

Abstract.—The impact of predation by staghorn sculpin, *Leptocottus armatus*, on newly settled Dungeness crab, *Cancer magister*, in the Washington coastal estuary of Grays Harbor was studied. Staghorn sculpin are known to be generalist, opportunistic feeders, with relatively high food requirements for estuarine growth during warm summer months. During late spring or early summer, vast numbers of crab megalopae reach the estuary and settle on intertidal flats and in subtidal channels. During the next two months the young-of-the-year (0+) crab population is rapidly reduced by predation, including cannibalism. Crab without appropriate refuge habitat are highly vulnerable to predation by fish, and accordingly survival of young crab is highest in intertidal shell and eelgrass beds. Abundance and summer growth of crab and sculpin within the estuary were documented by monthly trawling surveys (April to August) in 1989. Stomach contents of sculpin were analyzed to characterize the overall summer diet, to note monthly shifts in major prey items within two age classes of sculpin (0+ and 1+), and to contrast sculpin prey consumed in eelgrass with that consumed in shell habitats. The predominant prey species varied across the categories above but generally included ghost and blue mud shrimp, *Neotrypaea californiensis* and *Upogebia pugettensis*, a nereid polychaete (*Nereis brandti*), juvenile Dungeness crab, *Cancer magister*, and sand shrimp (*Crangon* spp.). Some combination of these species composed 85% of the total diet (on the basis of percentage of total Index of Relative Importance; %IRI) across time and between habitats. A comparison of diets of sculpin collected at eelgrass and shell habitats was significantly different; a strong preponderance of 0+ crab were consumed at the shell habitat. *Nereis brandti* was the most important prey for 0+ sculpin, whereas *Neotrypaea californiensis* was the most important for 1+ and older sculpin. The importance of shell as refuge habitat for *C. magister* and the apparent contradiction in the observation that a large number of 0+ crab were taken by sculpin at the shell habitat are discussed.

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Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister**

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Staghorn sculpin, *Leptocottus armatus*, are common in major estuaries throughout their range from Baja California through the Gulf of Alaska (Hart, 1974). Young sculpin inhabit brackish water streams and channels and move down into the estuary as they grow larger during their first year. Older juvenile and adult sculpin are broadly distributed throughout estuarine nursery areas utilized by juvenile crab and are known predators of Dungeness crab, *Cancer magister*, within estuaries (Reilly, 1983). Staghorn sculpin have wide gapes and relatively large mouth areas in relation to their size compared with other species of fish predators commonly found in estuaries during the summer.^{1,2} They are opportunistic, generalist predators (Jones, 1962; Hart, 1974; Birtwell et al., 1984) and feed heavily on decapod crustaceans such as the yellow shore crab, *Hemigrapsus oregonensis*, the ghost shrimp *Neotrypaea californiensis*, and pea crab, *Pinnixa* sp. (Tasto, 1975; Posey, 1986). Staghorn sculpin are described as visual predators that move onto estuarine tideflats with the incoming tide (Tasto, 1975); their foraging behavior may contribute to the high mortality rate of small 0+ crab (Wainwright et al., 1992).

The Grays Harbor estuary, Washington, contains extensive intertidal tracts of eelgrass and shell that serve as critical nursery areas for young-of-the-year (0+) and one-year-old (1+) Dungeness crab³ (Gutermuth and Armstrong, 1989; Gunderson et al., 1990; Jamieson and Armstrong, 1991). During high tides in May and June, vast numbers of crab megalopae reach estuaries, settle to the benthos, and metamorphose to the first juvenile instar (J1). Crab settle over broad expanses of the intertidal sandflats

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¹ Smith, J. L. 1976. Impact of dredging on the fishes in Grays Harbor. Appendix G in Maintenance dredging and the environment of Grays Harbor, Washington. Final Rep. by U.S. Army Corps of Engineers, Seattle District, 94 p.

² McGraw, K., and D. A. Armstrong. 1990. Fish entrainment by dredges in Grays Harbor, Washington. In C. A. Simenstad (ed.), Effects of dredging on anadromous Pacific coast fishes; workshop proceedings, Seattle, WA, 8–9 Sep. 1988. Washington Sea Grant Program, Univ. Washington, Seattle, WA 98195, 160 p.

³ Armstrong, D. A., T. C. Wainwright, J. M. Orensanz, P. A. Dinnel, and B. R. Dumbauld. 1987. Model of dredging impact on Dungeness crab in Grays Harbor, Washington, Final Rep. FRI-UW-8702 to Battelle Northwest Laboratories and U.S. Army Corps of Engineers, Seattle, District, Seattle, WA, 167 p.

and in subtidal channels but within a few weeks can be found only in areas that afford some refuge⁴ (Dumbauld et al., 1993; Fernandez et al., 1993a). First year survival, based on five years of trawl survey data in the estuary (Gunderson et al., 1990), has been estimated at approximately 8% (Wainwright et al., 1992). Different assemblages of predators affect survival of Dungeness crab during each phase of their life history (Reilly, 1983; Stevens and Armstrong, 1985; Thomas, 1985). Estuarine and nearshore fishes, wading birds, and older crab are known to prey upon the young crab instars (Stevens et al., 1982; Fernandez et al., 1993b), causing high mortality rates in the summer months (Wainwright et al., 1992).

Predation, including cannibalism, is considered to be the prime cause of the rapid decline in crab abundance through the summer. Stevens et al. (1982) showed that during years of high 1+ crab abundance, cannibalism can account for a significant portion of 0+ crab mortality. Even early settling 0+ crab are capable of cannibalizing later settlers of the same year class (Fernandez et al., 1993b). However, aside from Reilly's study (1983) in California estuaries, predation by estuarine fish and wading birds has received little attention as a source of crab mortality. Although sea birds are known to take a toll on megalopae⁵ and on newly settled crab (Mace, 1983), fish and crab predators are more likely to exert the greatest predation pressure on the highly abundant, small instars during settlement and early development.

In this study, we discuss the estuarine summer feeding patterns of staghorn sculpin with respect to a broad spectrum of crustacean prey but focus on their possible significance as predators of 0+ *C. magister* and on the role of refuge habitat on the basis of spatial patterns of predation in the estuary. A temporal shift in consumption of certain prey taxa is also discussed as indicative of opportunistic feeding by staghorn sculpins with seasonal patterns of prey abundance or with life history events which make prey more susceptible to predators.

Materials and methods

Sampling scheme

Grays Harbor (46°55'N, 124°05'W) is a major Washington coastal estuary of about 8,545 hectares

(Gunderson et al., 1988) marked by numerous subtidal channels. These channels extend across extensive sandflats that become exposed and represent 67% of surface area during spring low tides. Refuge habitat is provided by epibenthic shell exposed from remnant *Mya arenaria* and *Crassostrea gigas* bivalve populations and by eelgrass. Shell coverage has been calculated to account for 19% of the total intertidal area,⁶ whereas eelgrass (*Zostera marina* and *Z. noltii*) was reported to cover 42% of the tidal flat area.⁷

Staghorn sculpin were collected from Grays Harbor during six sampling trips from April through August 1989. Sampling was timed to coincide with the following periods: April–May prior to the main pulse of annual crab settlement, June (two trips) during recruitment of 0+ crab, and July–August during the post-settlement summer growth period. Two intertidal sandflat sites located about 10 km apart were routinely trawled at high tide as a means of contrasting diet in two common epibenthic habitats of the estuary: an eelgrass (*Zostera* spp.) bed in North Bay, and shell piles (*Mya arenaria*) in South Channel (Fig. 1). In order to ensure reasonable sample sizes of fish for each trip and site (target of $n > 20$), two trawls each were conducted at both an intertidal station (during slack flood tide) and at an adjacent subtidal station (at low slack) within 6 h on the same day, and fish were pooled for analyses of differences in diet over time. Additional subtidal trawls were made as time permitted for a total of 9–11 trawls per trip.

All trawl samples were collected with a 3-m beam trawl (Gunderson and Ellis, 1986) deployed from a 7-m Boston Whaler. The net had an effective fishing width of 2.3 m and a 4-mm codend liner to retain juvenile crab and fish. Trawls in subtidal channels were run for about four minutes at a speed of 3.7 to 5.6 km/h. Distance fished was determined by optical range finder fixes between buoys deployed at the beginning and end of each tow (see Gunderson et al., 1990, for details of trawl procedure); such distances ranged from 200 to 350 m. Intertidal tows were made between two staked points 160 m apart. Distance fished and fishing width of net were used to estimate area swept for calculation of catch per unit of effort (CPUE; number per hectare). Trawl contents were characterized as to type of vegetation (e.g. algae,

⁴ Armstrong, D. A., L. Botsford, and G. S. Jamieson. 1990. Ecology and population dynamics of juvenile Dungeness crab in Grays Harbor estuary and adjacent nearshore waters of the southern Washington coast. Rep. to U.S. Army Corps of Engineers, Seattle District, Seattle, WA, 140 p.

⁵ Armstrong, D. Personal observation at Whitcomb Flats sea gull nesting site, Grays Harbor, WA, May 1988.

⁶ Dumbauld, B. R., and D. A. Armstrong. 1987. Potential mitigation of juvenile Dungeness crab loss during dredging through enhancement of intertidal shell habitat in Grays Harbor, Washington. Final Rep. FRI-UW-8714 to U.S. Army Corps of Engineers, 64 p.

⁷ Smith, J., L. D. R. Mudd, and L. W. Messmer. 1977. Impact of dredging on the vegetation in Grays Harbor. Appendix F in Maintenance of dredging and the environment of Grays Harbor, Washington. Final Rep. by U.S. Army Corps of Engineers, Seattle District, 94 p.

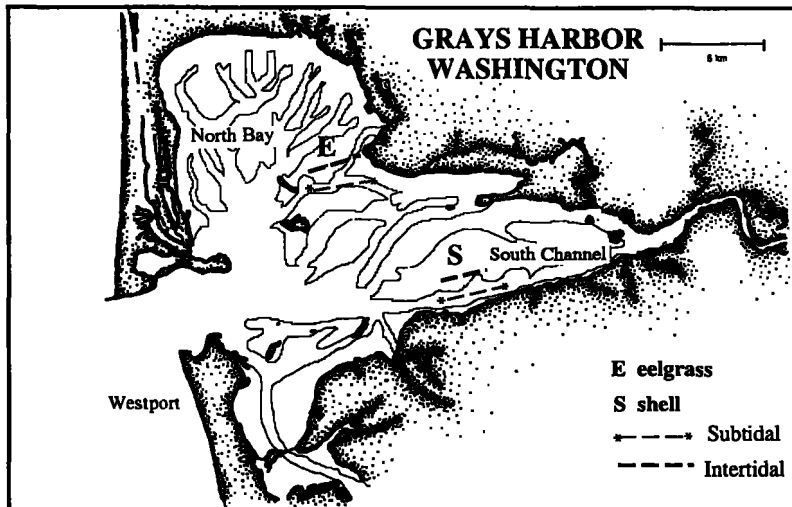


Figure 1

Grays Harbor, Washington, sampling locations for staghorn sculpin, *Leptocottus armatus*, and Dungeness crab, *Cancer magister*, at eelgrass (E) and shell (S) sampling sites. Bold dashed line denotes intertidal trawls and lighter dashed line indicates subtidal channel trawls.

eelgrass, terrestrial leaves), shell, and underlying substrate. All fish and crab were sorted from the catch, identified to species, and counted. Crab were measured (carapace width [CW] inside the 10th lateral spine), sexed, and returned to the water. Staghorn sculpin were picked from the catch and killed. Their body wall was slit, and the fish were preserved in 10% formalin in sea water and later transferred to 70% ethanol in the lab for measurement (total length, TL) and stomach content analyses.

Length-frequency data for sculpin and crab were used to determine instar and year-class composition. Crab length-frequency histograms by trip were used to establish the presence of the 1989 year class of 0+ crab from first tentative appearance in May, at peak settlement in early June, and at the time of summer growth through August. Size modes for crab instars (juvenile crab 6–40 mm CW) were visually determined from length-frequency histograms (hereafter crab instars 1 through 7 will be referred to as J1–J7 and conform to instar sizes specified by Wainwright and Armstrong [1993] and Dinnel et al. [1993]). Evaluation of size ranges and modes as compared with stage (CW for crab; TL for sculpin, Tasto, 1975) were used to set the upper size limits for 0+ and 1+ age classes each month during the summer.

Sculpin gape measurements

Sculpin mouth widths (measured for 466 sculpin) were used as an index of mouth gape size. The mouth

of a preserved specimen was gently pried open as far as possible and the internal distance from the intersections of upper and lower jaws was measured. Since fish body lengths are more commonly reported as standard lengths (SL), sculpin total lengths (TL) were converted to standard length for a discussion of mouth gape to body length relationship⁸:

$$SL = 0.87338 TL - 2.7584$$

$$(r^2 = 0.995, n = 53).$$

Stomach content analyses

Stomach contents of all staghorn sculpin from a trawl were examined up to a total of 20 fish. When catches were higher, the fish were separated into 5-mm size intervals, then proportionally subsampled until a total of 20 fish were selected for stomach analyses. Sculpin were measured (TL), blotted on paper towels, and weighed wet to the nearest 0.1 g. Then their stomachs were removed, blotted, and weighed with and without contents to derive stomach content weight. An estimate of relative stomach fullness was derived by using six categories corresponding to empty, 1/4, 1/2, 3/4 full, full, and "distended." In the latter case, quantity of prey within the stomach resulted in pronounced distention of the body wall beyond the normal lines and curvature of the fish. Sculpin stomachs were analyzed to document the frequency of occurrence of Dungeness crab, the overall proportion of the diet attributed to major prey categories, and the relationship between sculpin size and size of juvenile crab prey.

Food items were generally identified to species unless obscured by digestion. Prey species consumed frequently were analyzed as a distinct prey category, but species that were consumed infrequently were combined to form a more general prey taxon that also included prey items obscured by digestion. As an example, the amphipod *Eogammarus confervicola* was recorded as a separate prey category owing to its high frequency of occurrence, but several species of fishes (*Gasterosteus aculeatus*, *Lumpenus sagitta*, *Cymatogaster aggregata*, *Leptocottus armatus*, *Pleuronectes vetulus*, and *Citharichthys* sp.) were consumed infrequently and were thus grouped as "fish." Analysis of stomach content data was done by

⁸ Williams, G. Pacific Estuarine Research Labs., San Diego State Univ., San Diego, CA. Unpubl. data, 1991.

calculation of a modified form (Stevens et al., 1982) of the Index of Relative Importance (IRI) (Pinkas et al., 1971; Hyslop, 1980) based on estimated food weight rather than food volume. For a particular prey category, an IRI value was calculated as

$$IRI = (NC + GC)FO,$$

where *NC* (numerical composition) is the number of a particular prey item divided by the total number of all prey items in that sample multiplied by 100, *GC* (gravimetric composition) is the combined weight of a particular prey item divided by the total weight of all stomach contents in the sample multiplied by 100, and *FO* (frequency of occurrence) is the number of stomachs from a sample containing a given prey item divided by the total number of fish sampled multiplied by 100. IRI values from all prey categories were summed to derive a grand total IRI value. The relative importance of each prey category was then expressed as a percentage of this total IRI (hereafter referred to as %IRI).

Data analysis

Sculpin stomach content data were analyzed from four perspectives. First, an overall summer diet for staghorn sculpin was derived by combining all fish from both sites (E and S), inter- and subtidal, across months to determine dominant prey taxa. Second, a temporal comparison of sculpin diets from late spring through summer was made by examination of sculpin stomachs grouped by sampling trip. Third, the effect of sculpin size (and thus age) on diet was investigated for two size groupings derived from length-frequency histograms of sculpin caught during the six trips. Size ranges and age equivalents were set from the literature (Anaheim Bay, CA, [Tasto, 1975]; Yaquina Bay, OR [Bayer, 1985]) to group fish by age class as either 0+ ($n=210$) or $\geq 1+$ ($n=256$). IRI analyses were run separately on 0+ and $\geq 1+$ sculpin to determine whether there were changes in diet composition based on predator size. Fourth, prey composition of sculpins feeding at different epibenthic habitats was compared by examining diets of fish collected from the intertidal eelgrass site ($n=55$) and diet of sculpin caught at the intertidal shell site ($n=44$).

To compare dietary overlap of sculpin of the two size/age categories or of sculpin collected at the two different habitats (eelgrass vs. shell), Schoener's (1970) index of overlap (S_{IO}) was calculated as

$$S_{IO} = 1 - 0.5 \left(\sum_{j=1}^n |P_{x_j} - P_{y_j}| \right),$$

where P_{x_i} = the proportion of prey *i* (%IRI) in the diet of sculpin of size *x* (or from habitat *x*);
 P_{y_i} = the proportion of prey *i* (%IRI) in the diet of sculpin of size *y* (or from habitat *y*),
 and *j* = the number of prey types. An overlap value of $S_{IO} \geq 0.6$ (Schoener, 1970) was considered significant in this study.

Results

Overall summer diet

A total of 482 staghorn sculpin stomachs were collected from April to August 1989, of which 458 had some stomach contents. Sculpins averaged 118 mm TL (range: 61–215 mm TL) during the five-month sampling period (Table 1). Mouth gape width ranged from 13 to 17% of standard length (gape width = $0.1818 SL - 2.6487$, $r^2=0.909$; Fig. 2). Average fish length and weight varied by sampling month and were generally greater in April and May when samples were composed primarily of 1+ fish, decreased in June as 0+ sculpin moved into the sampling sites, and increased in July and August as individuals grew through summer (Fig. 3; Table 1). Size-frequency data indicated the presence of two modes equivalent to 0+ and 1+ age classes. Young of the year ranged from 60 to 94 mm TL in April and had grown to 75–119 mm by August (Fig. 3). For purposes of analyses of diet based on size-age composition of sculpin, 118 mm TL was used as the boundary between 0+ and 1+ groups. These size-age categories were corroborated by otolith annuli determinations of a similar size range of staghorn sculpins from Vancouver Island, British Columbia, estuaries by Mace (1983, p. 369).

The mean number of individual prey items per sculpin was 3.4, and gut fullness was generally high; 75% of all stomachs examined were rated 50% full or greater whereas fewer than 5% were empty (Fig. 4). Sculpin stomach contents included 23 prey taxa (Armstrong, 1991) which were grouped into 14 prey categories for IRI analyses (Table 2). Principal categories of sculpins' overall summer diet (% IRI) were the polychaete *Nereis* (*Neanthes*) *brandti* (30% IRI), the ghost shrimp *Neotrypaea californiensis* (27% IRI), sand shrimps *Crangon* spp. (13% IRI, including *C. franciscorum*, *C. nigracauda*, and *C. stylirostris*), juvenile *Cancer magister* (9% IRI), and the mud shrimp *Upogebia pugettensis* (6% IRI).

Temporal changes in diet

Stomach contents were analyzed on a per trip basis to note change in sculpin diet over the course of the

Table 1

Summary data for groups of staghorn sculpin, *Leptocottus armatus*, sampled during monthly trips and for all sculpin combined from April to August 1989 from Grays Harbor, Washington, for stomach content analysis. During each trip all sculpin were caught from both sites, eelgrass and shell habitats, inter- and subtidal trawls combined. SD = 1 standard deviation, TL = total length.

Dates	Fish size (mm TL)			Fish wet wt. (g)			Mean gape	No. stomachs examined	% empty	Mean no. prey per sculpin
	Mean	1 SD	Range	Mean	1 SD	Range	(mm)			
Apr 7-8	113	21	(61-190)	17	11	(2-70)	14.8	111	0	7.1
May 6-7	138	27	(94-215)	36	28	(9-133)	18.9	38	3	2.5
Jun 4-6	108	25	(72-173)	17	14	(3-62)	14.7	62	0	2.7
Jun 18-19	99	19	(70-162)	12	9	(4-55)	12.2	126	4	2.3
Jul 19-20	121	23	(78-169)	21	13	(4-53)	16	61	11	1.4
Aug 15-18	127	28	(84-213)	24	19	(6-102)	16.7	84	8	3.3
Combined grand mean	118	27	(61-215)	20	17	(2-133)	15.6	482	5	3.4

summer. Entry of small sculpin into our sampling areas in June was inferred by the decrease in mean sculpin size and wet weight (Table 1) and supported by examination of length-frequency histograms (Fig. 3).

Diet composition changed appreciably from month to month. During the spring, sculpin primarily consumed the gammarid amphipod *E. confervicola* (46% IRI), *Crangon* spp. shrimp (24% IRI), and fish (13% IRI) in April (Fig. 5), whereas the nereid polychaete *N. brandti* (34% IRI), the thalassinid shrimps *N. californiensis* (45% IRI), and *U. pugettensis* (12% IRI) were the most abundant prey in stomachs in May (Fig. 5). Sculpin consumed few crab, reflecting the relative scarcity of 0+ instars in late spring; J1 instars were found in only 5% of sculpin stomachs in May and represented less than 1% IRI. Minimal settlement of Dungeness crab during May was indicated by low catches of 0+ crabs (Fig. 6; only three J1 were caught in 10 trawls).

In early June, juvenile Dungeness crab recruited to the estuary (Fig. 6) and became the second most important diet category (24% IRI, Fig. 5). The nereid polychaete *N. brandti* was first in dietary importance, accounting for 59% IRI, and *Crangon* spp. shrimp ranked third (10% IRI) in early June. The major pulse of 0+ crab settlement had occurred during late May-early June (after the mid-May sampling; Fig. 6) and thus J1 and J2 crab had become readily available prey by the beginning of summer. Nereid polycha-

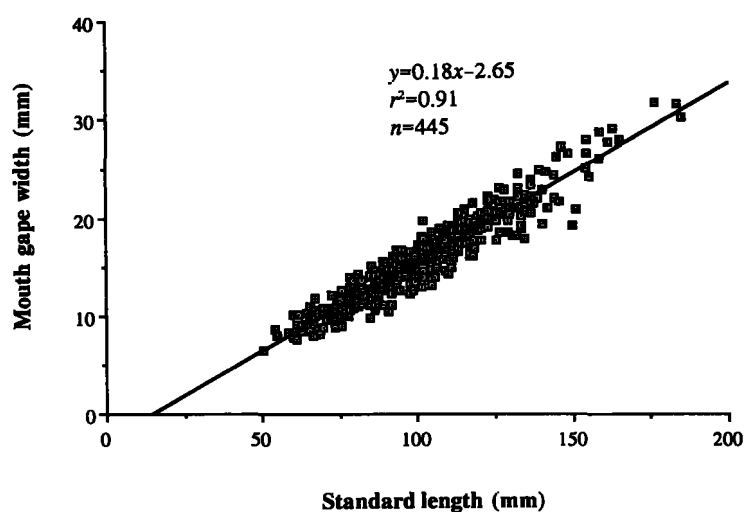
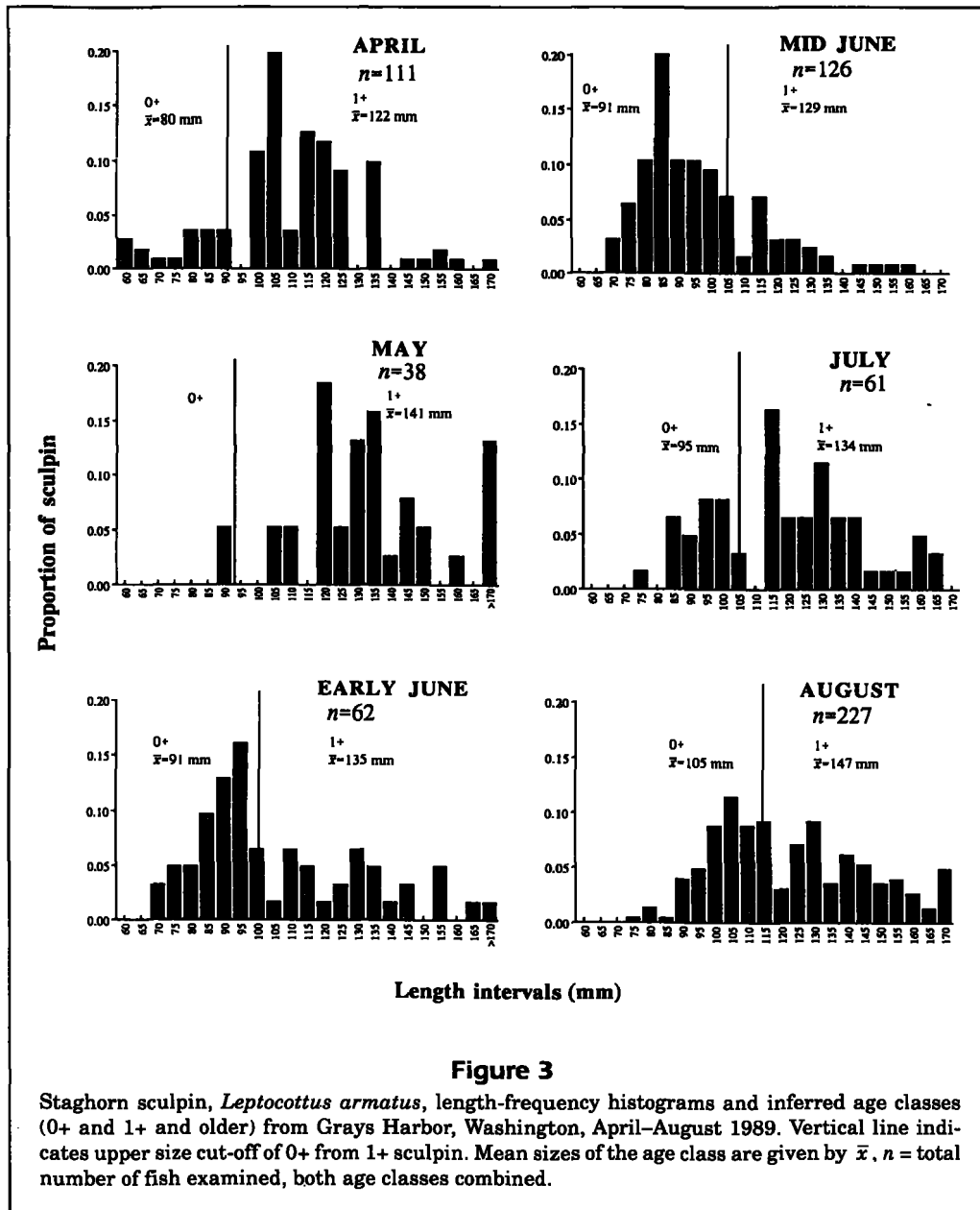


Figure 2

Staghorn sculpin, *Leptocottus armatus*, mouth gape width (y) to standard body length (x) relation based on 445 sculpin from Grays Harbor, Washington, April-August 1989.

etes continued as the most important prey item through mid-June (88% IRI), whereas *C. magister* juveniles accounted for only 4% IRI and were consumed by 24% of the sculpin examined.

During the mid and later part of summer, decapod crustaceans represented the majority of staghorn sculpin diet. In July and August nereid worms were rarely found in stomach contents, but thalassinid shrimp, *N. californiensis* and *U. pugettensis*, together totalled 70% IRI in July and 54% IRI in August (Fig. 5). Juvenile crab accounted for 15% and 13% IRI of

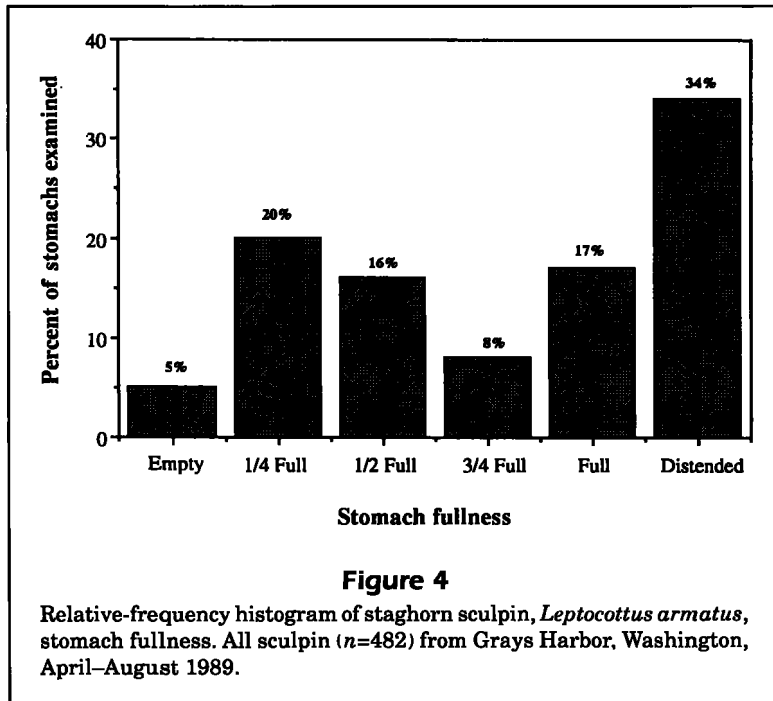


sculpin diets during these months and *Crangon* spp. for 10% and 11% IRI.

Sculpin age-class and prey composition

Sculpin length-frequency histograms by trip were examined and fish were separated into two age groups based on size (Fig. 3). The diets of 0+ and $\geq 1+$ sculpin were compared to determine whether there were differences in prey composition based on fish size. Both sculpin age groups had the same proportion of empty stomachs (5%) and the same mean number of prey species (3.4) per predator, indicating

similar feeding success rates. Small (0+) sculpins primarily consumed *N. brandti* (50% IRI), *N. californiensis* (13% IRI), *Crangon* spp. (11% IRI), *C. magister* (9% IRI), bivalve siphon tips, and miscellaneous or unidentified crustaceans (5% IRI each; Fig. 7). Larger sculpins consumed less *N. brandti* and crangonid shrimp (23% and 5% IRI) but more thalassinid shrimp (*N. californiensis* [31% IRI] and *U. pugettensis* [12% IRI]) and large gammarid amphipods (*E. confervicola* [8% IRI]). Dietary overlap was significant ($S_{10}=0.6$). Sculpins over the entire size range sampled (70–215 mm TL) consumed young *Dungeness* crab (9% of IRI in the summer diet of both



0+ and 1+ sculpin). Whole bodies of crab instars, J1–J4 (mean CW: 6–21 mm), were found in sculpin stomachs (Fig. 8).

Habitat comparison

Sculpin diets from two intertidal sites dominated by eelgrass and epibenthic shell (Fig. 1; E and S) were compared. At each site two trawls per trip were made at high tide after sculpin had moved from the adjacent subtidal channels up onto the flats to feed. Mean number of individual prey items per predator (about 3) was the same at both sites, but the percentage of empty guts was significantly lower among sculpin caught over the eelgrass compared with the percentage of empty guts among sculpin caught over shell habitat (2% vs. 11%; approximation of Fisher Exact Test, $Z=1.98$, $P=0.024$, Zar, 1984). Mean length of sculpin captured at the eelgrass and shell sites were 104 ± 24 mm (1 SD) and 123 ± 27 mm TL, respectively. The most pronounced difference in sculpin diets between sites was that juvenile *C. magister* composed 77% IRI over shell habitat but only 5% over eelgrass (Fig. 9). Frequency of occurrence of crab in sculpin stomachs was 3.6 times greater over shell habitat than over eelgrass habitat (69% FO vs. 19% FO). In addition to *C. magister*, the other top diet categories at shell habitat were ranked as *N. californiensis* (7% IRI), *U. pugettensis* (6% IRI), *N. brandti* (5% IRI), and unidentified amphipods (2% IRI). In contrast, primary prey at the eelgrass habitat were *N. californiensis* (27% IRI), *N. brandti* (25% IRI), and *Crangon* spp. (24% IRI). *Cancer magister* and bivalve siphons represented 5% and 4% IRI respectively (Fig. 9). There was not significant dietary overlap in sculpin diets between the two habitats ($S_{IO}=0.2$).

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Staghorn sculpin and 0+ crab densities

Relative density at intertidal and subtidal channels To assess the availability of crab as prey for sculpin predators, relative density was calculated for both sculpin and 0+ crab to contrast intertidal and subtidal eelgrass and shell habitats. At either site, relative crab densities were initially higher on the intertidal compared with adjacent subtidal channels during peak crab settlement in June. Intertidal densities in shell habitat at South Channel were about 9,500/ha in early June and declined to 6,000/ha later in the month. However, in the adjacent subtidal channel crab densities were less than 100/

Table 2

Summer diet composition of staghorn sculpin, *Leptocottus armatus*, from Grays Harbor, Washington, all data combined, April–August 1989. Values are percent composition by number (%NC), weight (%GC), frequency of occurrence (%FO), and percent of total Index of Relative Importance (%IRI) by prey categories. Bold values indicate the five most important prey categories as measured by % total IRI. The total cumulative percentage of the diet comprised by those five categories appears in the bottom line of the table.

Prey category	%NC	%GC	%FO	%IRI
<i>Nereis brandti</i>	9	30	30	30
<i>Neotrypaea californiensis</i>	9	27	30	27
<i>Crangon</i> spp.	12	7	27	13
<i>Cancer magister</i>	9	7	22	9
<i>Upogebia pugettensis</i>	3	17	11	6
<i>Eogammarus confervicola</i>	13	<1	12	4
Misc./unid. crustacea	9	2	12	3
Fish	4	6	12	3
Bivalve siphon tips	10	<1	10	2
Misc./unid. amphipods	6	<1	7	1
<i>Allochestes</i> spp.	5	<1	5	<1
<i>Corophium salmonis</i>	6	<1	5	<1
Misc./unid. polychaetes	2	<1	5	<1
Algae	3	<1	8	<1
Total cumulative percentage of diet within top 5 categories				85% IRI

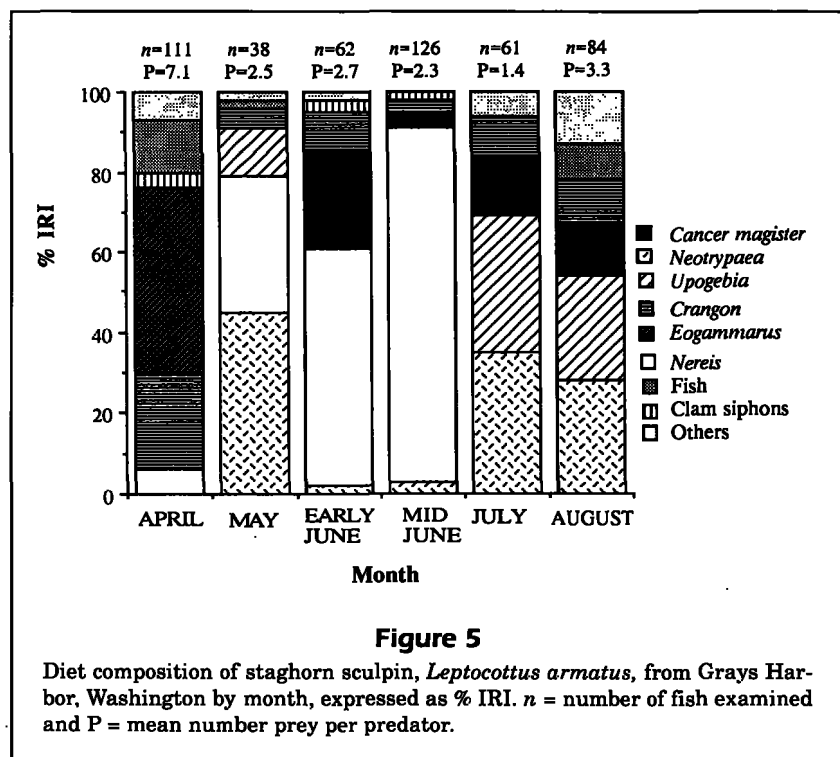
ha where the primary epibenthic cover is allochthonous leaves, branches, and bark. Initial mean crab densities were almost four times higher in the intertidal shell than at the intertidal eelgrass site (Fig. 10; 9,500 crab/ha vs. 2,500 crab/ha, t -test, $t=2.4$, $P=0.136$). At the eelgrass site, intertidal and subtidal crab densities were comparable by mid-June at about 2,500/ha. As the summer progressed, 0+ crab density declined in the intertidal at both the shell and eelgrass sites to about 900/ha and 320/ha, respectively, but increased in the subtidal channel adjacent to the shell habitat (Fig.10). The subtidal epibenthos at the shell site in South Channel is composed predominately of wood, bark, and leaves, whereas the subtidal benthic cover at the eelgrass site is primarily shell, eelgrass, and algae; these differences probably contribute to the density differences in mid-June between the two locations.

Relative density at shell habitats Sculpin densities at the shell habitat were always higher in the intertidal areas than in the subtidal channel except in mid-June (Fig. 10). In contrast, at the eelgrass site there were higher densities of sculpin in subtidal than in intertidal areas in early June (230 vs. 40 sculpin/ha), but by August higher mean sculpin densities occurred in the intertidal areas (138 vs. 30 sculpin/ha).

Discussion

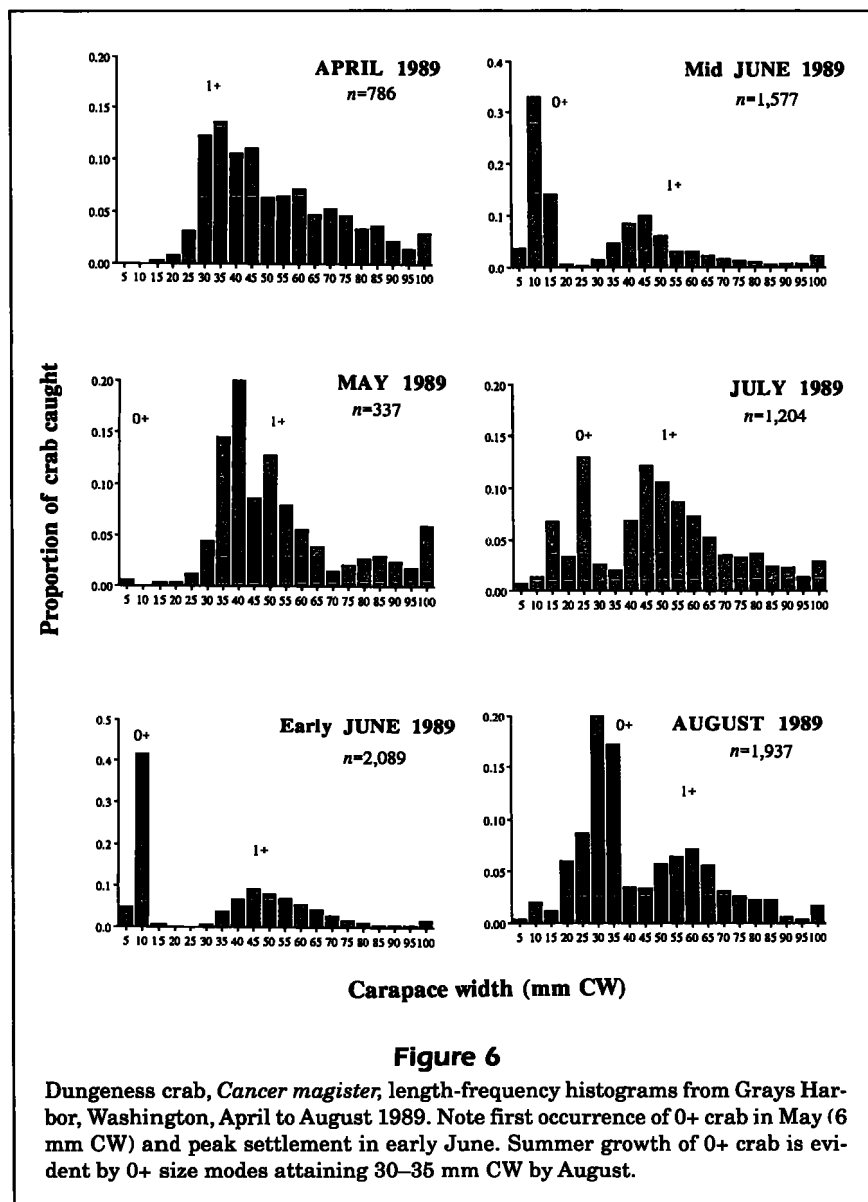
Importance of crustaceans as prey

Juvenile staghorn sculpins have been reported to feed heavily on small crustaceans including amphipods and isopods. Studies in Tomales Bay, California (Jones, 1962), and the San Juan Islands, Washington (Thornburgh, 1980), have shown that juvenile sculpin primarily consume amphipods, especially *Corophium* spp., mysids, and shrimp. Smith (1980) reported that juvenile staghorn sculpin (20–80 mm TL) in Skagit Bay, Washington, consume the amphipods *Corophium salmonis* and *Anisogammarus confervicolus*, tanaiids, and the polychaete *Neanthes limnicola*. Dinnel et al. (1990) showed ontogenetic diet shifts for staghorn sculpin from Padilla Bay,



Washington. The smallest sculpin (45–79 mm TL) consumed amphipods and isopods; sculpin 80–119 mm consumed amphipods, isopods, and crabs; and the largest sculpin (≥ 120 mm) consumed isopods, crabs, and fish. While juvenile sculpin less than 60 mm TL were not sampled in the present study, no significant diet shift was noted for the two size groups (60–119 mm and ≥ 120 mm) of the Grays Harbor prey assemblage, although relative importance of items differed between the size groups. Smaller fish did consume a relatively higher proportion of polychaetes, whereas larger sculpins consumed more thalassinid shrimp (Fig. 7).

Other studies have shown that adult staghorn sculpins consume crustaceans as a major portion of their diet when they are available. Dinnel et al. (1990) found that amphipods, isopods, and an assemblage of crab species (including *C. magister* and *Pinnixa* spp.) composed a majority (79% IRI) of the August diets of staghorn sculpins from Padilla Bay, Washington. Data presented by Jones (1962) and Boothe (in Tasto, 1975) showed that the majority of staghorn sculpin diet (92% IRI) consisted of decapod crustaceans, including *Crangon* spp., *Upogebia pugettensis*, and a crab assemblage of *Cancer* sp., *Hemigrapsus* sp., *Pinnixa* sp., and *Scleroplax* sp. Year-round sampling in Anaheim Bay, California, revealed that sculpin consumed primarily decapod crustaceans (78% of the diet by weight) including *N. cali-*



forniensis, *H. oregonensis*, and pea crabs, *Pinnixa* spp. (Tasto, 1975). A multi-species assemblage of crab including *Pugettia producta*, *Cancer productus* and *C. gracilis*, *Pinnixa* spp., *Scleroplax granulata* (pea crabs), *Hemigrapsus nudus*, *H. oregonensis*, and *Pagurus* spp. accounted for 25–30% of the spring diet (by volume) of staghorn sculpins >100 mm TL in an estuary of Vancouver Island, British Columbia (Mace, 1983).

The summer diet of staghorn sculpins from Grays Harbor, Washington, corroborates Tasto's (1975) observation that the diet of staghorn sculpin >70 mm TL consists of crustaceans, especially decapods including ghost and mud shrimp (*N. californiensis* and *U. pugettensis*), sand shrimp (*Crangon* spp.), and seasonally abundant 0+ *Cancer magister*. From IRI

analysis, it was determined that Dungeness crab represented about 9% of the overall total summer diet of sculpin. Over 30% of all staghorn sculpin collected during June and 23% during July and August had 0+ Dungeness crab in their stomachs. Two other decapods that composed even greater proportions of the overall sculpin summer diet were *Neotrypaea californiensis* and *Crangon* spp. (27% and 13% IRI, respectively).

Other prey

Staghorn sculpin also consume prey species such as nereid polychaetes, fish, and bivalves that are seasonally abundant and readily available (see Gunderson et al., 1990, for list of infaunal and epifaunal prey in Grays Harbor). These sculpin have relatively plastic feeding behavior and their diet changes month to month, fluctuating with relative prey abundance and accessibility. Despite this plasticity, the majority of this species' diet (85–99% IRI) generally consisted of only 4 or 5 prey species (Fig. 5; Table 2). In April, before crab were available, sculpin consumed amphipods, especially *E. confervicola*, and *Crangon* spp. shrimp. Nereid polychaetes and the thalassinid shrimp *Neotrypaea californiensis* were primary prey in May. Dungeness crab were incorporated into the diet as they

settled in June and were ranked second in IRI importance after *N. brandti*.

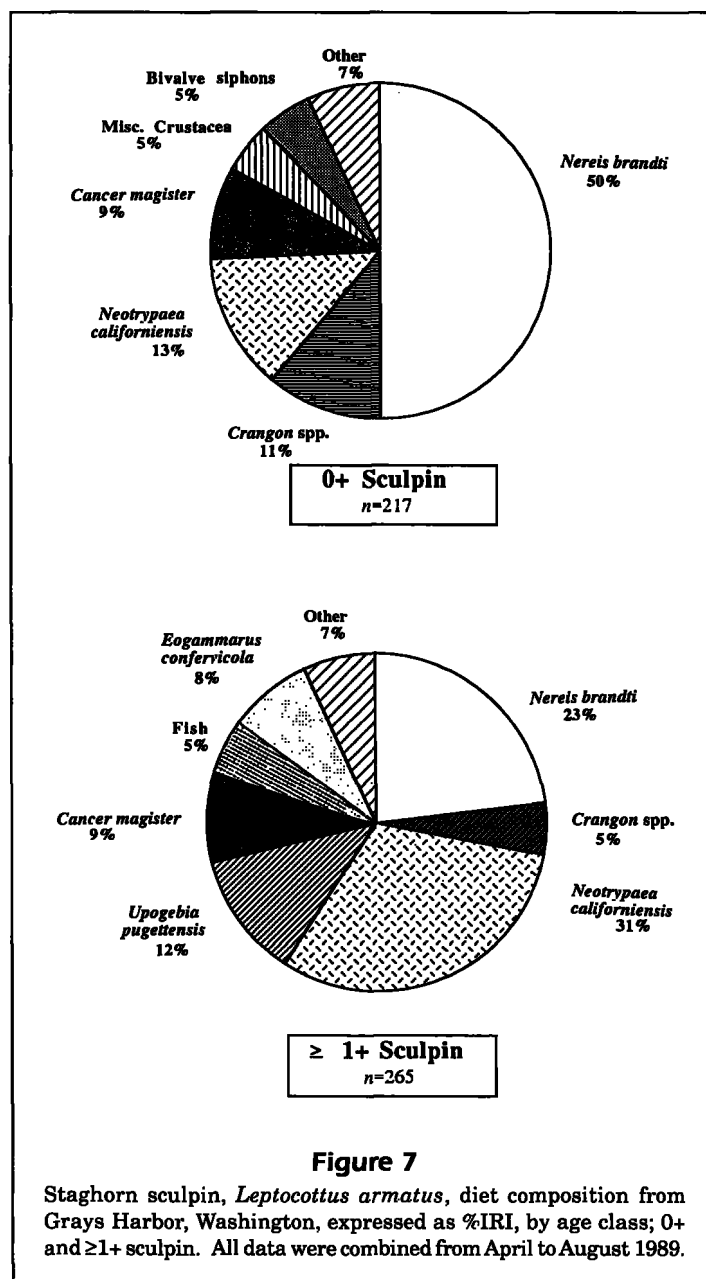
The late spring or early summer predominance of *N. brandti* polychaetes in the diet of sculpin was somewhat unexpected because polychaetes have not often been reported as a major diet item by other researchers from Washington (Smith, 1980; Thornburgh, 1980; Dinnel et al., 1990), or British Columbia (Mace, 1983), although they are mentioned as prey among fish from California (Jones, 1962; Tasto, 1975). The importance of this polychaete during spring and early summer to sculpin in Grays Harbor suggests that adult worm reproductive activity (Bass and Brafield, 1972; Giese and Pearse, 1975; Durchon, 1984) might make them vulnerable to sculpin preda-

tion at this time of year. We examined well-preserved specimens of this polychaete from stomach contents but found all were immature. High predation on immature stages of *N. brandti* may indicate worms are leaving their burrows to disperse as described by Dean (1978). By July and August, the behavior of the polychaetes may have changed, or their abundance may have declined since worms were rarely observed from stomach contents during those months.

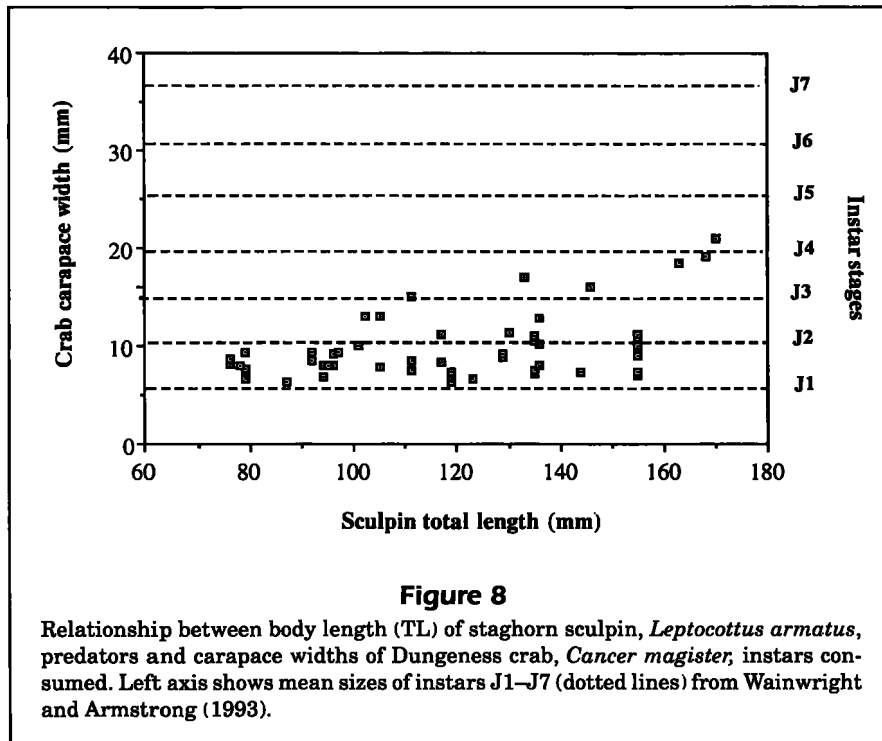
Dungeness crab

Predation on 0+ Dungeness crab by sculpin is of interest because of the substantial commercial value of the *C. magister* fishery from northern California through southeast Alaska (Botsford et al., 1989) and because of the ecological implications of this estuarine predator-prey relation that is dependent on the annual arrival of oceanic crab larvae. Estuaries are important nursery grounds for 0+ crab (Clever, 1949; Tasto, 1983; Gunderson et al., 1990) and provide refuge by means of several habitats including eelgrass and epibenthic shell (Stevens and Armstrong, 1985; Gunderson et al., 1990; Jamieson and Armstrong, 1991; Dumbauld et al., 1993). Fernandez et al. (1993a) demonstrated that megalopae and newly settled 0+ *C. magister* prefer heavy shell habitat over eelgrass, mud with scattered shell, or bare mud. In addition, field tethering of crab in Grays Harbor showed that shell provided the best protection from predation compared with other habitats and that crab tethered with attached hooks were most often attacked by staghorn sculpin.

During peak crab settlement in early June, juvenile crab were found in 42% of the sculpin stomachs examined and represented 10% of the total diet by weight (%GC), or 24% of IRI (Fig. 5). At this time crab are highly vulnerable to predation; the small J1 and J2 instars (6–11 mm CW) are very abundant (over 100/m²; Fernandez et al., 1993b), compete for limited refuge habitat, and molt frequently (every 2–3 weeks; Wainwright and Armstrong, 1993). The temporal pattern of 0+ intertidal density is consistent with inferences regarding both the rapid predation of much of the 0+ crab population shortly after settlement and with the relative importance of epibenthic shell as a refuge to ensure some survival of the year class. From early June to July, 0+ density decreased an order of magnitude at both the intertidal shell and eelgrass sites as measured by trawl, but density was generally about three times higher over shell habitat compared with eel-



grass habitat (Fig. 10). This difference in density between the two habitats is likely much greater than that indicated by the trawl data. Net efficiency is unknown, but the gear was designed to operate on a fairly uniform sand-mud substrate (Gunderson and Ellis, 1986) and, we assume, is less efficient over the shell habitat compared with eelgrass habitat (although much shell is taken in trawls). More importantly, the net "integrates" animals and material along the trawl path and cannot provide distinctions over smaller spatial scales of highly heterogeneous habitat such as intertidal shell. We know from previous intertidal work done in Grays Harbor that



megalopae settle and that J1 instars occur initially on both open tideflats and in refuge materials (e.g. shell, eelgrass) but are absent from the former within several tidal cycles and are virtually never found on open flats thereafter⁹ (Dumbauld et al., 1993). Detailed excavation of shell patches at low tide reveal post-settlement densities of J1 in excess of 100/m², but only a few per m² in eelgrass (Fernandez et al., 1993a), which suggests that trawl data collected at high tide are likely a substantial underestimate of 0+ crab in shell compared with crab in eelgrass.

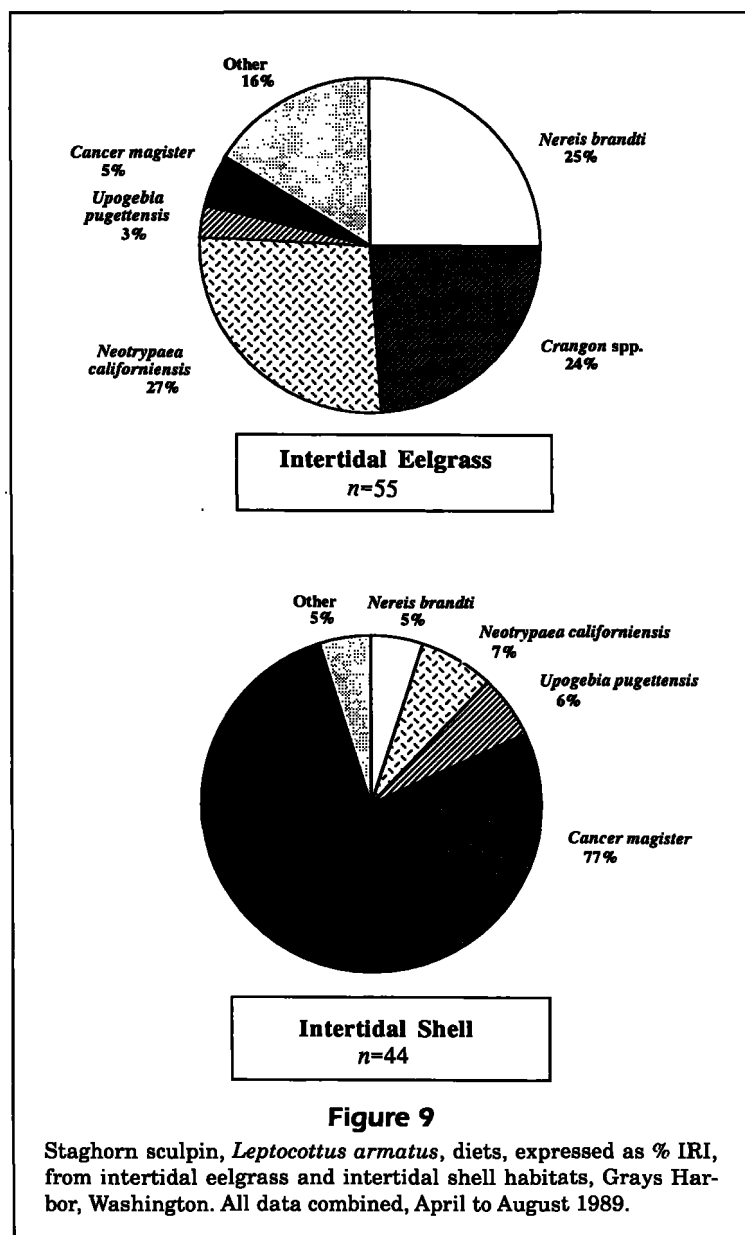
These observations reflect a paradox indicated by the data. Higher apparent crab consumption was measured among sculpin collected from the shell habitat (77% IRI) than from the eelgrass (5%) (Fig. 9), inconsistent with the notion that shell provides critical refuge habitat for small crab instars. The mean density of 0+ crab from eelgrass intertidal trawl sites decreased by an order of magnitude from 2,455 crab/ha in early June to 280 crab/ha in mid-July (Fig. 10). During the same period, mean 0+ crab density in shell habitat decreased from 9,452 crab/ha to 874

crab/ha, reflecting migration into the channels (Wainwright, 1994) and the impact of predation including cannibalism (1+ on 0+ instars [Stevens et al., 1982]; early 0+ on later 0+ [Fernandez et al. 1993b] fish on 0+ crab [Fernandez et al. 1993a]). There appears to be a short time period during peak crab settlement when staghorn sculpin eat many small instars, especially those that settle on bare sand or mudflats. In this respect Dungeness crab survival throughout much of the bay is dependent upon the availability of suitable refuge habitat^{2,10} (Fernandez et al., 1993a) as has been found for juveniles of other decapod species (Herrnkind and Butler, 1986; Barshaw and Lavalli, 1988; Howard, 1988; Warren, 1990).

This pattern may be explained by the short time scale of settlement and rapid predation on small instar crab (especially J1–J2). A possible explanation for the difference in observed crab consumption by sculpin between the two habitats is that crab settlement in eelgrass or on open tideflats is predated very rapidly and depleted from those areas compared with crab settlement in the shell habitat. Pulses of cohorts could be severely reduced in much less time than the interval between sampling trips and thereafter effectively be unavailable to sculpin in certain areas of the estuary because of virtual removal. Crab that recruit to areas of extensive shell may provide a more stable and persistent prey basis as the dynamics of small instars (agonistic interactions and foraging) make them vulnerable on the exterior of the shell matrix or as they move short distances between shell piles. Predation by sculpin on J1–J4 instars in shell habitats may occur over a longer period, thereby increasing the likelihood that sculpin in our samples contained crab later in the summer, long after they were depleted from less protected areas of open mud and light cover of eelgrass. This would be reflected both in greater numbers of crab consumed and in greater frequency of occurrence

⁹ Armstrong, D. A., K. A. McGraw, P. A. Dinnel, R. M. Thom, and O. Iribarni. 1991. Construction dredging impacts on Dungeness crab, *Cancer magister*, in Grays Harbor, Washington, and mitigation losses by development of intertidal shell habitat. Final Rep. FRI-UW-9110 to U.S. Army Corps of Engineers, Seattle District, Seattle, WA, 63 p.

¹⁰ Doty, D., D. A. Armstrong, and B. R. Dumbauld. 1990. Comparison of carbaryl impacts on Dungeness crab (*Cancer magister*) versus benefit of habitats derived from oyster culture in Willapa Bay, Washington. Univ. Washington, Fisheries Res. Inst., Seattle, WA. Rep. FRI-UW-9020, 69 p.



in sculpin sampled from the shell habitat (higher %NC and %FO in the IRI calculation).

Size at which 0+ crab were no longer vulnerable to sculpin predation was hypothesized to be about 25 mm CW (about instar J5) (Reilly, 1983) based on mouth gape width of the most prevalent size sculpin (gape limited predation [Zaret, 1980]). Theoretically, small crab newly settled to the estuary would be available and vulnerable to sculpin predation for much of their first full summer (as J1–J6), whereas 1+ crab resident in the estuary during summer would be too large (50–100 mm CW, Fig. 6; Stevens and Armstrong, 1985; Gunderson et al., 1990) for staghorn sculpin to consume. These assumptions were

confirmed because only J1–J4 (below 25 mm max. CW) were consumed (Fig. 8). Generally there were relatively few sculpin with an estimated gape width of 25 mm (Fig. 2), thus sculpin were restricted to J1–J4 crab. Carapace width is the larger body dimension of this species of crab, but if attacked from the side (i.e. laterally at the walking legs rather than face-on towards the chelae), then body length (from the posterior of the carapace to the orbit of eyes) could be the limiting dimension with respect to sculpin mouth gape. Based on data of Weymouth and MacKay (1936), the carapace length (CL) of J3, J4, and J5 instars is about 73%, 71%, and 70% of width, respectively. From this perspective, the average size sculpin of this study could possibly consume instars up to J5 with respect to length (approximately 18.8 mm CL). Very few sculpin longer than 175 mm TL were caught; even their estimated gape width was only about 24.6 mm, less than the average carapace width of most 0+ crab by September (Wainwright and Armstrong, 1993).

The six other potential fish predators of 0+ crab found in greatest abundance throughout the summer included juvenile English sole, *Pleuronectes vetulus*, shiner perch, *Cymatogaster aggregata*, snake prickleback, *Lumpenus sagitta*, saddleback gunnels, *Pholis ornata*, sand sole, *Psettichthys melanostictus*, and starry flounder, *Platichthys stellatus*.² The first five species have relatively small mouths, are most prevalent as juveniles within the Grays Harbor estuary (English sole) or are not documented as being important crab predators¹ (Williams, 1994). Starry flounder may prey on 0+ Dungeness crab both in Grays Harbor¹ and San Francisco Bay (Reilly, 1983) but are uncommon as adults in the former estuary (Rogers et al., 1989).

The results of this study expand current knowledge of staghorn sculpin's diet composition and feeding behavior, establish the importance of 0+ Dungeness crab as part of the estuarine summer diet of sculpin, and provide a perspective of the potential impact that sculpin predation has on juvenile Dungeness crab survival after settlement. Posey (1986) showed that staghorn sculpin predation limits the distribution of ghost shrimp *N. californiensis* on intertidal sandflats and labeled this fish a keystone predator controlling the depth distribution of newly settled ghost shrimp and the expansion of established beds of adult shrimp. Our data demonstrate that staghorn sculpin are a major predator of small

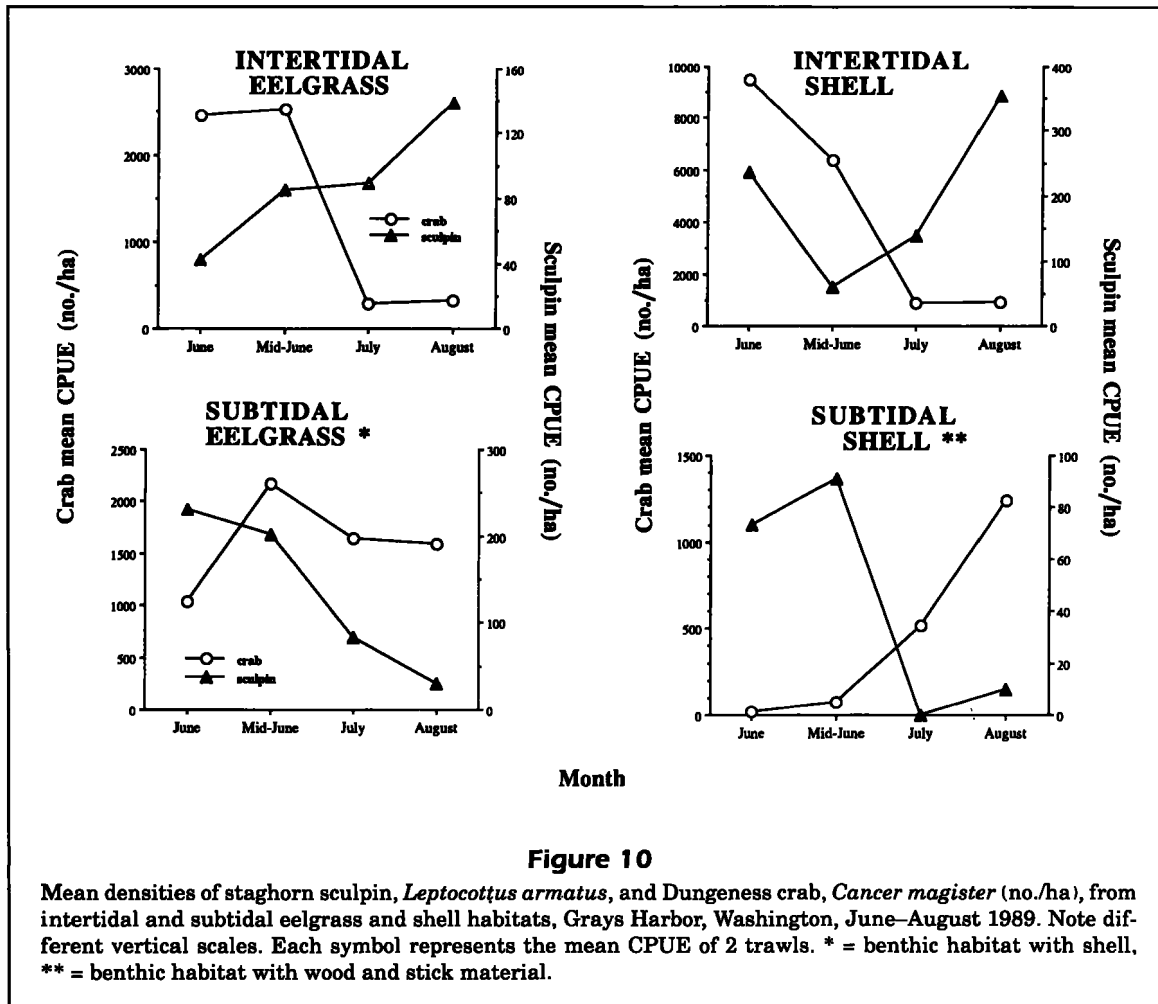


Figure 10
Mean densities of staghorn sculpin, *Leptocottus armatus*, and Dungeness crab, *Cancer magister* (no./ha), from intertidal and subtidal eelgrass and shell habitats, Grays Harbor, Washington, June–August 1989. Note different vertical scales. Each symbol represents the mean CPUE of 2 trawls. * = benthic habitat with shell, ** = benthic habitat with wood and stick material.

0+ Dungeness crab instars during a short period of late spring and early summer settlement and growth and that sculpin may be capable of exerting a pronounced effect on crab year-class strength within coastal estuaries (Armstrong, 1991).

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