Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats*

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ABSTRACT: Habitat selection by megalopae, and habitat preference and relative mortality of young-of-the-year (YOY) Dungeness crab *Cancer magister* Dana were evaluated in 4 habitat types: bivalve shell middens (*Crassostrea gigas*), eelgrass *Zostera marina*, mud with scattered shell and bare mud. Under laboratory conditions shell was the most preferred habitat by megalopae and YOY; eelgrass ranked second. Field tethering experiments showed that shell habitat provided the best protection from predation, and that the proportion of crab eaten was highest on bare mud. Field tethering experiments using small hooks attached to tether lines and glued to the crab showed that the sculpin *Leptocottus armatus* was the most important fish preying on YOY crab in this area. Cannibalism by larger instars of YOY, 1+ and 2+ Dungeness crab also may account for part of the YOY mortality. Most evidence suggests that intertidal shell habitat enhances Dungeness crab survival during the first several months of benthic life. It has led to the use of artificial shell habitat as a technique to increase juvenile crab abundance and compensate crab losses due to dredging.

INTRODUCTION

Dungeness crab *Cancer magister* Dana occurs along the west coast of North America from the Aleutian Islands to central California (Hart 1982, Jensen & Armstrong 1987) and supports an important invertebrate fishery through most of this range (Jamieson & Armstrong 1991). Ovigerous females move inshore (Diamond & Hankin 1985) where eggs are hatched and 5 zoeal stages develop (Lough 1976). After molting to megalopae, the last larval stage, they settle nearshore (Lough 1976, Reilly 1983, McConnaughey et al. 1992) and enter estuaries in high abundance (Reilly 1983, Armstrong & Gunderson 1985) which suggests that estuarine systems serve as 'nursery areas' (Armstrong & Gunderson 1985, Gunderson et al. 1990).

Little is known, however, of the natural history of early juvenile stages and factors that affect their survival through the first year of life. Young-of-the-year

(YOY) Dungeness crab are found at higher densities in intertidal or subtidal areas that offer some type of shelter (Dinnel et al. 1986, Jamieson & Armstrong 1991, Dumbauld et al. in press). In Lummi Bay (Washington, USA) significantly greater densities of YOY Dungeness crab are found in vegetated than in unvegetated areas (Dinnel et al. 1986). In coastal estuaries of the northwestern United States, Grays Harbor (Washington) and Willapa Bay (Washington), YOY crab density is higher within clam *Mya arenaria* and oyster *Crassostrea gigas* shell than on adjacent uncovered substrata (Armstrong & Gunderson 1985, Dumbauld et al. in press). Based on these observations, experiments have been conducted to assess the feasibility of using intertidal shell habitat to mitigate crab losses due to dredging of the Grays Harbor navigational channel (McGraw et al. 1988, Armstrong et al. 1991, 1992, Wainwright et al. 1992, Dumbauld et al. in press). Since 1990 intertidal oyster shell plots have been constructed in different parts of the estuary prior to crab settlement, and habitat quality and crab density monitored over time (Armstrong et al. 1992). The outcome consistently shows YOY Dungeness crab density ex-

ceeding 300 juvenile first instar (J1) crabs m^{-2} in shell habitat but less than 5 crabs m^{-2} on bare mud (Armstrong et al. 1992).

The full mitigation project was started in spring 1992 by deploying 8 ha of oyster shell in the intertidal zone of Grays Harbor. Yet supporting information concerning YOY population dynamics in shell does not indicate whether the observed pattern of higher density in shell plots is due to preference for shell habitat by megalopae, enhancement of local densities due to concentration of YOY, differential predation on YOY, or any combination of these 3 processes. In this paper we address 3 questions that may help to understand the role of different intertidal habitats for juvenile Dungeness crab: (1) do Dungeness crab megalopae or benthic instars prefer shell over other habitats, (2) does shell habitat increase survival rate of YOY crab, and (3) what are sources of mortality in each habitat?

MATERIAL AND METHODS

Study area. The Grays Harbor estuary is located along the southern Washington coast (46°55'N, 124°05'W). Over 60 % of the estuary is intertidal and uncovered by 1 of the 2 daily low tides from spring through fall when spring tides of up to 4 m occur. Extensive portions of the intertidal are covered by epibenthic bivalve shell (mostly soft shell clam *Mya arenaria* and oyster culture) and eelgrass *Zostera marina*. Field experiments were carried out in the southeast part of the estuary (South Channel; 46°56'N, 123°55'W) where all of these different habitat types coexist. The area of South Channel has been used for previous crab habitat experiments (Armstrong et al. 1991), and now is the major full-scale mitigation site.

Laboratory experiments. *Habitat selection by megalopae:* To test whether Dungeness crab megalopae settle preferentially in shell or mud, 40 l, aerated aquaria (n = 21) were conditioned with a 5 cm layer of mud collected in the intertidal zone and filled with estuarine water. The bottom of each aquarium was divided into 2 portions and each was randomly assigned to either shell or mud. Megalopae collected from the estuary in May 1991 were placed in groups of 10 in each aquarium. At the end of a 24 h trial the numbers of megalopae and first instar crab in each habitat were counted. Twenty-one trials were run. The null hypothesis that neither type of habitat was preferred was tested using a Wilcoxon test (Conover 1980).

Habitat selection by YOY crab: To test habitat preference of YOY crab, 4 circular pools (0.65 m², 40 cm depth) were conditioned with a 5 cm deep layer of mud and filled with estuarine water. Each pool contained a choice of 2 habitat types: (a) oyster shell versus mud

(13 trials), (b) oyster shell versus eelgrass (13 trials) and (c) eelgrass versus mud (10 trials). Pools were randomly assigned to each pair of habitats. Crabs were collected in intertidal areas of Grays Harbor and allowed to acclimate in the laboratory for 2 d at constant temperature (14 °C) prior to initiation of each experiment. Eight intermolt juvenile crabs, size range from 6 to 35 mm, were introduced into each pool and allowed to select from both habitats. Crabs in this size range are common in intertidal shell habitats (Armstrong et al. 1991). At the end of each 24 h experimental period a partition was inserted to separate the 2 habitats and number and size of crab in each were recorded. Individual crabs were used in only 1 trial. The null hypothesis of no habitat preference was tested using a Wilcoxon test (Conover 1980). A 1-way ANOVA was used to test for differences in the mean size of crabs used in the 3 habitat selection experiments. A t-test was used to test for differences in the mean size of crabs selecting each habitat in the 3 habitat selection experiments. Raw data were used given normality and homocedasticity assumptions were met.

Field experiments. *Relative mortality:* Tethered crabs (Heck & Wilson 1987) were used to examine relative predation rates (proportion of crab eaten per day) among habitat types and days. Tethering was repeated during several days to test whether mortality patterns between habitats were consistent over time. Comparison of predation rates across days was done for oyster shell piles, eelgrass, mud with scattered shell and bare mud. Crabs for tethering were collected from oyster shell piles located at South Channel. Second (J2) to sixth (J6) juvenile crabs were tethered; size ranged from 10 to 12.5 mm (J2), 13 to 15 mm (J3), 15.5 to 19 mm (J4), and 21 to 34 mm (J5-J6) (Dinnel et al. in press). J5 and J6 crab are less abundant in intertidal habitats than smaller instars and so were analyzed separately. Mean size of the crab used in the different habitat treatments was not significantly different ($F = 0.02$, df = 3,96, p > 0.5). Only hard intermolt crab were tethered to one end of a 0.5 m length of lightweight monofilament line attached with 'super glue' (cyanoacrylate cement) to the carapace. Each crab was placed in the habitat tethered by the line to a wire stake (1 crab per stake) pushed completely into the sediment. Daily, 8 to 9 measured crab were tethered in each habitat, left in place at low tide and inspected during the next low tide that uncovered the experimental site (about 19 h later). Loss due to predation was scored when a crab was missing from the tether and a piece of the glued carapace remained attached to the line. Crab remains attached to the line were identified as whole carapace or smaller pieces. A contingency table was used to test the null hypotheses of no differences in the frequency of dead or live crabs

among habitats and of independence between mortality rates and days in all habitat types (Zar 1984). Instances where crabs molted or when it was not clear whether they had escaped (rather than were eaten) were considered as loss data and not used for predation rate estimates. Losses were not significantly different among habitats ($\chi^2 = 2.99$, $0.1 < p < 0.25$).

Identification of predators: Three different approaches were used to identify major predators: (1) To identify fish predators crabs were attached with 'super glue' to small hooks (Mustad-Viking hook #10) and tethered to the end of a 0.5 m length of light-weight monofilament line. Twenty-nine trials were run in bare mud, 9 in mud with scattered shell, 12 in eelgrass, and 41 in shell. Tethered crab ranged in size from 10 to 18 mm (J2 to J4). (2) To investigate if 1 yr old (1+) and older crab, which are cannibalistic (Stevens et al. 1982), move from the subtidal to the study site on flood
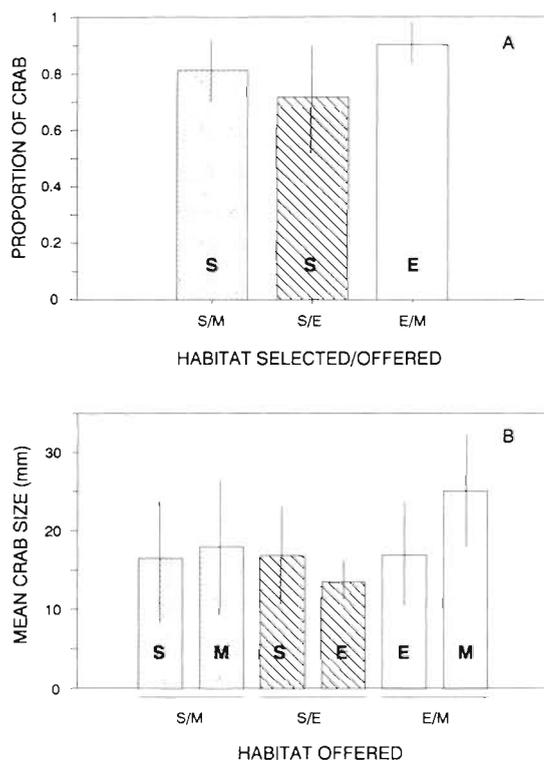

Fig. 1. *Cancer magister.* (A) Mean proportion (± 1 SD) of juvenile Dungeness crab selecting oyster shell (S) compared to mud (M) (S/M; $Z = -2.3$, n = 10, p < 0.01), oyster shell compared to eelgrass (E) (S/E; $Z = -2.7$, n = 13, p < 0.05), or eelgrass compared to mud (E/M; $Z = -2.8$, n = 13, p < 0.005). Letters in the x-axis indicate the habitat offered in each habitat selection experiment (e.g. S/M indicates that shell and mud were offered). Letters inside the bars indicate the habitat preferred. (B) Mean carapace width (±1 SD) of juvenile Dungeness crab that selected each habitat type when 2 habitats were offered. Letters inside the bars indicate the habitat for which each mean crab size was estimated

tide, a ring net baited with fish was used during high tide over intertidal shell and mud habitats. (3) To evaluate the relative importance of cannibalism within YOY we analyzed the characteristics of the pieces that remained attached to the line in the tethered experiments described above. The experiment was repeated in 1991 in shell and bare mud with 45 and 30 tethered crab respectively. Laboratory observations show that when YOY Dungeness crab prey on conspecifics they leave the entire carapace of preyed crab; fish and larger crab consume the whole crab or leave only small pieces (Fernandez unpubl.).

Survival and behavior of tethered crab: To examine the effect of tethering on crab survival a field experiment was performed. A total of 36 crab (J2 to J4) were randomly assigned to a treatment: (1) non-tethered crab as control, (2) tethered crab, and (3) tethered crab with hooks. Nine crabs, 3 crabs per treatment, were placed in a 0.15 m² cage. Cages (n = 4) were then placed in the intertidal zone for 24 h when the number of surviving crabs per treatment was recorded.

Observations of tethered and non-tethered juvenile crab behavior were carried out under experimental conditions to evaluate the effect of tethering. To observe tethered crab behavior in mud habitat aquaria were conditioned with a 5 cm deep layer of mud and filled with estuarine water. One (J2 to J4) tethered crab was introduced in an aquarium with another non-tethered crab of the same instar stage. Burying time was measured for each pair of tethered/non-tethered crab. Six trials were run and the mean time spent until burial between tethered and non-tethered crab was compared using a *t*-test. Observations on crab behavior in shell and eelgrass were carried out in the field when tethered experiments were performed.

RESULTS

Laboratory experiments

Habitat selection by megalopae. Under laboratory conditions Dungeness crab megalopae preferred shell over mud ($Z = -3.204$, n = 21, p < 0.05).

Habitat selection by YOY crab. Oyster shell habitat was preferred over eelgrass and over mud, and eelgrass was preferred over mud (Fig. 1A).

Mean crab sizes used in the 3 different treatments (2 habitat choices each) were not significantly different ($F = 0.014$, df = 2,237, p > 0.05). Mean size of crab that selected shell was not significantly different from those that selected eelgrass ($t = -0.42$, df = 76, p > 0.05) or mud ($t = -0.45$, df = 74, p > 0.5) (Fig. 1B). Crabs that selected eelgrass were significantly smaller than those that selected mud ($t = 4.43$, df = 76, p < 0.01) (Fig. 1B).

Field experiments

Relative mortality rates. No patterns in relative pre-dation rates between days were detected in shell, eel-grass, mud with scattered shell or on bare mud for J2 to J4 (χ^2 = 3.147, df = 9, p > 0.95) and in shell and mud for J5–J6 (χ^2 = 1.66, df = 1, 0.25 > p > 0.10). The mean pro-portions of crab eaten were always highest in bare mud, intermediate in mud with scattered shell and eel-grass, and lowest in shell for J2 to J4 (Table 1). Since there was no pattern across days within habitat type, relative predation values were pooled by habitat and

Table 1. *Cancer magister*. Relative mortality rates (± SD) by habitat type between days for second to sixth instar juveniles (J2 to J6) during July and August 1990. Each day 8 (J2 to J4) and 5 (J5 to J6) crabs were tethered per habitat type

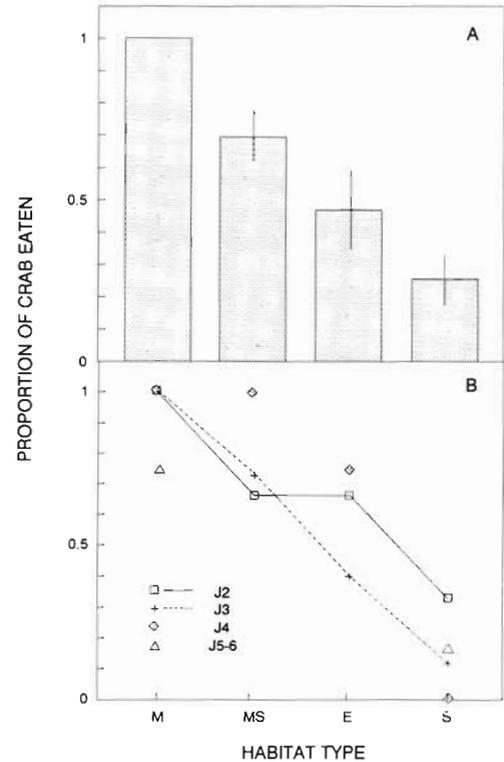| Day	Bare mud	Scattered shell	Eelgrass	Shell
J2 to J4				
Jul 9	1.0 (0.0)	0.6 (0.2)	0.7 (0.2)	0.1 (0.1)
Jul 10	1.0 (0.0)	1.0 (0.0)	0.4 (0.2)	0.1 (0.1)
Jul 11	1.0 (0.0)	0.7 (0.2)	0.3 (0.2)	0.3 (0.2)
Jul 12	1.0 (0.0)	0.4 (0.2)	–	0.3 (0.2)
J5 and J6				
Aug 7	0.7 (0.2)	–	–	0.3 (0.2)
Aug 8	0.8 (0.2)	–	–	0.0 (0.0)

Fig. 2. *Cancer magister*. Mean proportion of (A) YOY and (B) J2, J3, J4 and J5–J6 Dungeness crab eaten in tethering experiments carried out in July 1990 in 4 habitat types. M: mud; MS: mud with scattered shell; E: eelgrass; S: shell. All SD < 0.27

analyzed as a one-time experiment. Mean proportion of J2 to J4 crab eaten differed significantly among hab-itats (χ^2 = 37.27, p < 0.001) (Fig. 2A). Crabs tethered in shell habitat were preyed on at the lowest rate ($\bar{x}$ = 0.17, SD = 0.07, n = 29). The highest proportion of crab eaten was found on bare mud, where crab had no shel-ter ($\bar{x}$ = 1.0, SD = 0, n = 19). Relative predation discrim-inated by instar stage (J2 to J4) tended to increase with prey size in mud with scattered shell, and decrease as crab size increased in shell habitat (Fig. 2B). However there were no significant differences in the size of the crabs alive and dead in mud with scattered shell, in eelgrass, and in shell (Table 2). Mean proportions of J5–J6 crab eaten were highest in bare mud ($\bar{x}$ = 0.74, SD = 0.14, n = 10) and lowest in shell habitat ($\bar{x}$ = 0.16, SD = 0.12, n = 10) (Fig 2B).

Identification of predators. The sculpin *Leptocottus armatus* was the only fish captured (n = 9) using teth-ered crab with hooks. Size of fish ranged from 107 to 160 mm (total length) and was not related to size of crab prey. No fish were captured in eelgrass using J2 to J4 as prey, and on bare mud and shell habitats using J5 and J6 as prey. The proportion of J2 to J4 prey eaten by fish was 0.16 (SD = 0.07, n = 25) in bare mud, 0.28

(SD = 0.18, n = 7) in mud with scattered shell and 0.18 (SD = 0.09, n = 17) in shell habitat.

Larger Dungeness crab (1+ and 2+) were caught du-ring high tide on intertidal mud flats and shell plots but did not occur in these areas at low tide. Dungeness crab size ranged from 62 to 112 mm ($\bar{x}$ = 85.12, SD = 11.7, n = 43). Cannibalism among YOY was studied by the analysis of crab remains found attached to the line in the tethering experiment. The proportion of whole carapaces that remained attached to tether lines was

Table 2. *Cancer magister*. Mean size and 1 SD of crab eaten and crab that remained alive in the tethering experiment in 3 habitat types: scattered shell, eelgrass and shell. In mud habitat all crab were eaten. N: no. of replicates. Statistical comparison showed no differences in the mean size of crab alive or eaten in any habitat type (p > 0.05 in all cases)

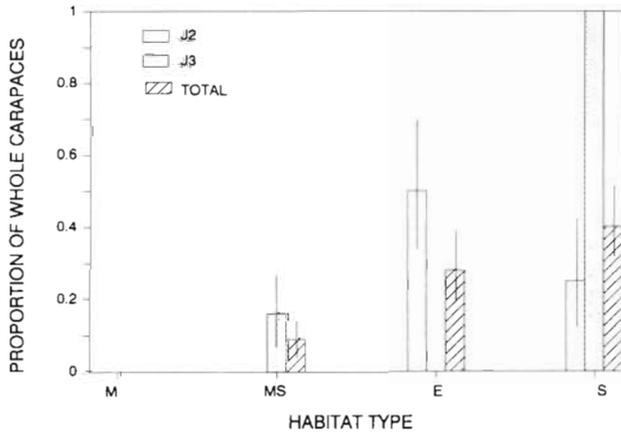|	Alive			Eaten		
	$\bar{x}$	SD	N	$\bar{x}$	SD	N
Scattered shell	13.4	0.7	8	13.3	2.3	2
Eelgrass	13.4	2.9	10	13.4	2.9	10
Shell	13.9	2.4	24	11.7	2.7	5

Fig. 3. *Cancer magister*. Mean proportion (± 1 SD) of whole carapaces that remained attached to the lines in mud, mud with scattered shell, eelgrass and shell in field tethering experiments carried out in 1990. Proportions were obtained based on analysis of pieces of crab eaten that remained attached to the line (no. of remaining whole carapaces / total no. of crab eaten). Total proportion includes J2 to J4; J4 not shown because no whole carapaces of J4 tethered crab eaten were found in any habitat type

zero on bare mud, intermediate in eelgrass and mud with scattered shell, and highest in shell (Fig. 3). Only whole carapaces of J2 and J3 remained attached to the line (Fig. 3). The pattern was similar in 1991; the proportion of whole carapaces from a mixture of J2 to J4 was 0 (SD = 0, n = 30) on mud and 0.4 (SD = 0.07, n = 45) in shell. When only J2 and J3 were considered the proportion of whole carapaces was 1.00 in shell habitat.

Survival and behavior of tethered crabs. No differential mortality was detected among tethered crab, tethered crab with hooks and non-tethered crab. None of the crab used in the experiment died. Laboratory observations showed that tethered crab were able to bury in the substrata and there were no significant differences in the mean time spent until burial between tethered and non-tethered crab ($t = 1.25$, df = 11, $0.2 < p < 0.5$). In the field tethered and non-tethered crab immediately hide among the oyster shells or eelgrass.

DISCUSSION

Habitat selection has been proposed as a process to explain the enhanced density of macrofauna in sheltered habitats (Bell & Westoby 1986). Dungeness crab megalopae select shell habitat over mud under still water conditions. Although the role of physical processes on settlement of the strong swimmer Dungeness crab megalopae is unknown, current speed similar to that in the field (40 cm s^{-1}) did not affect the swimming

ability of Dungeness crab megalopae (pers. obs.) Other decapod larvae also select habitats actively and prefer complex structures (*Homarus americanus*: Botero & Atema 1982; *Panulirus argus*: Herrnkind & Butler 1986). If this behavior is shaped by natural selection we should expect animals to select habitats where the risk of predation is lowest. In fact, megalopae and YOY Dungeness crab do select the habitat that provides lowest risk of mortality as evidenced by a preference for shell. Mortality rate of juvenile Dungeness crab in shell habitat is much lower than in any other habitat type; eelgrass ranked intermediate between shell and bare mud. Thus the between-habitat differences in YOY Dungeness crab density may be explained by a combination of habitat preference and differential mortality. The refuge value of various habitats has been reported for a variety of decapod crustaceans in vegetated habitats (e.g. Heck & Thoman 1981, Heck & Wilson 1987, Wilson et al. 1990). Shelters reduce the rate of predation on juvenile spiny lobster *Panulirus argus* (Eggleston et al. 1990), and cannibalism among *Hemigrapsus penicillatus* (Kurihara & Okamoto 1987). However predation rates on YOY Dungeness crab show more striking differences between habitat types than those reported for other decapod crustaceans (Heck & Wilson 1987, Wilson 1989, Wilson et al. 1990), which emphasizes the importance of shell habitat for recruitment success of Dungeness crab.

Predators of Dungeness crab in the intertidal habitat include staghorn sculpin *Leptocottus armatus*, and conspecifics. Sculpins, reported as one of the major predators of megalopae and juvenile crabs in the Grays Harbor estuary (Armstrong 1991), were the only fish predator captured by our hook-tethering technique. Hook efficiency was not estimated either in shell or mud; consequently our results most likely underestimate the actual predatory importance of this species and probably other fish species. Based on our results YOY Dungeness crab would not find better refuge against staghorn sculpin in shell than in mud habitat. Alternatively, and under the assumption of no differential hook efficiency between habitats, shell habitat may provide better refuge than mud for YOY crab but sculpin abundance may be higher in shell.

One year old and older Dungeness crab living in the estuary cannibalize smaller conspecifics (Stevens et al. 1982) although shell structures decrease predation rate (Fernandez unpubl.). Larger crab reside in subtidal channels during low tide and forage over the intertidal during high tide (Stevens et al. 1982). Our results show that 1+ and older crab also used shell habitat and surrounding areas as a foraging ground during high tide, which suggests that cannibalism by older crabs is a potential source of YOY mortality, mostly on bare mud. The analysis of remains left by conspecifics in previous

laboratory experiments suggests that intra-age class cannibalism accounted for a portion of tethered crab mortality, mainly in shell habitat where YOY density is higher (Armstrong et al. 1991). Together these observations present an interesting paradox: shell habitat enhances YOY crab density by the combined processes of habitat selection and increased survival compared to other habitats, but also increases intra-age class cannibalism. Although cannibalism among YOY was first found in artificial habitats where crab density is high it is also expected to occur in natural populations. In the Grays Harbor estuary crab densities similar to those found in artificial shell habitat are also observed in natural shell assemblages of soft shell clam *Mya arenaria* (pers. obs.) which cover around 19 % of the intertidal area of the estuary (Dumbauld et al. in press).

Although Dungeness crab settlement in Grays Harbor estuary can be high in both intertidal and subtidal areas, newly settled crab quickly disappear in the subtidal (Armstrong & Gunderson 1991). Intertidal crabs shelter in bivalve shell during the summer but by September, when 0+ crabs are ca 35 mm carapace width, they gradually move to the subtidal where they may be then able to avoid most predators by virtue of their greater size (Reilly 1983, Dinnel et al. 1986, Dumbauld et al. in press). If refuge value is considered over the period of time in which the Dungeness crab population may be most vulnerable to predation (spring to fall), then shell habitat may prove to be important for YOY crab survival and a useful technique to increase juvenile crab abundance and compensate crab losses due to dredging.

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