-2}

should be similar to that described for contrast (6).

Planned comparisons are examined regardless whether main effects are significant. Also, the a priori contrasts can be used to examine details of interactive factors by decomposing these sources of variation into single degree-of-freedom tests (Winer et al., 1991) that enables one to interpret complex, higher-order interactions in a biologically meaningful manner (Underwood, 1997). We adjusted type I error rate for all contrasts ($\alpha' = [1 - \alpha]^{1/n}$) where $\alpha = 0.05$ and $n =$ number of contrasts (Winer et al., 1991). To better understand spatial variability within a particular tidal height on a given sampling date, we partitioned sources of variation due to the nested block effects only when they were significant. We did not adjust type I error rate for these random effects for two reasons. First, the overall sum of squares for a given source of variation due to blocks is the sum of separate single-factor ANOVAs that could have been examined independent of the larger ANOVA (Neter et al., 1990). Second, block effects are random; as such, we had no a priori knowledge about these effects.

3. Results

3.1. Tidal inundation

Time of tidal submergence varied inversely with tidal height and lunar cycle (Table 1). Mean submergence time, pooled across sampling dates, increased 1:45 (h:min) from high to mid tide blocks and 1:52 from mid tide to low tide blocks. On 26 June, during

Table 1

Time (h:min) of submergence (during a 12-h tidal cycle) for individual blocks at the high ($n = 14$), mid ($n = 8$), and low ($n = 8$) intertidal sites at Flake Point Bar (FPB), Jonesport, ME on a neap (26 June) and spring (3 July) tide

Data are presented as if one were looking at the tidal flat from above. 0–180° represents a north–south plane at FPB. Submergence times represent individual blocks and the arrangement of times correlates precisely with the physical layout of blocks at each tidal height.

26 June 1996 (+ 0.33 m)									
180°———————————————————————————0°									
High	6:21	6:51	7:32	7:54	8:05		8:14	8:02	$\bar{x} = 7:42$
	6:58	7:45	7:38		8:08	8:10	8:14	8:02	$s = 0:35$
Mid	9:53	9:42	9:39						$\bar{x} = 9:52$
	10:05	10:05	9:57	9:57	9:42				$s = 0:10$
Low	12:00	12:00	12:00	12:00	12:00	12:00	12:00		$\bar{x} = 12:00$
		12:00							$s = 0:00$
3 July 1996 (− 0.71 m)									
180°———————————————————————————0°									
High	6:27	6:43	6:59	7:21	7:39		7:44	7:39	$\bar{x} = 7:20$
	6:53	7:13	7:05		7:42	7:46	7:44	7:39	$s = 0:26$
Mid	8:40	8:39	8:36						$\bar{x} = 8:40$
	8:46	8:43	8:40	8:37	8:37				$s = 0:03$
Low	10:13	10:13	10:13	10:18	10:20	10:20	10:24		$\bar{x} = 10:17$
		10:18							$s = 0:04$

neap tide, none of the low tide blocks became exposed. Conversely, these blocks were exposed for nearly 2 h within a 12-h cycle during a spring tide (Table 1). Regression of standard deviation of submergence times (dependent variable) on tidal height (low = 1; mid = 2; high = 3) also indicates that block-to-block variability (independent of lunar cycle) increased ($F_{1,4} = 16.27$; $P = 0.0157$) from the lower to upper shore and suggest microtopographic features were more pronounced at the upper intertidal site. For example, some blocks nearest the shore were submerged for as long as 8:14 while one was submerged for only 6:21 on the 26 June neap tide (Table 1). Similar variability was observed in the upper intertidal on the 3 July spring tide. Variation in submergence times within tidal height was lower at the two lower tidal levels where the greatest difference between blocks was 0:26 (e.g., mid tide on 26 June; Table 1).

3.2. Survival

Clam survival (Tables 2–5) varied significantly with each of the four fixed factors and one of eleven interaction sources of variation (Table 6). In addition, significant block effects were detected on several sampling dates, indicating variation on a spatial scale of 10s of meters (see below). Greatest clam losses occurred during the period when

Table 2

Fate of juvenile soft-shell clams ($\bar{x}_{SL} \pm 95\%$ CI $= 12.4 \pm 0.31$ mm; $n = 191$) from 6–9 April to 5 June 1996 (57–60 days) at Flake Point Bar, Jonesport, ME

Mean percent ($\pm 95\%$ CI) is given for living (% alive, A), dead with undamaged valves (% DU), dead with a countersunk hole drilled into a valve (% DD), dead with crushed or chipped valves (% DC), and missing (% M). Density (L, H, and M represent 330, 660, and 1320 individuals m^{-2}, respectively). Netting ($+$: present; $-$: absent). Means presented here are from the five pooled blocks. ($n = 10$).

Tide	Density	Netting	% A	% DU	% DD	% DC	% M
High	L	−	81.7 (37.6)	0.0 (0.0)	3.3 (8.1)	0.0 (0.0)	15.0 (36.5)
		+	85.0 (36.5)	1.7 (6.0)	6.7 (24.2)	0.0 (0.0)	6.7 (13.4)
	M	−	83.3 (38.5)	0.8 (3.0)	11.7 (28.2)	0.0 (0.0)	4.2 (9.2)
		+	97.5 (6.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.5 (6.4)
	H	−	86.7 (31.7)	0.8 (2.0)	6.7 (22.5)	0.0 (0.0)	5.8 (9.9)
		+	95.8 (3.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.2 (3.9)
Mid	L	−	91.7 (13.4)	1.7 (6.0)	1.7 (6.0)	0.0 (0.0)	3.3 (8.0)
		+	88.3 (12.9)	3.3 (8.1)	0.0 (0.0)	0.0 (0.0)	8.3 (13.5)
	M	−	95.0 (6.7)	0.8 (3.0)	0.0 (0.0)	0.0 (0.0)	4.2 (6.7)
		+	96.7 (9.2)	1.7 (6.0)	0.8 (3.0)	0.0 (0.0)	0.8 (3.0)
	H	−	90.0 (13.4)	0.0 (0.0)	2.1 (5.2)	0.0 (0.0)	7.9 (10.9)
		+	92.9 (11.7)	1.3 (2.3)	0.8 (3.0)	0.0 (0.0)	5.0 (10.8)
Low	L	−	80.0 (36.9)	3.3 (8.1)	3.3 (12.1)	0.0 (0.0)	13.3 (35.8)
		+	91.7 (13.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	8.3 (13.5)
	M	−	92.5 (9.5)	0.0 (0.0)	2.5 (4.6)	0.0 (0.0)	5.0 (8.1)
		+	95.0 (9.2)	0.0 (0.0)	0.8 (3.1)	0.0 (0.0)	4.2 (6.8)
	H	−	90.4 (9.6)	0.4 (1.5)	2.9 (4.5)	0.0 (0.0)	6.3 (6.5)
		+	95.4 (6.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.6 (6.5)

seawater temperatures were warmest (i.e., early August through late September; Table 4); however, losses were recorded for each sampling period. For example, mean percent loss between April and June was nearly 8%, primarily due to mortality by moon snails in the upper intertidal blocks and clams missing primarily from open enclosures at all tidal levels (Table 2). Mean survival $\pm$ 95% CI (pooled across all treatments) during this period was $92.2 \pm 4.48\%$ ($n = 180$). An additional mean loss of 5.6% occurred between June and August when $86.5 \pm 5.0\%$ were recovered alive (Table 3). Again, the proportion of clams missing from open enclosures (especially at the low intertidal) was relatively high ($9.7 \pm 3.5\%$). Clam losses were greatest between 6 August and 26 September (13.6%; Table 4) so that by the third sampling date, mean percent alive was $72.9 \pm 8.48\%$ ($n = 180$). The losses observed during this interval coincide with a concomitant increase in the incidence of crushed or chipped clams from mid and low enclosures (Table 4) suggesting that crabs may have been more active during this period. Table 7 provides additional evidence that *C. maenas* was more likely to be found in experimental units after the August sampling. In addition, there is a suggestion that mean survival actually increased between September and December as mean survival was $80.0 \pm 7.23\%$ ($n = 180$), but this difference ($+7.1\%$) was not significantly different from zero (contrast (3), Table 6, $P = 0.067$). This implies that after September, losses of relatively large juvenile clams ($\bar{x}_{SL} \pm 95\%$ CI $= 23.5 \pm 1.3$ mm [see below]) due to predation or other factors were unimportant. Although there were no two-, three-, or four-way interactions involving sampling date and the other three main factors (Table 6),

Table 3

Fate of juvenile soft-shell clams from 6–9 April to 6 August 1996 (119–122 days) at Flake Point Bar, Jonesport, ME

Column headings and row descriptors are the same as described in Table 2.

Tide	Density	Netting	% A	% DU	% DD	% DC	% M
High	L	−	93.3 (18.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	6.7 (18.5)
		+	98.3 (6.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.7 (6.0)
	M	−	88.3 (26.3)	0.8 (3.0)	4.2 (15.1)	0.0 (0.0)	6.7 (9.9)
		+	93.3 (11.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	6.7 (11.7)
	H	−	80.8 (20.9)	0.0 (0.0)	4.6 (16.6)	0.0 (0.0)	14.5 (13.7)
		+	89.2 (18.0)	0.0 (0.0)	0.4 (1.5)	0.0 (0.0)	10.4 (16.6)
Mid	L	−	91.7 (16.2)	0.0 (0.0)	1.7 (6.0)	0.0 (0.0)	6.7 (13.4)
		+	86.7 (19.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	13.3 (19.7)
	M	−	88.3 (16.3)	0.8 (3.0)	1.7 (6.0)	0.0 (0.0)	9.2 (15.9)
		+	95.0 (8.0)	1.7 (4.0)	0.0 (0.0)	0.0 (0.0)	3.3 (6.7)
	H	−	82.9 (23.7)	2.5 (7.5)	0.0 (0.0)	0.0 (0.0)	14.6 (16.9)
		+	97.1 (5.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.9 (5.9)
Low	L	−	61.7 (36.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	38.3 (36.1)
		+	98.3 (6.0)	1.7 (6.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	M	−	63.3 (32.5)	0.8 (3.0)	9.2 (22.3)	1.7 (6.0)	25.0 (33.9)
		+	95.0 (9.2)	0.0 (0.0)	0.8 (3.1)	0.0 (0.0)	4.2 (6.8)
	H	−	90.4 (9.6)	0.4 (1.5)	2.9 (4.5)	0.0 (0.0)	6.3 (6.5)
		+	95.4 (6.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.6 (6.5)

Table 4
Fate of juvenile soft-shell clams from 6–9 April to 26 September 1996 (170–173 days) at Flake Point Bar, Jonesport, ME
Column headings and row descriptors are the same as described in Table 2.

Tide	Density	Netting	% A	% DU	% DD	% DC	% M
High	L	−	73.3 (38.4)	1.7 (6.0)	10.0 (24.2)	0.0 (0.0)	15.0 (21.0)
		+	75.0 (39.5)	0.0 (0.0)	3.3 (12.1)	1.7 (6.0)	20.0 (30.9)
	M	−	64.2 (40.3)	0.8 (3.0)	11.7 (26.7)	0.0 (0.0)	23.3 (23.3)
		+	83.3 (22.5)	0.8 (3.0)	6.7 (21.0)	0.0 (0.0)	9.2 (11.4)
	H	−	66.7 (39.1)	0.0 (0.0)	12.1 (29.6)	0.0 (0.0)	21.2 (19.0)
		+	72.5 (31.9)	1.7 (6.0)	7.5 (20.9)	1.7 (6.0)	16.7 (19.8)
Mid	L	−	75.0 (42.5)	5.0 (12.9)	0.0 (0.0)	1.7 (6.0)	18.3 (40.7)
		+	93.3 (16.1)	3.3 (12.1)	0.0 (0.0)	3.3 (12.1)	0.0 (0.0)
	M	−	85.8 (21.1)	5.0 (10.3)	0.0 (0.0)	2.5 (9.0)	6.7 (11.7)
		+	77.5 (35.8)	0.8 (3.0)	7.5 (27.2)	9.2 (19.3)	5.0 (10.3)
	H	−	76.3 (25.1)	0.0 (0.0)	1.3 (3.2)	2.1 (7.6)	20.3 (23.4)
		+	56.7 (35.9)	7.1 (20.9)	0.0 (0.0)	20.0 (26.7)	16.3 (12.6)
Low	L	−	50.0 (32.5)	0.0 (0.0)	5.0 (12.9)	10.0 (13.4)	35.0 (29.1)
		+	91.6 (18.6)	5.0 (12.9)	1.7 (6.0)	0.0 (0.0)	1.7 (6.0)
	M	−	49.2 (18.3)	0.0 (0.0)	6.7 (12.6)	10.8 (13.5)	33.3 (12.7)
		+	91.7 (11.9)	0.8 (3.0)	0.0 (0.0)	0.0 (0.0)	7.5 (12.3)
	H	−	43.3 (18.9)	0.4 (1.5)	4.6 (7.9)	4.5 (6.9)	47.2 (17.4)
		+	87.9 (15.9)	0.4 (1.5)	0.0 (0.0)	1.7 (3.3)	10.0 (14.5)

the absolute difference in mean percent survival between September and December arose primarily due to differences between blocks at the high tide level (compare percent alive in the high blocks from Tables 4 and 5; see below).

We detected statistically significant density-dependent survival in this experiment (Table 6, contrast (7)), but only when comparing rates between the two highest density treatments. Overall mean survival of clams initially stocked at 1320 m^{-2} (80.1 ± 5.01%; $n = 240$) was significantly ($P = 0.0004$) lower than those stocked at 660 m^{-2} (84.7 ± 4.69%; $n = 240$). Mean survival of clams stocked at 330 m^{-2} and pooled over all treatments was intermediate between the two other stocking densities (82.3 ± 5.64%; $n = 240$).

Effects of tidal height and predator exclusion on mean percent survival were both significant ($P < 0.05$). However, excluding predators did little to enhance clam survival except at the lowest tidal height (interaction contrast (9); $P < 0.0001$; Table 6; Fig. 1) where difference in mean survival between protected and unprotected units was nearly 30% (Low$_{protected}$ = 91.1 ± 4.53% vs. Low$_{unprotected}$ = 63.3 ± 9.67%; $n = 120$). This differential mortality effect along the tidal gradient implies that predators are more important in controlling the distribution and abundance of soft-shell clam juveniles at lower tidal levels.

The field design permitted statistically powerful tests of spatial variation among blocks within each tidal height on each sampling date (Table 6; Fig. 2). To examine more closely the variation due to Block (Date × Tide), we partitioned the 48 *df* into 12

Table 5
Fate of juvenile soft-shell clams from 6–9 April to 10–13 December 1996 (245–248 days) at Flake Point Bar, Jonesport, ME
Column headings and row descriptors are the same as described in Table 2.

Tide	Density	Netting	% A	% DU	% DD	% DC	% M
High	L	−	81.7 (30.5)	0.0 (0.0)	1.7 (6.0)	0.0 (0.0)	16.7 (27.0)
		+	88.3 (29.9)	0.0 (0.0)	0.0 (0.0)	8.3 (30.2)	3.3 (8.1)
	M	−	94.2 (10.1)	1.7 (4.0)	2.5 (9.1)	0.0 (0.0)	1.7 (4.0)
		+	98.3 (4.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.7 (4.0)
	H	−	80.8 (11.3)	2.5 (6.4)	2.1 (6.1)	0.0 (0.0)	14.6 (11.5)
		+	96.3 (6.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	3.8 (6.1)
Mid	L	−	86.7 (19.7)	5.0 (9.2)	0.0 (0.0)	0.0 (0.0)	8.3 (13.5)
		+	71.7 (45.9)	8.3 (24.2)	1.7 (6.0)	10.0 (30.1)	8.3 (16.2)
	M	−	80.0 (22.6)	0.0 (0.0)	0.8 (3.0)	0.0 (0.0)	19.2 (22.5)
		+	80.8 (31.2)	0.0 (0.0)	0.0 (0.0)	3.3 (8.1)	15.8 (26.4)
	H	−	68.8 (35.3)	0.4 (0.4)	14.2 (37.1)	0.4 (1.5)	16.3 (15.7)
		+	90.4 (12.1)	0.0 (0.0)	0.0 (0.0)	0.8 (3.0)	8.8 (11.8)
Low	L	−	61.7 (34.9)	1.7 (6.0)	3.3 (8.1)	6.7 (24.1)	26.6 (25.8)
		+	90.0 (16.1)	1.7 (6.0)	0.0 (0.0)	3.3 (8.1)	5.0 (12.9)
	M	−	50.8 (26.4)	1.7 (4.0)	0.8 (3.0)	4.2 (12.1)	42.5 (26.0)
		+	90.8 (12.3)	0.8 (3.0)	0.8 (3.0)	1.7 (4.0)	5.8 (11.1)
	H	−	49.6 (9.4)	1.7 (6.0)	2.9 (5.9)	10.8 (14.6)	35.0 (20.8)
		+	79.6 (26.6)	1.7 (3.3)	0.0 (0.0)	11.3 (25.2)	7.5 (8.4)

orthogonal components and discovered that three of these explained 73% of the overall source of variation of this random effect. Two of three significant block effects were observed in June and September at the high tide location (Fig. 2). In both cases, atypically high predation by *Euspira* spp. was responsible (June, block 4 = 20.8% and September, block 3 = 42.3% mortality due to moon snails). Interestingly, although blocks were chosen randomly on each sampling date, these particular blocks were adjacent indicating that a high population density of moon snails resided in this vicinity or that relatively high numbers of naticids moved through these two blocks and preyed on clams. Further, examination of final mean SL ($\pm 95\%$ CI) of the drilled individuals suggested that predation events in each block occurred relatively close together in time (June SL: 12.9 ± 0.77 mm, $n = 35$; September SL: 13.7 ± 0.66 mm; $n = 71$). One other significant effect due to blocking occurred on the final sampling date at the low tide location (Table 6; Fig. 2). Unlike the other two significant block effects, the one at the low tide level presumably occurred because survival in one block was dramatically higher ($85.7 \pm 20.23\%$, $n = 12$) than in the other four blocks ($66.6 \pm 17.34\%$, $n = 48$).

Overall effects of excluding predators on mean clam survival also varied significantly from block-to-block within the combination of date and tidal height (i.e., Block $\times$ Netting [Date $\times$ Tide]), but, again, three orthogonal components explained most (ca. 60%) of the overall source of variation (Table 6). For example, the effect of netting in reducing clam mortality was most pronounced in September at the high tide location in the third block (Fig. 3). Here, as noted above, mortality due to moon snails was relatively high, but the

Table 6
ANOVA on the arc sine-transformed percent survival data
Main and interaction orthogonal contrasts (numbered sequentially) appear below main and interactive effects. Adjusted α values were used for all orthogonal contrasts ($\alpha' = 0.0253$ when number of contrasts = 2; $\alpha' = 0.0170$ when number of contrasts = 3). Partitioned sources of variation (lettered sequentially) that were significant appear below Block effects. ($n = 2$).

Source of variation/hypothesis test	df	Sum of squares	Mean square	F	Pr > F
DATE	3	22,567.94	7522.64	9.11	0.0001
(1) JUNE vs. REST	1	10,644.70	10,644.70	12.89	0.0008
(2) AUG vs. SEPT and DEC	1	9023.33	9023.33	10.92	0.0018
(3) SEPT vs. DEC	1	2899.90	2899.90	3.51	0.0671
TIDE	2	7066.04	3533.02	4.28	0.0195
(4) HIGH vs. MID and LOW	1	2427.95	2427.95	2.94	0.0929
(5) MID vs. LOW	1	4638.08	4638.08	5.62	0.0219
NETTING—NET vs. NO NET	1	20,348.87	20,348.87	45.94	0.0001
DENSITY	2	4580.93	2290.46	8.30	0.0005
(6) 330 m^{-2} vs. 660 and 1320 m^{-2}	1	799.61	799.61	2.90	0.0919
(7) 660 vs. 1320 m^{-2}	1	3781.31	3781.31	13.71	0.0004
DATE×TIDE	6	6852.65	1142.10	1.38	0.2408
DATE×NETTING	3	2151.77	717.25	1.62	0.1972
DATE×DENSITY	6	2769.68	461.61	1.67	0.1358
TIDE×NETTING	2	14,617.49	7308.74	16.50	0.0001
(8) NET vs. No NET×HI vs. MID and LOW	1	989.89	989.89	2.23	0.1415
(9) NET vs. No NET×MID vs. LOW	1	13,627.59	13,627.59	30.76	0.0001
TIDE×DENSITY	4	202.04	50.51	0.18	0.9467
NETTING×DENSITY	2	193.68	96.84	0.29	0.7459
DATE×TIDE×NETTING	6	4034.73	672.45	1.52	0.1925
DATE×TIDE×DENSITY	12	3077.46	256.45	0.93	0.5210
DATE×NETTING×DENSITY	6	2371.57	395.26	1.20	0.3129
TIDE×NETTING×DENSITY	4	1172.97	293.24	0.89	0.4728
DATE×TIDE×NETTING×DENSITY	12	4882.81	406.90	1.24	0.2705
BLOCK (DATE×TIDE)	48	39,648.36	826.00	3.00	0.0001
(a) Block (June, High)	4	13,452.84	3363.21	12.22	0.0001
(b) Block (Sept, High)	4	12,500.14	3125.03	11.35	0.0001
(c) Block (Dec, Low)	4	2931.84	732.96	2.66	0.0001
NETTING×BLOCK (DATE×TIDE)	48	21,262.63	442.97	1.61	0.0088
(d) Netting×Block (Sept, High)	4	5151.35	1287.83	4.68	0.0011
(e) Netting×Block (Sept, Low)	4	2892.19	723.05	2.63	0.0344
(f) Netting×Block (Dec, Mid)	4	4907.54	1226.88	4.46	0.0016

Table 6 (*continued*)

Source of variation/hypothesis test	df	Sum of squares	Mean square	F	Pr > F
DENSITY × BLOCK (DATE × TIDE)	96	26,480.93	275.84	1.00	0.4830
NET × DENS × BLOCK (DATE × TIDE)	96	31,613.19	329.30	1.20	0.1250
ERROR	360	99,120.26	275.33		
TOTAL	719	315,016.08			

presence of netting enhanced survival by nearly 50% in this block whereas the average difference in survival between protected and unprotected clams in the other four blocks on that sampling date and tide level was 0.7%. (A similar relationship may have existed in the fourth block at the high tide level in June (Fig. 3); however, the amount of variability associated with both means was too great to be statistically significant.) Spatial differences occurred in September among blocks at the low intertidal as well. In each block, mean survival in the open enclosures was lower than in protected containers; however, this difference varied from a high of nearly a 70% enhancement rate in block 5 (where mortality was high in open enclosures mainly due to moon snails and green crabs (Table 4)) to a low of only 25% in block 3 (Fig. 3). In December at the mid intertidal location, the effect of excluding predators also varied from block-to-block, but it was not
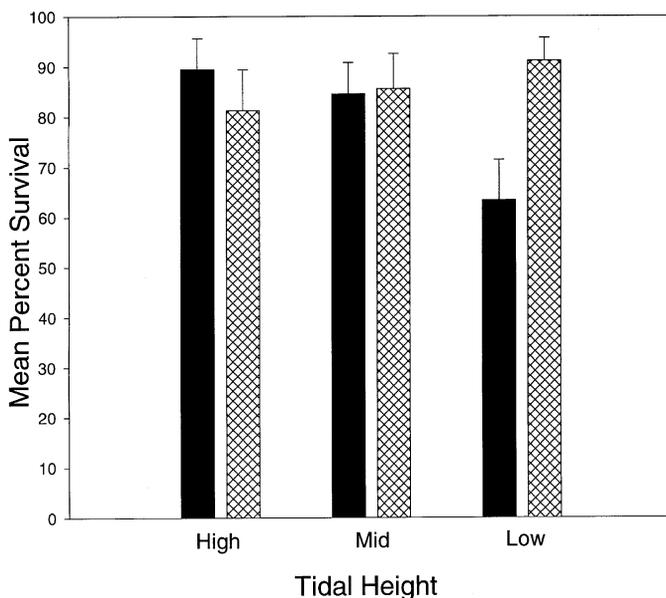
Fig. 1. Interactive effects of tidal height and predator exclusion on mean percent survival ($\pm$95% CI) of juveniles of *M. arenaria* at FPB. Bars (black = open enclosures; meshed = enclosures protected with flexible netting [6.4-mm aperture]) represent means pooled across sampling dates, blocks, and intraspecific density treatments. $n = 120$. See Table 6 (contrast (9)) for tests of significance.
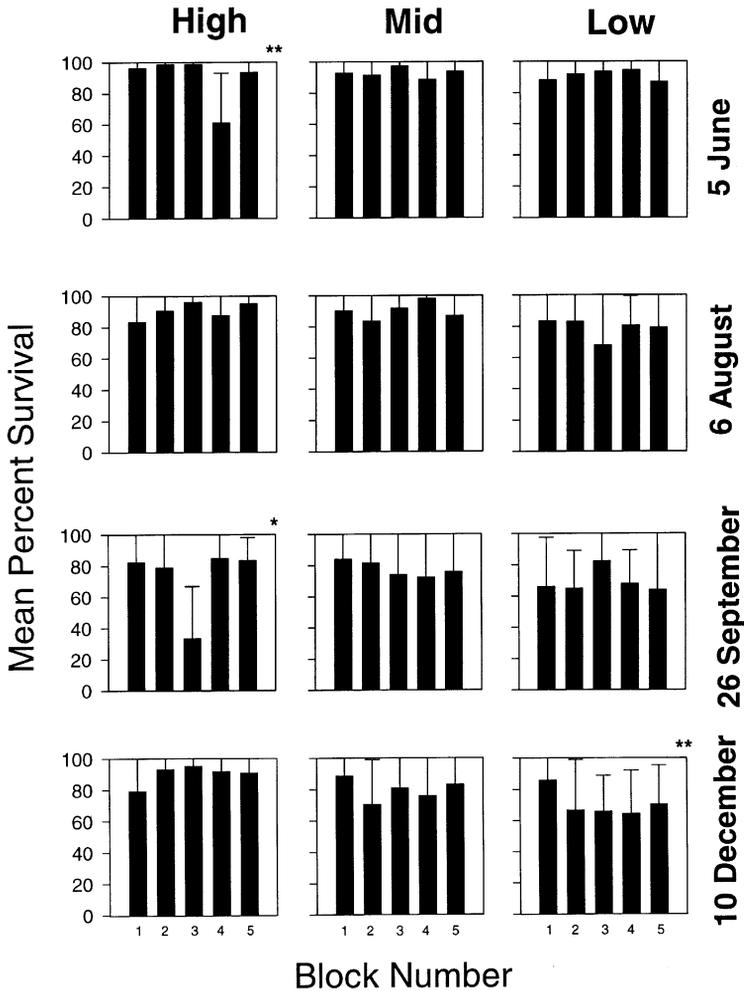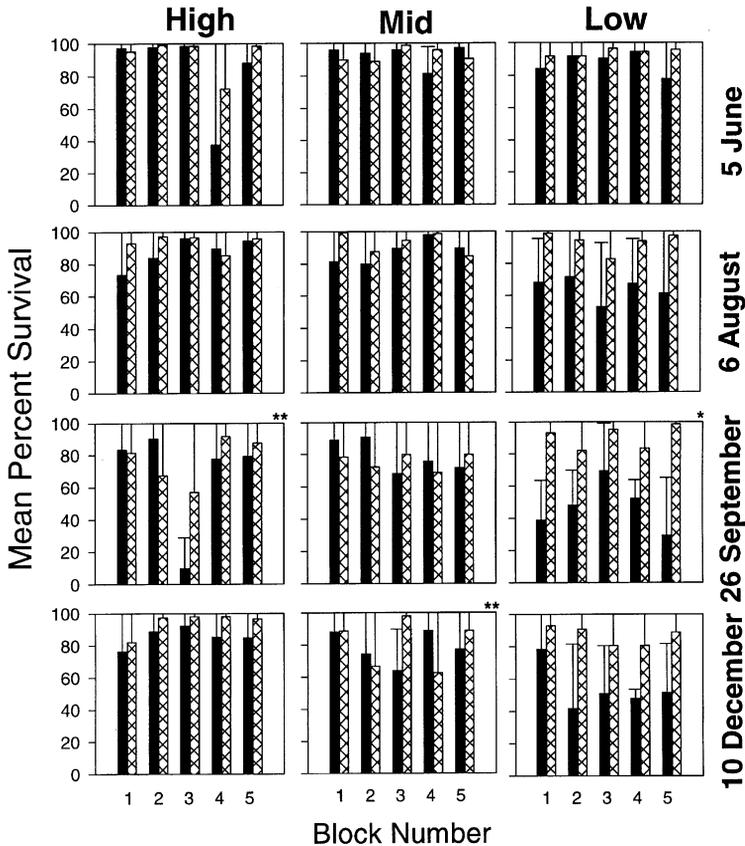
Fig. 2. Spatial effects of blocking on mean percent survival ($\pm 95\%$ CI) of juveniles of *M. arenaria* at FPB through time. Bars represent means pooled across intraspecific density and predator exclusion treatments. $n = 12$. $^{*} = P < 0.05$; $^{**} = P < 0.01$. See Table 6 for tests of significance concerning the Block (Date $\times$ Tide) source of variation.

consistent. For example, mean difference in percent survival between protected and unprotected experimental units in blocks 1, 2, and 5 was only 6%, whereas enhancement due to the presence of netting was 34% in the third block. Finally, survival was approximately 25% higher in open enclosures than protected units in the fourth block, which likely was due to green crabs as individuals of *C. maenas* were found within half of the six protected plots (Table 7).

The size of green crabs found within experimental units (Table 7) did not increase significantly through time ($F_{2,24} = 2.75$, $P = 0.0838$), but there was a significant increasing linear relationship between crab size and percentage of clams found dead

Fig. 3. Spatial effects of predator exclusion and blocking on mean percent survival ($\pm 95\%$ CI) of juveniles of *M. arenaria* at FPB through time. Bars represent means pooled across intraspecific density treatments. $n = 6$. $^{*} = P < 0.05$; $^{**} = P < 0.01$. See Table 6 for tests of significance concerning the Netting $\times$ Block (Date $\times$ Tide) source of variation.

within the same experimental unit ($r^2 = 0.298$; $n = 27$; $P = 0.0032$). None of the 29 green crabs sampled during the experiment was found in open enclosures (Table 7). It is unclear how most of these animals became entrapped in the protected units. We tested whether frequency of green crab occurrence depended on intraspecific clam density and found that it did not ($\chi_2^2 = 1.72$, $P = 0.4233$). These animals could have been in the sediments that were placed in the experimental units during 6–9 April, but, if this hypothesis were true, we would have expected to sample similar numbers of crabs within units on each date and this was not the case ($\chi_3^2 = 26.31$, $P < 0.0001$). Another possible hypothesis is that small crabs (< 6 mm CW) were present on the flat before August and that some entered protected units through the mesh aperture becoming trapped once they molted to a larger size. Berrill (1982) showed that green crabs grow from 5.5 mm CW in June to 13–25 mm CW by the winter on tidal flats in central Maine. If crabs grew similarly at FPB, this hypothesis might apply to some of the green

Table 7
Live predators discovered within experimental units and the percent mortality of cultured clams due to type of predator in those units on each sampling date

Netting (+: present; −: absent). Density (L, M, and H = 330, 660, and 1320 m^{-2}, respectively). Size of *Euspira* spp. represents distance (mm) from spire to apex. Size of *Carcinus* represents greatest carapace width (mm). (See Table 2 for actual sampling dates).

Date	Tidal height	Netting	Density	Species	Size	Sex	% Clams dead/unit
June	High	+	L	*C. maenas*	8.9	♂	33.3
	High	+	L	*E. heros*	11.1	−	66.7
	High	−	H	*E. heros*	11.5	−	62.5
	Low	−	H	*E. heros*	13.1	−	4.2
	Low	−	H	*E. heros*	14.7	−	4.2
August	High	+	H	*E. heros*	17.4	−	45.8
	High	−	H	*E. triseriata*	7.5	−	0.0
	Mid	−	L	*E. heros*	8.3	−	0.0
September	High	+	L	*C. maenas*	−	♂	16.7
	High	+	H	*C. maenas*	−	♂	16.7
	High	+	H	*E. triseriata*	10.6	−	12.5
	Mid	+	L	*C. maenas*	29.6	♂	16.7
	Mid	+	M	*C. maenas*	19.6	♂	25.0
	Mid	+	H	*C. maenas*	19.6	♂	12.5
	Mid	+	H	*C. maenas*	27.6	♂	33.3
	Mid	+	H	*C. maenas*	29.7	♂	37.5
	Mid	+	H	*C. maenas*	30.4	♂	58.3
	Low	+	L	*C. maenas*	23.9	♂	0.0
	Low	+	L	*C. maenas*	25.4	♂	33.3
	Low	+	M	*C. maenas*	16.1	♀	0.0
	Low	+	M	*C. maenas*	18.7	♂	8.3
	Low	+	H	*C. maenas*	21.0	♂	4.2
	Low	+	H	*C. maenas*	19.6	♂	12.5
	Low	+	H	*C. maenas*	20.7	♂	0.0
	Low	+	H	*C. maenas*	23.8	♂	4.2
December	High	+	L	*C. maenas*	30.4	♂	83.3
	High	+	M	*E. triseriata*	9.7	−	0.0
	Mid	−	L	*E. heros*	13.9	−	0.0
	Mid	+	M	*C. maenas*	20.0	♂	0.0
	Mid	+	M	*C. maenas*	17.4	♂	16.7
	Mid	−	M	*E. triseriata*	8.4	−	0.0
	Mid	+	M	*C. maenas*	36.9	♂	58.3
	Mid	+	H	*C. maenas*	19.3	♂	8.3
	Mid	−	H	*E. heros*	15.8	−	37.5
	Low	+	L	*C. maenas*	25.8	♀	16.7
	Low	+	L	*C. maenas*	13.7	♂	16.7
	Low	+	M	*C. maenas*	22.7	♀	8.3
	Low	+	M	*C. maenas*	10.2	♂	8.3
	Low	+	H	*C. maenas*	21.7	♀	12.5
	Low	+	H	*C. maenas*	21.4	♂	0.0
	Low	+	H	*C. maenas*	25.4	♂	70.8
	Low	−	H	*E. heros*	12.3	−	12.5

crabs found in experimental units in December, but it is doubtful that animals could have attained sizes between 16.1 and 30.4 mm CW (Table 7) from 6 August to 26 September.

3.3. Growth

Mean SL varied seasonally with tidal height, predator exclusion, and intraspecific clam density (Table 8). Variation in growth was most apparent across the tidal gradient (Fig. 4). For example, clams added 8.4% of their total SL between 6–9 April and 5 June at the high tide site, whereas this rate was 14.5% and 15.8% for clams at the mid and low tides, respectively. Most shell growth occurred between early June and 6 August, but rates depended, again, on tidal height (high, mid, and low tide blocks = 55%, 42.2%, and 45.2%, respectively). Between 6 August and 26 September 32–37% of total growth occurred across all tidal heights. Clams in high tide blocks stopped adding shell after late September, but animals continued to grow very slowly and at the same rate at the two lower tidal heights (Fig. 5a; Table 8).

Four of the six orthogonal contrasts associated with the Date × Tide interaction (Table 8) were significant ($P < 0.0001$). Generally, these contrasts showed that seasonal influences on growth were more dramatic at the lower tidal elevations. For example, contrast (8) (Table 8) examines the relationship between mean SL in June vs. the mean for the remaining three sampling dates and how this varied from the high tide blocks to the pooled mean of the mid and low blocks. A 43% increase in mean SL was observed at the high intertidal site (June = 13.1 ± 0.45 mm, $n = 60$ vs. August–December = 18.7 ± 1.07 mm, $n = 180$), whereas a 65% increase was observed in the mid and low blocks (June = 14.5 ± 0.31 mm, $n = 60$ vs. August–December = 23.9 ± 0.76 mm; $n = 180$). A similar disproportionate increase occurred when mean SL was compared between mid and low tide blocks over the same dates (Table 8; contrast (9)). Mean SL increased by 55% in mid tide blocks, when size in June (14.1 ± 0.40 mm; $n = 60$) was compared to average size from August to December (21.9 ± 0.81 mm; $n = 180$). However, a 75% increase was observed when the same comparison was made for clams in low tide blocks (June = 14.9 ± 0.38 mm, $n = 60$ vs. August–December = 25.8 ± 1.01 mm, $n = 180$). Both contrasts demonstrate that shell growth from early April to early June is relatively slow at all tidal heights, especially the high tide level, and that rates of shell accretion after June increase at faster rates lower on the shore. Contrast (10) (Table 8) provides further evidence for differential rates of shell accretion from August through December between the upper and lower shore.

Clams added shell at similar rates at the mid and low tide levels from late September to early December (Table 8, contrast (13); Fig. 5a), but, in both cases, this amounted to an average increase of only 1.2 mm (ca. 9.0% of total seasonal growth). Fig. 5a suggests that mean SL decreased from September to December at the upper intertidal site and this is likely why contrast (12) (Table 8) was highly significant. The reason for this apparent anomaly relates to high variability in time of tidal submergence between blocks within the upper intertidal site (Table 1) and the pattern of sampling high tide blocks through time. On the final sampling date, four of the remaining five blocks at the high tide location happened to be among those exposed, on average, for the longest periods during each tidal cycle. This difference in exposure times apparently led to a significant

Table 8
ANOVA on the mean shell length data
Main and interaction orthogonal contrasts (numbered sequentially) appear below main and interactive effects. Adjusted α values were used for all orthogonal contrasts ($\alpha' = 0.0253$ when number of contrasts = 2; $\alpha' = 0.0170$ when number of contrasts = 3; $\alpha' = 0.0127$ when number of contrasts = 4; $\alpha' = 0.0085$ when number of contrasts = 6). Partitioned sources of variation (lettered sequentially) that were significant ($P < 0.05$) appear below block effects. ($n = 2$).

Source of variation/hypothesis test	df	Sum of squares	Mean square	F	Pr > F
DATE	3	10,738.79	3579.59	348.53	0.0001
(1) JUNE vs. REST	1	8908.21	8908.21	867.35	0.0001
(2) AUG vs. SEPT and DEC	1	1830.28	1830.28	178.21	0.0001
(3) SEPT vs. DEC	1	0.30	0.30	0.03	0.8677
TIDE	2	3982.13	1991.06	193.86	0.0001
(4) HIGH vs. MID and LOW	1	2842.27	2842.27	276.74	0.0001
(5) MID vs. LOW	1	1139.86	1139.86	110.98	0.0001
NETTING—NET vs. NO NET	1	16.36	16.36	3.44	0.0696
DENSITY	2	18.80	9.40	2.48	0.0890
(6) 330 m^{-2} vs. 660 and 1320 m^{-2}	1	10.20	10.20	2.69	0.1041
(7) 660 vs. 1320 m^{-2}	1	8.60	8.60	2.27	0.1352
DATE×TIDE	6	1241.43	206.90	20.15	0.0001
(8) JUNE vs. REST×HIGH vs. MID and LOW	1	424.52	424.52	41.33	0.0001
(9) JUNE vs. REST×MID vs. LOW	1	204.99	204.99	19.96	0.0001
(10) AUG vs. SEPT and DEC×HIGH vs. MID and LOW	1	330.24	330.24	29.23	0.0001
(11) AUG vs. SEPT and DEC vs. MID vs. LOW	1	30.94	30.94	3.01	0.0890
(12) SEPT vs. DEC×HIGH vs. MID and LOW	1	279.40	279.40	27.20	0.0001
(13) SEPT vs. DEC×MID vs. LOW	1	1.34	1.34	0.13	0.7223
DATE×NETTING	3	43.75	14.58	3.07	0.0365
(14) JUNE vs. REST×NET vs. NO NET	1	3.51	3.51	0.74	0.3941
(15) AUG vs. SEPT and DEC×NET vs. NO NET	1	0.74	0.74	0.16	0.6946
(16) SEPT vs. DEC×NET vs. NO NET	1	39.50	39.50	8.32	0.0059
DATE×DENSITY	6	56.71	9.45	2.49	0.0276
(17) JUNE vs. REST×330 m^{-2} vs. 660 and 1320 m^{-2}	1	2.55	2.55	0.67	0.4139
(18) JUNE vs. REST×660 and 1320 m^{-2}	1	0.46	0.46	0.12	0.7276
(19) AUG vs. SEPT and DEC×330 m^{-2} vs. 660 and 1320 m^{-2}	1	31.18	31.18	8.23	0.0051
(20) AUG vs. SEPT and DEC×660 vs. 1320 m^{-2}	1	2.53	2.53	0.67	0.4151
(21) SEPT vs. DEC×330 m^{-2} vs. 660 and 1320 m^{-2}	1	16.55	16.55	4.37	0.0393
(22) SEPT vs. DEC×660 vs. 1320 m^{-2}	1	3.42	3.42	0.90	0.3444

Table 8 (*continued*)

Source of variation/hypothesis test	df	Sum of squares	Mean square	F	Pr > F
TIDE × NETTING	2	16.54	8.27	1.74	0.1861
TIDE × DENSITY	4	52.29	13.07	3.45	0.0112
(23) HIGH vs. MID and LOW × 330 m^{-2} vs. 660 and 1320 m^{-2}	1	38.68	38.68	10.21	0.0019
(24) HIGH vs. MID and LOW × 660 and 1320 m^{-2}	1	4.91	4.91	1.30	0.2577
(25) MID vs. LOW × 330 m^{-2} vs. 660 and 1320 m^{-2}	1	5.53	5.53	1.46	0.2298
(26) MID vs. LOW × 660 and 1320 m^{-2}	1	3.17	3.17	0.84	0.3636
NETTING × DENSITY	2	6.03	3.01	0.66	0.5202
DATE × TIDE × NETTING	6	58.14	9.69	2.04	0.0783
DATE × TIDE × DENSITY	12	25.37	2.11	0.56	0.8703
DATE × NETTING × DENSITY	6	22.49	3.74	0.82	0.5590
TIDE × NETTING × DENSITY	4	12.73	3.18	0.69	0.5979
DATE × TIDE × NETTING × DENSITY	12	81.13	6.76	1.47	0.1473
BLOCK (DATE × TIDE)	48	492.99	10.27	2.33	0.0001
(a) Block (Aug, High)	4	51.97	12.99	2.95	0.0235
(b) Block (Sept, High)	4	226.16	56.54	12.82	0.0001
(c) Block (Sept, Mid)	4	53.24	13.31	3.02	0.0181
(d) Block (Dec, High)	4	67.75	16.94	3.84	0.0045
NETTING × BLOCK (DATE × TIDE)	48	227.96	4.74	1.08	0.3441
DENSITY × BLOCK (DATE × TIDE)	96	363.82	3.79	0.86	0.8116
NETTING × DENSITY × BLOCK (DATE × TIDE)	96	440.25	4.58	1.04	0.3913
ERROR	360	1586.83	4.41		
TOTAL	719	19,484.61			

($P = 0.0045$) block effect (i.e., spatial variability within a tidal height–partitioned source of variation d, Table 8) as clams at the high tide level in December in four of the blocks grew 15% more slowly than those in the other (17.6 ± 0.35 mm, $n = 48$ vs. 20.2 ± 0.74 mm, $n = 12$). Three additional significant sources of spatial variability (i.e., Block [Date × Tide]) involving mean SL length occurred in this study (Table 8). Two of these occurred at the high intertidal site in August and September for similar reasons. The significant block effect detected at the mid tide site during September, where clams in one block were, on average, 8.8% smaller than those in the other blocks (21.3 ± 3.79 mm, $n = 12$ vs. 23.2 ± 0.85 mm, $n = 48$), may be related to a disproportionate amount
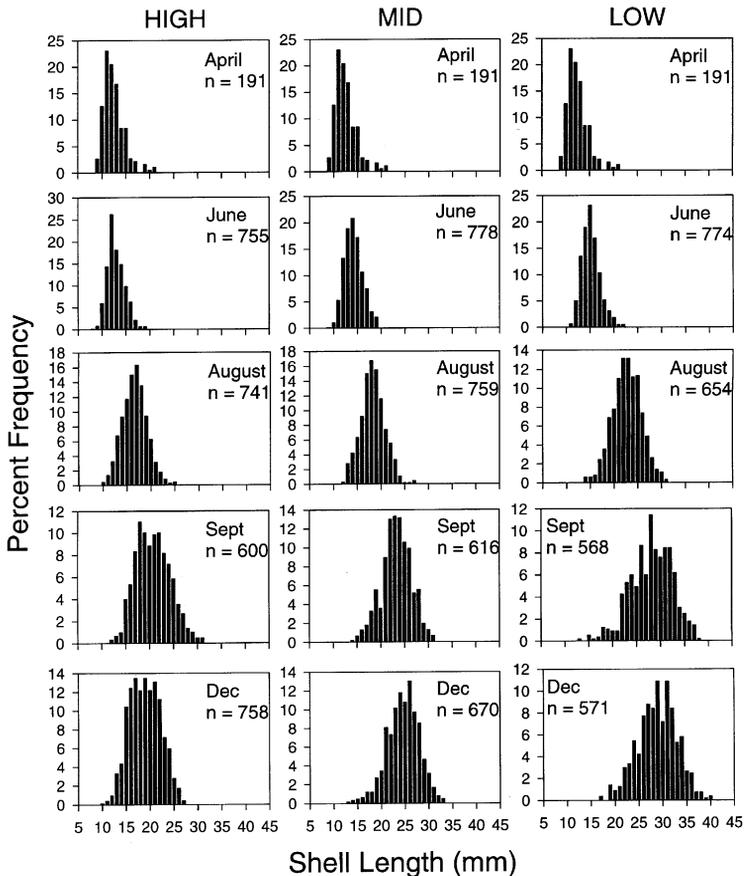
Fig. 4. Size–frequency distributions for live *M. arenaria* from all experimental units on each sampling date (June–December) along the tidal gradient (see Table 2 for exact dates). Initial size distribution was recorded on 5 April 1996.

of mortality observed in protected units of the two highest stocking densities (Table 4). That is, predator activity may have caused a reduction in feeding times for those animals that escaped predation (see Discussion).

The effect of excluding predators on mean SL varied seasonally ($P = 0.0365$, Table 8), but this probably was not biologically important (Fig. 5b). Through the August sampling, mean SL of clams within protected and unprotected experimental units was virtually identical. The significant Date × Netting interaction occurred because the relationship between protected and unprotected treatments and clam size changed from September to December (Table 8, contrast (16)). For example, in September, animals in protected experimental units (pooled across all tidal heights and stocking densities) were 5% larger than clams in open enclosures (i.e., 24.1 ± 2.19 vs. 22.9 ± 2.19 mm; $n = 90$). However, by December, mean SL of clams in both treatments was equal (protected = 23.5 ± 1.02 mm vs. open enclosures = 23.9 ± 1.03 mm; $n = 90$).
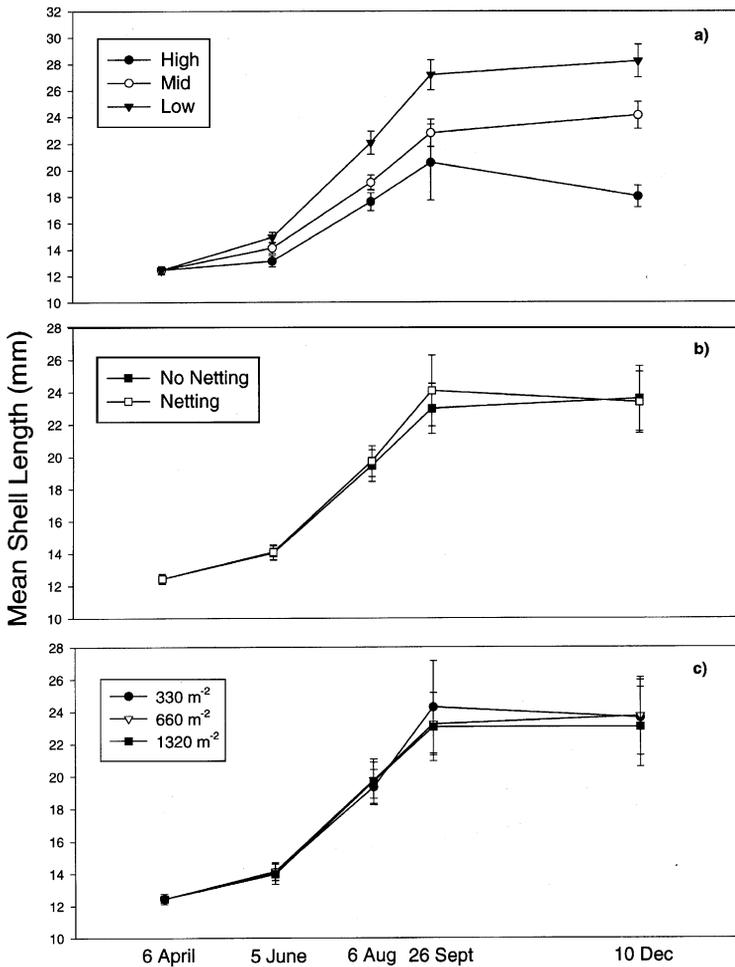
Fig. 5. (a) Effects of tidal height on mean SL ($\pm$ 95% CI) through time for juveniles of *M. arenaria* at FPB. See Table 8 (contrasts (8)–(13)) for tests of significance. Each point represents mean SL pooled across blocks, intraspecific density and predator exclusion treatments. $n = 191$ individuals for 6 April and $n = 60$ experimental units for June–December. (b) Effects of predator exclusion on mean SL ($\pm$95% CI) through time for juveniles of *M. arenaria* at FPB. See Table 8 (contrasts #14–16) for tests of significance. Each point represents mean SL pooled across blocks, tidal heights, and intraspecific density treatments. $n = 191$ individuals for 6 April and $n = 90$ experimental units for June–December. (c) Effects of intraspecific density on mean SL ($\pm$95% CI) through time for juveniles of *M. arenaria* at FPB. See Table 8 (contrasts #17–22) for tests of significance. Each point represents mean SL pooled across blocks, tidal heights, and predator exclusion treatments. $n = 191$ individuals for 6 April and $n = 60$ experimental units for June–December.

The effect of increasing intraspecific clam density on mean SL also varied through time ($P = 0.0276$, Table 8; Fig. 5c); however, only one of the six contrasts associated with Date × Density (contrast (19)) was significant. Mean SL of clams stocked at the lowest density on 6 August was 6.2% smaller than the mean of the two highest densities on that date (19.3 ± 0.54 mm, $n = 60$ vs. 20.5 ± 1.39 mm, $n = 120$). This relationship

differed from the one that existed from September–December. Mean SL of clams in the lowest density treatment was 10.2% greater than those in the two higher-density treatments (26.6 ± 2.65 mm, $n = 120$ vs. 23.9 ± 0.54 mm, $n = 240$; Fig. 5c).

There was a differential effect of density on mean SL along the tidal gradient; however, the crowding effect occurred only at the upper intertidal site ($P = 0.0112$, Table 8). Mean SL of animals at the lowest density in the upper intertidal site pooled across blocks, sampling date and predator exclusion treatments (17.9 ± 2.39 mm, $n = 80$) was nearly 6% larger than those stocked at the two higher densities (17.0 ± 1.64 mm, $n = 160$).

4. Discussion

4.1. Survival

This study followed the fate of a single cohort of relatively small (12.4 mm SL) clams through time and revealed differential rates and types of mortality from April to December (Tables 2–6). Peak mortality (13.6%) occurred during late summer (i.e., the 51-day period from early August to late September), when seawater temperatures were highest. Clam losses during that interval also coincided with increased numbers of live predators, such as green crabs, appearing in the experimental units (Table 7) and with an increase in percent crushed and chipped clams (compare the %DC column of Table 4 with Tables 2 and 3). Mortality during late summer was similar to cumulative losses during the 119- to 122-day period from 6–9 April to 6 August (13.4%) when most visible evidence of predation was by moon snails, *Euspira* spp. (Tables 2 and 3). Mortality was not significantly different from zero during the fall (i.e., 26 September–10 December; Table 6, contrast (3)) and is similar to results reported in Brousseau (1978) from Massachusetts and Brousseau and Baglivo (1991) for non-diseased soft-shell clams from Long Island Sound.

Decreased risk of clam mortality through the fall may be due to a combination of physical and biotic factors. For example, as seawater temperatures decrease, metabolic activity and predation rates of invertebrates such as moon snails and green crabs decline (Edwards and Huebner, 1977). In addition, clams that have survived the summer months and experienced the window of fastest growth are larger and, typically, burrow deeper than smaller clams do earlier in the spring or summer (Zaklan and Ydenberg, 1997). Zwarts and Wanink (1989) showed that there is a seasonal component to burial depth as *Mya* of a given size burrow deeper during fall and winter compared to spring and summer. Since clam survival increases with increasing burial depth (Virnstein, 1979; Blundon and Kennedy, 1982; Haddon et al., 1987; Zaklan and Ydenberg, 1997), the decreased rates of mortality of clams observed at FPB during the fall also may be due to a spatial refuge with depth.

Clam survival varied along the tidal gradient, but these effects cannot be interpreted without including a simultaneous examination of effects due to predator exclusion (Table 6). Survival was independent of tidal height for animals assigned to protected experimental units (88.7 ± 4.12%, $n = 360$; Fig. 2), but decreased from upper and mid

tidal heights ($82.9 \pm 6.12\%$, $n = 240$) to lower on the shore ($66.3 \pm 9.67\%$, $n = 120$) for animals within open enclosures. This differential effect of tidal position on predation rates suggests that predators were less important in limiting clam numbers near the mid and upper intertidal levels compared with lower on the shore. This conclusion would not be entirely correct. For example, *Euspira* spp. and/or *C. maenas* were found in some experimental units at all tidal heights (Table 7) on each sampling date. Although these predators left evidence (drilled or crushed valves) of their foraging within some experimental units (Tables 2–5), it is likely these and other predators (e.g., *Fundulus* spp., see Kelso, 1979) either excavate and then consume clams away from experimental units or crush their prey in situ leaving shell fragments too small to be detected. These clams would be considered "missing." If "percent missing" data from September and December (Tables 4 and 5) are combined with the other two predator-related columns (i.e., % DD and % DC) for open enclosures, then overall percent mortality due to predators at the high and mid intertidal blocks would be 22.2% and 18.7%, respectively. These rates are less than half the percent mortality observed in the low blocks (48.3%) when similar data are generated.

Although data in Table 5 suggest that crustacean predators were only marginally important in the lower shore blocks, the high rates of missing individuals, especially from open enclosures in low shore blocks, do not permit an unambiguous assessment of the relative role crustaceans play at that tidal height. Further, it is not possible to assign a specific mortality agent since there was no attempt to distinguish, based on the structure or form of shell damage, between *C. maenas* predation and, for example, rock crabs, *Cancer irroratus* Say, or lobsters, *Homarus americanus* Milne Edwards, that also are present in adjacent, subtidal waters (B. Beal, personal observation). Although live *C. maenas* was the only large crustacean predator observed in experimental units at any tidal height (Table 7), it is possible that other crustacean species forage within the intertidal at FPB during periods of high tide. For example, Beal (1994) observed that 22 of 51 crabs caught in modified lobster traps placed near the mid intertidal of a nearby mud flat in Cutler, ME ($44°41'13''$ N; $67°18'35''$ W) from 1 to 21 October 1993 were rock crabs, while the remaining were green crabs.

Predation seems the simplest and most straightforward explanation of observed patterns of wild soft-shell clam distribution at this and other intertidal sites. On flats that are commercially harvested as well as those closed to harvests for more than 25 years due to fecal contamination, relatively few animals occur at or near the low tide mark compared to the upper shore (B. Beal, personal observation). This study indicates that clam losses within open enclosures increase from the high to low shore due to molluscan and crustacean predators such as moon snails and crabs. During the period from April to December 1996, clam loss from unprotected units was ca. 30% higher at the lower shore than the upper shore (45.9% vs. 14.5%). Other field tests with *Mya* have demonstrated that mortality of adults and juveniles increases from high to low shore areas. Zaklan and Ydenberg (1997) found that the density of pits from foraging activities of red rock crabs, *Cancer productus* (Randall), in British Columbia increased with decreasing tidal elevation and so, too, did consumption of *Mya* by *C. productus*. Beal (1994) followed the fate of hatchery-reared individuals of *Mya* near the mid- and low-tide levels of an intertidal mud flat in eastern Maine from August 1989 to April 1990. Mean clam

survival (± 1 S.E.) at mid tide ($50.3 \pm 5.15\%$) was significantly higher than that observed at low tide ($34.4 \pm 5.43\%$).

It is unlikely that the observed pattern of clam abundance from high to low shore is set by recruitment. Beal and Fegley (1996) examined recruitment of soft-shell clams > 1.8 mm at FPB and five other intertidal sites within a 15 km radius of FPB from April to November 1995. Cumulative recruitment rates at FPB at high and low tide levels were low (e.g., < 25 individuals m^{-2}) in both protected and unprotected experimental units (0.002 m^{-2}) and no differences in density of recruits could be attributed to tidal height. Furthermore, at the other five eastern Maine sites, there was no consistent distribution pattern of *Mya* recruits from high to low shore levels. In addition, Fegley et al. (1996) examined short-term recruitment of soft-shell clams (< 1 mm SL) at FPB every 2 weeks from 28 April to 8 November 1995 and found no difference in mean number between upper and lower intertidal regions or between protected and unprotected experimental units. Passive dispersal of post-settled clams from one tidal height to another due to bedload transport potentially could play a role in the distribution of clams on sandflats (Emerson and Grant, 1991) where high rates of sediment transport occur. Although we did not deploy sediment traps (sensu Emerson and Grant, 1991) in the present study per se, the circular experimental units could be considered a type of sediment trap, especially those protected with flexible netting. In other studies (reviewed in Ólafsson et al., 1994), cages protected with netting have been shown to accumulate sediments at greater rates than uncaged controls. No noticeable sedimentation events were observed either in open or protected experimental units during the experiment at FPB. Had there been, these would likely have been reflected in a disproportionate percentage of dead clams with undamaged shells (presumably due to suffocation) in protected units, which was not observed.

This study also was designed to examine whether the effects of increasing intraspecific clam density (potential exploitative competition for food) could influence juvenile survival. (Competition for space was unlikely to occur since less than 10% of the available space within experimental units containing animals at the highest density was occupied.) We employed only three levels of intraspecific density and observed a small, but significant ($P = 0.0004$) overall reduction (4.5%) in mean percent survival between animals assigned to the highest densities (Table 6). Since this density-dependent mortality rate was independent of the other fixed factors (i.e., no significant higher-order interactions), one explanation for this result could be starvation or some other stress incurred by animals at the highest density. It is not appropriate to analyze statistically more than one fate category from Tables 2–5 because results from the separate analyses would not be independent as the sum of all fate categories taken together total 100%. However, after examining data from the percent "dead undamaged" category (which may be related to starvation, disease, or other stresses that kill clams without damaging their shell), there is little convincing evidence, that this density-dependent mortality is due to starvation because there is no pattern with density in this fate category.

It is possible that predators responded to increasing intraspecific clam density; however, since the reduction in survival occurred equally over both protected and unprotected units as there was no significant Netting × Density interaction ($P = 0.7459$; Table 6), this explanation also seems untenable. Other field investigations, focused

mainly on thick-shelled, shallow burrowers in the family Veneridae (Peterson and Andre, 1980; Peterson, 1982a,b; Walker, 1985; Peterson and Black, 1987, 1988; Peterson and Beal, 1989; Summerson et al., 1995; Whitlatch et al., 1997), or thin-shelled, deep burrowers in the family Tellinidae (Vincent et al., 1989; Skilleter and Peterson, 1994; Cummings et al., 1997; Hines et al., 1997), provide insights about how infaunal bivalves respond to increases in intraspecific density. Few field studies have demonstrated strong density-dependent mortality and, in those that have (e.g., Boulding and Hay, 1984; Summerson et al., 1995), predators concentrated their activities in high density rather than low density patches. Although crowding induced statistically significant mortality in the present study, as in Peterson (1982a) and Peterson and Black (1993), because mean percent survival in the lowest density treatment was intermediate between the other two treatments, it is likely this density-dependent response is not as important in regulating populations of juvenile *Mya* as predation.

We observed spatial differences in mean percent survival at scales of 10s of meters for some sampling dates and tidal heights. Typically, investigators who study how population parameters vary along tidal gradients allocate experimental units or sample individuals randomly within a small area within a particular tidal zone (Newcombe, 1935; Anderson, 1978; Peterson and Black, 1987, 1988; Borrero, 1987; Roseberry et al., 1991; Stiven and Gardner, 1992). Subsequent analyses to detect patterns or differences in means or frequencies between tidal heights assume that the area chosen is representative of that tidal height. Generally, little attention is paid to this issue (but see Andrew and Mapstone, 1987; Underwood, 1997; Underwood and Chapman, 1998). Nested experimental designs (Underwood, 1997), such as the generalized completely randomized block design, permit tests of within-tidal height variability. The trade-off for testing for the presence of within habitat heterogeneity, instead of using a completely randomized design that assumes homogeneity, is a statistically less powerful test for the main factors of interest (usually those that are fixed) because in ANOVA the mean square for the particular fixed factor is not tested over the mean square error, but another mean square with fewer degrees of freedom (Underwood, 1997). In the present study, significant variation in percent survival between blocks occurred on three sampling dates and at each of the three tidal heights (Table 6; Figs. 2 and 3). For example, three of the six significant sources of variation due to blocking were associated with the high tide site and, in each case, the heterogeneity was due to atypically high mortality caused by moon snails. Had there been no attempt to assess within-tidal height variation, and, had a random allocation of experimental units at the high tide level resulted in a majority of units being placed, for example, at or near blocks 3 (September) and 4 (June), results and inferences from this study would likely have been much different.

Until this study, the only field estimates of survival of juveniles of *Mya* (4–8 mm) in Maine were made by examining changes in size–class frequency histograms for three consecutive years from near the high tide level at a mud flat in Lubec, ME, USA. Commito (1982) inferred that mortality was 96.5% year^{-1} for the first 5 years and presumed that *E. heros* was primarily responsible because this naticid was abundant at that site and many dead valves in benthic cores were bored. *C. maenas* also occur at this flat (B. Beal, personal observation), and, because chipped or crushed valves from juvenile clams rarely remain intact, it is likely that this type of shell damage was

overlooked and that crabs play a larger role in that system, as they do at FPB. In addition, Commito's (1982) benthic cores were taken in the same general vicinity each year (B. Beal, personal observation). If within-flat habitat heterogeneity at that site is similar to FPB, then Commito's mortality estimates for small clams may be too high. In our study, of the 10,080 clams initially placed in experimental units, 267 (2.6%) were recovered with a countersunk bore hole. Of these, 139 (52.1%) were recovered from high intertidal blocks. Nearly all (87%) of these bored valves came from blocks within 30 m of each other and, of the seven live *Euspira* spp. discovered in experimental units within high intertidal blocks, all were recovered from blocks within 20 m of each other. Had our initial random placement of blocks not occurred in these patches of unusually high naticid snail density and/or foraging activity, our estimates of clam survival at that tidal height likely would have been greater. Furthermore, had we not attempted to assess small-scale spatial variability within a given tidal height, our results suggest that we risked overemphasizing the importance of naticid snail predation, especially at the high tide level.

4.2. Growth

The temporal pattern of shell growth paralleled closely that of survival (Table 8; Fig. 4), and was similar to that observed by Beal (1994) at other eastern Maine intertidal flats. That is, there were two periods of slow growth (April–June; September–December), and a period when growth was relatively rapid (June–September). Interestingly, this was nearly the same pattern observed by Newcombe (1935) who manipulated small (< 25 mm SL) individuals of *Mya* on several intertidal mud flats near St. Andrews, New Brunswick, Canada in 1930 and 1931, and by Spear and Glude (1957) who examined growth of clams (ca. 30 mm SL) in southwestern Maine on Georgetown Island during 1951–1952. For example, Spear and Glude (1957) determined that soft-shell clam growth began nearly a month earlier than in the present study, but no additional shell growth was observed after early October through the following February. Approximately 35% of the yearly growth at Georgetown occurred from April to early June, 50% from June to September, and 15% from September to mid-October. Brousseau (1979) followed monthly patterns of shell growth of clams > 35 mm SL near Gloucester, Massachusetts during 1973–1974. Growth began each year during February, was fastest in the late spring and early summer, and slowed in the fall and winter. In both years, periods of slower growth occurred during the time of spawning—March/April and June/July. Other growth studies of *Mya* in Long Island Sound (Brousseau and Baglivo, 1987; Cerrato et al., 1991) indicate a general pattern of growth starting as early as January that is related directly to seawater temperature and times of spawning. None of these studies examined whether temporal patterns of incremental shell growth were similar along a tidal gradient.

In this study, we observed a highly significant Date × Tide interaction (Table 8, $P < 0.0001$; Fig. 5a). The orthogonal contrasts indicated that clams not only grew slower at the high tide level but that percent of shell accretion through time differed from animals at the two lower tidal heights. For example, from April to June at the high tide level clams grew 8.5% of the way to their final mean SL, whereas rates of 14.5% and

15.8% were observed at the mid and low tide heights, respectively, during this same period. Fastest growth occurred at all shore levels between 5 June and 6 August; however, rates differed along the tidal gradient. Clams growing nearest the shore added 54.5% of their final mean SL during this interval whereas increases of 42% and 45% were recorded for animals at the mid and low, respectively. Rate of shell accretion slowed across all tidal heights from 6 August to 26 September, but, again, clams at the low and mid tide levels grew more similarly than those from the high tide region (37% of final mean SL occurred in clams at the high vs. a mean of 32% for the mid and low site). Fig. 5a and Table 8 (contrast (12)) suggest that from 26 September to 10 December clam growth differed from the high to the mean of the mid and low. The reason for this was the apparent negative growth of clams from the high intertidal compared to near-zero growth of clams at both the mid and low tidal heights. This anomaly was due to the fact that four of the remaining five blocks sampled at the high tide site in December were among those that belonged to a group of blocks that were exposed to air, on average, 15 to 53 min longer than other blocks during each 12-h tidal cycle (Table 1). In reality, it is likely that clams at each of the three tidal heights added no significant amounts of shell throughout the fall. Although this experiment was terminated in early December 1996, our data and that from Beal (1994), suggest that no significant shell growth was likely to occur again until the following April or May.

Average cumulative incremental shell growth varied inversely with tidal height at FPB. Newcombe (1935) showed experimentally that clams on beaches near St. Andrews, New Brunswick, Canada, grew 35% faster on the lower compared to upper shore levels. Similar results were observed for intertidal *M. arenaria* (Roseberry et al., 1991) and *Macoma balthica* (L.) (Vincent et al., 1989) near Rimouski, Quebec, Canada as well as several epibenthic suspension-feeding bivalves in more temperate areas (Jordan and Valiela, 1982; Bertness and Grosholz, 1985; Littlewood, 1988; Stiven and Gardner, 1992). On average, clams at the high tide level at FPB added only 8.2 ± 2.93 mm ($n = 60$) of new shell over the entire study (this estimate used mean SL for September from the high tide level, see above), whereas animals at the mid and low added 11.7 ± 1.03 and 15.8 ± 1.24 mm, respectively. Submergence time, averaged over both spring and neap tide, fails to explain completely these observed differences in shell growth. For example, blocks at the high tide level were submerged, on average, a total of 450 of 720 min every 12 h, whereas blocks at the mid and low averaged 556 and 669 min, respectively. Observed shell growth was 42% faster at the mid than at the high, but time of submergence of mid tide blocks was only 24% greater than high tide blocks. Similarly, clams grew 35% faster at low tide than animals at the mid tide level, yet low tide blocks were submerged only 20% longer than mid tide blocks. That the observed percent reductions in shell growth with increased elevation on the shore do not parallel directly the submergence times of these bivalves suggests additional factors, perhaps food depletion at the benthic boundary layer by suspension feeders (Carlson et al., 1984; Fréchette and Bourget, 1985) or physiological stresses, are important. Similar responses of infaunal, suspension-feeding bivalves to tidal elevation were observed by Peterson and Black (1987, 1988) at Shark Bay, Western Australia. In that system, four of five species that responded to experimental manipulation of tidal elevation (submergence time) showed the same pattern observed in the present study: faster growth occurred at

the lower tide level, but the magnitude of the enhanced growth could not be explained completely by average daily submergence.

Metabolic differences among animals at different tidal elevations may help to explain observed patterns of growth at FPB. Anderson (1978) found in the laboratory that metabolic rate (ml O_2 g dry weight^{-1} h^{-1}) of individuals of *Mya* (0.35 g dry tissue) varied inversely with decreasing tidal height. That study showed that low-shore *Mya* acclimate to changes in seawater temperatures more readily than those living at higher shore levels. Lewis and Cerrato (1997) demonstrated experimentally that shell growth in *Mya* was positively correlated with oxygen consumption. Their work, together with that of Tremblay and Pellerin-Massicotte (1997) may help explain why submergence time, by itself, only partially explains differences in clam growth along a tidal gradient. These investigators examined effects of tidal cycle on lysosomal membrane stability in the digestive gland of *Mya* (42–62 mm SL) near mid tide on the south shore of the St. Lawrence estuary near Rimouski, Quebec, Canada. Destabilization of lysosomal membranes in marine bivalves has been associated with the presence of environmental toxins as well as variations of temperature, salinity, hypoxia, and spawning (Bayne et al., 1978; Moore et al., 1979; Axiak et al., 1988). Tremblay and Pellerin-Massicotte (1997) demonstrated that air exposure and its associated hypoxia create a physiological condition in *Mya* that reduces their short-term ability to store and digest phytoplankton. Labilization periods increased in the middle of each emersion period. Autophagy followed with atrophy of digestive cells and failure of digestive and storage functions in the digestive gland. These functions returned and labilization decreased at the end of the emersion period. Interestingly, membrane destabilization did not occur when clams were submerged. Therefore, differential feeding times and/or food limitation from the low to high shore superimposed on cyclical changes in cell function affecting metabolism likely explain the failure of submergence times alone to account for differences in final SL between tidal levels.

Shell growth was affected by the level of predator exclusion, but the effect differed through time (Fig. 5b; Table 8, contrast (16)). For example, between 6 August and 26 September (interval when greatest seawater temperatures were noted), there appeared to be an enhancement of clam growth in experimental units protected with netting. Apparently, this condition was temporary because the effect did not extend to the December sampling. Enhanced growth of clams within protected experimental units may be possible because netting may act as a surface of attachment for benthic diatoms (B. Beal, personal observation). If diatoms growing on the netting became suspended, this might provide an additional food source. Since there was a problem with apparent negative growth of animals at the high tide level during the interval from September to December, we removed these 60 observations and reanalyzed the growth data to determine whether a significant enhancement occurred for clams in protected vs. unprotected units and/or if the Date × Netting interaction would disappear. The effect due to netting remained nonsignificant ($P = 0.0664$); however, the significant interaction disappeared ($P = 0.0969$).

Disturbance by predators may affect clam growth rates. Peterson and Black (1993) found a significant reduction in growth of nearly 50% for *Katelysia scalarina* Lamarck and *K. rhytiphora* Lamarck in fully protected cages vs. open enclosures during a

10-week study in Western Australia. The reduction apparently was due to increased disturbance by a predatory seastar that gained entrance to protected cages where it was protected from its predators. Irlandi and Mehlich (1996) observed small reductions in shell growth of hard clams when confined inside complete cages with pinfish, *Lagodon rhomboides* (L.), compared to predator-free cages. Nakaoka (2000) demonstrated that whelks can depress seasonal growth rates of hard clam shell and somatic tissue by nearly 100%. In the present study, two soft-shell clam predators were found accidentally trapped within experimental units on most sampling dates (Table 7), but the incidence of occurrence was relatively low (1.6–9.4% of experimental units sampled on a particular date). If predator presence were important in reducing clam growth, we would expect to see greatest differences between protected and unprotected units at the low tide. We reanalyzed our growth data for the period between April and December for animals within low tide blocks and compared mean SL between protected units with (27.1 ± 1.71 mm; $n = 8$) and without (28.9 ± 0.642 mm; $n = 22$) and predators. The 6.6% decrease in mean SL was significant ($F_{1,28} = 6.81$, $P = 0.0144$).

Density-dependent regulation of growth rates has been observed in populations of infaunal, suspension-feeding bivalves (Peterson, 1982a; Ólafsson, 1986; Peterson and Black, 1987, 1993; Peterson and Beal, 1989; Vincent et al., 1989; Jensen, 1992; Summerson et al., 1995; Montaudouin and Bachelet, 1996). These studies implied that local depletion of suspended phytoplankton can reduce individual growth rates. No overall effect of density occurred at FPB ($P = 0.089$); however, the fact that the Date × Density interaction (Table 8, contrasts (18) and (20)) was significant suggests that density-dependent growth occurred over at least one sampling period (Fig. 5c). Until 6 August, no significant depression in growth due to density occurred. Between August and September, growth of animals at the two highest densities was depressed approximately 7% ($P = 0.005$), but this trend did not continue between September and December ($P = 0.0393$; $\alpha' = 0.017$) as size of animals in the three density treatments converged. The strongest suggestion that growth was regulated by density-dependent processes occurred at the high intertidal site (Table 8, contrast (23); Fig. 5). Perhaps due to the interaction of physiological stress and reduced submergence times, animals held at the lowest density in the high tide blocks grew 5.3% faster than the mean of those in the upper two densities. No similar depression in growth occurred at mid- and low-tide levels. These results are similar to Peterson and Black (1987) showing density-dependent growth of other suspension feeders restricted to seasons and places (upper shore) of slowest growth. The generalization that emerges from these two observations is consistent with ecological theory that competition may be sporadic and limited to occasions when and where resources are in short supply (Weins, 1977).

As with the survival data, significant variability in shell growth was observed between blocks in four of twelve cases (Table 8). Three of these significant block effects occurred at the high intertidal site and, in each case, results could be explained by differences in submergence time between blocks.

4.3. Spatial scale of the experiment

Our experimental units were very small (0.018 m^2); as such, one might argue that we are unable to make realistic inferences about ecological processes involving *Mya* and

that our results are not valid compared to events that limit population growth of this bivalve over an entire mud flat or larger spatial scales. Ecological processes are scale-dependent and results observed at one scale may not be appropriate at another (Legendre et al., 1997). In an attempt to understand something about mechanisms that cause spatial and temporal heterogeneity in field populations, there is a trade-off between what can physically be accomplished given logistics and resources, which usually results in reducing number of treatments and/or replicates, and what should be done. We were able to observe predation and competition operating on the scale of our experimental units. Other investigators (Peterson and Black, 1987, 1993; Peterson and Beal, 1989; Skilleter and Peterson, 1994) using larger experimental units than ours (i.e., 1-m² scale), but that would still be considered small relative to the scale of water movement within a bay, sound, or estuary, detected similar processes.

Our decision, given the size of the experimental units in this study, was to incorporate a within-tidal height component in our field design that would allow us to estimate heterogeneity not only at the level of the experimental unit, but at the level of 10s of meters (i.e., the distances between blocks on any particular sampling date). Although this was, necessarily, another limited spatial scale, our results show surprising homogeneity in both growth and survival estimates within a particular tidal height. Microtopographic and sedimentary features of the upper intertidal rendered that site the most heterogeneous one in terms of responses by *Mya*. Another approach to better understand heterogeneity in this system was to sample over a period of time when most biotic processes were important. Although we did not extend the study through the winter months to examine the role that, for example, ice or black ducks, *Anas rubripes* Brewster, may play in redistributing and/or limiting clam abundance, we did observe processes that help explain patterns of distribution and abundance at FPB and other low-energy mud flats in eastern Maine.

The results presented here are relevant at least to the scale at which they were conducted. Future work at larger scales per experimental unit and over wider spatial and temporal settings is necessary to test the generality of our findings. That effort will enable fisheries managers to decide how best to manage wild and/or cultured populations of *Mya* and ecologists to understand the importance of scale-dependent processes (sensu Thrush et al., 1997b, 2000) in this intertidal system.

Appendix A

Mean square estimates (MSE) for the ANOVA tables. A_i = Sampling Date ($i = 4$), B_j = Tidal Height ($j = 3$), C_k = Netting ($k = 2$), D_l = Density ($l = 3$), E_m = Block ($m = 5$). All effects are considered fixed (α) except those due to blocks, which are considered random (σ^2). ($n = 2$).

Source of variation	df	Mean square estimates	F-ratio vs.	df for F-test
A_i	$a - 1$	$\sigma_e^2 + cdn\sigma_{E(AB)}^2 + bcden\alpha_A$	$E(AB)$	3, 48
B_j	$b - 1$	$\sigma_e^2 + cdn\sigma_{E(AB)}^2 + acden\alpha_B$	$E(AB)$	3, 48
C_k	$c - 1$	$\sigma_e^2 + dn\sigma_{CE(AB)}^2 + abden\alpha_C$	$CE(AB)$	1, 48
D_l	$d - 1$	$\sigma_e^2 + cn\sigma_{DE(AB)}^2 + abcen\alpha_D$	$DE(AB)$	2, 96
AB_{ij}	$(a-1)(b-1)$	$\sigma_e^2 + cdn\sigma_{E(AB)}^2 + cden\alpha_{AB}$	$E(AB)$	6, 48
AC_{ik}	$(a-1)(c-1)$	$\sigma_e^2 + dn\sigma_{CE(AB)}^2 + bden\alpha_{AC}$	$CE(AB)$	3, 48
AD_{il}	$(a-1)(d-1)$	$\sigma_e^2 + cn\sigma_{DE(AB)}^2 + bcen\alpha_{AD}$	$DE(AB)$	6, 96
BC_{jk}	$(b-1)(c-1)$	$\sigma_e^2 + dn\sigma_{CE(AB)}^2 + aden\alpha_{BC}$	$CE(AB)$	2, 48
BD_{jl}	$(b-1)(d-1)$	$\sigma_e^2 + cn\sigma_{DE(AB)}^2 + acen\alpha_{BD}$	$DE(AB)$	2, 96
CD_{kl}	$(c-1)(d-1)$	$\sigma_e^2 + n\sigma_{CDE(AB)}^2 + aben\alpha_{CD}$	$CDE(AB)$	2, 96
ABC_{ijk}	$(a-1)(b-1)(c-1)$	$\sigma_e^2 + dn\sigma_{CE(AB)}^2 + den\alpha_{ABC}$	$CE(AB)$	6, 48
ABD_{ijl}	$(a-1)(b-1)(d-1)$	$\sigma_e^2 + cn\sigma_{DE(AB)}^2 + cen\alpha_{ABD}$	$DE(AB)$	12, 96
ACD_{ikl}	$(a-1)(c-1)(d-1)$	$\sigma_e^2 + n\sigma_{CDE(AB)}^2 + ben\alpha_{ACD}$	$CDE(AB)$	6, 96
BCD_{jkl}	$(b-1)(c-1)(d-1)$	$\sigma_e^2 + n\sigma_{CDE(AB)}^2 + aen\alpha_{BCD}$	$CDE(AB)$	4, 96
$ABCD_{ijkl}$	$(a-1)(b-1)(c-1)(d-1)$	$\sigma_e^2 + n\sigma_{CDE(AB)}^2 + en\alpha_{ABCD}$	$CDE(AB)$	12, 96
$E(AB)_{m(ij)}$	$(m-1)(a)(b)$	$\sigma_e^2 + cdn\sigma_{E(AB)}^2$	MSE	48, 360
$CE(AB)_{km(ij)}$	$(c-1)(m-1)(a)(b)$	$\sigma_e^2 + dn\sigma_{CE(AB)}^2$	MSE	48, 360
$DE(AB)_{lm(ij)}$	$(d-1)(m-1)(a)(b)$	$\sigma_e^2 + cn\sigma_{DE(AB)}^2$	MSE	96, 360
$CDE(AB)_{klm(ij)}$	$(c-1)(d-1)(m-1)(a)(b)$	$\sigma_e^2 + n\sigma_{CDE(AB)}^2$	MSE	96, 360
Error = $e_{n(ijklm)}$	$(a)(b)(c)(d)(e)(n-1)$	σ_e^2		

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