Pre- And Post-Settlement Determinants of Estuarine Dungeness Crab Recruitment

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PRE- AND POST-SETTLEMENT DETERMINANTS OF ESTUARINE DUNGENESS CRAB RECRUITMENT[1]

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Abstract. Abundance of early juvenile Dungeness crab (*Cancer magister*) is dramatically higher in intertidal shell habitats compared to mud habitats in several coastal estuaries of the Pacific Northwest. To define the mechanisms underlying this habitat-specific pattern in abundance, we concurrently examined four components of recruitment to intertidal shell and mud habitats at two locations within the Grays Harbor estuary (Washington, USA): (1) water column supply of crab megalopae (postlarvae); (2) settlement patterns of crab megalopae 48 h after settlement substrates were deployed; (3) density of first benthic juvenile instars (*J*1) 48 h after deployment of such substrates; and (4) density of early juvenile crab in shell and mud habitats over a 4-mo period. We also describe the physical processes likely to be influencing postlarval supply within Grays Harbor, and take advantage of natural variation in postlarval supply between two locations, in combination with a predator exclusion experiment, to define the relative importance of postlarval supply vs. post-settlement survival in regulating population size of juvenile crab in certain intertidal habitats.

Water column postlarval supply (measured with plankton and neuston nets, and artificial settlement substrates) in terms of both megalopal density (number per cubic metre) and flux (number per hour) was significantly higher in the southern part of the estuary vs. the northern part during a week-long settlement pulse. Our field observations and measurements suggest that spatial variation in postlarval supply was due to local differences in wind-driven surface currents, since tidal current speeds in the two locations were similar. Moreover, there was no correlation between current speed and flux of megalopae over the bottom. There was generally no difference in postlarval supply between shell and mud habitats. Our experimental results further indicate that: (1) the abundance of recently settled crab megalopae in 0.25 m² settlement trays was significantly higher in shell than in mud habitats, irrespective of whether the trays were placed in 3–5 ha of shell vs. mud; (2) there was a positive and significant correlation between postlarval supply and density of megalopae in shell and mud habitats; and (3) there was a positive and significant correlation between postlarval supply and density of *J*1 instars only in habitats where specific predators were excluded. Once the number of *J*1 instars at both geographic locations was reduced to similar levels, equivalent but steadily decreasing densities persisted throughout the summer growing season. The decoupling of settlement patterns and density of *J*1 instars took place within our 48-h sampling interval. Thus, future attempts to examine the correspondence between larval supply and post-settlement abundance of marine benthic species with planktonic larvae should do so at extremely small temporal scales or a critical life history phase may be overlooked. The results from this study demonstrate that substrate selection can affect distribution of juvenile crab, and that predation (including cannibalism) is a key factor regulating local population size of early juvenile crabs in intertidal habitats where postlarval supply is relatively high.

Key words: Cancer magister; *Dungeness crab; Grays Harbor, Washington; habitat selection; intertidal; larval choice; mitigation; plankton; population regulation; predation; recruitment; settlement; surface slicks.*

INTRODUCTION

A central tenet in ecology is that biotic and physical mechanisms regulate the distribution and abundance of organisms. For species with complex life cycles (i.e.,

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species with ≥2 developmental stages requiring spatially separated habitats), this knowledge of biotic and physical processes that regulate abundance is gained by integrating the dynamics of several phases of the life cycle (Gaines and Roughgarden 1985, Underwood and Fairweather 1989, Bertness et al. 1992). Such integration is especially important in marine benthic communities where many invertebrates and demersal fishes have developed meroplanktonic reproductive strategies and release pelagic larvae that spend weeks

to months in the water column, dispersing great distances and subsequently settling in spatially separate habitats (Thorson 1950, Phillips 1981, Gaines et al. 1985).

Postlarval settlement patterns are the consequence of biological and physical processes operating on larval stages during the transition from a pelagic to a benthic existence. The intensity of local settlement is determined by the number of larvae or postlarvae that reach a location, settle, and metamorphose. Larval supply can be influenced by current patterns (Shanks 1983, Kingsford and Choat 1986, Shanks and Wright 1987, Kingsford et al. 1991, McConnaughey et al. 1992), whereas settlement of weakly swimming larvae can be influenced by benthic boundary layer flow processes that may lead to passive deposition (Eckman 1983, Hannan 1984, Butman 1987, Emerson and Grant 1991), or behavior to select substrate by strong swimming larvae or postlarvae (review by Meadows and Campbell 1972, Crisp 1974, Botero and Atema 1982, Herrnkind and Butler 1986, Hurlbut 1991). Moreover, post-settlement mortality and movements can also affect the distribution of marine benthic species and mask initial settlement patterns (Keough and Downes 1982, Luckenbach 1984, Connell 1985, McGuinness and Davis 1989, Rowley 1989, Holm 1990). Thus, for benthic organisms with strong-swimming planktonic larvae, recruitment (*sensu* Keough and Downes 1982) has three major components: (1) water column supply of larvae; (2) choices made by the larvae at the time of settlement; and (3) the survival of settlers to the age of initial census.

Recently, ecologists working in marine systems have begun to construct a new paradigm synthesizing the roles of pre-settlement and post-settlement processes in structuring communities of organisms with open populations. A growing body of theory (Roughgarden et al. 1985, Roughgarden and Iwasa 1986) and data (Sale 1977, 1990, Connell 1985, Gaines and Roughgarden 1985, Underwood and Fairweather 1989, Bertness et al. 1992, Milicich et al. 1992, Peterson and Summerson 1992, Doherty 1994) indicates that larval settlement can generate significant spatial and temporal variation in the size of open populations, their dynamics, and community structure. A number of criteria have been proposed for distinguishing between populations that are recruitment-limited (sensu Doherty 1983) vs. those regulated by post-settlement interactions such as intra- or interspecific competition and density-dependent mortality. One criterion for recruitment limitation is that mortality of larvae, postlarvae, or juveniles be density independent (i.e., population age or size structure be a direct reflection of previous settlement events) (Doherty and Williams 1988, Mapstone and Fowler 1988, Doherty 1994, see Holm 1990 for a discussion of density-dependent mortality under conditions of recruitment limitation). In instances where larval supply exceeds the carrying capacity of the habitat, density-dependent mortality or emigration will destroy the re-

lationship between larval settlement and subsequent recruitment (Connell 1985). Density-dependent mortality can also occur in habitats where resources are not limiting but local predators (or predator guilds) exhibit density-dependent functional responses (e.g., Lipcius and Hines 1986, Eggleston et al. 1992).

The relative contribution of pre-settlement and post-settlement processes in explaining variation in recruitment success is usually confounded because recruitment is often measured by censusing juveniles long after they have settled from the water column (Keough and Downes 1982, Bertness et al. 1992). Moreover, few studies have simultaneously considered the major components of recruitment within an experimental framework. This paper describes the results of a series of field experiments and observations that examine the mechanisms underlying recruitment success of juvenile Dungeness crab, *Cancer magister* Dana, in intertidal oyster shell and mud habitats at various spatial scales. We describe the physical processes influencing postlarval supply within a coastal estuary, and take advantage of natural variation in postlarval supply between two locations within the estuary, in combination with a predator exclusion experiment, to define the relative importance of postlarval supply vs. post-settlement processes in regulating population size of young-of-the-year (YOY: settlement to age 1) crab in several intertidal habitats.

The Dungeness crab (Crustacea: Decapoda: Cancridae) is a dominant, highly motile benthic marine invertebrate of shallow coastal and estuarine habitats in the Pacific coast of North America. Its complex life history is characteristic of marine invertebrates with planktonic larvae. Along the Washington coast, larvae are released during January through mid-March and proceed through five zoeal stages over a period of 130–150 d (Lough 1976). The larvae are planktonic in ocean waters and may be transported hundreds of kilometres (McConnaughey et al. 1992, 1994). The last larval stage then metamorphoses into the megalops stage in nearshore waters. The megalopa has behavior, morphology, and physiology that is transitional between the larval and early juvenile stages (Poole 1966, Brown and Terwilliger 1992). Actively swimming megalopae enter coastal and estuarine waters primarily during May–June (Gunderson et al. 1990), and metamorphose into first instar juveniles ($J1$) after settlement. At least two cohorts of megalopae per settlement season have been detected in Puget Sound (Dinnel et al. 1993), along the outer Washington coast (McConnaughey et al. 1992, 1994), and in Grays Harbor (Fernandez et al. 1993a). Throughout the summer, YOY juvenile crabs in the estuary are found in high numbers on the tideflats, whereas older subadults (1+, 2+ age classes) occur mainly in deeper channels (Stevens and Armstrong 1984).

Year class strength of coastal Dungeness crab populations has been linked through correlative analysis
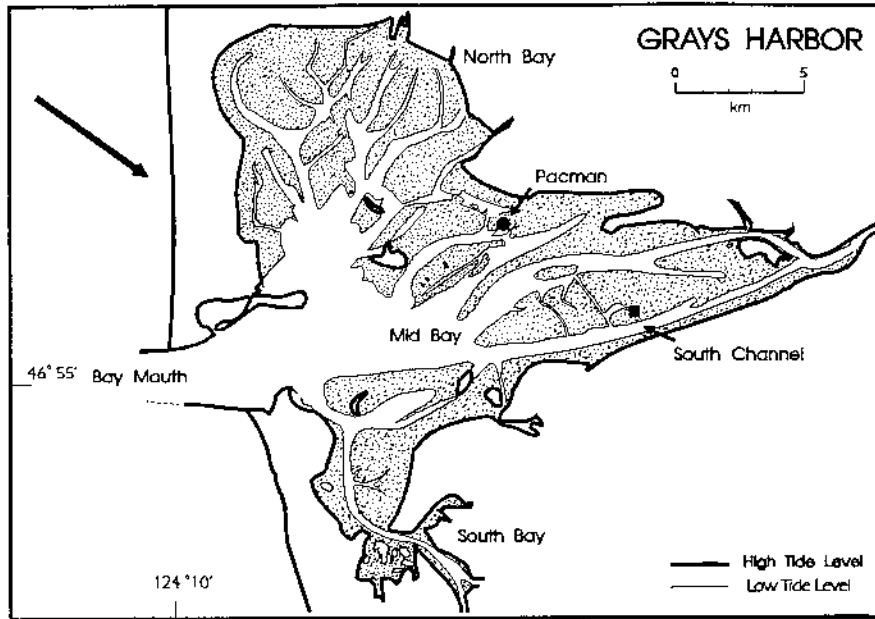
FIG. 1.   Study sites at Grays Harbor, Washington, USA. Wind vector arrow indicates predominant wind direction from the west-northwest and speed of 5–13 m/s. Stippling indicates intertidal habitats at mean low water.

to events operative during the larval stage for the most part (e.g., see reviews by Botsford et al. 1989, Jamieson and Armstrong 1991), but other studies indicate that 1st-yr survival of post-settlement juveniles probably accounts for very strong year classes that typify peaks in the fishery records (Gunderson et al. 1990, Mc-Connaughey et al. 1992). The species is dependent on nearshore (inside 50 m) refuge habitat that is patchy on the scale of tens of kilometres, and on movement of a portion of any year class into estuaries prior to settlement. Gunderson et al. (1990) estimated that abundance of surviving 1+ juvenile Dungeness crab was 3–8 times greater in the two major coastal estuaries of Washington State (Grays Harbor and Willapa Bay) compared to adjacent sections of open coast 8 times larger in area. Other comparative measures of crab density, abundance, growth rate, and biomass all indicate that estuarine populations of 0+ and 1+ equal and usually exceed coastal cohorts. First year growth is always faster in the estuaries than along the outer coast (Gutermuth and Armstrong 1989), and biomass is a minimum of 10–20 times greater per hectare in the former system. The Dungeness crab is an excellent species for examining recruitment dynamics in estuarine systems because they can be easily identified and collected in the water column, they often exhibit predictable settlement pulses, and settlement and survival in intertidal habitats is easily quantified. Moreover, the estuary used in this study was apparently large enough for surface currents to respond to local wind forcing, yet small enough to be tractable with small (7 m) boats.

Study system

Field observations and settlement experiments were conducted in Grays Harbor, a drowned river estuary characterized by expansive mudflats and a series of intervening channels, located on the Washington coast of North America (47° N, 124° W; Fig. 1). Grays Harbor is ≈24 km long and 18 km wide, with a water surface area ranging from 146 km² at mean high water to 61 km² at mean low water. The estuary is well mixed with tidally driven circulation and spring tidal currents reaching 40 cm/s. Grays Harbor serves as an important nursery habitat for juvenile Dungeness crab and supports a commercial fishery for adults.

In estuarine systems, large scale production of indigenous or exotic oyster species can result in extensive shell habitat in the form of living reefs or inert shell deposits. Previous observations in Grays Harbor and Willapa Bay, Washington indicate that Dungeness crab megalopae settle in oyster shell and relic deposits of the soft-shell clam, *Mya arenaria* (Armstrong and Gunderson 1985, Jamieson and Armstrong 1991). Shell habitats provided refuge for nearly 300 post-settlement stage Dungeness crab/m², and in excess of 20 crab/m² 3–4 mo after settlement (Fernandez et al. 1993a). These observations were striking in that post-settlement and early juvenile crab densities on adjacent open mudflats were seldom >1 crab/m². Hence, the general question we initially address in this paper is: what is the relative importance of megalopal supply, active substrate selection, and post-settlement distribution or mortality in explaining these different abundance patterns of early

juvenile Dungeness crab in shell and mud habitats? We then take advantage of natural variation in postlarval supply within Grays Harbor to examine the relative importance of postlarval supply vs. post-settlement processes in defining local population size of YOY crabs.

In 1990, the Port of Grays Harbor and the U.S. Army Corps of Engineers (COE) dredged the main navigation channel in Grays Harbor to widen and deepen the channel, killing an estimated 161 561 2-yr-old subadult Dungeness crabs in the process (Wainwright et al. 1992). In response to concerns of crab fishermen and resource managers over the extensive loss of subadult crabs due to the dredging operation, the COE constructed 8 ha of intertidal oyster shell habitat in 1992 in the first U.S. demonstration of this form of habitat enhancement mitigation for a decapod fishery. During March and April 1992, the COE constructed shell habitats in two independent intertidal locations in Grays Harbor: the so-called "Pacman" location on the north central side of Grays Harbor and "South Channel" (Fig. 1). These two locations were located ≈6 km apart and offered a complete cross section of intertidal habitats including the COE shell mitigation area, open mudflats, and sparse eelgrass (*Zostera marina*: <20 turions/m²). The sites were adjacent to numerous subtidal channels containing high densities of older juvenile *C. magister* and several dominant piscine predators (Cottidae, Gadidae, Plueronectidae, Embiotocidae, Salmonidae) (Rogers et al. 1988, Armstrong 1991). Site selection was also based on similar criteria of salinity, temperature, longevity of the shell (based on previous observations of shell sinkage), sediment type, and density of vegetation. Extant patches of relic *M. arenaria* shell deposits were located primarily in the northern part of the estuary.

Each intertidal location (i.e., Pacman and South Channel) contained an experimental (shell mitigation) and control site (open mudflat) of ≈4 ha each. Thus, this large-scale habitat manipulation, combined with a predicted, new-moon pulse of Dungeness crab megalopae into the estuary, allowed us to examine the joint effects of substrate type (shell vs. mud), location (Pacman vs. South Channel), type of available settlement substrate (i.e., shell vs. mud) surrounding substrate-filled, 0.25-m² settlement trays, and specific predators upon recruitment success of juvenile Dungeness crab.

METHODS AND MATERIALS

Our sampling and experimental approach concurrently examined four components of recruitment in intertidal shell and mud habitats at two different locations: (1) water column supply of megalopae (density and flux over the bottom), (2) settlement patterns of crab megalopae after 24 h and 48 h, (3) density of first-instar juveniles ($J1$) after 48 h, and (4) density of young-of-year (YOY) crabs ($J1$ to ≈$J6$) in shell and mud habitats over a 4-mo period. Initial field sampling

and settlement experiments were performed on 3–8 May 1992 during a major new-moon pulse of Dungeness crab megalopae into Grays Harbor. We recorded wind speed and direction, and water temperature (in degrees Celsius) twice daily during the study period in May 1992. We also quantified above-bottom current speeds (in centimetres per second) at both Pacman and South Channel during this time. To examine the correspondence between postlarval supply, initial patterns of settlement, and subsequent population structure, we measured the density of YOY crab in shell and mud habitats at Pacman and South Channel on four separate occasions from 15 May to 14 August 1992.

Postlarval supply: density and flux

We monitored daily water-column supply of Dungeness crab megalopae over the bottom during the new-moon settlement pulse in May 1992 with two techniques: plankton nets moored above the bottom and neuston nets pushed through surface slicks (i.e., estuarine water-mass fronts). Although both techniques targeted planktonic megalopae, we differentiate between plankton nets and neuston nets based on net configuration and deployment, and water depth sampled. Paired plankton nets 1 m apart were anchored in the middle of each 3–5 ha shell and mud site at both locations (Pacman and South Channel) for 1 h during the daytime mid-flood tide. The bottom of each net (0.5 mm mesh) rested just above the substrate and filtered an area 50 cm wide by 100 cm in height (0.5 m²). Each net was equipped with a flowmeter (General Oceanics model 2030) and fished passively on three days during the settlement pulse. Water volumes filtered per sample varied from 12 to 124 m³. Although filtration efficiency for plankton nets of the same design (but with 1-mm mesh) were ≈90% for blue crab (*Callinectes sapidus*) megalopae in Chesapeake Bay (Olmi, *in press*), we do not know whether or not net avoidance by strong swimming Dungeness crab megalopae was a problem in this study, nor if the plankton nets sampled in a biased way depending upon current speeds. However, our primary goal was to compare relative rates of postlarval supply between two locations in Grays Harbor (Pacman and South Channel). Since flood tide current speeds did not differ between locations (see *Results: Environmental conditions*), we assumed that the plankton nets were an adequate technique for measuring relative rates of postlarval supply, and that statistical comparisons between locations were valid. Moreover, temporal and spatial patterns of postlarval supply measured with the plankton nets were consistent with patterns generated by two independent techniques for quantifying postlarval supply: neuston nets and floating, artificial settlement substrates (see *Results: Postlarval supply*). Dungeness crab megalopae were enumerated in the field after retrieval of the plankton nets. Collections were standardized as one of two response variables: (1) megalopal density (megalopae per cubic metre per

hour), which was the daily mean number of megalopae per cubic metre of water sampled for the paired net samples, or (2) megalopal flux (megalopae per hour), which was simply the daily mean number of megalopae passing over a fixed area of bottom during 1 h of peak flood tide. Megalopal density provides a more traditional measure of postlarval supply by describing the concentration of megalopae passing over a fixed area of bottom, whereas megalopal flux provides a measure of the total number of megalopae passing over an area during a fixed amount of time. Both response variables were correlated with settlement and abundance of first benthic instars, and were also used in two separate three-way mixed-model ANOVAs with Site (shell mitigation site vs. open tideflat) and Location (Pacman vs. South Channel) as fixed factors, and sampling Date (4 May, 6 May, and 7 May) as the random factor. Location and Site were respectively treated as a fixed factors since the U.S. Army Corps of Engineers established only two shell mitigation sites in Grays Harbor, and each shell site was located adjacent to an open tideflat. Hence Locations and Sites were established a priori and our inferences are specific to the levels within each treatment (i.e., Pacman and South Channel; shell mitigation sites vs. adjacent open tideflats). Conversely, Date was treated as a random factor since postlarval supply was sampled on three of five days during which high densities of megalopae were recruiting into Grays Harbor. In this case we were interested in the effects of Location and Site averaged over a random sample of Dates. Megalopal densities were transformed as natural log of $(x + 1)$ to standardize variances.

Strong-swimming planktonic animals often form dense accumulations in zones along oceanic fronts (e.g., Zeldis and Jillett 1982, Epifanio 1987) because they are not under the influence of ambient vertical flow velocities (Franks 1992 and references therein). Historically, we have observed swarms of Dungeness crab megalopae, which are strong swimmers (see below), concentrated along convergent zones of tidal intrusion and axial convergent fronts, and wind-driven Langmuir cells in Grays Harbor during late spring new-moon, daytime flood tides (Eggleston, *unpublished data*). We sampled Dungeness crab megalopae during flood tide in fronts that bisected shell and mud sites at both Pacman and South Channel. Megalopae in the surface were sampled from a small boat (6 m) by holding a dip net (36 cm × 36 cm × 2-mm-mesh; equivalent to a neuston net) just below the water surface and pushing it through the center of a front for 2.5 min at idle speed. Four dip-net samples were taken at each location on three different days during the 7 d study period. As above, dip nets were equipped with a flowmeter; water volumes filtered per sample ranged from 13 to 52 m³. Daily collections were standardized as the mean number of megalopae per cubic metre. We examined whether or not megalopal density in the surface was different between Pacman and South Channel, and over time,

with a two-way mixed-model ANOVA with Location (fixed levels: Pacman vs. South Channel) and Date (random levels: 4 May, 6 May, and 7 May) as factors. Date and Location were treated as random and fixed factors as outlined above. Megalopal density was transformed as natural log of $(x + 1)$ to standardize variances.

Postlarval settlement and density of first instars

We used two techniques to measure settlement of crab megalopae during the new moon settlement pulse: floating, artificial settlement substrates and benthic mud and shell substrates.

Artificial substrates.—Artificial settlement substrates have been used successfully to examine settlement patterns of numerous decapod crustaceans (Witham et al. 1968, Phillips 1972, Beninger et al. 1986, van Montfrans et al. 1990). We examined megalopal settlement on artificial substrates because it provided another measure of settlement that was independent of the substrate types being tested, and that could be correlated with postlarval density and flux, and settlement on natural substrates. Three floating artificial settlement substrates were moored 5 m apart and adjacent to settlement trays at each Site (shell mitigation site and open tideflat) within a Location (Pacman and South Channel). Each artificial settlement substrate consisted of synthetic fiber air-conditioning filter material wrapped as a ring around an 80-cm section of 22 cm diameter PVC (polyvinyl chloride) pipe. Artificial substrates were suspended with floats attached to the inside of the PVC pipe and weighted at the bottom to maintain vertical position in the water column. Artificial substrates were deployed during the morning low tide and remained submerged through two high tides and a weak, evening low tide. These substrates were then recovered and the filter rings changed the following morning 24 h later as the tide was receding. This procedure was repeated 5 times during the new-moon settlement pulse (4–8 May 1992). The daily mean number of megalopae per substrate served as the response variable in a three-way fixed-factor ANOVA model with Site (shell mitigation site vs. open tideflat), Location (Pacman and South Channel), and sampling Date (4, 5, 6, 7, and 8 May) as factors. In this case, Date was treated as a fixed factor since sampling dates encompassed all possible sampling dates during the megalopal recruitment pulse into Grays Harbor.

Benthic substrates.—Settlement on benthic substrates was monitored by placing shell- or mud-filled square, plastic trays (0.25 m² × 9 cm height and lined with 1-mm mesh to cover the perforated bottom) on the sediment surface for two separate 48-h periods. The trays provided a convenient way of manipulating substrate type in the different intertidal habitats. Trays were filled to the top (9 cm deep) with oyster shells that had been air dried, or with mud removed from

below a depth of 20 cm at the control site (open tideflat), and hand sifted to remove larger fauna. The substrate surface in these trays stood 9 cm above the surrounding sediment surface. Elevation of settlement substrates above the tideflat surface presumably served two functions. First, it prevented passive bed load transport of sediments and animals into the trays (e.g., Levin 1984); thus settlement in trays was interpreted as the result of entry of animals from the water column (see *Results: Tray effects*). Second, it served as a partial barrier to immigration by predatory *J*2 conspecifics (Fernandez et al. 1993*a*) after settlement (see *Results: Tray effects*). The settlement experiment with plastic trays examined five treatments in relation to natural variation in postlarval supply: (1) Substrate (oyster shell vs. mud), (2) Site (intertidal shell mitigation site vs. open tideflat), (3) Location (Pacman vs. South Channel), Cage (predator exclusion cage vs. no cage), and sampling Date (experiment 1: 3–5 May vs. experiment 2: 6–8 May).

We used 12-mm mesh galvanized wire cages to ascertain whether or not exclusion of benthic predators would enhance settlement success of crabs in shell and mud substrates over 48 h. A mesh size of 12 mm was large enough to allow megalopae to pass through it, yet small enough to exclude the smallest staghorn sculpin (*Leptocottus armatus*; >70 mm total length [TL]), a dominant piscine predator of early juvenile Dungeness crab (Armstrong 1991), capable of preying on megalopae (70 mm TL minimum based on sculpin gape limitation when preying on megalopae; see Armstrong 1991). The 12-mm mesh did not exclude *J*1 and *J*2 crab, which can cannibalize newly settled recruits (Fernandez et al. 1993*a*).

The presence of predator exclusion cages may have altered hydrodynamics in the settlement substrates. For example, the cage and stakes holding it in place could have caused small-scale turbulence around the structures during tidal flows, thereby reducing water movement that in turn could produce positive or negative effects upon settlement (see Butman 1987 and references therein). Moreover, the increased above-bottom surface area provided by cages could enhance encounter rates with megalopae. However, given the strong swimming behavior of Dungeness crab megalopae (forward movement against a flow of 40 cm/s and 12 cm/s in still water; Fernandez et al. 1994), and the lack of a significant cage effect with megalopae (see *Results: Megalopal settlement . . . first instars: Benthic substrates*), we conclude that reduced current regimes (i.e., baffling effects) and enhanced encounter rates were not important in determining patterns of settlement in this study.

We included the Site treatment to test the hypothesis that settlement on a small (0.25 m²) area of substrate type (shell vs. mud) was not influenced by the surrounding 3–5 ha substrate type (e.g., oyster shell in 0.25-m² settlement trays positioned within 3–5 ha of

oyster shell vs. trays with shell being placed in ≥4 ha of open mud). This treatment also served as a control for the Substrate comparison in the event that larval supply differed between sites. The Location treatment allowed us to assess the other treatment effects at both a north and south point in the estuary, where postlarval supply would likely vary due to the effect of wind-driven surface transport of megalopae. Previous observations of surface drifters indicated that wind direction had a significant effect on the direction that surface drifters moved (D. Eggleston, *unpublished data*). The Date treatments accounted for potential variation in postlarval supply and settlement between the first and second experiments. The Dates of the first and second experiments were determined a priori and encompassed all logistically possible 48-h sampling periods during the recruitment pulse into Grays Harbor. The experimental design was orthogonal.

The experimental procedure involved placing two replicate settlement trays of each of four systematically interspersed (sensu Hurlbert 1984) treatment combinations (Substrate, Site, Location, Cage) on the exposed tideflats during the morning low tide of 3 May 1992, and retrieving trays 48 h after deployment at low tide. Samples were sieved through a 1-mm mesh screen and live sorted. Crabs were classified as megalopae, *J*1 benthic instars (5–8 mm carapace width [CW]), or *J*2 (9–12 mm CW). This experiment was performed a second time on 6–8 May 1992. The number of megalopae and first benthic instars per 0.25 m² per 48 h served as individual response variables in two separate five-way fixed-factor ANOVA models with Substrate, Location, Site, Cage, and Date as factors. We used natural log of $(x + 1)$ transformations when variances were heteroscedastic. When data transformations were unsuccessful in achieving homoscedasticity and data were distributed normally (normality tested with a Kolmogorov-Smirnov goodness of fit test), hypotheses were rejected at alpha values lower than the P values of Cochran's C test for homogeneity of variance (Underwood 1981:535).

Tray effects.—To evaluate potential biases associated with the use of plastic settlement trays and predator exclusion cages, we monitored settlement on shell and mud that was flush with the tideflat surface, but placed on top of a 1-mm mesh screen buried 7 cm below the substrate surface. Within a particular Site (shell mitigation site vs. open tideflat) during each 48-h settlement experiment, we deployed four of these benthic substrates flush with the substrate surface; two had predator exclusion cages and two were open. The "flush substrates" were recovered at low tide 48 h after deployment by pulling up the 1-mm mesh screen and placing the enclosed substrate in a large plastic bag. Samples were processed and data recorded as described above. In this case, flush substrates were the same as the surrounding substrate type (i.e., shell in shell, mud in mud). The flush cage and no cage treatments were

interspersed with the four treatment combinations described above (i.e., Substrate, Site, Location, Cage). Thus, there were two replicates of each of three orthogonal treatment combinations: Tray (plastic settlement tray present or absent), Cage (predator exclusion cage present or absent), and Location (Pacman vs. South Channel). This experiment was repeated on 6–8 May 1992. The number of megalopae and second benthic instars in shell or mud within a particular Site (e.g., oyster shell substrate in the shell mitigation site, and mud substrate in the open tideflat) were analyzed as separate response variables in a four-way fixed-factor ANOVA model with Date, Tray, Cage, and Location as factors. We included only megalopae and second instars as response variables for two reasons. First, megalopae served as a response for how the plastic trays may have influenced settlement. Second, the relative abundance of $J2$ was the measure of immigration of this potential predator into the tray. First instars were not included since they so quickly metamorphose from megalopae ($\approx$6–12 h post-settlement) and thereby confound settlement and migration.

Relationship between postlarval supply, settlement, and density of first benthic instars

We examined the statistical relationship between our two indices of postlarval supply (plankton nets and dip nets) and settlement on artificial substrates, with linear least-squares regression models. In this case, measures of postlarval density or flux at both geographic locations (independent variable) were related to settlement on artificial substrates the next day (dependent variable). For example, mean megalopal densities measured in the plankton on the afternoon of 4 May at Pacman and South Channel were compared with mean megalopal settlement on artificial substrates at these same locations the morning of 5 May. Fisher's transformation (Zar 1984) indicated that exponential or power transformations did not significantly improve the fit of the plankton and settlement data over linear functions (all $P > 0.39$).

We then examined the relation between megalopal supply and settlement on natural substrates with an analysis of covariance (ANCOVA). In this case, each measure of postlarval supply (plankton nets and dip nets) or settlement on artificial substrates served as separate covariates, substrate type was the independent variable, and the number of megalopae occupying mud- and shell-filled settlement trays served as the dependent variable. We then employed a similar approach to examine the relationship between postlarval supply and density of $J1$ in shell and mud. However, in this case, we performed a separate test depending upon whether a predator exclusion cage was present or absent. This criterion was based on our observation of significantly higher numbers of first instars beneath predator exclusion cages at South Channel compared to Pacman (see

Results: Megalopal settlement and density of first instars). Our goal here was to define the relative importance of postlarval supply on subsequent relative density of $J1$ in the absence of predation. The assumption of equal slopes (Underwood 1981) was met in all data sets, as evidenced by the lack of significant interaction between substrate and larval supply on $J1$ density. As above, Fisher's transformation (Zar 1984) indicated that exponential and power functions did not significantly improve the fit of the megalopal or first instar data over linear functions (all $P > 0.21$; except for the relationship between settlement on artificial substrates and density of first instars, which was best fit by a hyperbolic, second-order polynomial: Fig. 9F).

Population structure

We quantified the density of recruits in each study site during the summer of 1992. This allowed us to assess the relative importance of postlarval supply and initial patterns of settlement as determinants of distribution and abundance of YOY crabs in these intertidal habitats at the end of the summer growing season. Towards the end of the summer, intertidal YOY crabs gradually move to subtidal habitats (Gunderson et al. 1990) where they are able to avoid most predators by virtue of their greater size (>25 mm CW; Armstrong 1991). Thus, the majority of early juvenile crabs remain in the intertidal until they reach a relative refuge in size from predation. Therefore, we assumed that any significant reduction in the numbers of YOY crab during the summer at Pacman and South Channel was due primarily to predation rather than emigration.

Crabs in the shell habitat were sampled by hand excavating all shells within a 30 cm $\times$ 30 cm area and 5 cm into the substrate beyond the shell–sediment interface. Shell material was washed in a bucket containing estuarine water, and the elutriate filtered through a 1-mm mesh-size screen. Additional samples were taken similarly from open tideflat areas. We quantified the density of YOY crab at each site on 4 separate occasions: 14–16 May, 13–15 June, 12–14 July, and 11–13 August. Six to fifteen replicate 30 cm $\times$ 30 cm quadrats were taken at each Site (shell mitigation site vs. open tideflat) within a Location (Pacman vs. South Channel). The density of 0+ crab (crabs/0.1 m^2) served as the response variable in a three-way fixed-factor ANOVA model with Site, Location, and Time (May, June, July, August) as factors.

RESULTS

Environmental conditions

On 3–4 May 1992, at the beginning of our water column sampling and field settlement experiments in Grays Harbor, the wind was blowing from the west-northwest WNW; ($\approx$300°) at $\approx$13–15 m/s (25–30 knots). From 5–6 May, although the wind continued to blow from the WNW ($\approx$280°), there was an appreciable

TABLE 1. Effects of sampling date (4, 6, and 7 May), site (open tideflat vs. shell mitigation site), and location (Pacman vs. South Channel) upon three megalopal water column supply response variables: (1) log-transformed $(x + 1)$ megalopal densities (measured as no. per cubic metre per hour) collected with plankton nets moored above the bottom; (2) flux of megalopae over a fixed area of bottom with moored plankton nets; and (3) megalopal densities collected with neuston nets in surface slicks. Analysis was by a three-way ANOVA model III. NA = not applicable.

Source of variation	Megalopal densities (plankton nets)			Megalopal flux (plankton nets) (no./h)			Megalopal densities (neuston nets in slicks) (no./m³)		
	df	F	P	df	F	P	df	F	P
Date (random factor)	2, 12	0.07	0.93	2, 12	2.16	0.32	2, 18	0.84	0.54
Site (fixed factor)	1, 12	0.61	0.45	1, 12	7.14	0.02	NA	NA	NA
Location (fixed factor)	1, 12	11.31	0.01	1, 12	34.57	0.01	1, 18	20.15	0.01
Date × Site	2, 12	0.32	0.73	2, 12	0.50	0.62	NA	NA	NA
Date × Location	2, 12	0.22	0.80	2, 12	7.36	0.01	2, 18	7.19	0.01
Site × Location	1, 12	0.01	0.98	1, 12	1.14	0.31	NA	NA	NA
Date × Site × Location	2, 12	1.42	0.28	2, 12	2.21	0.15	NA	NA	NA

drop in wind speed from 13–15 m/s to 5–8 m/s. Towards the end of the tide series on 7–8 May, wind speed increased from 5–8 m/s to 13–15 m/s. During the study period surface salinity was 17 g/kg and temperature averaged 14°C at both locations. There was no significant difference in above-bottom current speed, as measured by the flowmeters, between Pacman (13.3 cm/s) and South Channel (12.5 cm/s; t test: $t = 0.26$, df $= 22$, $P = 0.80$) when averaged over the three plankton net sampling dates.

Postlarval supply

Megalopae in the water column were 2.5 to 6 times more abundant at South Channel than at Pacman, regardless of the technique used to measure larval supply. The plankton nets moored just above the bottom indicated megalopal density was significantly higher at South Channel than at Pacman (Table 1, Fig. 2A,B). Megalopal densities did not differ between the shell mitigation sites and open tideflats, nor among the three sampling dates (Table 1, Fig. 2A,B). None of the interaction effects were significant (Table 1). However, the plankton nets indicated that megalopal flux across a fixed area of bottom was significantly higher over the open tideflats compared to the shell mitigation sites (Table 1, Fig. 2C,D), and varied significantly according to sampling date (Table 1). However, a significant date × location interaction effect precluded contrasts across the location main effect (Underwood 1981). The interaction effect was due to significantly higher numbers of megalopae at South Channel compared to Pacman on 4 May and 7 May, compared to no difference between locations on 6 May ($P < 0.05$, Ryan's Q test; Fig. 2C).

The use of a hand-held dip net and small boat allowed us to sample directly along the center of a surface slick regardless of the degree to which the slick meandered. Megalopal density in surface slicks varied significantly according to location (Table 1); however, a significant date × location interaction effect precluded contrasts across the location main effect. The interaction effect was similar to that observed for megalopal

flux: significantly higher megalopal density on 4 and 7 May compared to no difference between locations on 6 May ($P < 0.05$, Ryan's Q test; Fig. 2E). Megalopal density in the neuston averaged 1 individual/m³ at both locations, but was 6 individuals/m³ at South Channel early in the tide series of the May new moon (Fig. 2E).

Megalopal settlement and density of first instars

The initial patterns of settlement by megalopae on floating, artificial substrates and benthic substrates tended to mirror those observed in the plankton.

Artificial substrates.—The mean number of megalopae that settled on artificial substrates was significantly higher at South Channel than at Pacman (three-way ANOVA: df $= 1$, 38, $F = 26.63$, $P = 0.01$), and significantly higher on 4 and 5 May, compared to later dates during the new-moon sampling period (three-way ANOVA: df $= 4$, 38, $F = 12.09$, $P = 0.01$; Ryan's Q multiple comparison test, Fig. 3A, B). On average, megalopal settlement was twice as high at South Channel compared to Pacman (Fig. 3). Settlement also decreased 75% from an average of 4 to 1 megalopae per substrate per day going from 4 May to 7 May, respectively (Fig. 3). There were no significant differences in megalopal settlement between the shell mitigation sites and open tideflats (three-way ANOVA: df $= 1$, 38, $F = 2.96$, $P = 0.09$; Fig. 3A, B), nor were there any significant interaction effects (all $P > 0.08$).

Benthic substrates.—The mean number of megalopae that settled on natural substrates in plastic trays was significantly higher in oyster shell than mud (five-way ANOVA: df $= 1$, 32, $F = 41.2$, $P = 0.0001$; generally 8 to 10 times higher, Fig. 4), significantly higher during the first experiment compared to the second experiment (five-way ANOVA: df $= 1$, 32, $F = 10.2$, $P = 0.003$; Fig. 4A), and significantly higher at South Channel compared to Pacman (five-way ANOVA: df $= 1$, 32, $F = 15.8$, $P = 0.001$; Fig. 4B). Megalopal settlement did not differ according to whether the trays were located in the open tideflat or shell mitigation sites (five-way ANOVA: df $= 1$, 32, $F = 1.6$,
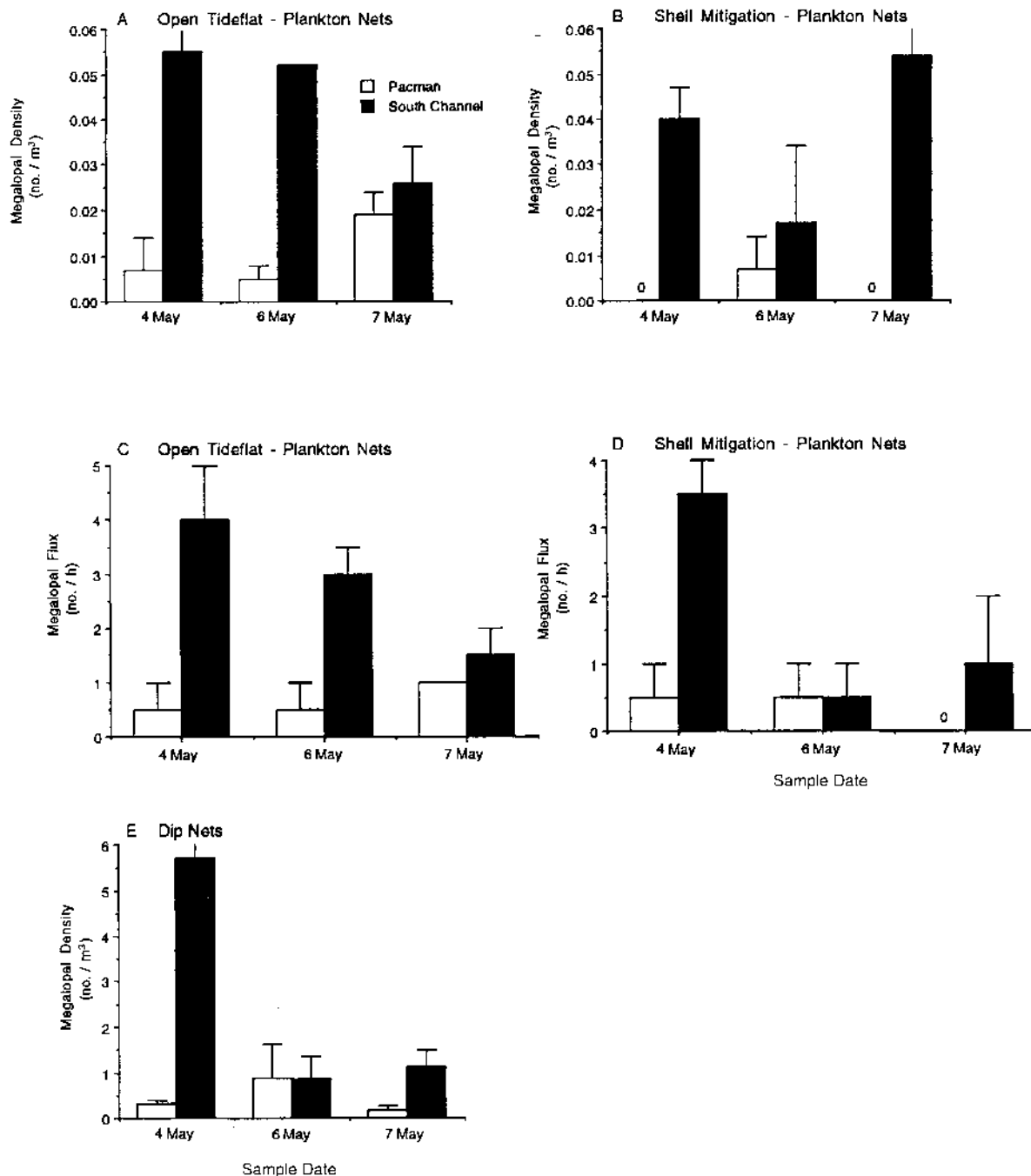
FIG. 2. Water column supply of Dungeness crab megalopae measured on three dates during the new-moon settlement pulse in May 1992, as a function of location (South Channel vs. Pacman) and: (A) megalopal density measured with plankton nets moored above the open tideflats; (B) megalopal density measured with plankton nets moored above the shell mitigation sites; (C) megalopal flux measured with plankton nets moored above the open tideflats; (D) megalopal flux measured with plankton nets moored above the shell mitigation sites; and (E) megalopal density measured with dip nets pushed through surface slicks that bisected both sites. Graphs show means and 1 SE. Note different scales on y-axes.

$P = 0.21$; Fig. 4C), nor whether a predator exclusion cage was present or absent (five-way ANOVA: df = 1, 32, $F = 0.32$, $P = 0.58$; Fig. 4D). None of the interaction effects were significant (all $P > 0.04$; Coch-

ran's C test rejected homogeneous variances at $P < 0.004$).

We quantified the density of $J1$ instars in the settlement experiment to examine the correspondence be-

A Open Tideflats
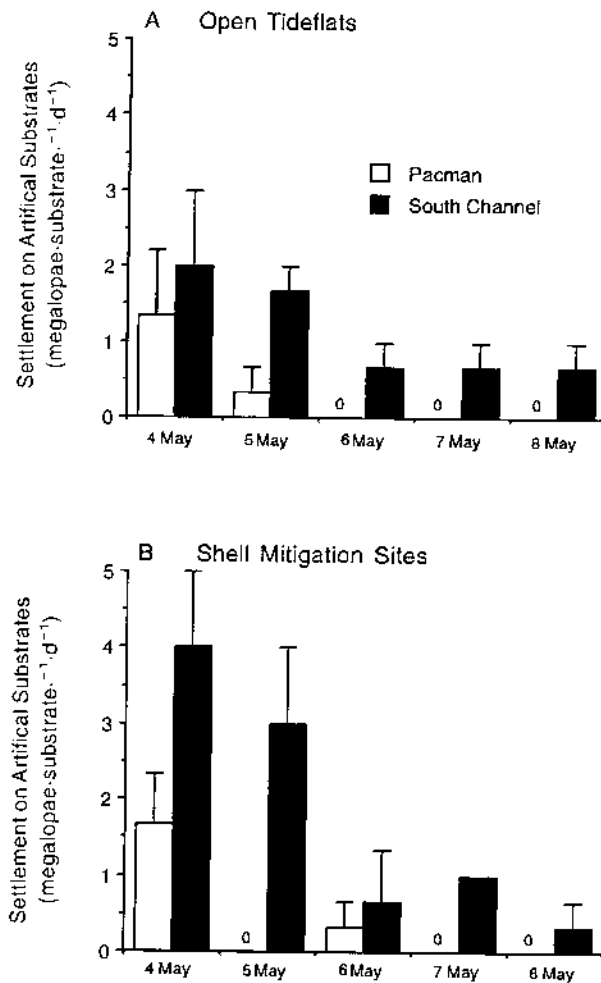

B Shell Mitigation Sites

FIG. 3. Settlement of Dungeness crab megalopae on floating, synthetic fiber substrates on six dates during the new moon settlement pulse in May 1992, as a function of location (South Channel vs. Pacman) and whether substrates were moored above the (A) open tideflats, or (B) shell mitigation sites. Graphs show means and 1 SE.

tween initial patterns of megalopal settlement, and subsequent densities of crabs during a 48-h period. Because $J1$ are motile, their density after 48 h not only reflects megalopal settlement, but also includes migration as well as losses due to natural mortality. The mean number of $J1$ in settlement trays was significantly higher in shell vs. mud substrates (Fig. 5, Table 2), reflecting the substrate-specific trend in settlement observed for megalopae (compare Figs. 4 and 5). There was no significant difference in the numbers of first instars occupying substrate-filled trays in the open tideflats vs. shell mitigation sites (Fig. 5C, Table 2), and in general $J1$ were about 3.5 times more dense in shell than mud after 48 h. This trend was also consistent with the previous result of nonsignificant differences in megalopal settlement between the shell mitigation sites and open tideflats. The number of $J1$ varied significantly according to sampling date (first experiment vs. second

experiment), location (Pacman vs. South Channel) although this difference was slight, and whether a predator exclusion cage was present or absent (Fig. 5, Table 2). However, there were significant substrate × date and location × cage interaction effects, which precluded contrasts across main effects upon which the interactions were based (Underwood 1981). The significant substrate × date interaction effect was due to significantly higher numbers of $J1$ in shell during the first experiment compared to the second, whereas there was no significant difference between the first and second experiments in mud ($P < 0.05$, Ryan's Q test; Fig. 5B). The significant cage × location effect was due to significantly higher numbers of $J1$ beneath predator exclusion cages compared to open plots at South Channel, whereas no such difference was found at Pacman ($P < 0.05$, Ryan's Q test; Fig. 5E). All remaining interaction effects were not significant (Table 2).

Tray effects.—We compared megalopal settlement in substrate-filled plastic trays with settlement on substrates that were flush with the sediment surface to assess potential positive or negative effects these trays may have had upon settlement. There was no significant difference between the number of megalopae that settled in oyster shell placed in plastic trays above the sediment surface at the shell mitigation site and settlement in shell that was flush with the sediment surface (Fig. 6; four-way ANOVA: df = 1, 16, $F = 0.01$, $P = 0.93$). However, significantly more megalopae settled in shell at South Channel than at Pacman ($≈7$ times as many; four-way ANOVA: df = 1, 16, $F = 39.34$, $P = 0.01$), similar to the trend observed for settlement in plastic trays only (compare Figs. 4B and 6B). The presence or absence of predator exclusion cages had no significant effect upon the numbers of megalopae in shell substrates (Fig. 6C; four-way ANOVA: df = 1, 16, $F = 0.01$, $P = 0.93$). Although there was a significant date main effect (four-way ANOVA: df = 1, 16, $F = 26.02$, $P = 0.01$), a significant date × location interaction effect (four-way ANOVA: df = 1, 16, $F = 16.79$, $P = 0.01$) precluded contrasts across the date main effect. The date × location interaction was due to significantly higher densities of megalopae during the first experiment compared to the second at South Channel, whereas there was no difference in abundance of megalopae across experiments at Pacman (Fig. 6A; Ryan's Q multiple comparison test). All other interaction effects were nonsignificant (all $P > 0.37$). We were unable to evaluate potential biases associated with using plastic trays to measure settlement in mud because of the paucity of settlement on that substrate.

We compared the density of $J2$ in substrate-filled plastic trays with the density of crabs in plots that were flush with the sediment surface (inverted mesh buried in sediment and filled with shell or mud) to assess any positive or negative effects these trays may have had upon crab immigration. For shell substrates placed in the shell-mitigation site, there were significantly more
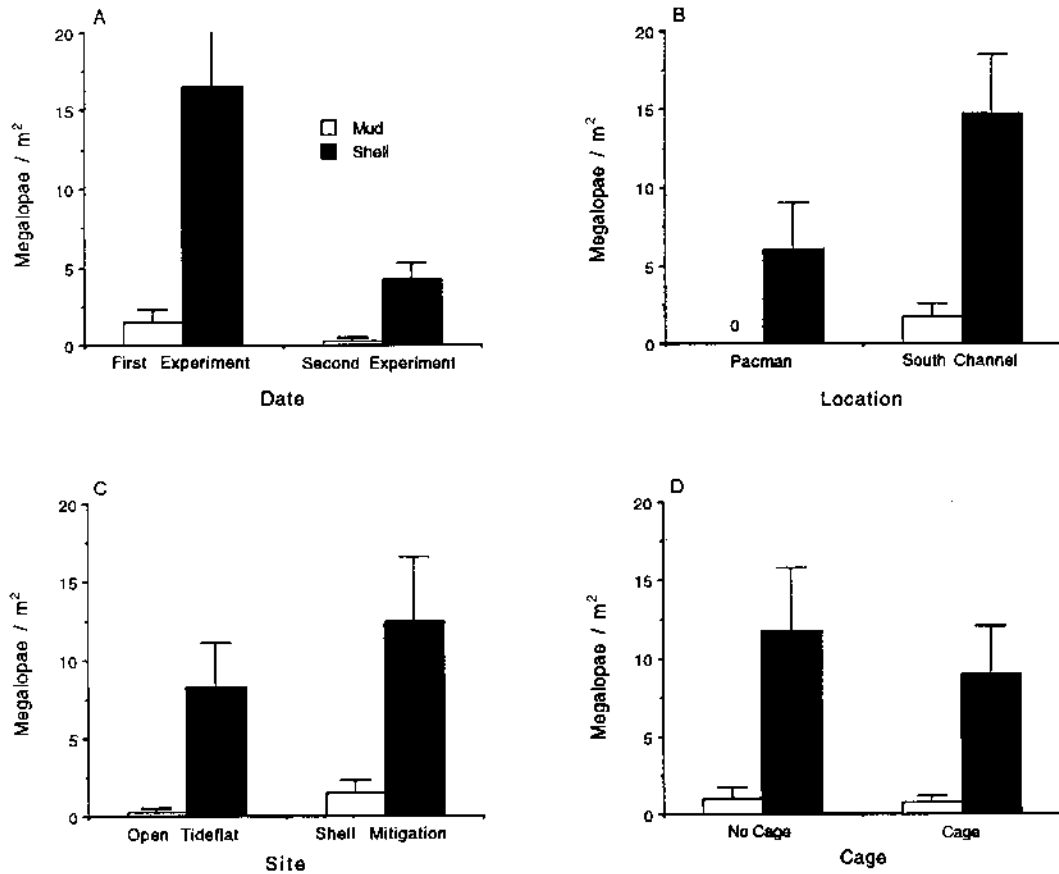
FIG. 4. Density of Dungeness crab megalopae in 1992 in shell- or mud-filled plastic trays placed on the tideflat surface, as a function of (A) sampling Date (first experiment [3–5 May] vs. second experiment [6–8 May]); (B) geographic Location (Pacman vs. South Channel); (C) Site (shell mitigation sites vs. open tideflats); and (D) presence vs. absence of a predator exclusion Cage. Data were back-transformed and pooled for graphical purposes. Graphs show means and 1 SE.

J2 in shell which was flush with the sediment surface compared to the shell-filled plastic trays (Fig. 7; four-way ANOVA: df = 1, 16, F = 17.19, P = 0.01), significantly more J2 at Pacman compared to South Channel (Fig. 7C; four-way ANOVA: df = 1, 16, F = 31.37, P = 0.01), and significantly more J2 during the second experiment compared to the first experiment (Fig. 7A; four-way ANOVA: df = 1, 16, F = 12.70, P = 0.01). The presence or absence of predator exclusion cages had no significant effect upon the numbers of J2 in shell substrates (Fig. 7E; four-way ANOVA: df = 1, 16, F = 3.05, P = 0.10). None of the interaction effects were significant (all P > 0.07).

For mud substrates placed in the open tideflats, there were significantly more second instars in mud-filled plastic trays compared to mud that was flush with the sediment surface (Fig. 7; four-way ANOVA: df = 1, 13, F = 8.51, P = 0.01), opposite to the pattern observed in shell (compare parts A, C, E and B, D, F of Fig. 7). There were also significantly more J2 at Pacman than at South Channel (Fig. 7D; four-way ANOVA: df = 1, 13, F = 9.22, P = 0.01), similar to the trend observed for J2 in shell (compare parts C and D

of Fig. 7). There was no significant effect of either the predator exclusion cage or date upon the density of J2 in mud (Fig. 7B, F; four-way ANOVA: cage effect: df = 1, 13, F = 0.29, P = 0.60; date effect: df = 1, 13, F = 2.58, P = 0.13). None of the interaction effects were significant (all P > 0.09).

Relationship between postlarval supply, settlement, and density of first benthic instars

Megalopal settlement on artificial substrates reflected postlarval supply as measured in the water column (moored plankton nets) and in surface slicks (neuston nets). There was a positive and significant relationship between both the density of megalopae in the water column and flux of megalopae past a given point, as measured by moored plankton nets, and megalopal settlement on artificial settlement substrates (Fig. 8A, B). Similarly, there was a positive and significant relationship between density of megalopae in surface slicks, as measured by neuston nets, and megalopal settlement on artificial substrates (Fig. 8C).

Megalopal settlement on natural substrates also reflected water column postlarval supply. For example,
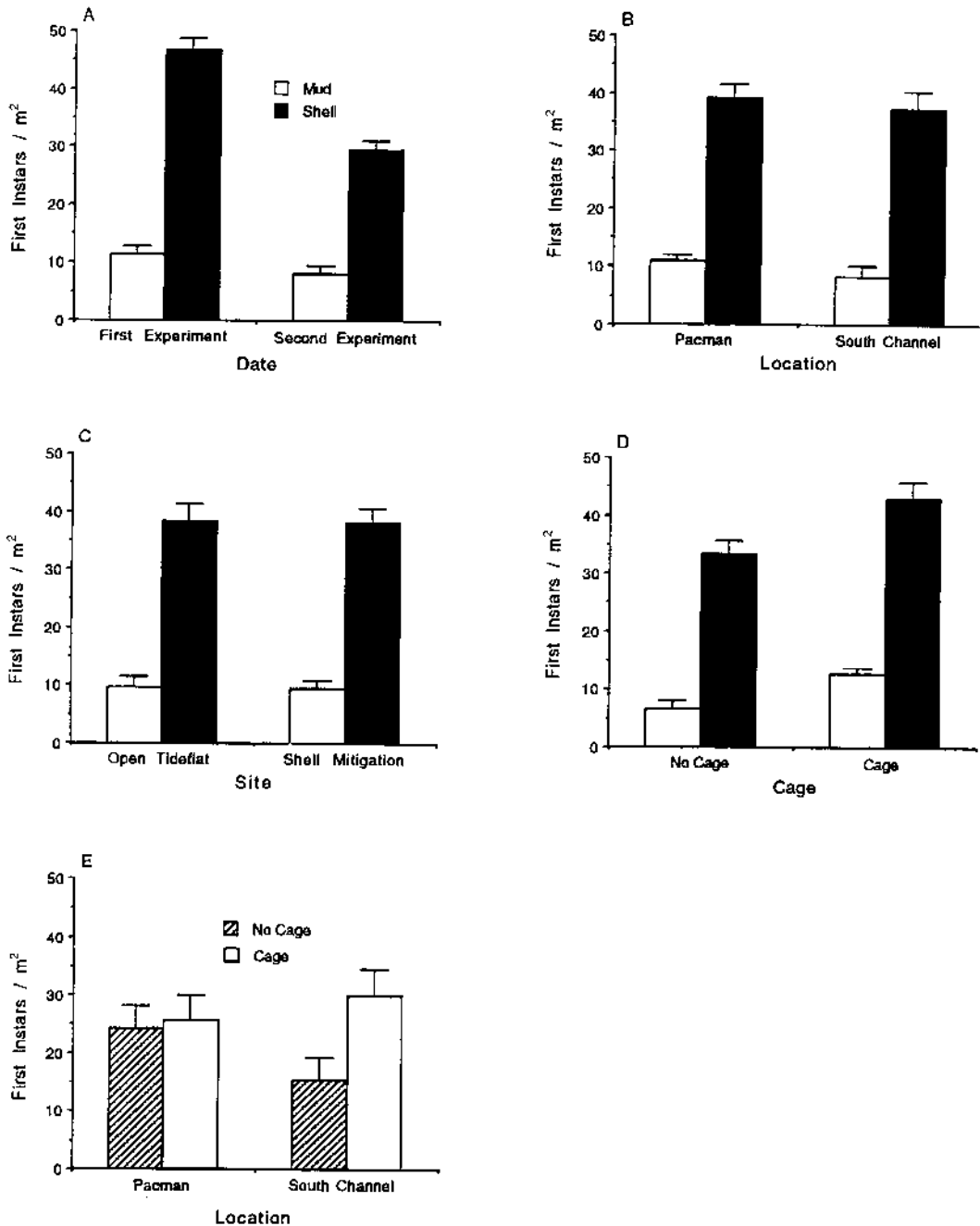
FIG. 5. Density of first benthic instar Dungeness crab (J1, carapace width 5–8 mm) in 1992 in shell- or mud-filled plastic trays placed on the tideflat surface, as a function of (A) sampling Date (first experiment [3–5 May] vs. second experiment [6–8 May]); (B) geographic Location (Pacman vs. South Channel); (C) Site (shell mitigation sites vs. open tideflats); and (D) presence vs. absence of a predator exclusion Cage. Graph E illustrates a significant Cage × Location interaction effect (see Table 2 for significance levels). Data were pooled for graphical purposes. Graphs show means and 1 SE.

there was a positive relationship between megalopal settlement in mud- and shell-filled plastic trays, and both the density and flux of megalopae (Fig. 9A, B) above these substrates as measured with moored plankton nets (Table 3). There were also significantly higher numbers of megalopae in shell-filled trays vs. mud-

filled trays (Fig. 4, Table 3). Similarly, there was a positive relationship between megalopal settlement in substrate-filled plastic trays and density of megalopae in surface slicks (measured by neuston nets) within the vicinity of the settlement trays (Fig. 9C, D, Table 3). There were significantly more megalopae in shell vs.

TABLE 2. Effects of substrate type (oyster-shell vs. mud; sampling date (first experiment: 3–5 May 1992 vs. second experiment: 6–8 May 1992); site (open tideflat vs. shell mitigation site); location (Pacman vs. South Channel); and presence or absence of a predator exclusion cage; upon the number of first benthic instars ($J1$) residing in substrate-filled, plastic trays (0.25 m²) placed on the tideflat surface for 48 h. Analysis was by a five-way ANOVA model I.

Source of variation	MS	df	F	P
Substrate	812.25	1	684.0	0.01
Date	105.06	1	88.47	0.01
Site	0.06	1	0.05	NS
Location	5.06	1	4.26	0.04
Cage	64.00	1	53.89	0.01
Substrate × Date	49.00	1	41.26	0.01
Location × Cage	42.25	1	35.58	0.01
Error*	1.19	32		

* All other interactions were nonsignificant (all $P > 0.18$).

mud substrates (Fig. 4, Table 3), and there was a positive relationship between settlement on artificial substrates and settlement in mud- and shell-filled plastic trays (Fig. 9E, F, Table 3). Thus, settlement on artificial substrates appears to provide a useful index and convenient means of measuring both water column supply and magnitude of megalopal settlement.

In general, there was a significant positive correlation between postlarval supply and the density of benthic $J1$ only when predators were excluded from the settlement trays. For example, there was no correlation between postlarval density or flux, as measured by plankton nets, and density of $J1$ in mud- and shell-filled trays when a predator exclusion cage was absent (Table 3). However, when a predator exclusion cage was present, there was a positive correlation between both postlarval density and flux (Fig. 10A, B), and the density of $J1$ (Table 3). Similarly, there was a positive correlation between postlarval density, as measured with neuston nets, and the density of $J1$ in mud and shell only in the presence of predator exclusion cages (Figs. 10C, D, Table 3). This pattern held for the correlation between megalopal settlement on floating, artificial substrates and the density of $J1$ as well (Fig. 10E, F, Table 3). In all cases, there were significantly higher numbers of megalopae and $J1$ in shell vs. mud substrates (Fig. 10, Table 3).

Population structure

Early juvenile Dungeness crab inhabiting intertidal habitats within the vicinity of Pacman and South Channel were primarily in shell habitat. During the summer of 1992 using the excavation technique, we found a mean density of 55.8 ± 3.5 YOY crabs/m² (mean ± 1 SE; $N = 115$ excavation samples) in the shell mitigation sites, compared to 0.4 ± 0.3 YOY crabs/m² ($N = 91$ excavation samples) in the open tideflats. These crabs comprised a mixture of $J1$ to $J5$ crabs (see below), reflecting a molt interval of ≈2–3 wk. Hence, we re-

stricted our statistical contrasts to crab density measurements in shell.

To examine the correspondence between Location differences in settlement by megalopae and subsequent abundance of $J1$ in the shell mitigation sites, we quantified the density of $J1$ 7 d after the new-moon settlement pulse in May 1992. In this case, significantly more first instars were found at Pacman (mean ± 1 SE = 62.0 ± 11 $J1$/m², $N = 14$ excavation samples) than at South Channel (49.0 ± 6.0 $J1$/m², $N = 15$ excavation samples; two-tailed variance-ratio test: $F = 29.5$, df = 27, $P = 0.05$). Although this result is of borderline
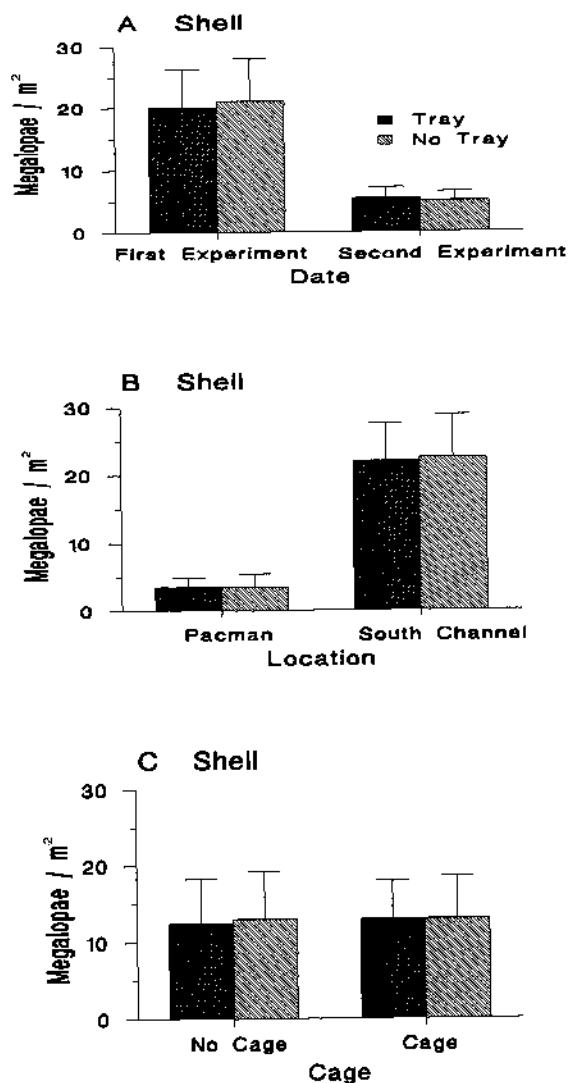

FIG. 6. Density of Dungeness crab megalopae in 1992 in oyster shell flush with the tideflat surface (No Tray), or in plastic trays 9 cm above the tideflat surface (Tray), as a function of (A) sampling Date (first experiment [3–5 May] vs. second experiment [6–8 May]); (B) Location (Pacman vs. South Channel) and (B) presence vs. absence of a predator exclusion Cage. Data were back-transformed for graphical purposes. Graphs show means and 1 SE.
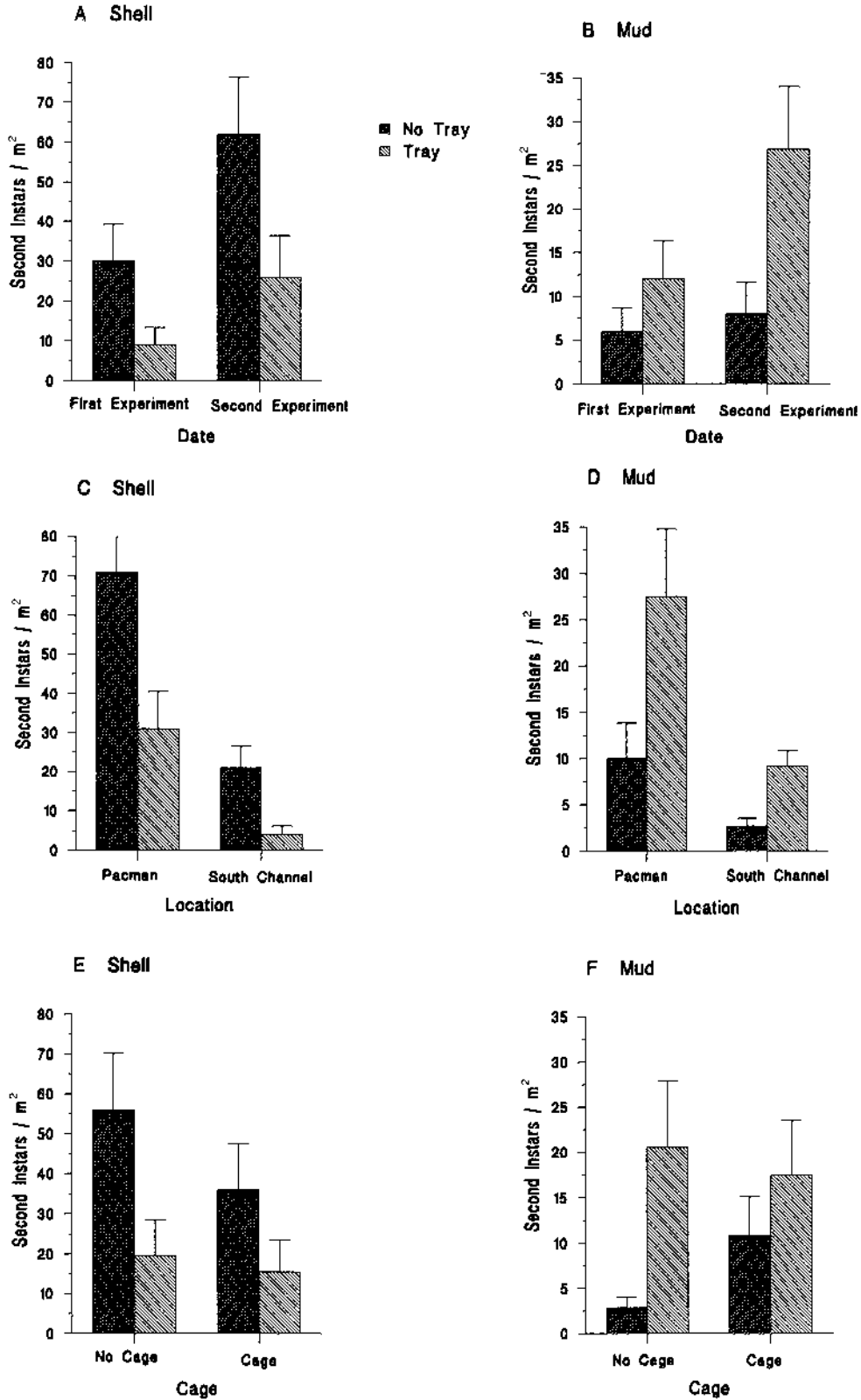
FIG. 7. Density of second benthic instar (J2) Dungeness crab in 1992 in substrates flush with the tideflat surface (No Tray), or in plastic trays 9 cm above the tideflat surface (Tray), as a function of sampling Date (first experiment [3–5 May] vs. second experiment [6–8 May]) using (A) oyster-shell or (B) mud; Location (Pacman vs. South Channel) using (C) oyster-

significance (i.e., $P = 0.05$), we conclude that it is biologically meaningful given that the statistical power of the test (see Zar 1984:137) was low (≈ 0.55). This geographic trend in abundance was exactly opposite to that observed for megalopae (Fig. 4B). During the summer growing season, early juvenile crabs ranged in size from a mean $J1$ size (carapace width) of 5.8 mm in May to 23.7 mm as $J5$ instar in August. The density of early juvenile crab in the two intertidal shell mitigation sites decreased significantly during the summer (Date: two-way ANOVA; $F = 23.27$, df $= 3$, 107, $P = 0.0001$), with significantly higher densities in May and June compared to July and August (Fig. 11; Ryan's Q multiple comparison test). There was no significant difference in the density of YOY crabs between Pacman and South Channel (Fig. 11; Location: two-way ANOVA; $F = 1.05$, df $= 1$, 107, $P = 0.31$), nor was there a significant interacton effect (Date $\times$ Location: $F = 1.73$, df $= 3$, 107, $P = 0.17$).

DISCUSSION

Although most animals have complex life cycles (e.g., frogs, salamanders, fish, holometabolous insects, and most marine organisms), the relative contribution of spatially separated life history phases to ultimate patterns of juvenile and adult distribution and abundance are seldom known. In marine systems, spatially separated life history phases such as planktonic larvae and benthic juveniles are often linked by physical transport mechanisms such as wind-driven surface currents or tidal transport. The linkage between physical transport processes and local or regional variation in larval supply is of fundamental interest to ecologists working in marine systems.

Postlarval supply, substrate selection behavior, and post-settlement survival jointly explained the observed distribution and abundance patterns of early juvenile Dungeness crab in two intertidal locations in Grays Harbor, Washington during this study. Our ability to partition the relative importance of these components to recruitment success of Dungeness crab was greatly facilitated by our capacity to anticipate the arrival of swarms of megalopae into the estuary, and the ease with which these large postlarvae (3 mm diameter) could be quantified in the water column and in intertidal settlement substrates. Moreover, the shell mitigation project conducted by the U.S. Army Corps of Engineers, at a cost of nearly 10^6, allowed us to assess substrate selection behavior at two dramatically different spatial scales (0.25 m^2 vs. 4 ha). By using plankton nets moored over shell and mud habitats, and dip nets to sample neuston where megalopae are concentrated in surface slicks, we identified significantly high-

er numbers of megalopae in the water column at the southern portion of the estuary (South Channel) compared to the northern portion (Pacman). We attributed this difference to a buildup of megalopae in the south due to wind-driven surface currents flowing from the northwest to the southeast, since tidal current speeds were similar between locations. Moreover, there was no significant correlation between current speed above the bottom and flux of megalopae as measured by the plankton nets ($r = 0.27$, $N = 24$, $P = NS$).

The use of mud- and shell-filled plastic settlement trays and predator exclusion cages placed in the shell mitigation sites and open tideflats allowed us to examine the interactive effects of substrate type, type of substrate surrounding shell and mud settlement habitats, and predation upon patterns of settlement and survival. Megalopae actively chose to settle in oyster shell vs. mud habitats, irrespective of the scale at which these substrates were available (i.e., 0.25 m^2 vs. 3–5 ha). This inference stems from the findings of significantly higher numbers of megalopae in settlement trays containing shell, whether placed on the open tideflat or within large shell mitigation sites, compared to trays filled with mud. Exclusion of predators, as well as plastic settlement trays elevated 9 cm above the tideflat, had no effect on these initial patterns of settlement. Settlement patterns in both shell and mud also reflected the high supply of megalopae measured at South Channel. Settlement patterns on floating, synthetic-fiber substrates corroborated our measures of higher postlarval supply and settlement at South Channel compared to Pacman, and the lack of observed differences in these measures between the shell mitigation sites and open tideflats. Moreover, there was a positive correlation between settlement on floating artificial substrates, and postlarval supply (measured with plankton nets) and settlement on benthic substrates. Thus, megalopal settlement on artificial substrates appears to provide a useful index of natural postlarval supply and relative post-settlement density of megalopae.

Differences in megalopal settlement between South Channel and Pacman disappeared when we focused on recruitment success of $J1$ instars. In this case, post-settlement mortality at South Channel reduced $J1$ densities to levels similar to those observed at Pacman where postlarval supply was low. This predation inference stems from the findings of significantly higher numbers of $J1$ beneath predator exclusion cages at South Channel compared to Pacman where there was no significant cage effect. Moreover, there was a significant correlation between postlarval supply and density of $J1$ instars only when predators were excluded. If density-dependent emigration was the primary mech-

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shell or (D) mud; and presence vs. absence of a predator exclusion Cage using (E) oyster-shell or (F) mud. Note larger scale on y-axis for graphs A, C, and E. Data show means and 1 SE.

A   Plankton Nets versus Artificial Substrates

$y = -0.19x + 36.30 \quad R^2 = 0.72 \quad P = 0.03$

Postlarval Density
(megalopae / m³)

B   Plankton Nets versus Artificial Substrates

$y = 0.55x + 0.04 \quad R^2 = 0.98 \quad P = 0.0002$

Postlarval Flux
(megalopae / h)

C   Dip Nets versus Artificial Substrates

$y = 0.19x + 1.30 \quad R^2 = 0.97 \quad P = 0.0003$

Postlarval Density
(megalopae / m³)

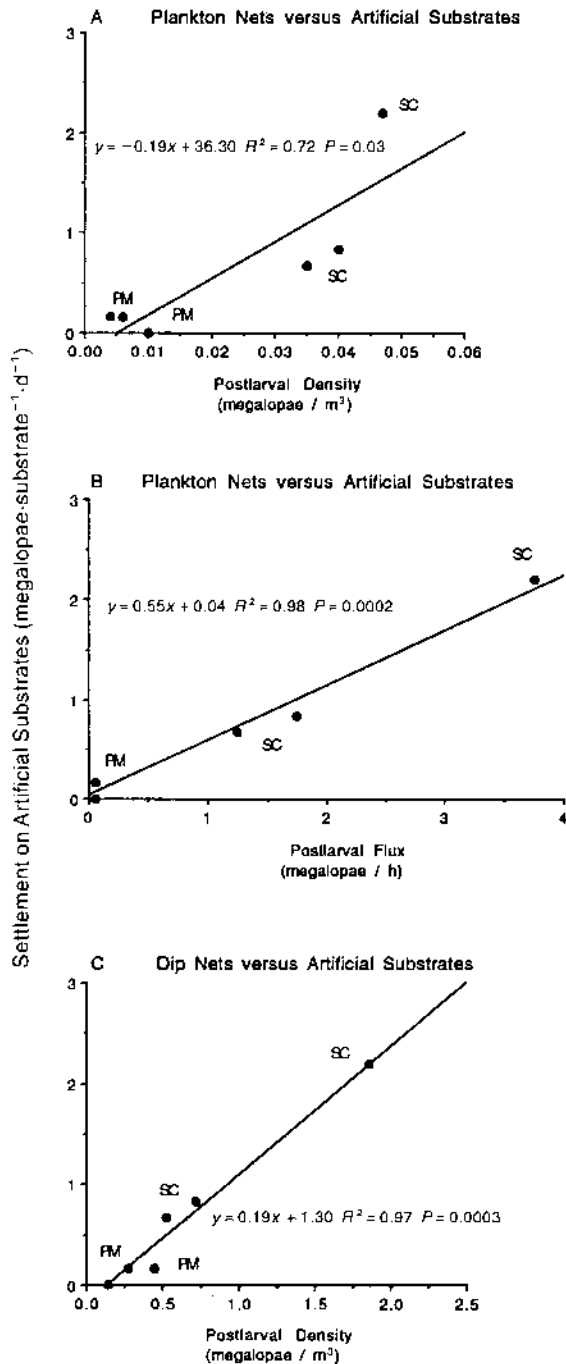Settlement on Artificial Substrates (megalopae·substrate⁻¹·d⁻¹)

FIG. 8. Relationship between postlarval supply (sampled on 4, 6, and 7 May), as measured with (A) moored plankton nets (mean megalopal density, measured daily at each site), (B) moored plankton nets (megalopal flux), and (C) neuston (dip) nets (megalopal density); and mean megalopal settlement on floating artificial substrates (sampled on 5, 7, and 8 May). Measurements at South Channel and Pacman are denoted by SC and PM, respectively.

anism responsible for decoupling postlarval supply and density of $J1$ instars, then there should have been no correlation between postlarval supply and density of $J1$ instars whether a predator exclusion cage was present or absent. Thus, although Dungeness crab megalopae actively select to settle in structurally complex shell habitats where survival is presumably enhanced, post-settlement mortality due to predation appears to conceal any recruitment patterns that may be related to high postlarval supply.

Wind-driven surface currents and postlarval supply

Strong flood tidal currents associated with spring tides during new-moon cycles seem the process whereby megalopae move from the outer coast into the mouth of the estuary. But, wind-driven surface currents appear to be a key factor controlling local (kilometre-scale) rates of Dungeness crab larval supply within Grays Harbor. Localized oceanographic features in shelf and estuarine waters can greatly influence the distribution and abundance of benthic larvae (Alldredge and Hamner 1980, Kingsford and Choat 1986, Oliver and Willis 1987, Clancy and Epifanio 1989). Specific oceanographic features such as surface slicks formed by tidal intrusion fronts, internal waves, or Langmuir circulations can also influence the direction of larval transport (Shanks 1983, Hamner and Schneider 1986, Kingsford and Choat 1986, Kingsford et al. 1991). However, the overall importance of these oceanographic features relative to adjacent water masses in determining larval delivery rates to the benthos remains unclear.

During settlement pulses in Grays Harbor in 1992, surface slicks contained one order of magnitude higher density of megalopae than occurred in adjacent water masses (D. Eggleston, unpublished data). Additional observations indicated that surface drifters dropped seaward of frontal zones were quickly entrained in these features and were rapidly transported along the axis of a front during flood tide (D. Eggleston, unpublished data). Wind direction had a dramatic effect upon the path drifters tracked during flooding tides. For example, on days when the wind was blowing from the west-northwest (WNW), drifters consistently moved from the entrance of Grays Harbor to the extreme southern portion of South Bay (Fig. 1) during a single flood tide (D. Eggleston, unpublished data). These observations, combined with our field measurements of strong winds (13–15 m/s) blowing from the WNW on days corresponding to the settlement experiment (4 and 7 May), and no difference in above-bottom current speeds between locations during this time, are consistent with the notion that wind-driven surface currents were facilitating the accumulation of megalopae in surface slicks, resulting in higher postlarval supply to our South Channel location compared to Pacman (Fig. 1). An unequivocal test of this hypothesis would require concurrent measures of wind speed and direction, sur-
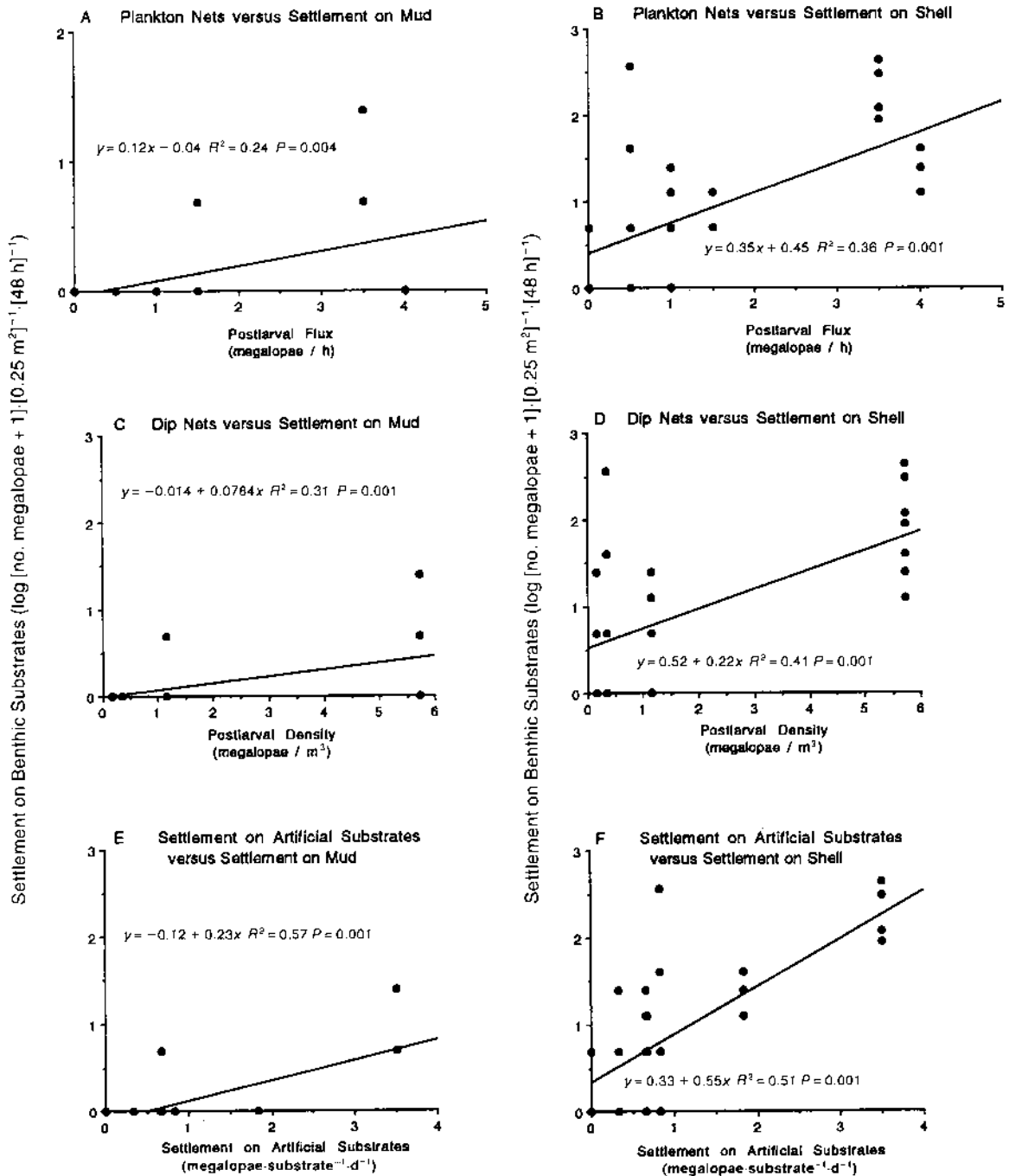
FIG. 9. (A and B) Relationship between mean postlarval flux as measured with moored plankton nets (sampled on 4 and 7 May), and density of megalopae in 16 0.25-m² trays, each filled with (A) mud or (B) shell. (C and D) Relationship between mean postlarval density as measured with neuston (dip) nets (sampled on 4 and 7 May), and density of megalopae in 16 trays, each filled with (C) mud or (D) shell. (E and F) Relationship between megalopal settlement on artificial substrates (mean settlement on 4–5 May and 7–8 May) and density of megalopae in 16 trays filled with (E) mud or (F) shell. The regression in each figure represents 32 individual data points (2 Sites × 2 Locations × 2 Replicates × 2 Dates × Cage vs. No Cage); however, many of these have the same x and y values, which masks numerous points in some instances. See Table 3 for additional significance levels associated with the regression of settlement on artificial substrates vs. settlement on natural substrates.

TABLE 3. Results from the analysis of covariance of postlarval supply (covariate) and substrate type (mud vs. shell) on the numbers of megalopae (transformed as log[x + 1]) or first benthic instars in substrate-filled settlement trays.

Benthic response variable	Regression against postlarval supply			Substrate effects			Substrate × postlarval supply interaction		
	df	MS	F	df	MS	F	df	MS	F
A) Postlarval density measured with plankton nets									
Megalopae	1, 60	3.45	10.69‡	1, 60	10.21	31.68‡	1, 60	0.83	2.56 NS
First instars: No cage	1, 28	13.68	3.00 NS	1, 28	457.53	100.47‡	1, 28	0.25	0.05 NS
First instars: Cage	1, 28	22.22	6.45†	1, 28	357.78	103.86‡	1, 28	0.51	0.15 NS
B) Postlarval flux measured with plankton nets									
Megalopae	1, 60	6.51	25.25‡	1, 60	10.21	39.64‡	1, 60	1.65	6.41 NS^v
First instars: No cage	1, 28	4.82	1.23 NS	1, 28	357.78	91.44‡	1, 28	4.82	1.23 NS
First instars: Cage	1, 28	40.02	11.53†	1, 28	457.53	131.86‡	1, 28	4.27	1.23 NS^v
C) Postlarval density measured with dip nets									
Megalopae	1, 60	7.57	31.79‡	1, 60	10.21	42.88‡	1, 60	1.75	7.36 NS'
First instars: No cage	1, 28	1.86	0.46 NS	1, 28	357.78	89.53‡	1, 28	5.44	1.36 NS
First instars: Cage	1, 28	47.22	15.16‡	1, 28	457.53	146.85‡	1, 28	6.98	2.24 NS
D) Postlarval supply measured with artificial settlement substrates									
Megalopae	1, 60	10.58	55.93‡	1, 60	10.21	54.02‡	1, 60	1.70	8.99 NS^v
First instars: No cage	1, 28	0.15	0.40 NS	1, 28	357.78	92.52‡	1, 28	10.76	2.78 NS
First instars: Cage	1, 28	51.01	17.97‡	1, 28	457.53	161.18‡	1, 28	10.94	3.85 NS

NS: $P > 0.05$; † $P < 0.017$; ‡ $P < 0.0002$.
NS': $P > 0.007$ (Cochran's C test rejected homogeneous variances at $P < 0.007$).
NS^v: $P > 0.004$ (Cochran's C test rejected homogeneous variances at $P < 0.004$).

face and above-bottom current speed and direction, and postlarval supply under varying wind regimes. Thus, future attempts to integrate the dynamics of postlarval and juvenile survival in understanding recruitment variation in local populations of Dungeness crab should incorporate oceanographic processes that modify postlarval supply rates.

Mechanisms underlying habitat-specific abundance of crabs

Megalopal abundance was generally 3–4 times higher in shell habitats vs. mud, irrespective of the particular treatment combination considered (e.g., Tray, Cage, Site, Location, Date; Figs. 4 and 6). These measurements are consistent with our previous observations in Grays Harbor (Gunderson et al. 1990, Jamieson and Armstrong 1991). There are four possible explanations for this pattern, which are not mutually exclusive: (1) enhanced passive deposition of megalopae in shell habitat due to an increase in benthic boundary layer shear stress leading to reduced current speeds (e.g., Butman 1987, Wright et al. 1991); (2) higher postlarval supply over shell habitats than mud; (3) enhanced post-settlement survival in shell due to its refuge capacity; and (4) active selection for shell by megalopae (e.g., Fernandez et al. 1993b).

We argue against the passive deposition hypothesis as a mechanism explaining the high settlement patterns in shell based on several lines of evidence. First, recent laboratory experiments indicate that Dungeness crab megalopae prefer to settle on oyster shell instead of mud (Fernandez et al. 1993b), and can easily swim and maneuver in turbulent boundary layers encountered above oyster shell, even at the highest current velocities

(10–40 cm/s) found in Grays Harbor during tidal exchange (Fernandez et al. 1994). Second, we presumed that if passive deposition was responsible for the high settlement patterns observed in shell, this effect would be most apparent for substrates placed in the large, 3–5 ha shell mitigation site. In this case, there was no significant difference in megalopal settlement between the shell mitigation site and the open tideflat, irrespective of substrate type. Thus, passive deposition does not appear to explain much of the variation in settlement patterns observed in this study.

Based on the results of our plankton measurements, we can also eliminate the second mechanism of differential postlarval supply based on our general findings of no significant difference in postlarval supply, whether measured with plankton nets or neuston nets, between the shell mitigation sites and open tideflats. Additional support for this inference is provided by megalopal settlement patterns on standardized artificial substrates, which were similar between sites.

Although shell habitat probably enhances immediate post-settlement survival of megalopae compared to mud, it does not appear to explain much of the substrate-specific variation in megalopal densities observed. For example, if settlement rates, time to metamorphosis, and frequency of molting to $J1$ were similar in mud and shell habitats, and the refuge provided by shell was primarily responsible for the high numbers of post-settlement megalopae in this habitat, we would have expected to see a cage × substrate interaction effect whereby abundance of megalopae would be enhanced in mud habitats containing a predator exclusion cage. However, the presence of a predator exclusion cage did not enhance survival of megalopae in mud or
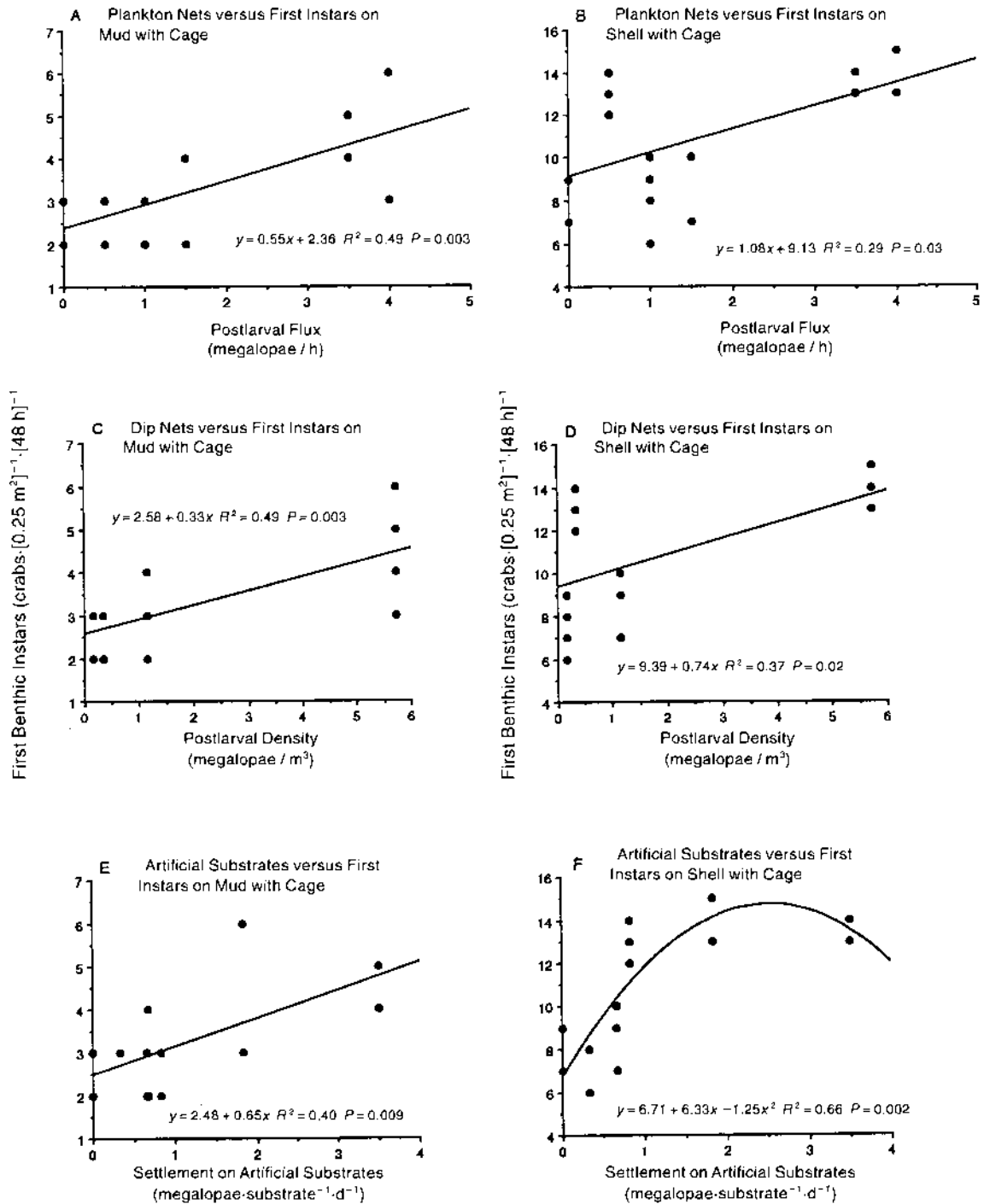
FIG. 10. (A and B) Relationship between mean postlarval flux as measured with moored plankton nets (sampled on 4 and 7 May), and density of first benthic instars in 0.25-m² trays filled with (A) mud or (B) shell, both with predator exclusion cages. (C and D) Relationship between mean postlarval density as measured with neuston (dip) nets (sampled on 4 and 7 May), and density of first benthic instars in trays filled with (C) mud or (D) shell, both with predator exclusion cages. (E and F) Relationship between mean megalopal settlement on artificial substrates (settlement on 4–5 May and 7–8 May), and density of first benthic instars in plastic trays filled with (E) mud or (F) shell, both with predator exclusion cages. Each figure represents 16 individual data points (2 Sites × 2 Locations × 2 Replicates × 2 Dates); however, many of these have the same x and y values, which masks numerous points in some instances. See Table 3 for additional significance levels associated with the regression of first instars against postlarval supply. Note larger scale on y axis for graphs B, D and F.
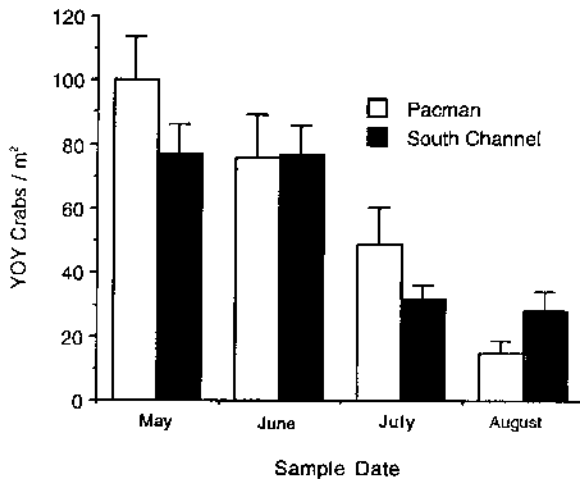
FIG. 11. Number of YOY (young-of-the-year) Dungeness crab in intertidal shell habitats during the summer of 1992 as a function of geographic location (South Channel vs. Pacman). Instar composition generally ranged from $J1$–$J2$ in May to $J4$–$J5$ in August. Graph shows means and 1 SE.

shell substrates, whereas cages increased abundance of $J1$ in both substrate types. A caveat to this line of evidence is that predator exclusion cages do not control for substrate-specific differences in frequency of molting and time to metamorphosis of recent settlers. Thus, final conclusions concerning the influence of shell and mud on frequency of molting and time to metamorphosis require laboratory investigations of these factors under realistic flow conditions. However, another line of evidence against this enhanced survival mechanism for megalopae concerns the positive and significant relationship between postlarval supply and settlement in shell and mud substrates. This result suggests that immediate post-settlement survival has very little, if any effect on abundance patterns of megalopae in shell and mud habitats. The time from settlement to metamorphosis into $J1$ is extremely short ($\approx$6–12 h). This short time interval prior to molting combined with their cryptic nature after settlement probably greatly reduces their detection by predators.

The propensity for megalopae to settle in shell and reside at high numbers in the absence of predator exclusion cages (this study), combined with the results from recent tethering experiments in Grays Harbor which demonstrated that survival of early juvenile crab is significantly higher in intertidal shell vs. mud or eelgrass habitats (Fernandez et al. 1993b), suggests that directed megalopal settlement in structurally complex habitats such as oyster shell enhances survival of juveniles more than settled megalopae. Settlement by most marine benthic invertebrates (e.g., hydroids, ascidians, echinoids, molluscs, barnacles) reflects habitat requirements of the adult stage (e.g., Meadows and Campbell 1972). However, for invertebrates such as decapod crustaceans with mobile adult stages, larvae

or postlarvae should select to settle in habitats where juvenile survival is high (e.g., Botero and Atema 1982, Herrnkind and Butler 1986). Reduced predation pressure in structurally complex habitats such as oyster reefs, should produce strong selective preferences for these habitats (e.g., Huffaker 1958, Hacker and Steneck 1990, Eggleston and Lipcius 1992).

The most parsimonious explanation for the settlement patterns observed in this study is active substrate selection by settling megalopae for shell habitats, even though active substratum selection behavior has seldom been demonstrated in the field (but see Hurlbut 1991 and references therein). Specific environmental cues are believed to trigger neural or hormonal processes that lead to settlement and metamorphosis in habitats that offer greater survival for subsequent life stages (Meadows and Campbell 1972). The spatial scale at which active choice may be possible depends on the settling-stage characteristics of the species such as sinking velocity, sensitivity to cues, and swimming capabilities under realized flow conditions (Boudreau et al. 1990). A previous laboratory flume study indicated that swimming and sheltering behavior of Dungeness crab megalopae in shell was unrelated to flow velocity, even at high current speeds of 40 cm/s (Fernandez et al. 1994). Dungeness crab megalopae in this study responded similarly to oyster shell and mud placed in 0.25-m² trays irrespective of whether trays were placed in 3–5 ha of shell or mud. Since the oyster shell used in this study was azoic, it is likely that megalopae were responding more to a tactile stimulus (physical and hydrodynamic) rather than a chemical one in their choice of shell over mud.

Recent laboratory and field experiments on habitat selection by marine benthic invertebrates have demonstrated that the sensitivity of active settlement responses to boundary-layer flow conditions is species-specific. Habitat selection by larvae of the hydroid *Tubularium crocea*, the bryozoans *Bugula turrita* and *Schizoporella unicornis*, and the tube-building polychete *Hydroides dianthus* were studied in manipulated field flows in Great Harbor, Massachusettes, USA (Mullineaux and Garland 1993). Although boundary layer flows influenced settlement of all four species examined, the bryozoan *B. turrita* settled most prominently in regions of reduced shear stress, exhibiting settlement patterns that closely approximated predictions from a model of passive particle contact (Mullineaux and Garland 1993). Similarly, laboratory still-water and flume-flow experiments demonstrated that although near-bottom flow influenced settlement distributions of the bivalve *Mulina lateralis* and the polychete *Capitella* sp. I, hydrodynamic effects were greater for *M. lateralis* (Snelgrove et al. 1993). Numerous field studies have also demonstrated strong correlations between the distribution and abundance of relatively weak-swimming epifaunal species such as barnacles (Wethey 1986), scyphozoans (Keen 1987), and fora-

minifers (Mullineaux and Butman 1991), and various components of boundary layer flows. Conversely, larval settlement in decapod crustaceans is presumed to be primarily an active response to chemical or tactile cues (Botero and Atema 1982, Herrnkind and Butler 1986, Jensen 1989). Among invertebrates, decapods demonstrate the highest swimming speeds (e.g., Phillips et al. 1978, Calinski and Lyons 1983, Cobb et al. 1989, Luckenbach and Orth 1992, Fernandez et al. 1994). Thus, our use of active substrate selection behavior as a mechanism for explaining distribution and abundance patterns of Dungeness crab megalopae in intertidal shell vs. mud habitats is consistent with other studies of larval settlement in decapod crustaceans.

Relationship between postlarval supply, settlement, and density of juvenile crabs

The positive correlation between postlarval supply and settlement extended to $J1$ instars only in habitats where predators were excluded. These results suggest that mortality due to predation is a key factor regulating local population size of early juvenile Dungeness crab in intertidal habitats where postlarval supply is relatively high (perhaps in excess of local carrying capacity). Megalopal abundance was significantly higher at South Channel compared to Pacman, reflecting the higher postlarval supply in the southern portion of the estuary. However, once the number of $J1$ instars was reduced to similar levels at these two locations, equivalent but steadily decreasing densities persisted throughout the summer growing season. The decoupling of settlement patterns and density of $J1$ in the absence of predator exclusion cages took place within our 48-h sampling interval. Recruitment studies of marine benthic organisms seldom demonstrate such a short interval between settlement and sampling. Analogous situations where the relationship between initial settlement and subsequent recruitment is decoupled have been described for populations of bryozoans (Keough and Downes 1982), infaunal bivalves (Luckenbach 1984), barnacles (Connell 1985), sea urchins (Rowley 1989), colonial ascidians (Osman et al. 1992), and reef fishes (Jones 1990).

The effects of post-settlement competition for space, as well as habitat-specific differences in predation pressure or predator functional responses, probably influenced recruitment success and local population size in shell habitats in this study. Although we did not observe the exact behavioral mechanism responsible for decoupling settlement patterns and density of $J1$ instars, we hypothesize that it involves a combination of agonistic interactions and possibly cannibalism between first instars within a cohort, inter-cohort cannibalism (Fernandez et al. 1993a), and predation by demersal fishes. For example, laboratory observations indicate that $J1$ are very agonistic towards each other, and may exhibit cannibalism (Fernandez et al. 1993a). Moreover, recent field observations and manipulations

of crab density and food availablity in small shell plots on an open tideflat in Grays Harbor, demonstrated that early juvenile crab at high densities are agonistic towards each other and emigrate from shell plots even under conditions where food resources were enhanced (Iribarne et al., *in press*). Post-settlement competition in shell appears to be in response to limited space rather than food. When settlement in shell habitats is high, density-dependent agonistic interactions between $J1$ could lead to increased emigration from the interstices of the shell matrix, which could then lead to increased encounter rates with demersal predators. Sources of predation likely included fish such as staghorn sculpin (Armstrong 1991) and redtail surfperch, *Amphistichus rhodoterus* (G. Williams, University of Washington, *unpublished data*), as well as cannibalism by juvenile and adult crabs (Stevens et al. 1982). Recent calculations based on crab and sculpin population estimates, the proportion of sculpin diet containing crab, predator–prey size relationships, and sculpin-length-based daily consumption estimates indicate that a significant proportion (64%) of the first summer mortality of newly settled intertidal crab could be due to sculpin predation (Armstrong 1991). However, the predatory impact of transitory species such as salmonids also could be significant. Flood tide faunal surveys performed 2 wk after our study revealed significantly higher numbers of predatory fish and crabs at South Channel compared to Pacman (G. Williams, *unpublished data*). Moreover, stomachs from many of the fish collected during this time contained high amounts of $J1$ and $J2$ Dungeness crab (G. Williams, *unpublished data*). Cannibalism by $J2$ did not appear to be a major source of mortality of $J1$ since there were similar numbers of $J2$ in shell between open plots and plots with predator exclusion cages (Fig. 7E). Instars larger than $J2$ were absent from intertidal habitats during this time. This scenario suggests that differences in the density of $J1$ due to variable settlement, combined with habitat-specific differences in the abundance or functional response of predators, should be incorporated into models of early juvenile crab survival in intertidal habitats. Previous studies have shown survival of marine benthic invertebrates affected by differences in prey availability caused by variable settlement (e.g., barnacles: Connell 1985, Fairweather 1988; and ascidians: Osman et al. 1992), as well as habitat-specific predation intensity and variable functional responses (infaunal bivalves: Luckenbach 1984, Lipcius and Hines 1986, Eggleston et al. 1992; sea urchins: Rowley 1989; and ascidians: Osman et al. 1992).

Ecological models of the mechanisms regulating populations of marine benthic organisms have traditionally incorporated processes that affect growth, movements, and mortality of settled recruits or adults (Connell 1985, Roughgarden et al. 1985 and references therein). The renewed interest in incorporating the supply of recruits into these models (Gaines and Rough-

garden 1985, Underwood and Fairweather 1989, Bertness et al. 1992, Doherty 1994) has contributed to our understanding of how larval dynamics can regulate the dynamics of juvenile and adult populations. Our results for Dungeness crab suggest that active substrate selection behavior by megalopae can affect the distribution of early juvenile crab, and that predation on $J1$ instars is more important than postlarval supply in regulating the dynamics of early juvenile crab in certain intertidal habitats. However, we offer the following caveat: our measures of postlarval supply, settlement, and recruitment were replicated in time (two 48-h experiments) and space (two locations: South Channel and Pacman); however, they were not replicated across settlement events within a season or among years. Since it appears that wind-driven surface currents can influence local rates of postlarval supply, it is possible that variable wind speeds and directions within a settlement season could distribute megalopae throughout the estuary in approximately equivalent densities, precluding post-settlement processes regulating population size. Similarly, on an annual temporal scale, strong offshore winds (i.e., east-southeast) during major settlement events (e.g., new-moon, spring tides in May and June), could effectively weaken tidal transport of megalopae into Grays Harbor, resulting in early juvenile dynamics that are regulated primarily by larval supply rather than by post-settlement events, particularly in shell habitats where habitat carrying capacity is greater. A recent study of Dungeness crab recruitment and alongshore transport (McConnaughey et al. 1992, 1994), suggests that high storm activity and correspondingly strong alongshore transport may deplete the larval pool from which Washington recruits are drawn, resulting in a poor year class and weak fishery 4 yr hence. Thus, final conclusions regarding the relative importance of pre-settlement vs. post-settlement processes in regulating population dynamics of juvenile Dungeness crab in intertidal habitats warrant integrating the major components of recruitment with processes influencing both intra- and interannual variation in postlarval supply.

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