DISTRIBUTION, ABUNDANCE, AND GROWTH OF JUVENILE DUNGENESS CRABS, *CANCER MAGISTER*, IN GRAYS HARBOR ESTUARY, WASHINGTON[1]

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ABSTRACT

Dungeness crabs, *Cancer magister*, were collected biweekly or monthly from May 1980 to July 1981 in Grays Harbor, Washington. Age of each crab was estimated from width-frequency analyses, and the population density and growth rate were monitored for each age class over the 14-month period. In April 1980 and 1981, crabs entered the estuary either as megalops larvae that metamorphosed to first instar postlarvae or directly as first instars. Intertidal mudflats with beds of eelgrass (*Zostera* spp.) were important habitats for the first few postlarval stages. Some crabs may have emigrated from the estuary during their second year of life, whereas others dispersed throughout the estuary and appeared to emigrate at sexual maturity (about 2 years). No gravid females were ever found in the bay. Population size was estimated to range from 3.3 million crabs (winter) to 39.0 million crabs (summer); 74% of the summer population were early instars. Growth of early instars was rapid and resulted in a 282-fold increase in dry weight from May to September, but little growth occurred during the remainder of the year. Based on summer population abundance, it is estimated that this estuary could account for a substantial portion of recruitment to the offshore commercial fisheries.

The biology of the Dungeness crab, *Cancer magister*, has been studied by numerous investigators for several decades (Weymouth and MacKay 1936; MacKay 1942) because of its importance to commercial fisheries and its position as a benthic predator in estuaries and offshore communities (Gotshall 1977; California Department of Fish and Game 1981). Previous studies of *C. magister* biology have been conducted largely along the open coast (MacKay 1942; Cleaver 1949; Butler 1960, 1961; Gotshall 1978b, c). The few studies of crab populations in estuaries or shallow-water habitats (Butler 1956; Tegelberg and Arthur 1977; Gotshall 1978a; California Department of Fish and Game 1981) have indicated that such areas may be extremely important nursery grounds, but the size and dynamics of estuarine populations have not been statistically determined and, furthermore, the contribution of estuarine habitats to offshore stocks has not been adequately assessed. Orcutt et al. (1978) estimated that 50-80% of crabs caught by the fishery in the Gulf of the Farallones spend some of their life cycle in the San Francisco-San Pablo Bay complex. Benefits derived from estuarine early life history may include enhanced growth rates, more abundant food, and refuge for postlarval and juvenile crabs from larger, older age classes that act as competitors and predators (Botsford and Wickham 1978).

Quantitative studies of *C. magister* in major estuaries are timely and imperative. The demise of the San Francisco fishery prompted a 5-yr investigation of *C. magister* biology in that region (California Department of Fish and Game 1981), and hypotheses for the decline include alterations of estuarine habitat and water quality. In addition, channel dredging practices in west coast estuaries kill hundreds of thousands of crabs annually (Stevens 1981). Armstrong et al. (1982) estimated that a proposed channel modification project in Grays Harbor, Wash., could entrain and kill 2.5 million crabs over a 2-yr period. Knowledge of estuarine crab population dynamics and ecology of juveniles is required to gauge the relative importance of such habitat to the species, and to mitigate impacts of estuarine development on juvenile stages.

MATERIALS AND METHODS

Study site

Grays Harbor is a shallow drowned river basin

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estuary with an extensive littoral zone and a wide variety of substrate types (Fig. 1). Sampling stations were established primarily along the existing navigation channel in accord with a concurrent study to assess the impact of dredging on Dungeness crabs (Armstrong et al. 1982). Habitats represented include deeper sandy channels (stations 1-3), shallow sand (station 4), sand-mud (stations 6 and 7), mud (stations 8-12), and those adjacent to eelgrass (*Zostera marina* and *Z. noltii*) beds (station 5) (Table 1; Fig. 1). Fifteen sublittoral strata were established for the purpose of estimating population abundance, and sampling stations were located approximately at the center of each (Fig. 1). However, strata 14 and 15 contained no regularly sampled stations because these areas were outside the primary focus of our contract. The boundaries of each stratum were defined by the midpoint between sampling stations, or the bottom contours at −5.5 m or 0.0 m (for detailed

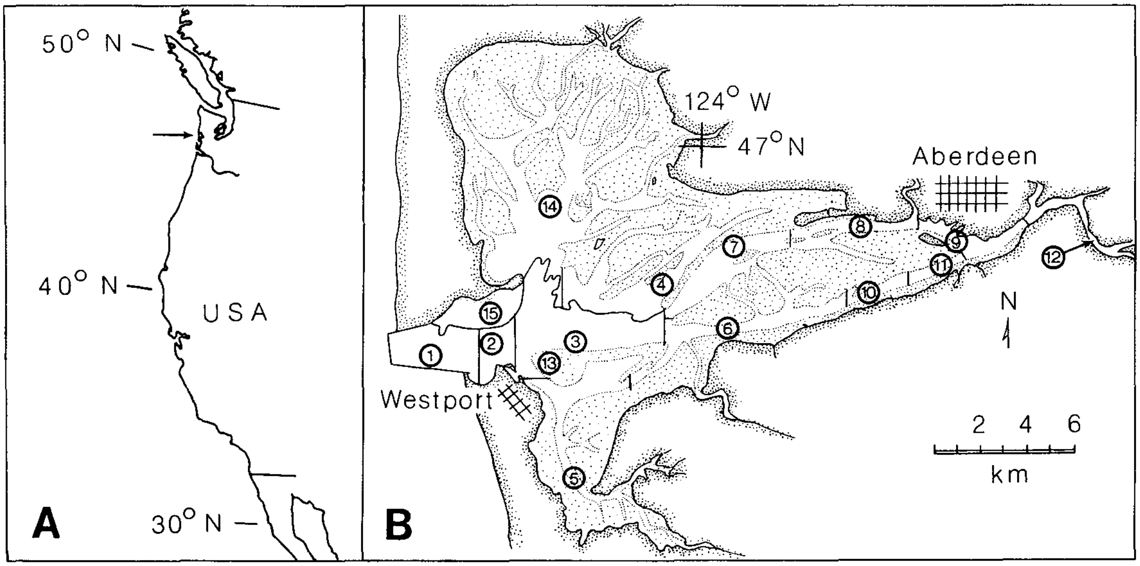

FIGURE 1.—A. West coast of North America. Arrow indicates site of Grays Harbor, Wash.; B. Map of Grays Harbor, showing sites of *Cancer magister* collection (1-13). Stations 14 and 15 represent unsampled strata. Lines separating strata were defined arbitrarily for use in determining crab population size.

TABLE 1.—Location and description of sampling sites for *Cancer magister* in Grays Harbor, Wash.

Station no.	Area (ha)	Gear type[1]	Latitude N	Longitude W	Depth (m)	Bottom type	Comments
1	837	T	46°54′30″	125° 9′ 0″	15-18	Sand, cobble	Not sampled in 1981 due to rough water conditions.
2	496	T	46°55′15″	124° 7′20″	13-15	Hard sand	Dredged sediment disposal site.
3	1,507	T	46°55′15″	124° 4′20″	10-15	Sand	Outer harbor channel bottom.
4	1,120	T	46°56′40″	124° 1′10″	3-5	Sand, mud	Shallow outer harbor habitat.
5	658	T	46°51′55″	124° 4′15″	5-8	Sand, mud	Adjacent to extensive eelgrass beds.
6	680	T	46°55′40″	123°59′ 5″	6-8	Sand, mud, leafy debris	Near mudflats without eelgrass.
7	656	T	46°57′30″	123°59′ 0″	11-14	Mud, sand	Adjacent to eelgrass beds.
8	418	T	46°58′10″	123°55′20″	11-15	Mud	Inner harbor channel bottom.
9	221	T	46°57′40″	123°50′50″	12	Mud	Numerous snags; adjacent to shipping terminals, inner harbor.
10	96	RN	46°56′20″	123°54′15″	3-4	Mud, snags	
11	86	RN	46°57′12″	123°51′15″	3-4	Mud, snags	
12	—	RN	46°57′37″	123°46′18″	3-4	Mud, cobble	Along shore of deep (20 m) river channel.
13		T	46°54′45″	124° 5′15″	0-3	Sand	Intertidal sand flat; no eelgrass.
14	2,653					Mud, sand, eelgrass	Not sampled. Used for population estimate.
15	414					Sand	Not sampled. Used for population estimate.

[1] T = otter trawl; RN = ring net.

descriptions see Stevens 1982). The area of each stratum was determined by planimetry at the level of mean lower low water (NOAA Chart No. 18502 Grays Harbor, 1979 edition).

Sampling Design

Crabs were sampled at stations 1-9 and 13 with a 4.9 m, 4-seam, semiballoon otter trawl net, having 38 mm stretch nylon mesh throughout and a 6 mm cod end liner. Working width of the net was about 3.0 m. Distance towed was measured between buoys placed at the beginning and end points of each trawl, by compass triangulation to stationary objects whose positions were predetermined and located on 7.5-min topographic maps (U.S. Geological Survey). Distances were then converted to area swept and catches expressed as crabs/ha. At stations 10-12, underwater snags prevented trawl operation so crabs were collected by setting collapsible ring nets (76 cm diameter) covered with 12 mm mesh. A "set" consisted of 4 baited nets set 50 m apart and fished for 20 min. Catches were expressed as crabs/net. Trawls and ring net sets were made within 1-2 h of slack low tide in daylight. Occasional plankton tows were made with a 0.5 m diameter conical net of 500 μm mesh, in the spring of 1980 and 1981, to determine if crabs entered the bay as larvae.

Stations 3, 6, 8, and 9 were sampled biweekly from May through October 1980 and at intervals of 4-5 wk thereafter through July 1981. Other stations were generally sampled monthly except when weather or boat problems precluded operations. Most stations were sampled on 13-19 occasions during the 14-mo field study (May 1980 to late June 1981), with the exception of stations 1 and 2 (6 and 10 samples, respectively). Station 13 was sampled quarterly on a diel basis, and complete results from that diel study are reported elsewhere (Stevens and Armstrong 1984). No samples were taken at stations 14 and 15 which were used only to calculate crab populations based on data from adjacent areas (see below).

All crabs were measured to the nearest millimeter across the carapace between the notches just anterior to the 10th anterolateral spines ("carapace width" or cw), sexed, and released. Subsamples were used for width frequencies only in May and June of 1980 and 1981, when early instars were collected in large quantities. Surface and bottom-water samples were collected during each trawl with a modified Van Dorn bottle; temperature was measured to 0.1°C, and salinity determined with a refractometer at room temperature.

Growth Analysis

Cumulative width frequencies of all crabs caught during a given week were plotted on probability paper, and width limits were subsequently defined as the curve inflection points (arbitrarily nonoverlapping) to delimit the size range of each year class through time, according to the method of Cassie (1954). These were compared with frequency graphs for verification. Values were interpolated during weeks in which too few crabs were caught for accurate analysis. Each crab was then assigned to an age-group on the basis of the width limits for each sampling week. Age was defined as the number of years since metamorphosis. Mean widths were calculated for each age group (0+, 1+, 2+, and 3+) and plotted by sampling week. Eighty-seven males (12-132 mm cw) and 74 female crabs (15-115 mm cw) were frozen and returned to the University of Washington where they were opened at the epimeral line and dried to constant weight at 60°C (48-72 h). Only hardshell intermolt crabs were used. Log_{10} dry weight (g) was plotted against $\log_{10}$ carapace width (mm) and regression equations determined for each sex. Mean weights for each age group of crabs were calculated at monthly intervals from mean widths using the regression equation (the 1977 year class was omitted because the regression equation did not represent these larger animals). Weight-specific growth rates (k) per month were calculated by use of the equation

$$W_t = W_0 \, e^{kt}.$$

The monthly percent weight increase was calculated as $e^k - 1$.

Crab Density Analysis

Because counts of benthic invertebrates usually show a contagious distribution (Elliott 1977), all density data were transformed prior to analysis of variance or regression by

$$X_t = \text{Log}_{10} \, (\text{density} + 1),$$

where X_t is the transformed variable.

Density was plotted against bottom-water salinity, temperature, and estimated Chehalis River flow by a stepwise multivariate procedure (SPSS REGRESSION) for all trawl and ring net samples.

The effects of season and location on crab density were examined by analysis of variance (SPSS ANOVA procedure). The sampling year was divided into two seasons: spring-summer (March-August) and fall-winter (September-February). The navigation channel was divided into two areas: the outer estuary (stations 2, 3, and 4: station 1 deleted due to lack of winter data points), and the inner estuary (stations 7, 8, and 9). A two-way ANOVA was performed with these two seasons and two station groups as the independent variables, and crabs/ha as the dependent variable.

Population Estimation

Two basic assumptions were made concerning the trawl data: 1) Sampling efficiency of the net was not 100% and varied for each age class of crabs. Efficiency was estimated to be 0.33 for the 0+ age class during summer, and 0.25 in winter, based on comparisons between net catches and visual counts of young instars on mudflats at low tide (see Discussion). Sampling efficiency was estimated to be 0.50 for all other age groups in accordance with Gotshall (1978a). 2) Sampling efficiency was assumed to remain constant and not to vary as a function of changes in crab behavior (e.g., burial or diel activity variations).

Data on crab densities were used from a 12-mo period, June 1980 to May 1981, which was divided into three "seasons": summer (June-August 1980), fall-winter (September 1980-February 1981), and spring (March-May 1981). Population estimates were made for three age groups (0+, 1+, and 2+, the latter including all 3+ animals which were identifiable only in summer 1980) in each of the three defined seasons. A *stratified* random technique was used, using the following variables (see Cochran 1953):

h = stratum of harbor
C_{ih} = catch of crabs in tow i, stratum h
a_{ih} = area (ha) covered by tow i, stratum h
n_h = number of tows in stratum h
x_{ih} = individual estimates of crabs ha^{-1}, from tow i, stratum h
$\bar{x}_h$ = mean catch (crabs ha^{-1}) in stratum h for a given season
A_h = area of harbor in stratum h (ha)
$s^2{}_{(\bar{x}_h)}$ = variance of mean $\bar{x}_h$ in stratum h
T = total number of crabs in harbor.

Data used for population estimates were not transformed as done for ANOVA comparisons because that would have led to complications in the determination of confidence intervals, but only minor changes in the resultant mean densities of crabs. Mean crab density in each stratum was calculated for each age group and season by

$$\bar{x}_h = \frac{\sum_{i=1}^{n} (c_{ih}/a_{ih})}{n_h} .$$

The total number of crabs in each stratum was calculated as $T_h = A_h\ (\bar{x}_h)$, and the total for the harbor by the sum of all stratum totals,

$$T = \sum_{h=1}^{15} T_h .$$

For strata 1-9, the variance of each stratum total was calculated by

$$V_{(T_h)} = \frac{A_h^2 s^2(\bar{x}_h)}{n} ,$$

and the variance of the total was calculated by summing the individual variances

$$V_{(T)} = \sum_{h=1}^{9} V_{(T_h)} .$$

Confidence intervals for T were approximated at the 95% level by

$$T \pm t_{(\text{df},\, 0.05)}\, V_{(T)}^{1/2} .$$

Crab abundances in strata which were not sampled by trawl (10, 11, 14, and 15) were calculated using mean density values from nearby strata of similar ecological characteristics. Data were used from strata 6 (for 10 and 11), 5 (for 14), and 3 (for 15). Totals by age group and season for those strata were added to totals for strata 1-9, to obtain totals for the entire estuary. The estuary totals were divided by the estimated trawl efficiency factors to obtain final corrected estimates of crab abundance by age group and season. Confidence intervals for these final estimates could not be computed.

RESULTS

Temperature-Salinity Profile

Grays Harbor has a strong horizontal salinity gradient (Fig. 2). Temperature and salinity were

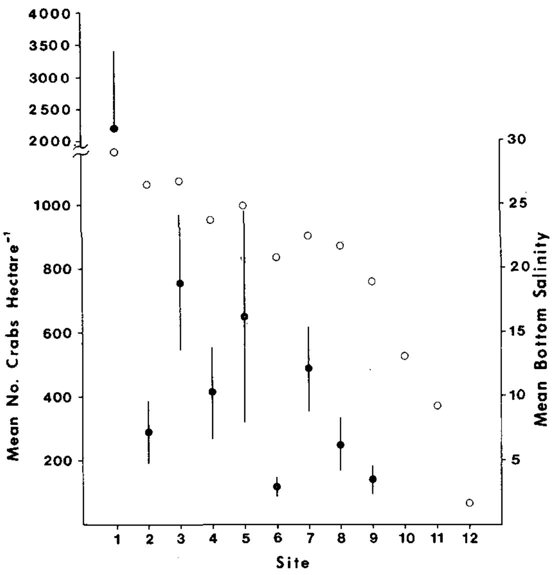

FIGURE 2.—Temperature-salinity profile for crab sampling sites 1-12, Grays Harbor, Wash. Filled circles indicate mean density +1 SE of crabs for the entire study, as determined by trawl; open circles indicate mean bottom salinity at low tide. Crab densities are not plotted for stations 10-12 where ring nets were used.

more stable in the outer estuary, but less so as distance increased eastward from the harbor mouth. At station 3, bottom temperatures ranged from 7°C (winter) to 14°C (summer), while at station 9 they ranged from 5° to 18°C. Vertical stratification was greater toward the head of the estuary and less so in the outer estuary as a result of turbulent mixing. Greatest vertical salinity difference measured during the study was 17‰ at station 9. Grays Harbor receives 70-100 in of rainfall annually, and stratification was greatest during November-March, the period of peak rainfall. Flow rates of the Chehalis River, which contributes 80% of the freshwater inflow, varied from 22.3 m^3s^{-1} in August 1980 to 2,322 m^3s^{-1} in February 1981 (data provided by U.S. Geological Survey).

Spatial Distribution of Crab Population

Complete records (width, sex, age) were obtained for 14,556 crabs. Coefficients of variation averaged 0.53 for the trawls and 0.46 for the ring nets, implying that both techniques had a similar degree of precision.

Mean density of crabs during the 14-mo sampling period was greatest at station 1 (2,190 crabs ha^{-1}), and catches declined with increasing distance from the estuary mouth and decreasing bottom salinity (Figs. 2, 3A). Notable exceptions to this pattern were low densities at stations 6 and 2 (120 and 290 crabs ha^{-1}, respectively; Fig. 3). Station 2 was concurrently being used as a dredged sediment disposal site by the U.S. Army Corps of Engineers.

Crabs caught by ring net were more abundant at station 11, near the eastern (upstream) end of the estuary than at station 10, and averaged 22.9 and 12.7 crabs net^{-1}, respectively, from June to October (Fig. 3F). No crabs were caught at station 12 except in August and September 1980.

Temporal Distribution of Crab Population

Megalops larvae were found as early as 1 April 1980 at station 6, and in densities up to 810/1,000 m^3 at station 5 on 22 April 1980.

Crab densities at all stations were greatest from May to August 1980 (Fig. 3A-E) and declined from September 1980 through January 1981. Lowest densities occurred in October and November 1980, none being >200 crabs ha^{-1} except at station 1. Although monthly variation was great at each station, this general decline in crab density during fall-winter occurred throughout the estuary.

Crab abundance at the three ring-net stations (10, 11, and 12) increased dramatically from June through October 1980, then dropped in November 1980 to a low of <1.0 crabs net^{-1} at all three stations (Fig. 3F). No crabs were caught at station 12 except during August and September 1980, when the salinity reached 9 and 7‰, respectively. Salinity at station 12 was 1.0‰ or less during all other sampling periods.

The *F*-tests showed that mean crab density in the outer estuary (stations 2, 3, and 4) was significantly greater ($P = 0.011$) than in the inner estuary (stations 7, 8, and 9; Table 2). Crab density at all six stations (2, 3, 4, 7, 8, and 9) was significantly greater ($P = 0.001$) in spring-summer than in fall-winter 1980-81. Regression analysis of $\log_{10}$-transformed density data on bottom salinity, temperature, and Chehalis River flow rate showed no significant dependence of trawl catches on these variables, but salinity alone was responsible for about 40% of the variance in crab abundance at the ring net stations (10, 11, and 12; $r^2 = 0.398$, $P = 0.001$).

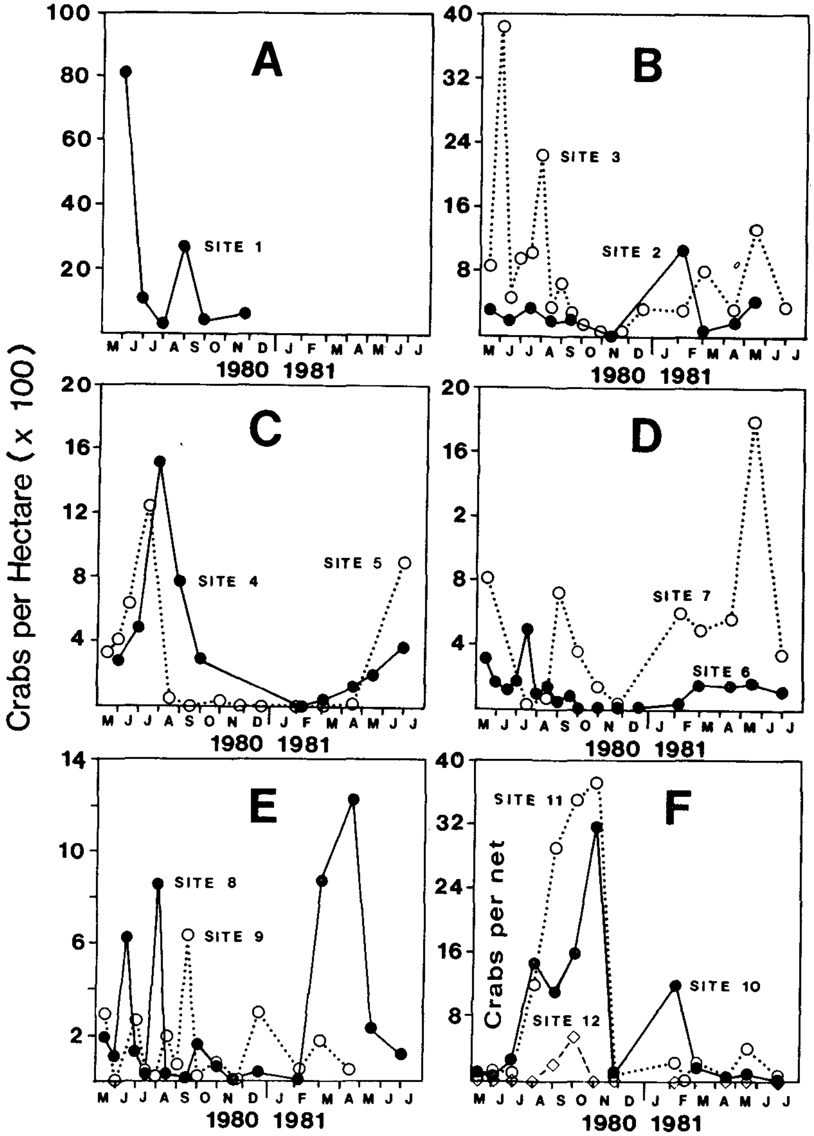

FIGURE 3.—Crab density for all sampling sites in Grays Harbor, Wash., sampled in 1980-81. Trawl sampling sites 1-9 are shown as crabs ha^{-1}; ring-net sampling sites 10-12 are shown as crabs per ring net. Each point represents a single sample.

Age-Structure of Crab Population

Width-frequency distributions for all crabs caught by trawl in the estuary are presented by sampling week in Figure 4. Width limits for each age class were selected so as to be nonoverlapping (Table 3).

The distribution of crabs within the estuary varied with age group. Animals in the 0+ age group were commonly found from station 2-8 at an average of 46 crabs ha^{-1}, and represented 16.6% of total crabs caught in the estuary throughout the entire 14-mo sampling period (Fig. 5). The greatest annual mean density of this age group occurred at station 5 near an area of dense eelgrass. The density of this age group was very low during October-December.

Summer populations of 0+ crabs were about twice as dense at station 5 than at any other (Fig. 6). Visual inspection of mudflats adjacent to this

TABLE 2.—Mean densities of *Cancer magister* in Grays Harbor, Wash., areas and seasons compared by ANOVA. Values are means of original data expressed as crabs ha^{-1}, ± SE, with n in parentheses. F tests were performed on log-transformed data.

Mean densities:	Outer harbor (sites 2-4)	Inner harbor (sites 7-9)	Season means
Spring-summer (March-Aug.)	658 ±146 (29)	358 ±73 (32)	500 ±81 (61)
Autumn-winter (Sept.-Feb.)	229 ±104 (10)	120 ±42 (16)	162 ±47 (26)
Area means	548 ±114 (39)	279 ±53 (48)	

Results of F-tests:

Comparison	df	F-value	Probability level
Seasons	1/83	15.181	0.001
Areas	1/83	6.744	0.011
Interaction	1/83	0.607	0.438

site in May 1982, and at a similar site in stratum 14 in May 1981, revealed that first instar crabs were abundantly distributed on the mudflats at low tide in slight depressions, buried just beneath the sediment surface and in burrows of *Callianassa* spp. Estimated densities were 1-5 crabs m^{-2}, based on random visual observations within an area of the mudflats measuring about 100 m^2. This density was 1-2 orders of magnitude greater than that calculated from trawl catches of this age group. Therefore, it is likely that 0+ crabs were grossly underrepresented in the trawl catch, especially at stations near mudflats such as 4 through 8. The 0+ age group formed <1% of the catch at station 1 and were virtually absent from the ring net stations (10-12).

Crabs in the 1+ age group were by far the most

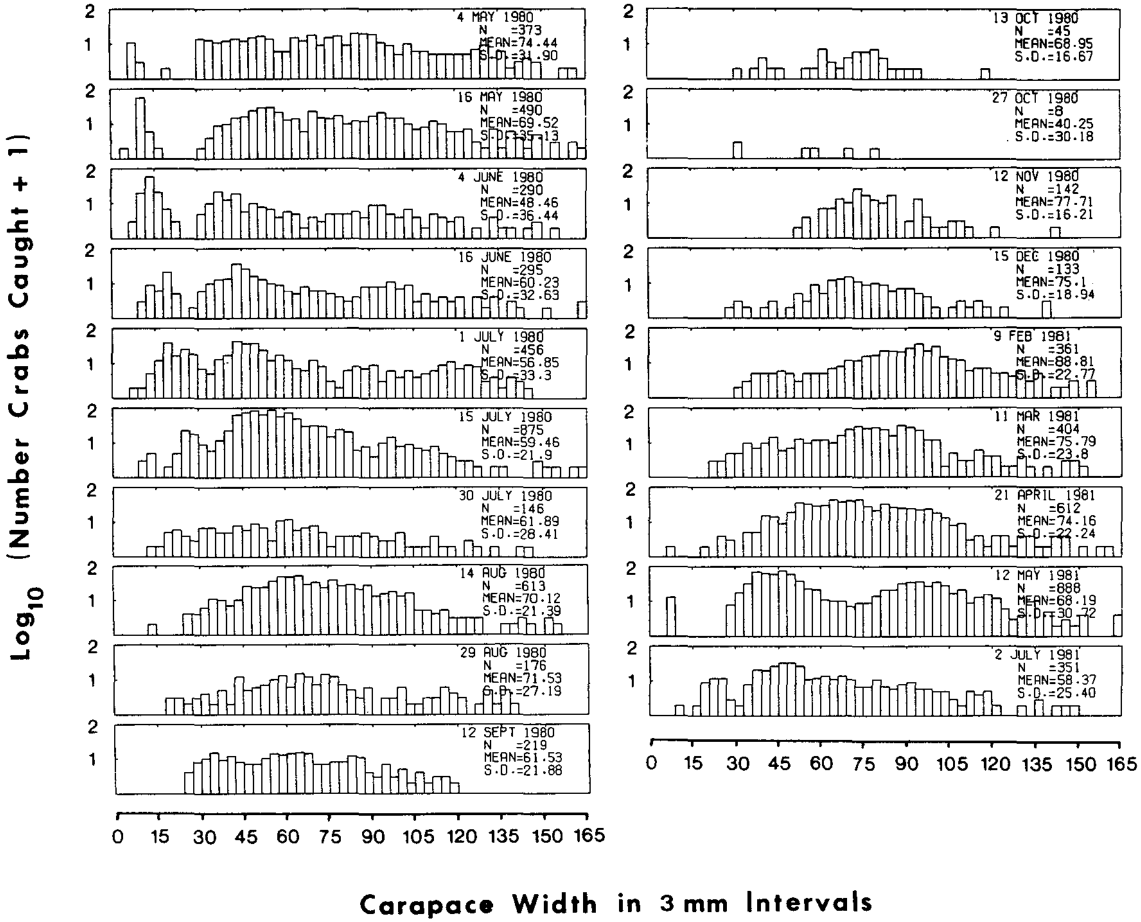

FIGURE 4.—Carapace width frequencies of all crabs caught by trawl at stations 1-9 in Grays Harbor, Wash., 1980-81. Numbers expressed as $\log_{10}$ (catch + 1). Box for each sampling period shows date, number of crabs measured, mean carapace width overall (mm), and standard deviation.

abundant at all stations except 3, averaging 268 crabs ha^{-1} and 54.7% of all crabs over the entire sampling period. Greatest densities occurred at station 1, but these crabs were also abundant at stations 3, 4, 5, and 7 (Fig. 5), i.e., the outer estuary. This group was least abundant at stations 6, 8, and 9, but comprised the largest proportion (73-78%) at the ring net stations (10-12).

The average density of the 2+ age group was 121 crabs ha^{-1} (stations 1-9) equal to 21.3% of all crabs caught. Greatest densities occurred at stations 1 and 3 (Fig. 5). This group was the most abundant at station 3, the only area where the 1+ age group did not predominate.

The 3+ age group was difficult to separate from the 2+ group because the former were caught in low numbers. Of all samples taken during the study, they represented 3% with an average density of 17 crabs ha^{-1}. This group occurred primarily at stations 1-3, with greatest densities at station 1 (Fig. 5).

TABLE 3.—Upper limit of carapace width range (mm) of *Cancer magister* in Grays Harbor, Wash., for each age/sex group. Selection method was cumulative probability (P) or interpolation (I). The upper limit for age 2+ crabs (lower limit of 3+) was not distinguishable in fall-winter due to low numbers caught. nd = not distinguishable.

	Males				Females			
		Age groups				Age groups		
Date	Method	0+	1+	2+	Method	0+	1+	2+
5/4/80	P	25	60	115	P	30	60	120
5/16/80	I	26	65	120	I	28	69	124
6/4/80	P	27	70	124	P	25	77	127
6/16/80	I	29	70	132	I	27	79	126
6/21/80	P	30	70	136	P	28	80	126
7/1/80	I	32	75	136	I	31	87	127
7/15/80	P	34	85	136	P	37	90	130
7/30/80	I	37	88	134	I	36	91	nd
8/14/80	P	40	92	132	P	36	92	nd
8/29/80	I	43	92	nd	I	41	93	nd
9/12/80	I	45	94	nd	I	45	94	nd
9/26/80	P	46	96	nd	P	50	95	nd
10/13/80	P	46	105	nd	P	50	96	nd
10/27/80	I	46	106	nd	I	52	98	nd
11/12/80	P	46	107	nd	P	54	100	nd
12/15/80	P	46	101	nd	P	52	104	nd
1/17/81	P	44	121	nd	P	55	125	nd
2/9/81	I	44	121	nd	P	54	126	nd
3/11/81	P	45	121	nd	P	61	126	nd
4/4/81	P	47	120	nd	P	56	133	nd
4/21/81	I	15	55	nd	I	15	63	120
5/21/81	P	26	70	127	P	29	75	120
7/1/81	P	29	75	nd	P	29	86	nd

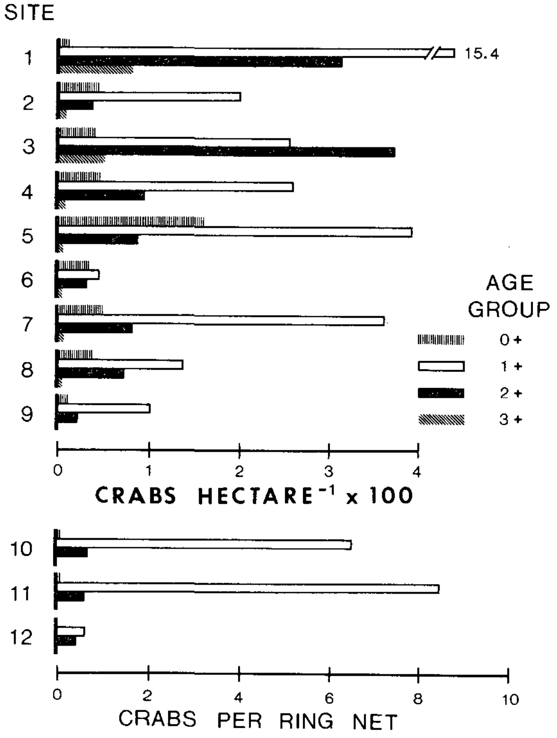

FIGURE 5.—Mean number of crabs per hectare (sites 1-9) and crabs per ring net (sites 10-12) in Grays Harbor, Wash., over the entire study period, by age group.

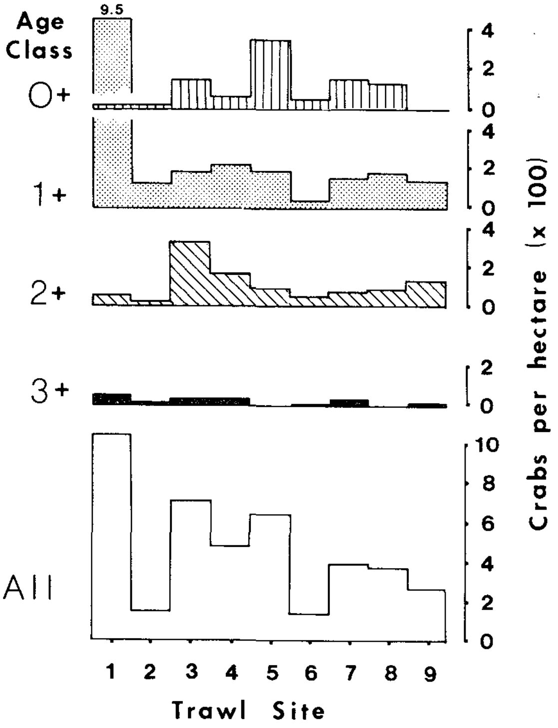

FIGURE 6.—Actual density of crabs caught by trawl at sites 1-9 in Grays Harbor, Wash., June 1980, by age class. Sites 2, 5, and 7 sampled on 4 June; sites 1, 4, and 9 sampled on 16 June; sites 3, 6, and 8 sampled on both dates and averaged. Note greatest abundance of 0+ age group at site 5.

Growth: Width

Crabs in the 0+ age group (1980 year class) increased in width by a factor of 4, from 10 mm in May to 40 mm in October 1980, but growth slowed from then to the following April 1981 when they were about 50 mm wide (Fig. 7). The same pattern of rapid growth during spring and summer was evident among the 1+ and 2+ age groups (1979 and 1978 year classes, respectively), although measurable increases in carapace width were recorded into winter 1981 for these older crabs. Crabs of the 1979 year class grew from 45 to 73 mm between May and October 1980 (factor of 1.6), while the 1978 year-class crabs grew from 84 to 118 mm during the same period, an increase of 1.4. Females had slightly greater mean widths than males up to about 125 mm cw, but the differences were minor (Table 3).

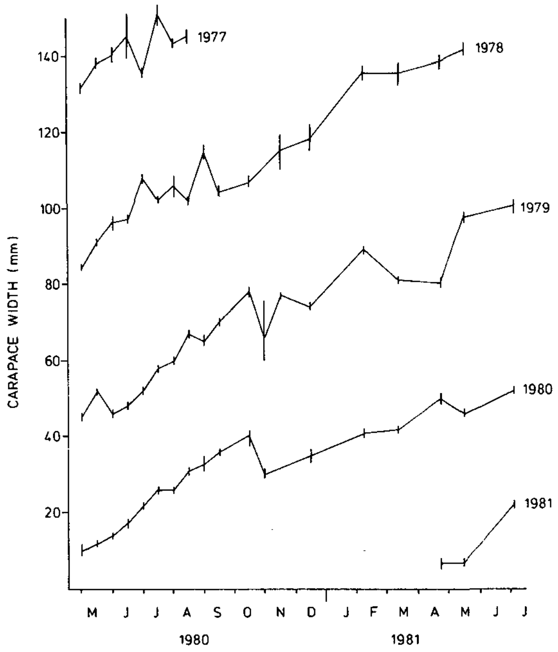

FIGURE 7.—Mean width of four age groups of crabs (0+, 1+, 2+, 3+) in Grays Harbor, Wash., 1980-81. Mean width (+1 SE) shown for each sampling period was determined by graphical analysis of width-frequency data or interpolation (see Table 3).

Growth: Weight

Regression equations for $\log_{10}$ dry weight (g) on $\log_{10}$ carapace width (mm) were derived separately for male and female crabs, but were not significantly different. Therefore, a pooled regression equation was calculated for both sexes combined:

$$\text{Log}_{10}\ \text{Weight (g)} = -4.064 + 2.832\ (\text{Log}_{10}\ \text{Width, mm})$$

or

$$\text{Weight (g)} = (8.63 \times 10^{-5})\ \text{Width}^{2.832}$$

$$(r^2 = 0.985, P = 0.0001;\ \text{Fig. 8}).$$

Differences in width/weight and width/age relationships between male and female crabs would probably increase at sexual maturity, which occurs about 2 yr after metamorphosis, and at widths of 93-122 mm for males and 100-105 mm for females (Butler 1960, 1961; Poole 1967). Growth data presented herein are probably valid only for male crabs <132 mm and female crabs <115 mm width.

Changes in mean weight with time (Fig. 9) probably represent a continuous curve, but there appeared to be an inflection point in late August that separated spring-summer and fall-winter growth stanzas. Therefore, *k* values were calculated for the periods May-August and September-April.

Monthly weight-specific growth rates were greater in spring-summer than in fall-winter for all age groups but decreased with size (Fig. 9). Specific growth rates were greatest for 0+ age group crabs in their first summer during which the average monthly weight increase was 206% (Table 4). Growth decreased to an average 15.8% per month during the winter. Growth rates increased again for age 1+ crabs in their second summer (31% per month), but were lower than experienced in their first year. This pattern was found for all age groups. Crabs in the 2+ age group (probably at sexual maturity) increased in weight 25% per month in the summer of 1980, but only 6.5% per month during the following winter (Table 4). First

TABLE 4.—Weight-specific growth rates (*k*) and percent weight increase of three year classes of *Cancer magister* in Grays Harbor, Wash. Weight calculated from mean carapace widths of each year class by regression equation (see Figure 8). Growth per month calculated for spring-summer (May-August) and fall-winter (September-April) growth stanzas (see also Figure 9).

				Mean growth per month			
	Dry weight (g)			Spring-Summer		Fall-Winter	
Year class	4 May 1980	29 Aug. 1980	22 Apr. 1981	*k*	% weight increase	*k*	% weight increase
1980	0.02	1.75	5.56	1.118	206	0.147	15.8
1979	4.02	11.75	21.46	0.268	31	0.075	7.8
1978	24.30	59.70	98.71	0.225	25	0.063	6.5

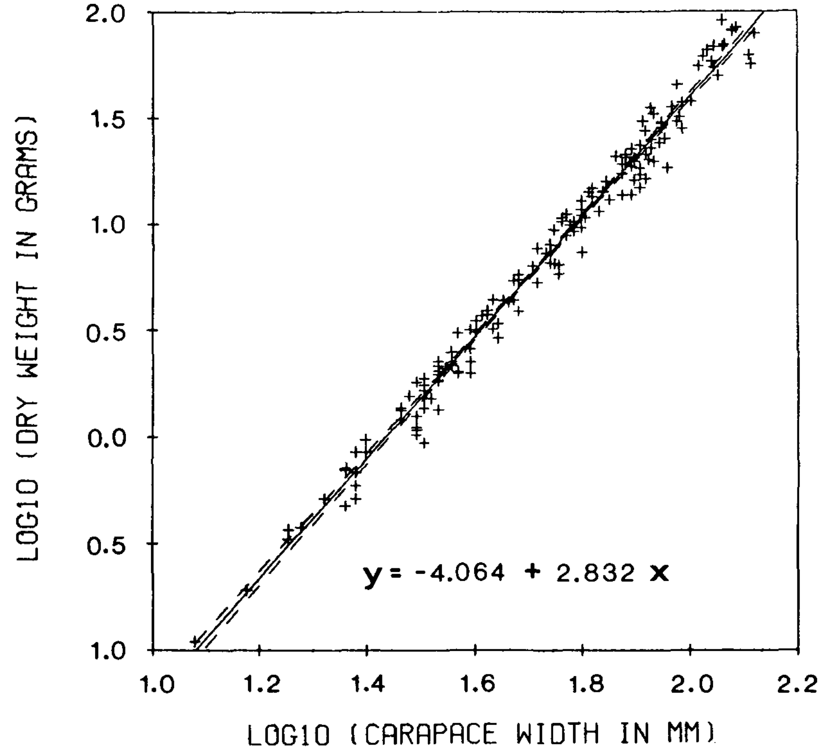

FIGURE 8.—Regression of $\log_{10}$ dry weight (g) on $\log_{10}$ carapace width (mm) for 87 male (12-132 mm) and 74 female (15-115 mm) *Cancer magister* from Grays Harbor, Wash. Observations (+), regression line (solid), and 95% confidence interval about the regression line (dashed) are shown.

instar crabs (7 mm cw) of 0.02 g dry weight increased in dry biomass 282 times by the time they reached the 6th or 7th instar (about 50 mm cw), weighing 5.7 g the following April (Fig. 9). Some may have reached 70 mm by that time, weighing 14.7 g, an increase of over 700-fold. Second-year crabs increased in dry biomass 5.3 times, from 4.0 to 21.5 g. Third-year crabs increased from 24 to 99 g, a dry biomass increase of 4.1 times.

DISCUSSION

Recruitment and Distribution in the Estuary

Megalops larvae probably metamorphosed to the first postlarval stage in Grays Harbor, since trawl collections included second instars on 4 May 1980 and first instars in April and May 1981. Cast exuviae of these stages were abundant on beaches of the outer estuary in early May 1982. Larval densities in the estuary were at the low end of the range of densities found by Lough (1976) off the Oregon coast in 1970-71 (100-8,000/1,000 m^3). In contrast, no megalops larvae were found in San Francisco-San Pablo Bays during 4 yr of surveys by the California Department of Fish and Game, which concluded that crabs entered that estuarine system only after metamorphosis (Orcutt et al. 1975, 1976).

Once inside Grays Harbor, *C. magister* showed an ontogenetic change in habitat selection, i.e., centers of abundance changed with age. Eelgrass beds may be the preferred habitat of the first postlarval stages, because catches of 0+ crabs were most abundant near those areas (Figs. 5, 6). Butler (1956) also found that the most abundant concentrations of early instars along the northern shore of Graham Island, Canada, were associated with the presence of *Zostera marina* in sheltered inlets. However, this age class was widely distributed from stations 1 to 9.

Crabs in the 1+ age group (size range 50-90 mm cw) were the most abundant. Although their dis-

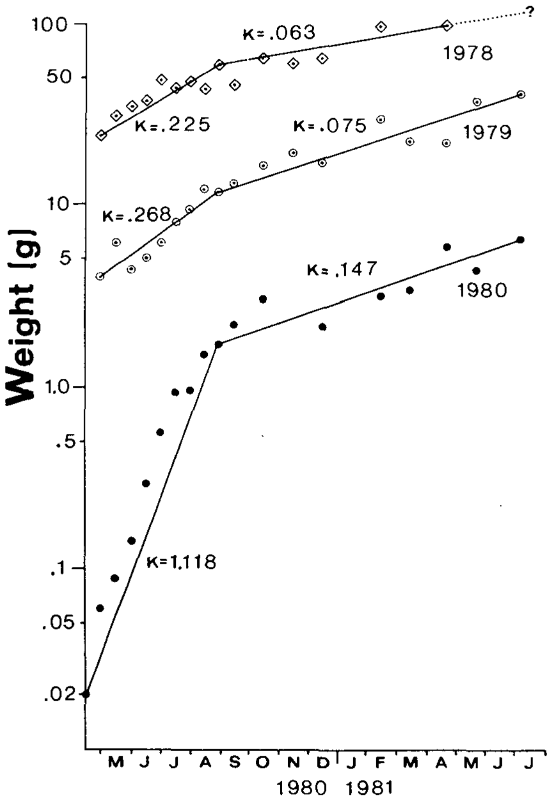

FIGURE 9.—Growth rates of *Cancer magister* from Grays Harbor, Wash. Points represent $\log_{10}$ mean dry weight calculated from mean width by regression equation. Straight lines (fitted visually) show slope of growth curve (k) for summer and winter growth stanzas of 1980 (0+), 1979 (1+), and 1978 (2+) year classes. Growth stanzas arbitrarily separated at 28 August 1980.

tribution greatly overlapped that of the 0+ age class, age 1+ crabs showed proportionally less use of low-salinity stations such as 6, 8, and 9. Although this group was also abundant near eelgrass beds, they were restricted to the subtidal channels and showed only intermittent use of mudflat areas during high tides, whereas many crabs of the 0+ group remained in the littoral zone at low tide.

The 2+ age group, consisting of sexually mature crabs (Poole 1967), was abundant only at the outer estuary stations (1, 3, 4, 6, and 7). Many crabs probably migrate out of the harbor before reaching age 3+. This hypothesis is supported by the scarcity of age 3+ crabs east of station 3 and the total absence of gravid females from trawls taken in the estuary, although many trawls were made during the spawning season (October-March). Apparently, most mature females leave the harbor to spawn. Stressful salinity and temperature, high larval predation in the estuary, or inadequate larval food supplies might have created selection pressures for spawning females to seek water offshore with the proper environmental conditions for higher egg and larval survival.

Crab Population Estimates

A more important question than that of local crab densities at several stations is that of total population abundance throughout the estuary, determined for different seasons and age classes. Such a calculation is of interest in order to gauge 1) the potential use of the estuary by the species and the 0+ age class in particular; 2) the theoretical contribution made by the estuarine population to the commercial fishery; and 3) the potential impacts of estuarine development (e.g., dredging and landfill) on resident populations. The former two points are addressed in this discussion.

Trawl Efficiency Estimates

In order to extrapolate crab density values at each station to abundance within the corresponding stratum, some measure of trawl efficiency was needed. Examinations of mudflat areas (stations 5 and 14) in May of 1981 and 1982 showed very high densities of 0+ age crabs, ranging from 1 to 5 crabs m^{-2}. This estimate was conservatively reduced to 1 crab m^{-2}, and we assumed that only 50% of the available estuarine bottom (Fig. 1B) was utilized by early instars (excluding the inner estuary and perimeter which had lower salinities and had produced few or no crabs of this age group). This "corrected" density of 0.5 crabs m^{-2} (5,000 crabs ha^{-1}) was about 30 times the mean summer density of age 0+ crabs at station 5 (162 crabs ha^{-1}) as estimated by trawl; thus trawl efficiency in that season was about 0.033 (more recent studies have shown early instar densities to equal or exceed 10 m^{-2} in 1983; D. Armstrong, unpubl. data). In winter and spring, 0+ age group crabs were large enough to be sampled more effectively, but probably not as effectively as larger crabs; thus a factor of 0.25 was used in both of those seasons. An efficiency factor of 0.5 was applied to all other age groups, in accordance with Gotshall (1978a).

Abundance Calculation

For the nine strata of Grays Harbor sampled by trawl, the total number of trawl-catchable crabs present in 1980-81, ±95% confidence intervals, were summer, 4.3 ± 1.7 million crabs; winter, 1.3 ± 0.7 million crabs; and spring, 2.6 ± 1.2 million crabs (Table 5). However, stratum 1 (837 ha) was excluded from the spring estimate due to lack of data, but was reincluded later, using density estimates from adjacent stratum 3. Totals for the other nonsampled strata (10, 11, 14, and 15) were added to totals for the trawl-sampled strata, and the sums for each age group were divided by the trawl efficiency estimates described above. Final calculated numbers for the total crab population were summer, 39.0 million crabs; fall-winter, 3.3 million crabs; spring, 7.8 million crabs (Table 5).

The 1980 year class, which was extremely abundant in the summer of 1980, virtually disappeared during the following winter, and reappeared in spring of 1981. Some hypotheses for this decline and recovery include winter hibernation, migration to nonsampled areas (e.g., stratum 14), and temporary egress from the estuary. Natural mortality probably contributed substantially to the decline as well.

Due to the speculative nature of these estimates and the underlying assumptions concerning trawl efficiency and proportion of habitat utilized, it was not possible to compute confidence limits on these final estimates. The estimates of total population abundance in the estuary suggest a tremendous increase in summer with the influx of 0+ crabs as megalopae and first instars, and an increase in 1+ animals as well. This estimate of 39 million crabs is the highest estuarine crab population abundance yet reported. The only other reported estimate, that of 9.3 million crabs in the San Francisco-San Pablo estuary complex during 1975 (Orcutt 1978), is based on a much less systematic survey than ours and does not correct for poor gear efficiency in regards to the small size of early instars. Furthermore, this latter estuarine system represents an area (500 km^2) five times that of Grays Harbor.

The accuracy of our estimates of population abundance can be qualitatively assessed by comparison of trawl density data with that of other studies (Gotshall 1978a; Orcutt et al. 1975, 1976; Orcutt 1977, 1978; Table 6). Generally, there is great seasonal variation, but densities estimated in Grays Harbor are in accord with values for Humboldt Bay and San Francisco Bay. Extrapolations to total abundance indicate that large populations of juvenile crabs may use other coastal estuaries as well. Even relatively small estuaries in Oregon, such as Tillamook, Netarts, Yaquina, and Coos Bay, could support large populations of 0+ crabs, considering their small biomass (0.2 g dry weight). The principal benefits of these estuaries are probably refuge from larger cannibalistic conspecifics (Botsford and Wickham 1978; Stevens et al. 1982), more abundant food, and possibly accelerated growth as a result of food supplies and warmer temperatures than offshore waters.

TABLE 5.—Estimation of *Cancer magister* population in Grays Harbor, Wash., for 1980-81. All values are numbers of crabs except efficiency factors and percentages. C.I. = confidence interval.

	Strata sampled by trawl (sites 1-9)								
Season/ Age Class[1]	n (×10^3)	Variance of n (×10^9)	df	C.I.[2] (×10^3)	Strata not sampled[3] (n×10^3)	Sum of crabs (×10^3)	Efficiency factor	Total crabs (×10^3)	% of total
Summer									
0+	485	9	36	188	470	955	0.033	28,942	74.2
1+	2,979	555	36	1,511	982	3,961	0.5	7,922	20.3
2+	851	19	36	279	228	1,079	0.5	2,160	5.5
Total	4,315	687	36	1,681	1,680			39,024	100.0
Winter									
0+	182	14	28	244	6	188	0.25	753	23.0
1+	1,070	82	28	588	87	1,157	0.5	2,311	70.7
2+	97	10	28	65	7	104	0.5	207	6.3
Total	1,349	123	28	720	100			3,271	100.0
Spring									
0+	146	8	13	189	87	233	0.25	931	11.9
1+	1,176	181	13	918	307	1,483	0.5	2,965	38.0
2+	1,246	342	13	1,262	707	1,953	0.5	3,904	50.1
Total	2,568	290	13	1,163	1,101			7,800	100.0

[1] See Table 3 and Figure 7 for size of these age classes throughout the year 1980-81.
[2] Values for $t_{(0.05)}$: summer = 2.029, winter = 2.048, spring = 2.160.
[3] See text for explanation of estimates based on data of adjacent trawl stations.

TABLE 6.—Comparison of *Cancer magister* densities in Grays Harbor, Wash. (this report); Humboldt Bay, Calif. (Gotshall 1978a); and San Francisco-San Pablo Bay, Calif. (Orcutt et al. 1975, 1976; Orcutt 1977). Data are not corrected for gear efficiency.

Bay	Season	Year	Transect Method	Transect Area (m²)	No. crabs/ha
San Francisco-San Pablo, *Calif.*	Summer	1975-77	Trawl	[1]1,500	90-340
	September	1977-78	Trawl	1,500	13-170
Humboldt Bay, Calif.	January	1967	Trawl	2,400	4,910
	August	1967	Trawl	2,400	300
	April	1968	Trawl	2,400	140
	August	1968	Trawl	2,400	1,280
	October	1968	Trawl	2,400	930
		(Mean of trawl samples, 1967-68 = 890)			
	August	1967	Scuba	140	520
	April	1968	Scuba	140	0
	August	1968	Scuba	140	4,480
	October	1968	Scuba	140	280
		(Mean of scuba samples, 1967-68 = 1,080)			
Pacific Ocean, near Humboldt Bay, Calif.	October	1968	Trawl	[2]6,667	0-9,400
	November	1968	Trawl	6,667	0-36,000 ($\bar{x}$ = 800)
Grays Harbor, Wash. Outer Harbor	June	1980	Trawl	variable	200-1,000
	December	1980	Trawl	1,400	310
	May	1981	Trawl	2,000	1,320

[1] Distance estimated as 50 m/min.

[2] Area estimated as distance (given) × ⅔ (headrope length).

Growth

Dry weight increased 282 times between first instar (0.2 g) and sixth instar (5.7 g) during the first year. Other authors have not presented growth data as changes in weight, but rather as increases in carapace width. Crabs in Grays Harbor grew from about 7 mm to 50+ mm cw during 1980-81, which is similar to values reported by Cleaver (1949) and Butler (1961). However, Poole (1967) concluded that crabs in Bodega Bay, Calif., reached 75 mm (range 50-100 mm) by 1 yr after metamorphosis. This would represent fairly rapid growth, but close to the upper limits of crab growth rates in Grays Harbor.

In contrast to Grays Harbor, Tasto (1983) stated that juvenile crabs spend only 1 yr in San Pablo Bay, and reach 100 mm by the end of that time (twice the growth rate of ocean crabs and Grays Harbor crabs). He concluded that the estuarine population was a single year class and was almost completely replaced by a new year class each spring, a situation very different from Grays Harbor where at least three year classes are present constantly. The San Francisco data may have been misinterpreted, perhaps caused by use of collecting gear (mostly ring nets) that selected larger crabs and resulted in a frequency mode near 100 mm cw that may have actually represented older 1+ age group crabs.

Unfortunately, growth data are not available for 0+ age Dungeness crabs that metamorphose directly offshore for comparison with estuarine populations. Presumably, colder bottom-water temperatures offshore (8°-10°C) would cause metabolic, growth, and general energetic depression of these animals relative to rates in warmer (14°-18°C) estuaries. Studies of offshore juvenile populations are much needed in this regard.

Importance of Grays Harbor to Commercial Fisheries.

The potential contribution of Grays Harbor to the commercial landings of *Cancer magister* was calculated by assigning various mortality rates to the 1980 year class for a period of 3.5 yr, i.e., until recruitment to the fishery. Jow (1965) estimated annual natural mortality of adult male crabs to be 15% per year ($M = 0.165$, exponential). Mortality rates for juveniles are unknown, so we have assumed a range of 0.5-0.8. From an initial population (N_0) of 28.9 million juvenile crabs in summer of 1980, the number surviving 3.5 yr (N) was calculated from the equation

$$N = N_0 e^{-zt}$$

where z represents the annual mortality rate and t is the time interval. Values of z used were 0.8 for the first half year ($t = 0.5$), 0.5 for the second half year, and 0.2 (as above) for the remaining 2.5 yr necessary to reach legal size, assuming crabs enter the fishable population at that age, as suggested by Cleaver (1949). At these mortality rates, about 9.2 million adult crabs might remain by

December 1983, of which about half, 4.6 million, would be males subject to the commercial fishery. If an equivalent number of crabs were available from the 1980 recruitment to Willapa Bay, a large bay equaling or exceeding Grays Harbor in area and located about 20 km south, then about 9.2 million legal male crabs of estuarine origin might be available to the commercial fishery in 1984-85 from larvae and early instars that utilized these two Washington estuaries in 1980-81.

Washington coastal crab landings for the period 1971-80 have averaged 3,500 t/yr (PMFC 1981), or about 3.85 million crabs (at 0.9 kg/crab). Thus, these two bays could theoretically serve as nursery grounds for more than enough crabs necessary to maintain a viable commercial fishery in Washington. However, landings over the past 40 yr have fluctuated from 1,000 to 8,000 t, with a 9-12 yr period, so it is impossible to predict how the estimated contribution of the 1980 year class will compare to 1984 commercial landings.

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