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ABUNDANCE, SETTLEMENT, GROWTH AND HABITAT USE BY JUVENILE DUNGENESS CRAB, CANCER MAGISTER, IN INLAND WATERS OF NORTHERN PUGET SOUND, WASHINGTON

Russell O. McMillan

August 1991

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Abundance, Settlement, Growth and Habitat Use by Juvenile Dungeness Crab, *Cancer magister*, in Inland Waters of Northern Puget Sound, Washington

by

Russell O. McMillan

A thesis submitted in partial fulfillment
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Approved by ______________________
(Chairperson of Supervisory Committee)

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to Offer Degree ___School of Fisheries___

Date ___August 20, 1991___

MASTER'S THESIS

University of Washington

Abstract

Abundance, Settlement, Growth and Habitat Use
by Juvenile Dungeness Crab, Cancer magister,
in Inland Waters of Northern Puget Sound,
Washington

by

Russell O. McMillan

Chairperson of the Supervisory Committee: Professor David A. Armstrong
School of Fisheries

Abundance, growth and habitat use by early post-larval Dungeness crab, Cancer magister, were examined at 5 northern Puget Sound sites between June 1984 and September 1987. Sampling was conducted in intertidal habitats biweekly during settlement and approximately monthly or bimonthly thereafter. Northern Puget Sound Dungeness crab populations appear to be largely supported by recruitment from inland parental stocks with occasional recruitment originating from coastal or oceanic stocks. Settlement of Dungeness crab in inland waters typically peaked in August and interannual variation in yearclass strength at settlement was low relative to that reported for coastal crab populations. Spatial and interannual differences in settlement densities were mediated by high post-settlement mortality. Post-settlement growth rates corresponded to seasonal water temperatures and were greatest for the coastal cohort that settled in early summer. These crab grew rapidly to a size that allowed emigration from

intertidal to subtidal areas by September. Emigration of the late summer cohort which settled in August occurred the following spring, about 10 months after settlement when crab appear to have acquired refuge from predation in size. Mean seasonal densities of 0+ age juvenile crab corresponded to habitat complexity. Densities were highest in mixed sand and gravel with an overstory of attached or drift macroalgae, intermediate in eelgrass (*Zostera marina*) and lowest on bare sand.

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Dedication

This manuscript is dedicated to my wife Judy, whose support, understanding and encouragement made it possible.

INTRODUCTION

Dungeness crab, Cancer magister Dana, support the largest commercial crustacean fishery in the inland marine waters of Washington State. Despite this, little is known regarding settlement, early life history, habitat requirements or population dynamics of crab from these waters. Several studies of 0+ age C. magister have identified coastal estuaries and, particularly, estuarine intertidal habitat as important nursery areas which contribute substantially to recruitment to the coastal Dungeness crab fisheries (Cleaver 1949, Gotshall 1978, Stevens and Armstrong 1984, Gunderson et al. 1990). Advantages attributed to these areas are warmer temperatures, greater standing stock biomass of food organisms and refuge from predation (Gunderson et al. 1990). Substantially higher rates of growth are reported for crabs that settle or reside in estuaries and shallow embayments than members of the same yearclass found in adjacent coastal regions (Tasto 1983, Armstrong and Gunderson 1985, Gunderson et al. 1990). Higher survival is associated with estuarine intertidal habitats that provide refuge from predation (Dumbauld and Armstrong 1987, Doty et al. 1990).

Timing of settlement is quite similar along the outer coast and coastal estuaries from California to British Columbia (BC). Larval Cancer magister are planktonic for 105 to 125 days in California waters (Reilly 1983a) and 130 days in Oregon waters (Lough 1976). Larvae pass through 5 zoeal stages to megalopae which occur nearshore and enter estuaries along the coast in April and May. First and second instar (J1 and J2) crab are observed in May and June in San Francisco Bay (Tasto 1983), Humboldt Bay (Gotshall 1978), and in Grays Harbor, Washington, (Cleaver 1949, Stevens and Armstrong 1984). In the Queen Charlotte Islands, BC, Butler (1961) observed J2 and J3 crab in early June, suggesting that settlement occurs during May.

In contrast to early summer settlement along the coast, C. magister settlement occurs in late summer in inland waters of the Strait of Georgia. MacKay and Weymouth (1935) reported peak settlement in August at Boundary Bay, BC, and Orensanz and Gallucci (1988) observed a pulse of settlement in August at Garrison Bay, Washington. Such late settlement may have implications on the population level (e.g. different stocks), but certainly suggests effects on growth rate during the first year following settlement.

Interannual and seasonal variability in density of 0+ age C. magister have been characterized for coastal systems. Recruitment varies dramatically with interannual differences in density of newly settled crab from 2 to 3 orders of magnitude (Tasto 1983, Dumbauld and Armstrong 1987, Armstrong et al. 1989, Gunderson et al. 1990). Seasonal patterns in density are marked by a rise during settlement in early summer followed by a rapid decline over the next several weeks with density stabilizing thereafter at lower levels (Armstrong and Gunderson 1985).

Within the inland waters of Washington and BC, eelgrass (Zostera marina) beds are known to serve as habitat for juvenile Dungeness crab (Butler 1956, Thayer and Phillips 1977). However, the relative importance of eelgrass is unknown both with respect to other habitats or the degree of refuge from predation that it provides. Mortality rates are high immediately following settlement and smaller crab below 25 - 30 mm carapace width (CW) are subjected to disproportionately higher predation than larger instars (Reilly 1983b). A number of intertidal habitats provide physical refuge from predation during the critical first several months after settlement. Recent studies in Washington coastal estuarine systems have compared the post-settlement survival of Dungeness crab in intertidal habitats of varying structural (= habitat) complexity. These were, in decreasing order of complexity: shell deposits from natural sources and oyster culture; eelgrass beds; and bare sand flats. Consistently higher 0+ age crab densities in shell material were attributed to its greater structural complexity and protection provided from predation and possibly to attenuation of environmental stresses associated with intertidal existence (Armstrong and Gunderson 1985, Dumbauld and Armstrong 1987, Doty et al. 1990, Gunderson et al. 1990).

A number of studies have examined the effects of habitat complexity and predation on abundance and distribution of benthic invertebrates. Juvenile blue crab, Callinectes sapidus, are more abundant in vegetated than in open habitats as are juveniles of a number of other crustaceans species (Orth et al. 1984, Leber 1985, Main 1987, Orth and van Montfrans 1987, Wilson et al. 1987, 1990). Predation is mediated by habitat structure through a number of mechanisms such as reduction of foraging efficiency and interference of visual cue predators (Coen et al. 1981, Heck and Thoman 1981, Crowder and Cooper 1982). Habitat complexity is positively associated with faunal abundance (Heck and Wetstone 1977, Heck and Orth 1980, Lewis and Stoner 1983, Rader 1984, Zimmerman and Minello 1984). The interaction of these two factors, predation and habitat complexity, contributes to small scale distribution of benthic invertebrate prey species (Heck and Wetstone 1977, Nelson 1979, 1981, Rader 1984, Summerson and Peterson 1984, Wilson et al. 1987, 1990).

This study examines post-settlement, 0+ age C. magister in the inland waters of northern Puget Sound, Washington. The objectives were to: 1) characterize interannual and seasonal patterns of settlement, survival and growth of C. magister in the intertidal zone, and 2) examine intertidal habitat use by juvenile crab. The study area is located in northern inland waters of Washington from the Canadian border to Anacortes, Washington, referred to herein as northern Puget Sound. This region is noteworthy in that 75 - 90% of Washington's inland commercial crab fishery landings originate here. The impetus for much of this work was the need to better understand the ecology of this commercially important species and particularly its dependence on intertidal habitats. Saltwater and estuarine tidelands have been substantially impacted by human activity over the last 50 years and their continued destruction or alteration could significantly impact inland crab stocks. Bortleson et al. (1980) examined historical trends in 11 of the largest Puget Sound river deltas and found that nearly 60% of the coastal wetlands (tidelands) had been converted to other uses since 1800. These tidelands continue to be at risk from pressure to develop or expand existing marina and port industrial facilities through dredging, filling and bulkheading. In order to best manage these tidelands and the fisheries stocks which are critically dependent upon them, it is necessary to understand the values and functions these intertidal regions provide.

METHODS AND MATERIALS

INTERTIDAL SURVEYS

Intertidal sampling for juvenile C. magister was conducted in five bays located in northern Puget Sound, Washington (Fig. 1). The sites were selected based on presence of extensive intertidal flats and eelgrass (Z. marina) beds. From north to south these were Semiahmoo Spit, Birch Bay, Lummi Bay, Samish Bay and Padilla Bay. Intertidal regions at each of the sites are typically a mosaic of different habitats, although eelgrass over a silt/sand substrate is the most prevalent habitat. Other habitats are interspersed within or between eelgrass beds and include patches of open silt or sand and patches of gravel and cobble either bare or covered by attached or free drifting macrophytes (e.g. Ulva fenestrata or Enteromorpha intestinalis).

Sampling was initiated in July 1984 and continued through September 1987. Sites were visited on approximately two week intervals during summer months with less frequent sampling during winter months. At each site a transect was established and, during 1984 and 1985, all habitats encountered along the transect were sampled randomly. Where practical, three or more 0.25 m^2 samples were collected from within each habitat. Beginning in June 1986, samples were selected randomly from within a plot (50 X 100 m) located adjacent to the original transects. Macrophyte cover was categorized by the dominant species, percent cover was visually estimated, and substrate composition (e.g.

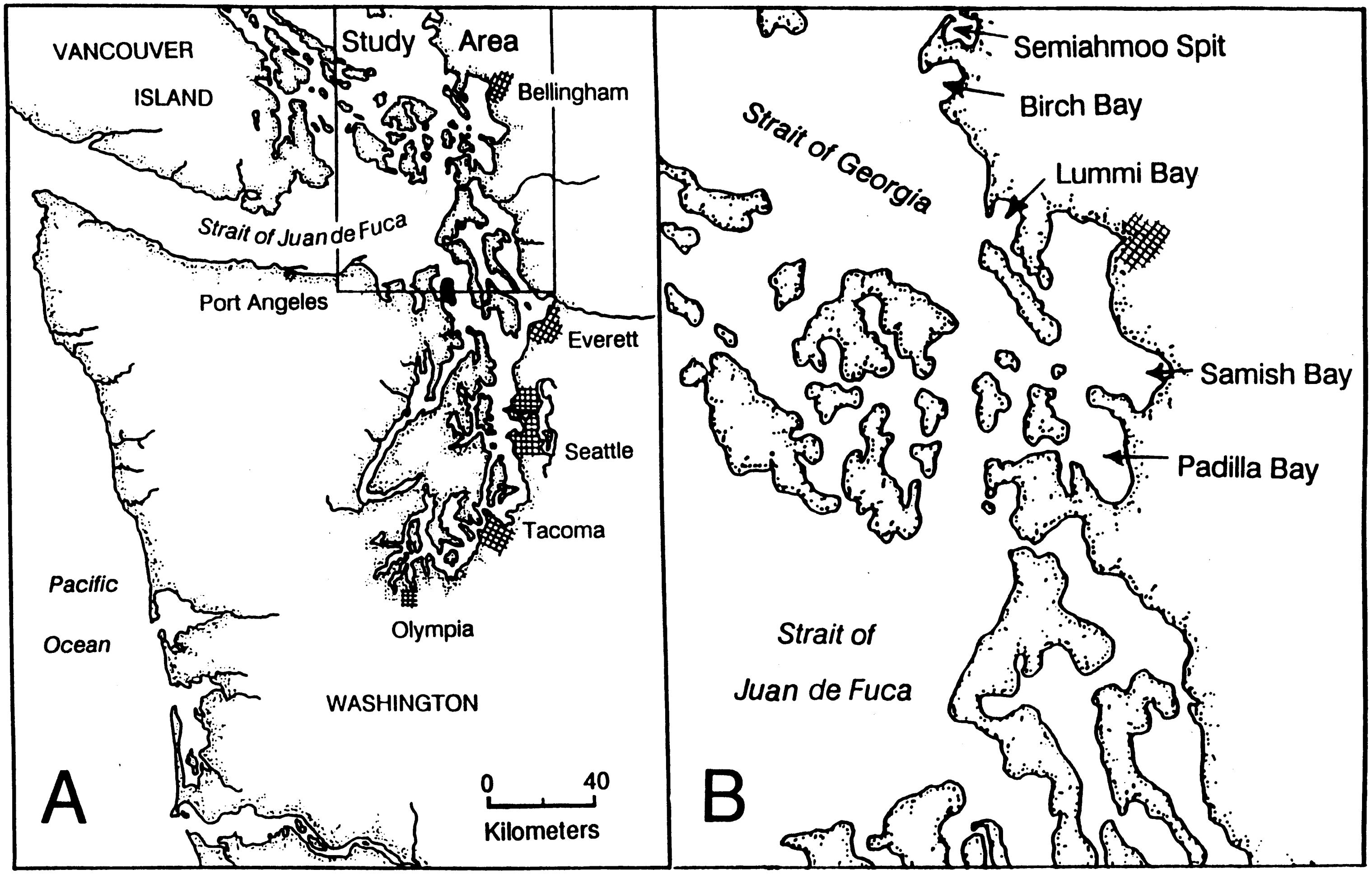

Figure 1. A) Map of western Washington showing northern Puget Sound study area.
B) Study sites.

silt, sand, gravel or cobble) were noted for each sample. Larger macrophytes and cobbles were removed from the sample and inspected for the presence of megalopae or juvenile crab instars. The remainder of the substrate was excavated to a depth of 3 - 5 cm and wet seived through a 3 mm mesh. All crab were counted and measured for CW (measured immediately anterior to the tenth anterolateral spine) then returned to the beach.

DATA ANALYSIS

Three seasonal periods were defined based on life history phases and seasonal variation in crab density occurring in the intertidal zone. These were summer, 15 July to September 30; winter, 1 October to 30 March; spring, 1 April to 31 May. The period of 1 June to 14 July was marked by emigration of late 0+ age crab from the intertidal region which varied in timing between years. This period was not included in comparisons of crab density across years or across bays, but was included in subsequent comparisons of crab density among habitats.

Five habitat categories were defined according to substrate type and macrophyte cover. Substrates were divided into two categories: sand (comprised of silt and sand), and "gravel" (comprised of a matrix of gravel, cobble or shell, mixed with sand). Where macrophyte cover was present, it was grouped according to dominant forms as either eelgrass or macroalgae (e.g. *U. fenestrata* or *E. intestinalis*). The five habitat categories were; 1) open silt/sand (bare-sand), 2) silt/sand with macroalgae cover (sand-with-algae), 3) open gravel/cobble (gravel), 4) silt/sand with eelgrass cover (eelgrass) and 5) gravel/cobble with macroalgae cover (gravel-with-algae) (Table 1).

Crab density in eelgrass was used as the basis of spatial and temporal comparisons considered in this study. Mean seasonal crab density was calculated for each combination of site and season and these mean densities were compared across sites and years. Nonparametric procedures (Mann-Whitney and Kruskal-Wallis tests) were used for comparisons of mean densities as a result of non-normally distributed counts and unequal sample sizes. Where Kruskal-Wallis tests indicated significant differences (alpha = 0.05), a nonparametric multiple comparisons test was performed to determine which differences were significant (Zar 1984).

Comparisons of crab density among habitats were conducted for three seasonal periods to examine distribution of crab among habitats and to observe change in distribution over time. Comparisons were performed on the three most commonly encountered habitats; bare-sand, eelgrass, and gravel-with-algae. Seasonal periods were settlement (summer) 1 July to 30 September, overwintering (winter) 1 October to 31 March, and spring, 1 April to 30 June. Crab densities among habitats were compared using Friedman's test, a nonparametric, analysis of variance on ranked data. Data were first grouped by season and then blocked to isolate the effects of year, sampling trip and bay. Where all three habitats were sampled within a block, mean density of crab was

Table 1. Habitat categories used in intertidal surveys.

HABITAT CATEGORY	SUBSTRATE MATERIAL	MACROPHYTE COVER
Gravel-with-Algae	"Gravel" (Matrix of Gravel, Cobble and Sand)	*Ulva fenestrata* *Enteromorpha intestinalis* *Laminaria sp.* *Fucus gardneri*
Eelgrass	Silt/Sand	*Zostera marina* *Zostera japonica*
Gravel	"Gravel" (Matrix of Gravel, Cobble and Sand)	----
Sand-with-Algae	Silt/Sand	*Ulva fenestrata* *Enteromorpha intestinalis* *Laminaria sp.*
Bare Sand	Silt/Sand	----

calculated for each habitat. These means were then ranked and Friedman's test was performed on the ranked means. Where Friedman's tests indicated significant differences among habitats, a least significant difference test was performed to determine which differences were significant (Conover 1980).

RESULTS

PATTERNS OF SETTLEMENT

Seasonal occurrence of *C. magister* in the intertidal is characterized by an abrupt increase in numbers during settlement in summer, followed by a rapid decline to lower more constant numbers through winter and into spring (Fig. 2). Peak densities typically occurred in August and were as high as 104 crab/m^2 (single 0.25 m^2 sample, Birch Bay, 16 August 1985). However, in most years mean (seasonal) summer density of 0+ age juvenile crab in eelgrass ranged from 5 - 32 crab/m^2. Mean densities declined by approximately 50% during the winter and ranged from 0.3 - 1.6 crab/m2 in spring. Density declined sharply again around mid-June or mid-July as late 0+ age crab emigrated from the intertidal to the subtidal. This resulted in few of the previous yearclass occupying the intertidal region at the onset of settlement by a new yearclass.

A protracted period of settlement was observed for *C. magister* in inland waters as indicated by the presence of first instar crab in samples. J1 instars were seen as early as June in the north Puget Sound region and were observed in samples through September (Fig. 3). Most of the crab sampled from June through August were J1 and J2 and the latter were still the most prevalent instars in September samples.

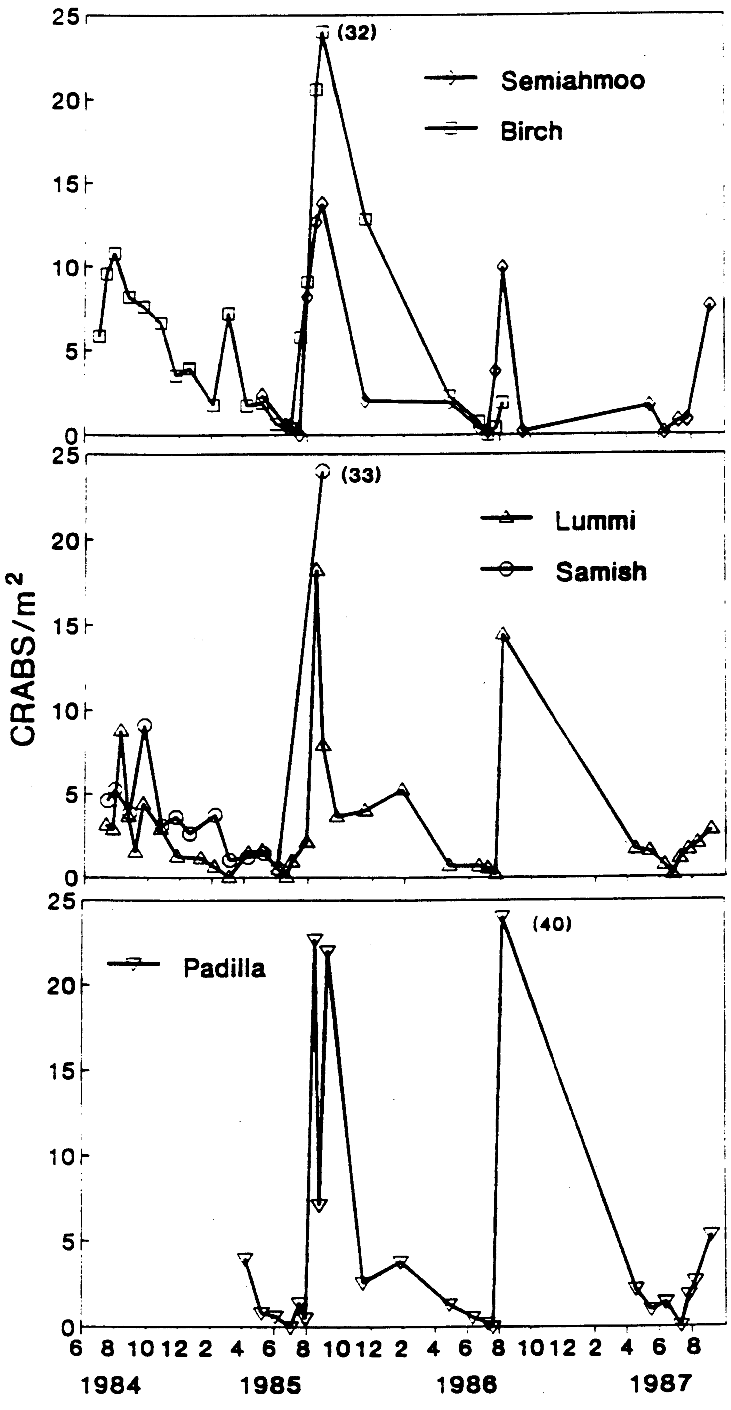

Figure 2. Mean density of 0+ age C. magister by sampling trip for five study sites in northern Puget Sound, from June 1984 to September 1987. Sites are listed from north to south: Semiahmoo Spit and Birch Bay; Lummi and Samish Bays; and Padilla Bay (Data combined for all habitats.)

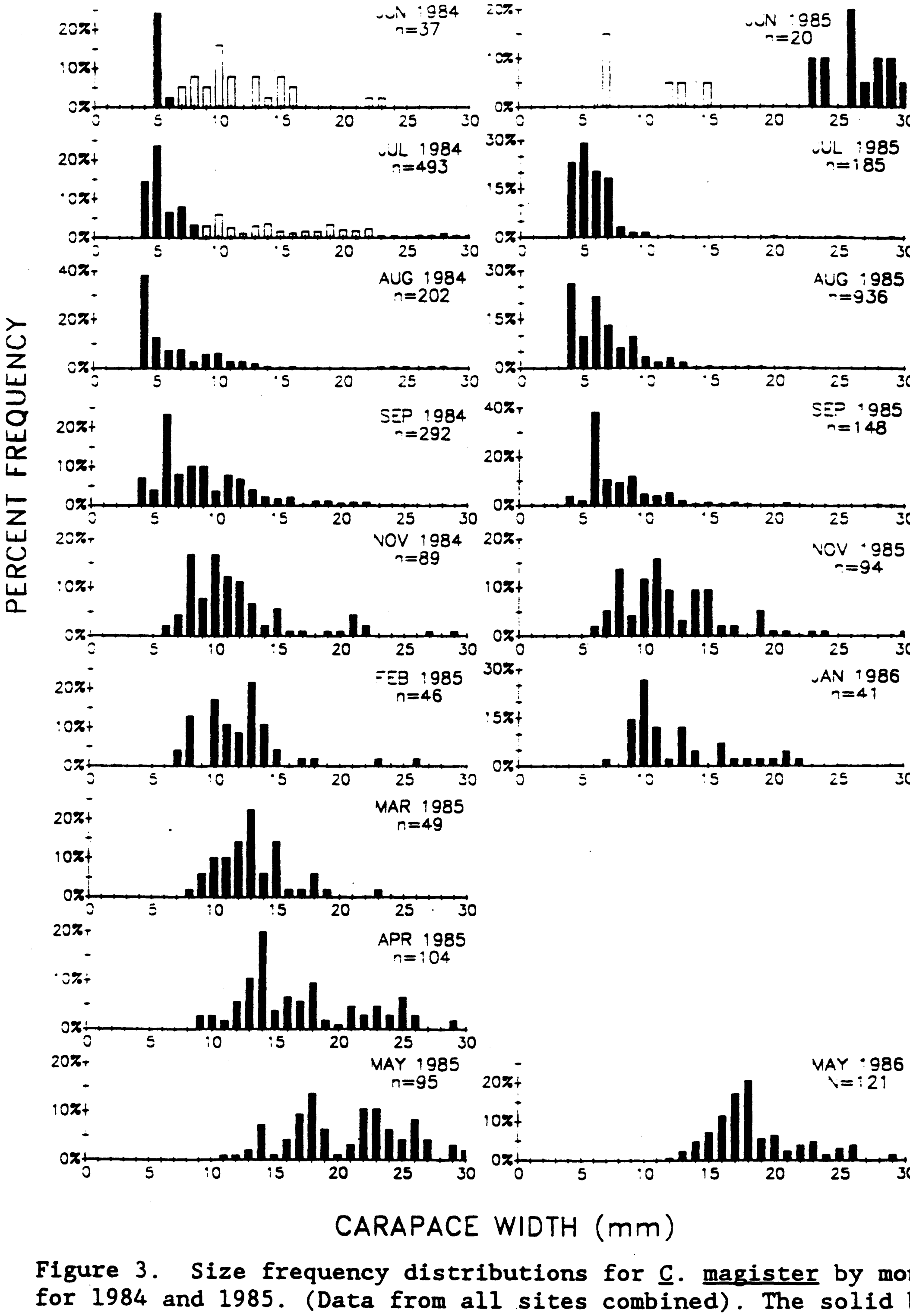

Figure 3. Size frequency distributions for C. magister by month for 1984 and 1985. (Data from all sites combined). The solid bars represent crab originating from inland parental stocks (Puget Sound cohort) the open bars represent crab from coastal stocks (oceanic cohort).

Settlement in 1984 was notably different from that observed in subsequent years. The presence of J1, J2 and J3 instars in late June, 1984, indicated an earlier pulse of settlement had occurred around late May. This first pulse preceded the more typical, protracted settlement seen during July and August (Fig. 3). This early settling oceanic cohort represented about 24% of the settling crab sampled from the 1984 yearclass. An early settling cohort was observed again in 1985, but in smaller numbers.

TEMPORAL AND SPATIAL VARIABILITY

Significant differences between yearclass strength (alpha = 0.05) were exhibited when summer or winter mean densities were compared across years (Table 2). Comparison of yearclass strength during spring showed interannual differences were not significant except at Lummi Bay. The 1985 yearclass had the highest mean summer densities (recruitment) at all sites (6.6 - 32.9 crab/m^2). However, this yearclass had the lowest mean densities in spring (0.5 - 1.4 crab/m^2) for all sites except Padilla Bay. The 1987 yearclass had the lowest recruitment observed over the four consecutive years (Table 2).

Patterns of crab abundance among bays were not consistent from one year to the next. Significant differences in crab density among bays occurred during summer and winter, except for the summer of 1987. In spring, differences between bays were not significant (Table 2).

Table 2. Comparison of C. magister density among years (columns) and among sites (rows) by season. (Kruskal-Wallis 1-way ANOVA using Chi-square corrected for ties, where only two values were compared the Mann-Whitney U Test Z statistic is given.)

SEASON Year (Year-class)	STUDY SITE Semiahmoo Spit	Birch Bay	Lummi Bay	Sammish Bay	Padilla Bay	Statistic X^2	Probability P
SUMMER							
1984 (1984)	-	11.21	4.57	7.73	-	24.169	.0000
1985 (1985)	16.70	21.60	7.77	32.89	6.62	67.989	.0000
1986 (1986)	4.83	1.33	6.89	-	0.00	12.899	.0049
1987 (1987)	3.51		2.12	-	2.30	3.218	.2001
Statistic	X^2=44.847	X^2=33.149	X^2=15.305	Z=-4.148	X^2=10.357		
Probability	P=.0000	P=.0000	P=.0016	P=.0000	P=.0056		
WINTER							
1984-85 (1984)	-	5.22	1.66	3.52	-	22.277	.0000
1985-86 (1985)	2.00	10.67	4.62	-	3.65	8.801	.0321
1986-87 (1986)	-	-	-	-	-		
Statistic	-	Z=-2.158	Z=-3.05	-	-		
Probability	-	P=.0309	P=.0023	-	-		
SPRING							
1985 (1984)	2.80	1.69	1.89	1.22	1.43	4.782	.3104
1986 (1985)	1.40	0.53	0.84	-	1.31	4.326	.2283
1987 (1986)	1.75	-	1.72	-	0.53	5.534	.0629
Statistic	X^2=3.185	Z=-1.489	X^2=7.887	-	X^2=2.899		
Probability	P=.2035	P=.1364	P=.0194	-	P=.2347		

GROWTH

The pattern of growth for the inland cohort was relatively consistent between years. Mean CW was about 5 mm during peak settlement in August, and increased to approximately 8 mm by late September (Fig. 4). From September to November, CW increased approximately 4 mm to a mean of 12 mm. Growth was very slow between November and early March, with an increase of only 1 mm during this time. This period of slow growth rates coincided with lowest mean monthly water temperatures which ranged from 2.5 - 7.5°C (Fig. 5). After March, mean CW increased markedly from about 13 mm to 40+ mm by July, after which the late 0+ age crab were rarely present in the intertidal samples (App. A).

Growth of the early settling cohort (seen in 1984 and to a lesser extent in 1985) was markedly greater than that of the later settling cohort (Fig's. 4 and 5). By September, mean CW of these crab had exceeded 40 mm, although, few were present in the intertidal samples after that time.

HABITAT USE

Eelgrass was the most prevalent habitat and accounted for 46 - 75% of the sampling effort from the five sites. Bare-sand was the second most abundant habitat followed by gravel-with-algae. Comparisons of crab density among habitats were limited to these three habitat categories. The remaining two habitats, sand-with-algae and gravel, were the least

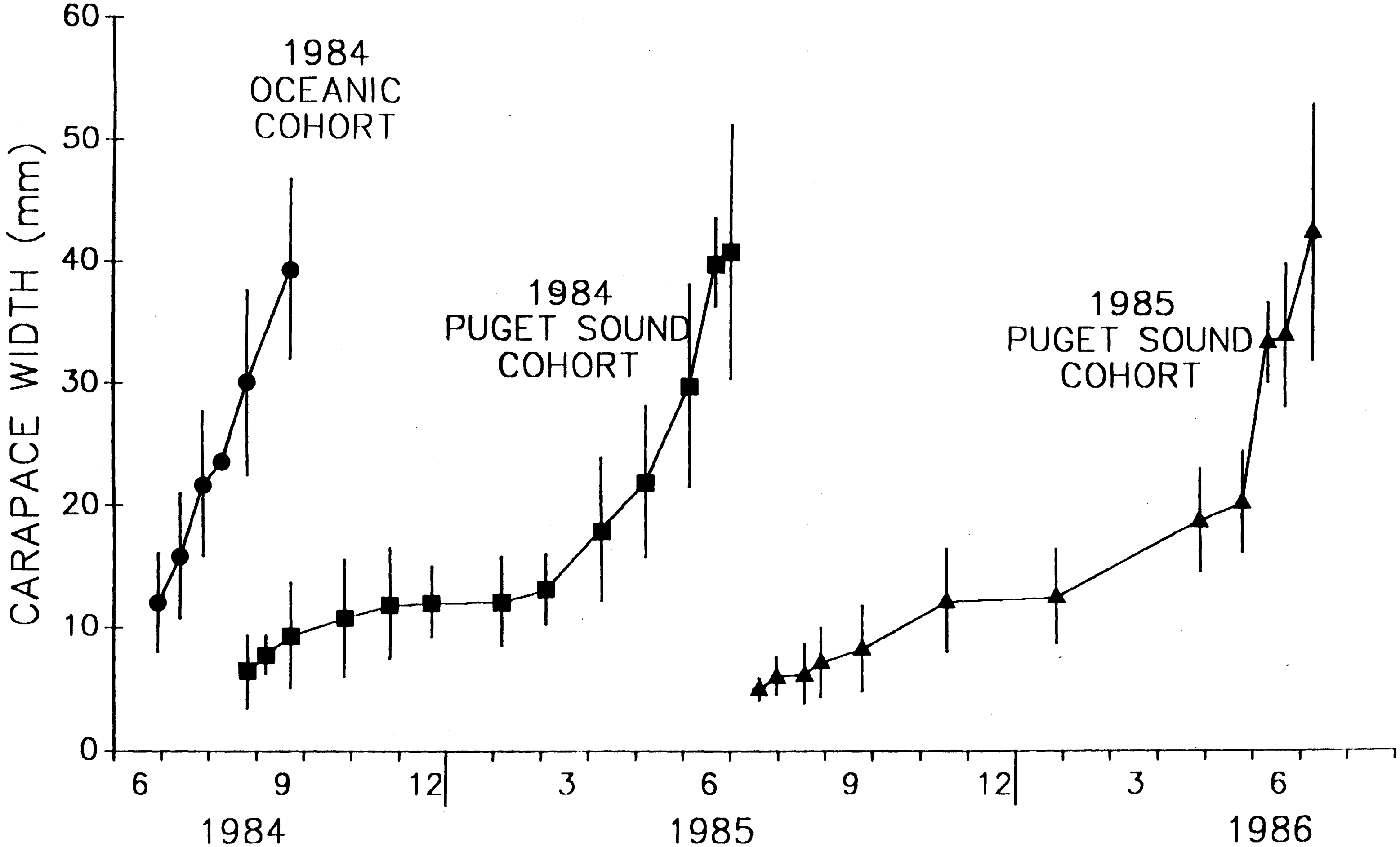

Figure 4. Mean carapace widths (± 1 SE) over time for C. magister yearclasses 1984 and 1985. Filled circles represent the 1984 oceanic cohort, filled boxes represent the 1984 Puget Sound cohort and filled triangles represent the 1985 Puget Sound cohort.

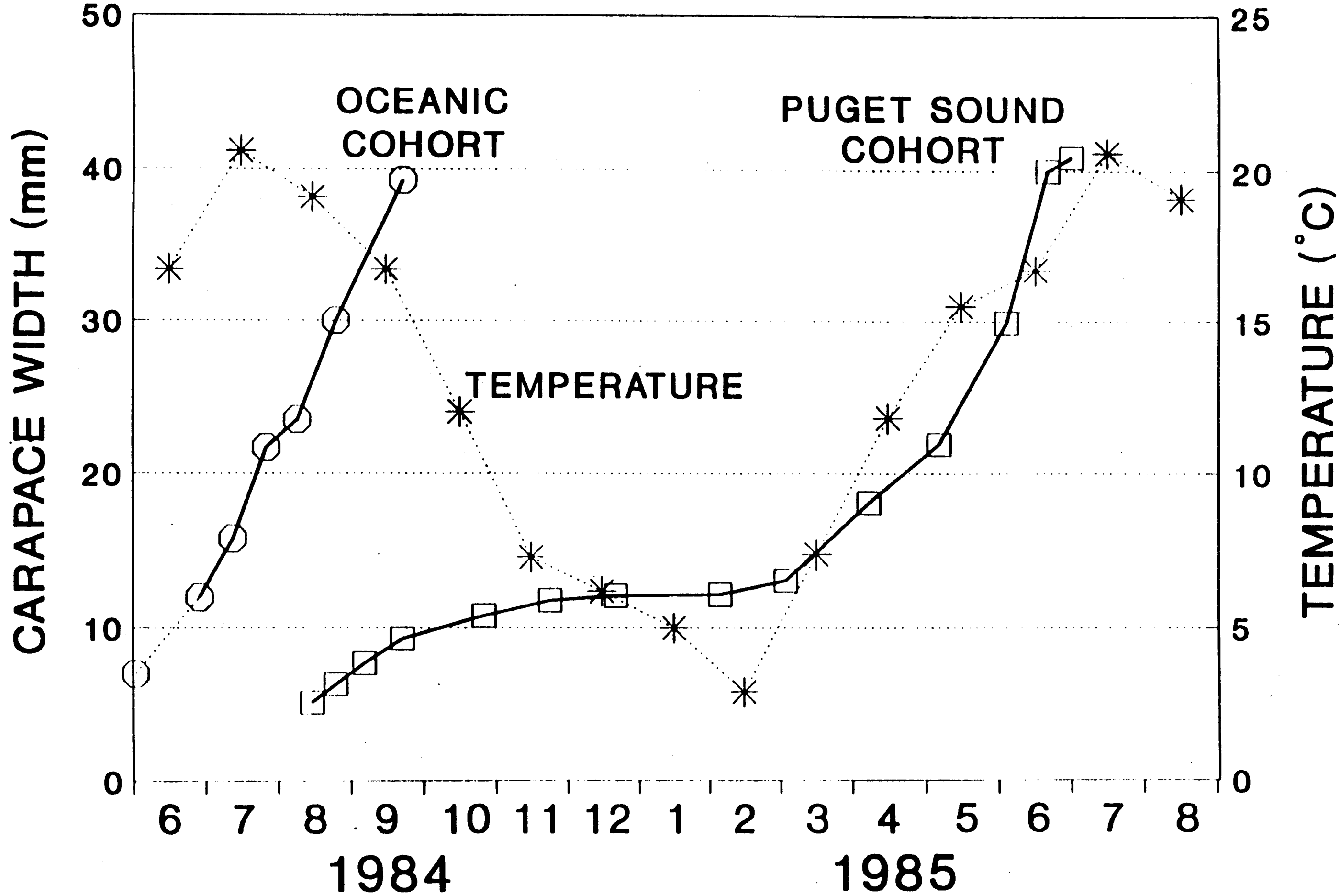

Figure 5. Growth of C. magister (mean carapace widths) and monthly mean water temperatures. Two cohorts are shown (oceanic and Puget Sound) representing the 1984 yearclass. Initial size and timing of the oceanic cohort is interpolated from the data.

abundant and together represented from 3 - 12% of the samples from the five sites.

Mean seasonal crab density was highest in gravel-with-algae for all seasons, intermediate in eelgrass, and lowest in bare-sand (Fig's. 6 and 7). In summer, mean crab densities were not significantly different between gravel-with-algae and eelgrass (7.0 and 6.3 crab/m^2, respectively), but these were both significantly higher than crab density on bare-sand (0.6 crab/m^2)(Table 3). Crab densities were significantly different between all three habitat categories in winter (5.4, 4.0 and 0.2 crab/m^2 in gravel-with-algae, eelgrass and bare-sand, respectively). Crab were virtually absent from bare-sand in spring (less than 0.1 crab/m^2) and crab density in gravel-with-algae and eelgrass were significantly higher than sand (2.5 and 1.2 crab/m^2, respectively), although not significantly different from one another (Table 3). Density in sand-with-algae was generally intermediate between other habitats but this was not consistent. Gravel was the least frequently sampled habitat and patterns of density relative to other habitats were not evident (App. B).

Data from all sites and years were combined to examine the effect of eelgrass density (percent cover) on _C. magister_ density. Crab density in summer was highest (11.3 crab/m^2) in eelgrass cover of 61 - 80% and lowest (6.1 crab/m^2) in cover of 81 - 100% (Fig. 8). Crab density in winter declined about 50% from summer densities and crab densities (3 - 4 crab/m^2) varied little across the range of eelgrass density. In

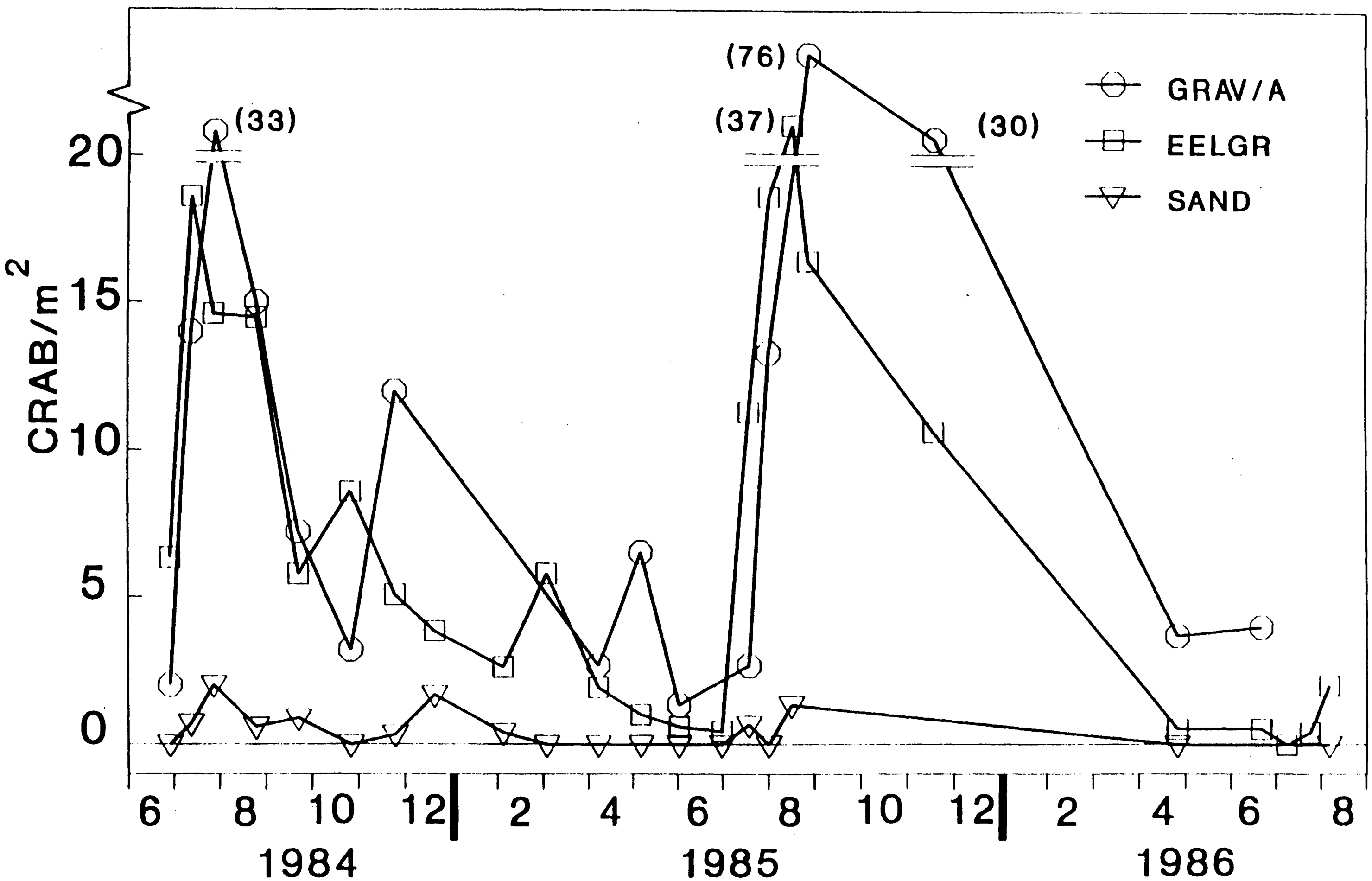

Figure 6. Mean density of C. magister by sampling trip for three habitats. 1984 and 1985 year classes are shown (Data from Birch Bay only.) Habitats: GRAV/A, gravel-with-algae; EELGR, eelgrass; and SAND, bare-sand (see Table 1).

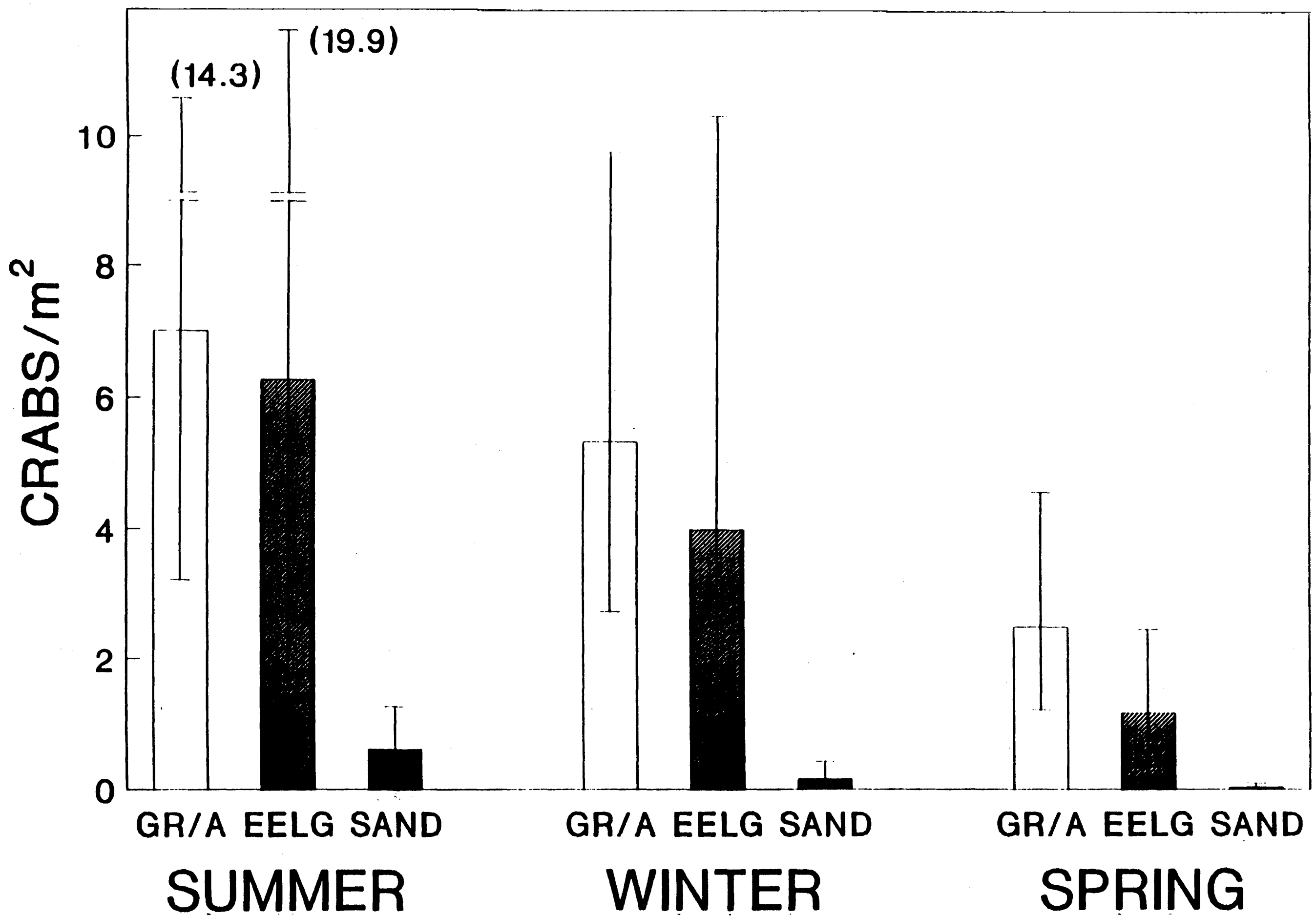

Figure 7. Mean seasonal density (± 1 SE) of C. magister by habitat. Habitats: GR/A, gravel-with-algae; EELG, eelgrass; and SAND, bare-sand (see Table 1). Data was grouped by season and blocked for the effects of year, sampling trip, and site. Data was weighted by sample size, lognormal transformed, means and standard errors were calculated and then untransformed for graphic presentation.

Table 3. Tests for differences in mean seasonal density of *C. magister* among habitats: gravel-with-algae (GRAV/A); eelgrass (EELGR) and bare-sand (SAND). Underline denotes no significant differences between habitats. Data was grouped by season and then blocked for year, sampling trip and site (bay). Friedman's test was performed on ranked mean densities and where significant differences were indicated among habitats (alpha = 0.05) a protected least significant difference test was performed to determine which differences were significant (Conover 1980).

SEASON	df	F Value	Probability	HABITATS (High)	Mean Rank	(Low)
Summer	2	17.51	<0.0001	EELGR	GRAV/A	SAND
Winter	2	33.09	<0.0001	GRAV/A	EELGR	SAND
Spring	2	28.65	<0.0001	GRAV/A	EELGR	SAND

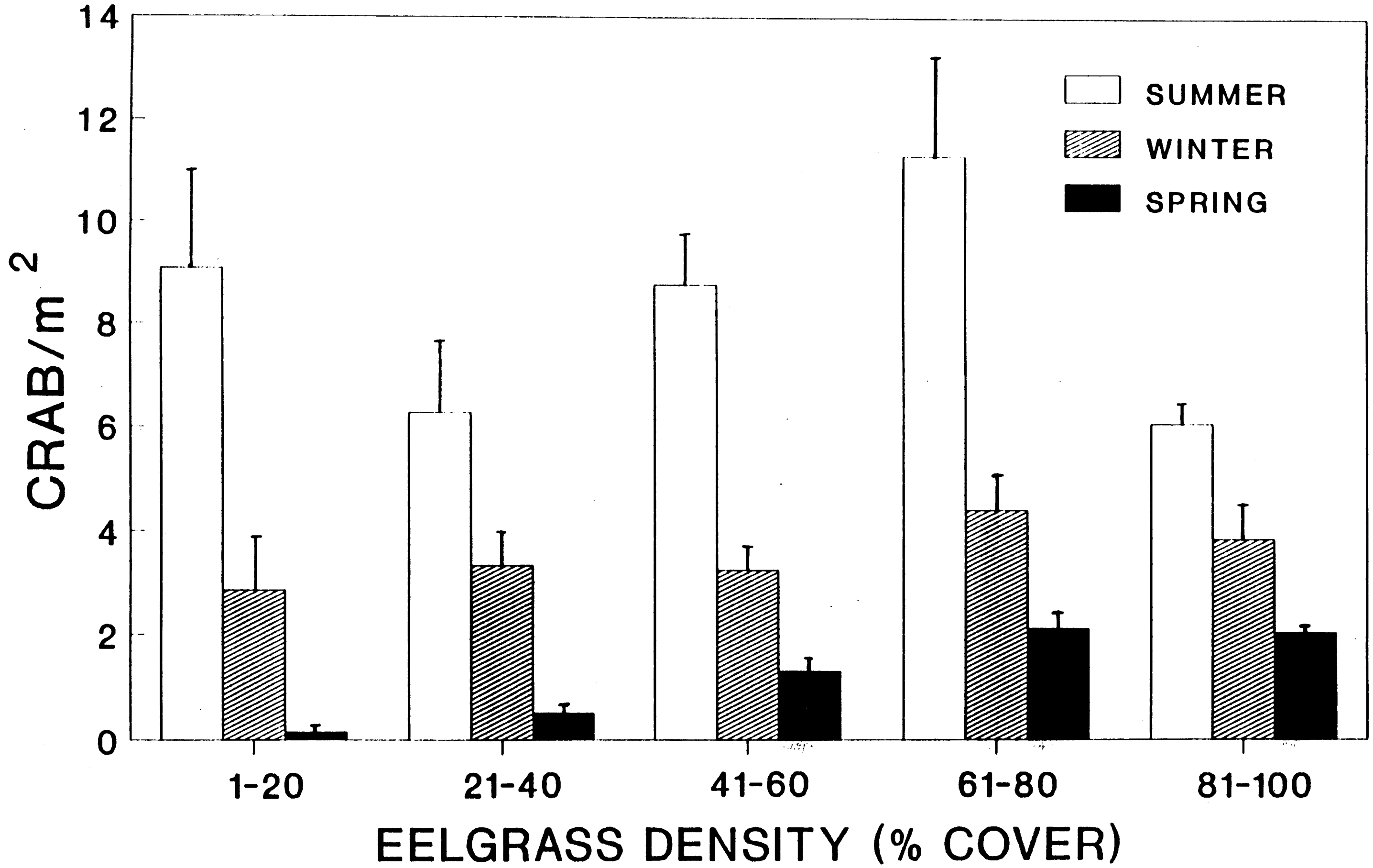

Figure 8. Mean seasonal density (+ 1 SE) of C. magister as a function of percent cover of eelgrass (Z. marina). (Data combined for all years and sites.)

spring, crab density corresponded to percent eelgrass cover and crab were nearly absent (less than 0.5 crab/m^2) from eelgrass providing less than 40% cover, while in cover greater than 40%, densities ranged from 1.3 to 2.1 crab/m^2 (Fig. 8).

DISCUSSION

PATTERNS OF SETTLEMENT

Dungeness crab settlement in inland waters of northern Puget Sound occurred later and over a longer period of time than off the outer coast of Washington. In most years, settlement in inland waters extended from late June through September and peaked in August (Fig's. 2 and 3). This follows the pattern of timing described for Boundary Bay, BC, in the Strait of Georgia (Mackay and Weymouth 1935). In contrast, settlement along the Washington coast is characterized by a strong, short term pulse of settlement during May or June (Stevens and Armstrong 1984, Dumbauld and Armstrong 1987, Gunderson et al. 1990).

A bimodal pattern of crab settlement occurred in the study area, in 1984 and to a lesser extent in 1985, similar to that described by Orensanz and Gallucci (1988) for Garrison Bay, San Juan Island, and other sites in the northern Puget Sound area (Dinnel et al. in preparation). The two cohorts appear to be derived from different parental stocks. The larger size at settlement and timing of the early cohort corresponded to coastal stocks (oceanic cohort), while the later cohort of smaller sized individuals resembled the pattern attributed to south Strait of Georgia stocks (referred to herein as Puget Sound cohort) (MacKay and Weymouth 1935, Orensanz and Gallucci 1988, Dinnel et al. in preparation). At the northern Puget Sound study sites, the oceanic cohort comprised about 24% of the juvenile crab that were sampled during summer (settlement) in 1984. Contribution of the oceanic cohort was negligible for the 1985 yearclass.

High settlement in 1985 at the five study sites is consistent with a similarly strong yearclass along the outer coast (Gunderson et al. 1990). However, it is unknown whether a this was coincidence or if factors contributing to a high settlement on the coast may also affect inland settlement. Contribution by the (early settling) oceanic cohort could not account for the high settlement in inland waters (Fig. 3) and except for 1985, patterns of yearclass strength were not consistent between inland study sites and coastal systems.

TEMPORAL AND SPATIAL VARIABILITY

Magnitude of recruitment varied significantly between years, however, interannual variation in northern Puget Sound was notably less than that described for coastal Washington. The maximum difference in recruitment observed in this study was an order of magnitude, whereas, in Grays Harbor and adjacent nearshore areas, interannual differences in recruitment as great as three orders of magnitude have been reported (Dumbauld and Armstrong 1987, Armstrong et al. 1989).

The dynamics of larval transport are implicated in the higher variability of recruitment in oceanic versus inland stocks of _C. magister_. The planktonic zoeal stages of oceanic stocks are dispersed progressively farther offshore by oceanic and atmospheric events

(Lough 1976, Reilly 1983a, Jamieson and Phillips 1988). It is hypothesized that zoea are carried in longshore currents and dispersed offshore by Ekman transport, upwelling events and estuarine plumes. Some megalopae may then return to shallow nearshore regions or estuaries in order to successfully settle and metamorphose (Lough 1976, Hatfield 1983, Reilly 1983a). Successively later developmental stages of megalopae are reported to occur closer towards shore (Hatfield 1983, Jamieson and Phillips 1988). However, it is unknown what mechanism of transport accounts for this or whether larvae carried offshore are able to return. Jamieson and Phillips (1988) suggest that offshore transport may result in larval wastage with few larvae actually returning to nearshore areas to settle successfully. If this were the case, lower settlement would be expected when conditions such as upwelling, Ekman transport or estuarine plumes increased offshore transport. Alternatively, storms, gyres or near bottom currents are proposed as possible mechanisms of retaining larvae nearshore (Lough 1976, Hatfield 1983, Jamieson and Phillips 1988).

Whether settlement is from larvae that are retained nearshore or dispersed offshore and then transported back onshore, the oceanic and atmospheric conditions that drive retention or transport mechanisms are highly variable. An example of the broadest scale of variation was given by Jamieson and Phillips (1988) who suggest that larvae off Vancouver Island could theoretically have originated anywhere from northern California to southern Alaska, given the currents in the area. The possible effect of currents on distribution and transport of megalopae off Vancouver Island was reported by Jamieson and Phillips (1988). Settlement was low during the 1985 season despite relatively abundant megalopae located 38 - 148 km offshore. These megalopae were concentrated between surface currents flowing in opposite directions and it was concluded that the northward flowing Vancouver Island Coastal Current may sometimes serve as a barrier to onshore movement and successful settlement. Storm events may be required to transport megalopae through such a barrier (Armstrong et al. 1989). Lough (1976) examined larval abundance off Oregon during 1970 and 1971 and reported a substantial difference between years in abundance of megalopae. The lower abundance in 1971 occurred despite similar abundance of early stage zoea for the two years and was attributed to unusually severe weather in February and March, 1971.

A similar model of larval dispersal and transport is believed to contribute to variability in recruitment of blue crab, Callinectes sapidus (Sulkin and Van Heukelem 1982, Epifanio et al. 1984, Sulkin and Epifanio 1986, Lipcius et al. 1990). Modeling of wind and current induced drifts of blue crab larvae revealed that the wind component had the greatest effect on recruitment and that it could either increase or decrease recruitment (Johnson and Hess 1990). The stochastic nature of environmental stresses (including storm events, current strength and direction, wind-driven Ekman transport, etc.) are thought to contribute to the variable settlement along the coast for

Dungeness crab, though the extent is subject to debate (Armstrong 1983, Hankin 1985, Botsford 1986).

In contrast to the wide dispersal of larvae in coastal waters, larvae in waters surrounded by land may remain nearshore throughout their planktonic phase (Jamieson and Phillips 1988). This could explain the lower interannual variability in settlement observed in northern Puget Sound, since these larvae were not subjected to the magnitude of dispersal or variability in transport experienced by larvae in coastal waters. Despite lower variability between years in inland waters, significant differences in settlement did occur between years and between bays (Table 2). Further, patterns of settlement among bays were not consistent between years (i.e. Birch Bay had the highest settlement in 1984, but the second lowest in 1986). It appears that variable environmental factors (winds, circulation, etc.) that contribute to widely variable settlement along the coast, may also affect distribution of larvae, and subsequent settlement in inland waters, though to a lesser degree. These factors probably account for the differences in settlement seen over the scale of several kilometers between bays in the study area.

Northern Puget Sound stocks of C. magister do not appear to be recruitment limited. The number of crab surviving ten months to a year after settlement was independent of the magnitude of settlement for that yearclass. For example, the 1985 yearclass had the highest settlement of four consecutive years but the lowest mean spring densities (Fig. 2, Table 2). Further, yearclass strength in spring did not differ significantly among years (except at Lummi Bay), despite significant differences in settlement among years. This suggests that factors other than recruitment drive the population size of late 0+ age crab in northern Puget Sound.

GROWTH

Growth of post-settlement, 0+ Dungeness crab is strongly temperature-dependent with considerably higher rates attributed to warmer estuarine than oceanic environments (Tasto 1983, Armstrong and Gunderson 1985, Gunderson et al. 1990). Growth of the two 1984 cohorts within Puget Sound reflect different temperature regimes following settlement. The oceanic cohort which settled early (May/June) in the intertidal region reared in water temperatures that increased to over 15°C for most of summer (Fig. 5). In contrast, the Puget Sound Cohort settled in August and was exposed to only one month of temperatures exceeding 15°C. Four months after settlement, mean CW's for the oceanic cohort and Puget Sound cohort were 39 mm and 12 mm, respectively (Fig. 5). By late September, the oceanic cohort had apparently emigrated from the intertidal to subtidal since very few occurred in intertidal samples. The Puget Sound cohort was present in the intertidal through the winter and into the following spring. During the period from late November through early March growth of the inland cohort was virtually halted when water temperatures fell below about 7.5° C. As temperatures increased the following March the rate of growth for the Puget Sound cohort rose dramatically until these crab moved to the subtidal in June. In addition to differences in rearing temperatures, the smaller size of the Puget Sound cohort at the time of settlement also contributed to the greater time required to reach a given CW. Puget Sound J1 crab had a mean CW of 5.3 mm CW and had to undergo one additional molt to reach the initial size (7.2 mm CW) of the oceanic cohort J1 instar (Orensanz and Gallucci 1988, Dinnel et al. in preparation).

HABITAT USE

Intertidal habitats such as eelgrass, shell material, and macroalgae provide small juvenile Dungeness crab with refuge from predation (Butler 1961, Stevens and Armstrong 1984, Dumbauld and Armstrong 1987, Doty et al. 1990). Availability of refuge is especially important immediately following settlement and for the ensuing few months as predation appears to be size dependent and contributes significantly to natural mortality during this time. In the San Francisco area, fish predation on juvenile C. magister was almost exclusively on crab of 30 mm CW or less (Reilly 1983b). Staghorn sculpin (Leptocottus armatus) in Grays Harbor estuary also feed predominantly on small instars J1-J4 and seldom on larger crab (D. Armstrong, UW unpublished data). The marked decrease in predation on larger crab suggests that refuge from predation is gained in size, reducing dependence on intertidal habitat as refuge. The hypothesis of a size refuge against predation is supported by the observed emigration of crab from Puget Sound intertidal eelgrass beds into the unvegetated subtidal channels upon their reaching a CW of approximately 30 mm (Dinnel et al. 1986, 1987). This is consistent with habitat partitioning by size reported for C. magister in coastal estuaries. During summer, juvenile crab were abundant in intertidal habitats but abundance declined rapidly once crab had grown to about 30 mm CW in Willapa Bay (Doty et al. 1990) and Grays Harbor where they subsequently appeared in subtidal trawl catches (Stevens and Armstrong 1984, Armstrong and Gunderson 1985, Dumbauld and Armstrong 1987, Gunderson et al. 1990). Orth and van Montfrans (1987) report a similar ontogenetic shift in habitat for the blue crab, Callinectes sapidus, though refuge appears to be gained at a smaller size for this species.

In the northern Puget Sound study area, intertidal habitat categories, gravel-with-algae and eelgrass, provide refuge for newly settled C. magister. Highest seasonal crab densities were consistently associated with gravel-with-algae although means were not significantly different from eelgrass for summer or spring (Fig. 7, Table 3). Crab density on bare-sand was significantly lower than the other two habitats for all three seasons and fewer than 0.1 crab/m^2 were present on bare-sand in spring. Survival from summer to spring varied among habitats and presumably reflects the quality of refuge provided by the different habitats. Mean spring crab densities, expressed as percent survival from summer densities were: 36% for gravel-with-algae; 19% for eelgrass and only 5% for bare-sand.

For coastal estuarine systems, high survival of crab in shell was attributed to the three dimensional structure or complexity which provides refuge from predation (Dumbauld and Armstrong 1987, Doty et al. 1990). Likewise, the higher survival of 0+ age crab in the habitat category, gravel-with-algae, appears to be a function of the highly structured substrate surface in combination with an overstory of attached or drifting macroalgae. The highly complex surface topography may directly reduce predation by visual or physical interference and, combined with the additional effects of the vegetative overstory, may explain the higher crab densities. The intermediate survival of crab in eelgrass, relative to other habitats, is in accord with the relative complexity of this habitat. The low survival of crab (only 5%) on bare-sand is consistent with the low complexity of this habitat and the poor quality of refuge that it provides.

The association of increasing crab density (or survival) with increasing habitat complexity was also observed within eelgrass. Percent cover (= density) of eelgrass serves as a measure of relative habitat complexity. Crab appear to recruit to eelgrass in summer without regard to density of the plants (Fig. 8). However, survival of crab over time was dependent on percent cover of eelgrass. This shift in distribution conforms to predation-influenced patterns for crustacean fauna in vegetated aquatic habitats. Density of many crustacean species is positively correlated to density of, or degree of refuge provided by, Z. marina (Nelson 1979, Heck and Orth 1980, Heck and Thoman 1984, Summerson and Peterson 1984, Orth and van

Montfrans 1987, Wilson et al. 1987) or other seagrasses (Heck and Wetstone 1977, Coen et al. 1981, Nelson 1981, Orth et al. 1984, Leber 1985, Heck and Wilson 1987). Additionally, 0+ crab were nearly absent in spring where eelgrass cover was less than 40% (Fig. 3). This was consistent with other studies that reported a minimum or threshold level of vegetation density required to significantly reduce predation (Nelson 1979, Heck and Thoman 1981).

Structured or complex habitats provide protection from the environmental rigors of the intertidal environment as well as refuge from predation. The author observed an episode of settlement at Semiahmoo Spit during late July, 1986, in which megalopae that occurred on bare-sand did not survive exposure at low tide. Megalopae were observed among eelgrass and on exposed bare-sand where estimated densities were up to $10/m^2$. These had apparently sought refuge by burying just below the surface of the sand during the outgoing tide. However, over the course of exposure at low tide, most appeared to have succumbed to heat and desiccation. Perhaps as a reaction to stress, megalopae had struggled partly out of the sand, and were exposed at the sand surface. Glaucous winged gulls and crows were observed foraging over the bare-sand for the abundant megalopae. Those in adjacent eelgrass beds were protected from desiccation, high temperatures, and foraging birds and were alive and vigorous just prior to inundation by the incoming tide.

Eelgrass provides similar protection from moderate freezing in winter, although severe winter conditions may kill crab outright or indirectly through extensive reduction in eelgrass beds. Outflow of cold air masses from the Fraser River canyon can create conditions of extended below-freezing weather in the study area. During 1990, periods of high winds and freezing temperatures in combination with low tides contributed to the loss of extensive intertidal beds of eelgrass in Padilla Bay (R. Thom, Battelle Mar. Sci. Lab., pers. commun.). I speculate that if crab were able to survive the extreme conditions by burial in the substrate, they would still be subject to increased predation due to loss of refuge provided by eelgrass.

In summary, stocks of Dungeness crab in northern Puget Sound are primarily supported by recruitment from inland parental stocks. Settlement varied significantly over the scale of several kilometers between bays in the study area and between years. Variability in settlement, both across bays and across years is mediated by high post-settlement mortality which appears to be the result of heavy predation. Small scale spatial distribution of 0+ age Dungeness crab (among intertidal habitats) corresponded to habitat complexity. This association is at least partly driven by predation although other factors may contribute. For example, active selection among habitats may occur at the time of settlement. Following settlement, juvenile crab are dependent upon intertidal habitats for refuge from predation until they reach a size refuge (about 30 mm CW). Crab then emigrate from the intertidal to subtidal areas. This occurs after a period of intertidal residency of about ten months for crab originating from inland parental stock. Larvae of oceanic parental stocks are occasionally are transported into, and settle in, the northern Puget Sound area. These crab reside intertidally for only three to four months due to earlier settlement, faster growth through the warmer summer months and larger initial size.

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APPENDIX A

INTERTIDAL SURVEY DATA
Juvenile Dungeness Crab Mean Carapace Widths
Summarized by Trip and Yearclass

TRIP[1]	YEAR-CLASS[2]	MEAN CW[3] (mm)	STDDEV	No. of CRAB
1	84C	12.00	4.07	27
1	84I	5.10	.32	10
2	84C	15.80	5.13	115
2	84I	5.40	1.04	94
3	84C	21.68	5.92	73
3	84I	6.03	2.08	220
4	84C	23.50	.71	2
4	84I	8.33	3.08	9
5	84C	30.00	7.60	22
5	84I	6.29	2.94	178
6	84I	7.67	1.53	3
7	84C	39.31	7.41	16
7	84I	9.26	4.34	288
8	84C	33.33	2.08	3
8	84I	10.75	4.82	141
9	84C	43.00	.	1
9	84I	11.81	4.51	89
10	84C	52.25	4.86	4
10	84I	12.08	2.93	62
11	84C	59.00	.	1
11	84I	12.15	3.68	46
12	84I	13.12	2.93	49
13	84I	18.10	5.87	101
14	84I	21.92	6.17	103
15	84I	29.87	8.35	31
16	84I	40.00	3.61	3
17	85I	5.61	1.27	23
18	85I	4.86	.91	57
19	85I	5.98	1.51	133
20	85I	6.17	2.41	402
21	85I	7.12	2.87	548
22	85I	8.24	3.56	148
23	85I	12.22	4.25	94
24	85I	12.61	3.90	41
25	85I	18.91	4.26	124
27	85I	33.60	3.36	5
28	85I	34.13	5.91	8
29	85I	42.67	10.61	6
29	86I	5.67	1.53	3
30	85I	39.50	12.27	8

TRIP	YEAR-CLASS	MEAN CW (mm)	STDDEV	No. of CRAB
30	86I	6.00	2.13	12
31	86I	5.32	1.17	192
33	86I	5.00	.	1
35	86I	16.87	3.42	31
36	86I	26.07	5.60	45
37	86I	33.24	6.03	17
38	86I	32.00	.	1
39	86I	46.07	8.58	14
40	86I	47.71	9.78	7
40	87I	4.68	.90	38
41	87I	6.30	1.94	50
42	87I	7.80	3.40	125

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[1] Trip numbers were designated for a study of entire Puget Sound region and only those trips in which sampling occurred at one of the five northern Puget Sound study sites are included here. Trip dates are included in Appendix B.

[2] Yearclass designates year of settlement and parental stock (e.g. 84I - 1984 Yearclass from Inland parental stock; 84C - 1984 Yearclass from Coastal (or Oceanic) parental stock).

[3] Carapace Width measured anterior to tenth anterolateral spine.

APPENDIX B

INTERTIDAL SURVEY DATA
Juvenile Dungeness Crab Density
Summarized by Sampling Trip, Site and Habitat

TRIP[1]	YEAR	MONTH	DAY	SITE[2] (Bay)	HABITAT[3]	DENSITY (crab/m^2)	STDERR	No. of SAMPLES
1	84	6	29	3	5.00	2.00	2.83	2
1	84	6	29	3	1.00	6.29	9.20	7
1	84	6	29	3	3.00	.00	.00	5
1	84	6	29	3	2.00	10.67	10.58	9
1	84	6	29	3	4.00	2.67	2.31	3
2	84	7	13	3	5.00	14.00	14.79	4
2	84	7	13	3	1.00	18.59	19.08	17
2	84	7	13	3	3.00	.67	1.53	18
2	84	7	13	3	2.00	9.09	9.14	11
2	84	7	13	3	4.00	4.00	.	1
2	84	7	12	6	1.00	2.10	4.84	21
2	84	7	12	6	3.00	.67	1.63	6
2	84	7	12	6	2.00	5.71	7.80	14
2	84	7	14	9	1.00	9.26	15.38	19
2	84	7	14	9	3.00	.00	.00	14
2	84	7	14	9	2.00	1.50	4.24	8
3	84	7	28	3	5.00	33.33	23.42	6
3	84	7	28	3	1.00	14.60	11.98	20
3	84	7	28	3	3.00	2.00	4.09	24
3	84	7	27	6	5.00	.00	.00	2
3	84	7	25	6	1.00	3.34	8.37	67
3	84	7	25	6	3.00	.19	.87	21
3	84	7	27	6	2.00	5.07	5.34	15
3	84	7	27	6	4.00	.00	.	1
3	84	7	29	9	1.00	6.92	10.84	48
3	84	7	29	9	3.00	.00	.00	15
4	84	8	9	6	1.00	14.67	12.86	3
4	84	8	9	6	3.00	.00	.	1
4	84	8	9	6	2.00	.00	.	1
5	84	8	25	3	5.00	15.00	16.45	4
5	84	8	25	3	1.00	14.48	14.17	21
5	84	8	25	3	3.00	.60	1.96	20
5	84	8	25	3	2.00	.00	.	1
5	84	8	24	6	5.00	.00	.00	2
5	84	8	24	6	1.00	6.00	8.97	40
5	84	8	24	6	3.00	.00	.00	19
5	84	8	24	6	2.00	.67	1.63	6
5	84	8	26	9	1.00	4.86	6.33	37

TRIP	YEAR	MONTH	DAY	SITE (Bay)	HABITAT	DENSITY (crab/m^2)	STDERR	No. of SAMPLES
5	84	8	26	9	3.00	.22	.94	18
5	84	8	26	9	2.00	13.33	12.86	3
6	84	9	6	6	5.00	.00	.	1
6	84	9	6	6	1.00	3.00	3.83	4
6	84	9	6	6	2.00	.00	.	1
6	84	9	6	6	4.00	.00	.00	2
7	84	9	22	3	5.00	7.20	20.12	10
7	84	9	22	3	1.00	5.76	10.07	25
7	84	9	22	3	3.00	.89	1.76	9
7	84	9	22	3	4.00	35.00	42.25	4
7	84	9	21	6	5.00	.00	.	1
7	84	9	21	6	1.00	4.60	6.66	60
7	84	9	21	6	3.00	.00	.00	16
7	84	9	21	6	2.00	20.00	16.97	4
7	84	9	23	9	5.00	18.67	6.11	3
7	84	9	23	9	1.00	12.00	15.22	34
7	84	9	23	9	3.00	.00	.00	13
7	84	9	23	9	4.00	.00	.	1
8	84	10	26	3	5.00	3.20	4.54	10
8	84	10	26	3	1.00	8.59	11.88	27
8	84	10	26	3	3.00	.00	.00	9
8	84	10	26	3	4.00	13.33	11.78	6
8	84	10	26	6	5.00	.00	.	1
8	84	10	25	6	1.00	3.35	4.96	31
8	84	10	25	6	3.00	1.23	2.52	13
8	84	10	26	6	2.00	16.00	.	1
8	84	10	26	6	4.00	.00	.	1
8	84	10	27	9	5.00	12.00	8.00	3
8	84	10	27	9	1.00	2.77	5.40	26
8	84	10	27	9	3.00	.00	.00	5
8	84	10	27	9	4.00	.00	.	1
9	84	11	24	3	5.00	12.00	4.00	3
9	84	11	24	3	1.00	5.07	4.65	15
9	84	11	24	3	3.00	.33	1.15	12
9	84	11	24	3	4.00	2.22	3.53	9
9	84	11	25	6	5.00	8.00	.	1
9	84	11	25	6	1.00	1.18	2.53	44
9	84	11	25	6	3.00	.00	.00	14
9	84	11	25	6	2.00	8.00	11.31	2
9	84	11	23	9	5.00	16.00	4.00	3
9	84	11	23	9	1.00	3.33	5.66	30
9	84	11	23	9	3.00	.44	1.33	9
10	84	12	20	3	1.00	3.83	4.93	24
10	84	12	20	3	3.00	1.67	2.06	12
10	84	12	20	3	4.00	7.50	3.34	8
10	85	1	9	6	1.00	1.78	2.91	9
10	85	1	9	6	3.00	.00	.00	4
10	85	1	9	6	2.00	.00	.	1
10	84	12	19	9	5.00	4.00	.	1

TRIP	YEAR	MONTH	DAY	SITE (Bay)	HABITAT	DENSITY $(crab/m^2)$	STDERR	No. of SAMPLES
10	84	12	19	9	1.00	3.60	5.34	20
10	84	12	19	9	3.00	.00	.00	7
10	84	12	19	9	4.00	.00	.	1
11	85	2	3	3	1.00	2.61	3.74	23
11	85	2	3	3	3.00	.40	1.26	10
11	85	2	3	3	4.00	.67	1.63	6
11	85	2	4	6	1.00	.40	1.26	10
11	85	2	4	6	3.00	1.33	2.31	3
11	85	2	5	9	1.00	7.47	6.57	15
11	85	2	5	9	3.00	.00	.00	12
11	85	2	5	9	4.00	.00	.00	3
12	85	3	4	3	1.00	5.78	5.70	9
12	85	3	4	3	3.00	.00	.00	6
12	85	3	4	3	4.00	13.33	16.49	9
12	85	3	4	6	1.00	.00	.00	12
12	85	3	4	6	3.00	.00	.00	4
12	85	3	5	9	1.00	1.56	3.11	18
12	85	3	5	9	3.00	.00	.00	6
12	85	3	5	9	4.00	.00	.00	3
13	85	4	8	3	5.00	2.67	3.27	15
13	85	4	8	3	1.00	1.92	3.50	48
13	85	4	8	3	3.00	.00	.00	7
13	85	4	8	3	2.00	.00	.00	5
13	85	4	8	3	4.00	1.33	2.00	9
13	85	4	10	6	1.00	1.86	3.30	71
13	85	4	10	6	3.00	.00	.00	19
13	85	4	9	9	5.00	4.67	4.68	6
13	85	4	9	9	1.00	.86	2.08	42
13	85	4	9	9	3.00	.27	1.03	15
13	85	4	9	9	2.00	4.00	4.00	3
13	85	4	7	10	5.00	5.33	4.84	6
13	85	4	7	10	1.00	7.33	7.34	6
13	85	4	7	10	3.00	.00	.00	6
13	85	4	7	10	2.00	2.67	4.62	3
14	85	5	7	1	5.00	3.33	4.68	6
14	85	5	7	1	1.00	2.80	4.94	30
14	85	5	7	1	3.00	.00	.00	9
14	85	5	7	3	5.00	6.50	7.07	8
14	85	5	7	3	1.00	1.00	2.31	16
14	85	5	7	3	3.00	.00	.00	12
14	85	5	7	3	4.00	1.60	2.19	5
14	85	5	6	6	5.00	.00	.00	2
14	85	5	6	6	1.00	1.93	2.83	58
14	85	5	6	6	3.00	.00	.00	10
14	85	5	6	6	2.00	.00	.	1
14	85	5	6	6	4.00	2.00	4.00	4
14	85	5	9	9	5.00	2.00	3.35	6
14	85	5	9	9	1.00	1.78	3.20	27
14	85	5	9	9	3.00	.00	.00	9

TRIP	YEAR	MONTH	DAY	SITE (Bay)	HABITAT	DENSITY $(crab/m^2)$	STDERR	No. of SAMPLES
14	85	5	8	10	5.00	1.33	2.31	3
14	85	5	9	10	1.00	.96	1.96	75
14	85	5	8	10	3.00	.00	.00	3
14	85	5	8	10	2.00	.00	.00	6
14	85	5	8	10	4.00	.00	.00	3
15	85	6	2	3	5.00	1.33	2.83	9
15	85	6	2	3	1.00	.59	1.45	27
15	85	6	2	3	3.00	.00	.00	6
15	85	6	2	3	2.00	.00	.00	3
15	85	6	5	6	5.00	.00	.	1
15	85	6	5	6	1.00	.63	1.62	70
15	85	6	5	6	3.00	.00	.00	19
15	85	6	5	6	2.00	.00	.00	2
15	85	6	4	9	5.00	.00	.00	3
15	85	6	4	9	1.00	1.11	1.84	18
15	85	6	4	9	3.00	.00	.00	12
15	85	6	4	9	2.00	.00	.00	3
15	85	6	4	9	4.00	.00	.00	3
15	85	6	6	10	5.00	1.33	1.97	12
15	85	6	4	10	1.00	.46	1.29	78
15	85	6	3	10	3.00	.00	.00	9
15	85	6	3	10	2.00	1.33	2.07	6
15	85	6	6	10	4.00	2.67	2.31	3
16	85	6	21	1	5.00	.00	.00	6
16	85	6	21	1	1.00	.67	1.52	24
16	85	6	21	6	5.00	.00	.	1
16	85	6	21	6	1.00	.00	.00	7
16	85	6	21	6	3.00	.00	.00	2
17	85	6	30	1	5.00	.00	.00	9
17	85	6	30	1	1.00	.89	1.71	18
17	85	6	30	1	3.00	.00	.00	3
17	85	7	1	3	1.00	.44	1.29	18
17	85	7	1	3	3.00	.00	.00	9
17	85	7	1	3	4.00	.67	1.63	6
17	85	7	1	6	1.00	1.16	3.07	38
17	85	7	1	6	3.00	.00	.00	6
17	85	7	1	6	4.00	.00	.00	3
17	85	7	3	10	1.00	.00	.00	68
17	85	7	3	10	2.00	.00	.00	4
18	85	7	17	1	4.00	.00	.	1
18	85	7	19	3	5.00	2.67	3.27	6
18	85	7	19	3	1.00	11.33	15.14	12
18	85	7	19	3	3.00	.67	1.63	6
18	85	7	19	3	2.00	5.33	2.31	3
18	85	7	19	3	4.00	.00	.00	3
18	85	7	18	10	5.00	.00	.00	9
18	85	7	18	10	1.00	1.85	3.51	13
18	85	7	18	10	2.00	2.67	3.27	6
19	85	7	31	1	5.00	.00	.00	3

TRIP	YEAR	MONTH	DAY	SITE (Bay)	HABITAT	DENSITY $(crab/m^2)$	STDERR	No. of SAMPLES
19	85	7	31	1	1.00	14.50	16.32	16
19	85	7	31	1	3.00	.50	1.41	8
19	85	7	31	1	2.00	.00	.00	2
19	85	8	1	3	5.00	13.33	13.78	6
19	85	8	1	3	1.00	18.67	10.07	3
19	85	8	1	3	3.00	.00	.00	6
19	85	7	29	6	5.00	.00	.00	6
19	85	7	29	6	1.00	3.50	5.30	40
19	85	7	29	6	3.00	.19	.87	21
19	85	7	29	6	2.00	1.33	2.31	3
19	85	7	30	10	1.00	.57	1.63	49
19	85	7	31	10	2.00	.00	.00	4
20	85	8	17	1	5.00	2.00	2.83	2
20	85	8	17	1	1.00	18.12	18.17	17
20	85	8	17	1	3.00	.00	.00	3
20	85	8	17	1	2.00	1.33	2.31	3
20	85	8	16	3	1.00	37.82	33.15	11
20	85	8	16	3	3.00	1.33	2.07	6
20	85	8	16	3	2.00	4.00	.00	2
20	85	8	16	3	4.00	.00	.00	2
20	85	8	16	6	1.00	18.22	22.17	18
20	85	8	17	10	5.00	57.33	6.11	3
20	85	8	17	10	1.00	28.44	11.39	9
20	85	8	17	10	3.00	.00	.00	3
20	85	8	17	10	2.00	16.00	4.00	3
20	85	8	17	10	4.00	11.33	7.76	6
21	85	8	28	1	1.00	17.17	12.40	24
21	85	8	28	1	3.00	.00	.00	6
21	85	8	27	3	5.00	76.00	47.94	7
21	85	8	27	3	1.00	16.44	14.06	9
21	85	8	27	3	2.00	3.33	5.32	6
21	85	8	28	6	5.00	.00	.	1
21	85	8	28	6	1.00	12.14	13.22	28
21	85	8	28	6	3.00	.00	.00	12
21	85	8	28	6	2.00	4.00	8.00	4
21	85	8	27	9	1.00	32.89	19.47	9
21	85	8	26	10	5.00	10.67	2.31	3
21	85	8	25	10	1.00	6.83	9.85	41
21	85	8	25	10	3.00	.00	.00	2
21	85	8	25	10	2.00	8.29	11.68	14
22	85	9	23	6	1.00	4.22	5.65	37
22	85	9	23	6	3.00	.00	.00	6
22	85	9	10	10	5.00	38.67	22.15	6
22	85	9	10	10	1.00	18.46	23.86	13
22	85	9	10	10	3.00	4.00	4.00	3
23	85	11	17	1	1.00	2.00	3.27	16
23	85	11	17	1	3.00	2.00	2.83	2
23	85	11	17	3	5.00	30.67	15.14	3
23	85	11	17	3	1.00	10.67	8.49	9

TRIP	YEAR	MONTH	DAY	SITE (Bay)	HABITAT	DENSITY (crab/m^2)	STDERR	No. of SAMPLES
23	85	11	17	3	4.00	1.33	2.31	3
23	85	11	15	6	1.00	4.00	7.46	24
23	85	11	14	10	5.00	4.00	3.81	12
23	85	11	14	10	1.00	1.33	2.00	9
23	85	11	14	10	3.00	.00	.00	2
24	86	1	25	6	1.00	5.25	6.15	16
24	86	1	25	10	1.00	5.14	6.74	14
24	86	1	25	10	4.00	2.00	2.83	10
25	86	4	26	1	5.00	6.22	6.96	9
25	86	4	26	1	1.00	1.40	3.50	57
25	86	4	26	1	3.00	.00	.00	6
25	86	4	26	3	5.00	3.70	5.86	27
25	86	4	26	3	1.00	.53	2.07	15
25	86	4	26	3	3.00	.00	.00	3
25	86	4	26	3	4.00	.00	.00	3
25	86	4	25	6	1.00	.84	2.36	57
25	86	4	25	6	3.00	.00	.00	10
25	86	4	25	6	2.00	.00	.00	4
25	86	4	28	10	5.00	3.33	3.93	6
25	86	4	28	10	1.00	1.31	2.64	150
25	86	4	27	10	3.00	.00	.00	3
25	86	4	28	10	2.00	.00	.00	3
27	86	6	10	10	5.00	.31	1.11	13
27	86	6	10	10	1.00	2.00	3.35	6
27	86	6	10	10	3.00	.00	.00	3
27	86	6	10	10	4.00	.00	.00	6
28	86	6	21	1	1.00	.43	1.67	28
28	86	6	21	1	3.00	.00	.00	2
28	86	6	21	3	5.00	4.00	.	1
28	86	6	21	3	1.00	.53	2.07	15
28	86	6	20	6	1.00	.67	1.84	30
29	86	7	8	1	1.00	.20	.89	20
29	86	7	8	3	1.00	.00	.00	20
29	86	7	7	6	1.00	.55	1.76	29
29	86	7	7	6	2.00	.00	.	1
29	86	7	9	10	1.00	.24	.97	17
30	86	7	23	1	5.00	.00	.	1
30	86	7	23	1	1.00	2.67	3.94	12
30	86	7	24	1	3.00	20.00	.	1
30	86	7	24	3	1.00	.40	1.26	10
30	86	7	22	6	1.00	.20	.89	20
30	86	7	22	6	3.00	.00	.00	5
30	86	7	19	10	5.00	.00	.00	8
30	86	7	19	10	1.00	.00	.00	12
31	86	8	6	1	1.00	10.48	17.87	21
31	86	8	6	1	3.00	4.00	.00	2
31	86	8	6	3	1.00	2.00	4.37	14
31	86	8	6	3	3.00	.00	.	1
31	86	8	5	6	1.00	15.25	7.33	16

TRIP	YEAR	MONTH	DAY	SITE (Bay)	HABITAT	DENSITY (crab/m^2)	STDERR	No. of SAMPLES
31	86	8	5	6	3.00	8.00	.00	2
31	86	8	7	10	5.00	26.00	25.46	2
31	86	8	7	10	3.00	.00	.	1
31	86	8	7	10	2.00	62.67	37.17	3
33	86	9	14	1	1.00	.20	.89	20
35	87	4	17	6	1.00	1.82	3.85	22
35	87	4	17	6	3.00	.00	.00	2
35	87	4	18	10	5.00	6.91	6.71	11
35	87	4	18	10	1.00	.38	1.20	21
35	87	4	18	10	3.00	.00	.	1
35	87	4	18	10	2.00	.57	1.51	7
36	87	5	15	1	1.00	1.75	2.85	48
36	87	5	15	1	3.00	.00	.00	2
36	87	5	14	6	1.00	1.67	2.65	43
36	87	5	14	6	3.00	.00	.00	3
36	87	5	14	6	2.00	.00	.	1
36	87	5	17	10	5.00	1.87	3.66	15
36	87	5	17	10	1.00	.71	1.57	17
36	87	5	17	10	2.00	.00	.00	7
36	87	5	17	10	4.00	.00	.	1
37	87	6	12	1	1.00	.11	.68	35
37	87	6	12	1	3.00	.00	.00	4
37	87	6	12	1	2.00	.00	.	1
37	87	6	11	6	1.00	.74	1.57	38
37	87	6	11	6	3.00	.00	.00	2
37	87	6	13	10	5.00	.92	1.75	13
37	87	6	13	10	1.00	2.29	2.14	7
37	87	6	13	10	2.00	1.60	3.58	5
38	87	6	26	6	1.00	.13	.73	30
39	87	7	8	1	1.00	.92	2.06	26
39	87	7	8	1	3.00	.00	.00	4
39	87	7	9	6	1.00	1.19	2.17	27
39	87	7	9	6	2.00	.00	.00	2
39	87	7	11	10	5.00	.00	.00	7
39	87	7	11	10	1.00	.11	.67	36
39	87	7	11	10	3.00	.00	.00	6
39	87	7	11	10	2.00	.00	.00	30
39	87	7	11	10	4.00	.00	.	1
40	87	7	24	1	1.00	1.00	2.27	32
40	87	7	24	1	3.00	.00	.00	6
40	87	7	24	6	1.00	1.69	2.81	26
40	87	7	24	6	3.00	.00	.	1
40	87	7	25	10	5.00	6.00	4.00	4
40	87	7	25	10	1.00	1.00	3.39	24
40	87	7	28	10	3.00	.00	.00	9
40	87	7	25	10	2.00	3.29	5.70	17
40	87	7	28	10	4.00	.00	.00	2
41	87	8	10	6	1.00	2.00	3.78	20
41	87	8	6	10	5.00	3.30	3.75	23

TRIP	YEAR	MONTH	DAY	SITE (Bay)	HABITAT	DENSITY (crab/m^2)	STDERR	No. of SAMPLES
41	87	8	6	10	1.00	3.33	6.09	24
41	87	8	11	10	3.00	.00	.	1
41	87	8	6	10	2.00	.62	1.50	13
41	87	8	6	10	4.00	.00	.	1
42	87	9	4	1	1.00	8.24	6.55	17
42	87	9	4	1	3.00	.00	.	1
42	87	9	4	1	4.00	4.00	.	1
42	87	9	4	6	1.00	2.80	4.12	20
42	87	9	4	10	5.00	11.11	9.76	18
42	87	9	4	10	1.00	2.67	5.13	18
42	87	9	6	10	3.00	.00	.00	6
42	87	9	4	10	2.00	3.73	7.17	15

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[1] Trip numbers were designated for a study of entire Puget Sound region and only those trips in which sampling occurred at one of the five northern Puget Sound study sites are included here.

[2] Site:
1 - Semiahmoo Spit
3 - Birch Bay
6 - Lummi Bay
9 - Samish Bay
10- Padilla Bay

[3] Habitat:
1 - Eelgrass (_Zostera marina_) over sand or silt
2 = Macroalgae over sand or silt
3 - Bare sand
4 - Mixed gravel, cobble and sand
5 - Mixed gravel, cobble and sand with Macroalgae

[a]Macroalgae - _Ulva fenestrata_, _Enteromorpha intestinalis_ _Laminaria sp_. _Fucus gardneri_