# OCCURRENCE OF CANCER CRAB (C. MAGISTER AND C. OREGONENSIS) MEGALOPAE OFF THE WEST COAST OF VANCOUVER ISLAND, BRITISH COLUMBIA

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#### ABSTRACT

The seasonal and cross-shelf occurrences of *Cancer* crab (*C. magister* and *C. oregonensis*) megalopae in 1985 along a transect line perpendicular to the coast off Tofino, British Columbia, are presented. Megalopae of both species were generally absent from surface waters during daylight hours. The two species may have slight temporal differences in nocturnal surface abundance, with *C. magister* occurring later in the evening and earlier in the morning than *C. oregonensis*. Their relative occurrence at the surface during the night was used to calibrate cross-shelf megalopal abundance data. Cross-shelf megalopal intermolt stage proportions were calculated, relating degree of megalopal development to proximity of nearshore habitat required for successful settlement of larvae.

Cancer magister megalopae were present from April to August, with peak abundance in May and June. Megalopae were abundant in a broad band 37-148 km from shore, with peak abundance  $(2,871 10 \text{ m}^{-2})$  56 km offshore in June. In May, some late stage megalopae were collected in coastal inlets but settlement appeared low in coastal study areas. Megalopal abundance decreased abruptly shoreward of 28 km from the coast.

Cancer oregonensis megalopae were also present from April to August, with their pattern of crossshelf abundance basically similar to that of C. magister. However, in contrast to C. magister, abundance of late stage megalopae in coastal inlets was relatively high (313 10 m<sup>-2</sup>) in June, indicating that a significant settlement of megalopae of this species could have occurred.

Evidence for cross-shelf movement of Cancer megalopae is discussed.

Dungeness crab, *Cancer magister*, range from the Aleutian Islands to northern Mexico in the eastern Pacific (Hart 1982) and are commercially exploited from northern California to Kodiak Island, AK. As part of an ongoing study of Dungeness crab recruitment off the west coast of Vancouver Island, the abundance and distribution of larvae off Tofino, British Columbia, are being studied to determine how variability in annual recruitment is affected by larval settlement.

Dungeness crab larvae are planktonic and pass through five zoeal stages and one megalopal stage before settling to the sea bottom. Studies of larvae prior to the 1970s primarily involved descriptions of larval morphology (Mir 1961; Poole 1966), and it was not until Reed (1969) developed laboratory culture methods that larval environmental requirements were first described. Optimal ranges of temperature and salinity for laboratory-cultured zoeae were  $10.0^{\circ}-13.9^{\circ}$ C and 25-30% respectively, but their survival was not significantly affected by the temperature and salinity ranges occurring in the

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cantly from that in open coast waters. Larval settlement, which typically occurs in May and June off the outer coast of Washington, can occur as late as mid-September in northern Puget Sound (D. Armstrong<sup>2</sup>).

waters off Oregon, where Reed's study was con-

ducted, at the time of year when larvae are com-

monly found. Lough (1976) suggested offshore lar-

val movement would allow larvae to avoid lower

nearshore salinities, and that normal oceanic salinity

levels probably favor survival over the long term.

The temporal occurrence of larvae in open coast

Temporal and spatial distributions of crab larvae have been documented for the years 1975–80 in the Gulf of Farallones and the San Francisco-San Pablo-Suisun Bay complex in central California (Reilly

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1983) and for the years 1969-70 along a transect off Newport, OR (Lough 1975, 1976). These studies suggest that while larvae are hatched in the nearshore, shallow-water environment preferred by adult Dungeness crab, they subsequently move alongshore and offshore, and then inshore, often over considerable distances. Larvae hatched off California and Oregon in late winter have been hypothesized to move northward with the Davidson Current before its reversal in March-April, and offshore as a result of upwelling, Ekman transport, estuarine runoff, and geostrophic flow, depending on location and season (Lough 1976; Wild and Tasto 1983). Later stage zoeae are typically found progressively further offshore, and it seems to be the megalopal stage that returns inshore (Lough 1976; Reilly 1983). The megalopal stage is the strongest swimming stage (Jacoby 1982), but there is no direct evidence to indicate that their inshore movement is active.

There are five species of crabs of the genus Cancer in British Columbia (Hart 1982), and larvae of C. oregonensis also occur in abundance in offshore waters along with C. magister (Lough 1975). Cancer oregonensis has no commercial importance, but since it occurs with *C. magister*, data on both species of crabs are included in this study. Comparisons of occurrence between the two species may provide insight into possible environmental mechanisms or processes that influence transport from offshore areas to the inshore juvenile habitats, which the larvae of both species must reach.

This study establishes the seasonal and spatial occurrences of Cancer megalopae along a transect over and beyond the continental shelf off the west coast of Vancouver Island (Fig. 1). The geographical area is of particular interest because of the location of a major regional crab fishery near Tofino (Jamieson 1985; Noakes and Jamieson 1986) and the resulting importance of understanding factors influencing the magnitude of local larval crab settlement. The oceanography off Vancouver Island has been relatively well studied (Freeland et al. 1984; Thomson 1981), and because of the intrusion of Juan de Fuca Strait waters into the general longshore oceanographic regime and the relative increase in topographical complexity of the continental shelf, it is considerably more complicated than that found



FIGURE 1.-The survey transect line, with stations, over which this study was conducted.

south of Cape Flattery (Hickey 1979). Along the eastern Pacific coast, Cape Flattery marks a significant change in nearshore oceanography, and this study to investigate larval crab distribution in open coast waters is the first one north of this landmark.

## GENERAL OCEANOGRAPHY OFF VANCOUVER ISLAND

A seasonal surface current moving northward from about lat. 32°N to 51°N (northern Vancouver Island) typically exists in nearshore waters from October to March (Fig. 2). South of Cape Flattery, this is called the Davidson Current (Hickey 1979) whereas off British Columbia, it appears to consist of two components. Nearshore, there is the yearround, northward flowing Vancouver Island Coastal Current, about 20-30 km wide, and further offshore, there is the seasonal Shelf-Break Current, perhaps a continuation of the Davidson Current, which reverses direction in response to changes in the large-scale wind field (Freeland et al. 1984). The Davidson Current off Oregon has an average northward flow of 50 cm/s for 30% of the time (Boisvert 1969), sufficient to transport larvae significant distances northward during their developmental period if they remained continuously in the current. The California Current is a seasonal, southward moving, surface current of similar magnitude and location to the Davidson Current. It occurs off Vancouver Island (Hickey 1979) in the spring and summer, along with the seasonal, southward flowing, Shelf-Break Current on the outer continental shelf (Freeland et al. 1984). These currents could transport larvae located off Vancouver Island during the spring and summer southwards (Fig. 2). North of Vancouver Island, outer continental shelf currents are poorly described, but off Cape St. James (southern tip of the Queen Charlotte Islands). the surface flow is strongly southward almost yearround, turning northward only in March and April (Freeland et al. 1984). The Vancouver Island Coastal Current originates at the mouth of Juan de Fuca Strait, and so could transport larvae out of the Puget Sound-Georgia Strait complex.

### MATERIALS AND METHODS

### General Methodology

Sampling was largely done along an offshore transect line perpendicular to the coast off Tofino, British Columbia (Fig. 1), with stations located at 0, 9.3, 18.5, 27.8, 37, 46, 55.6, 74.1, 92.3, 111.2, 148.2, and 185.3 km from shore. Stations were more closely spaced nearshore where larval abundance was expected to be greatest, but the transect extended well beyond the shelf break to determine what the seaward distribution of megalopae might be.

Six offshore samplings were made along the transect from February through August 1985, but only three extended the full 185 km. Dates of sampling were 27 February-4 March, 17 and 18 April, 30 and 31 May, 14 and 15 June, 6 and 7 July, and 24 and 25 August. February-March, June, and July samplings were terminated 74 km, 130 km, and 111 km offshore, respectively, because of poor weather and time constraints.

At each station, a neuston tow and an oblique bongo tow to 250 m, or to within 5 m of bottom, were made, and a temperature profile was recorded by means of an expendable bathythermograph. On all cruises, bongo tows were done during daylight hours and neuston tows at night; late-stage crab larvae congregate near the water surface at night (Booth et al. 1985). On 17 June 1985, an hourly, nocturnal series of neuston tows was made at one location, 9.3 km offshore, to identify patterns of nighttime abundance of megalopae in surface waters.

To supplement offshore sampling along the transect, neuston tows were made after dusk in the inlets around Tofino biweekly from early May through August 1985 to monitor presence and movement of larvae. In addition, a beam trawl and epibenthic sled were used in inshore waters in July 1985 to sample for newly settled larvae in an effort to establish time and magnitude of larval settlement.

The RV G. B. Reed was used for all offshore sampling except for the June sample, which was collected from a 27 m charter vessel. Inshore sampling was conducted from a 7 m aluminum herring skiff except for mid-June, when the charter vessel was again used.

### Gear

The neuston sampler was a modified otter surface sampler (Mason and Phillips 1986) with a square mouth opening 45 cm on each side; under calm sea conditions, it sampled the top 35 cm of the water column. A General Oceanics flowmeter<sup>3</sup> in the mouth of the net was used to establish volume of water filtered. Netting was black, 500  $\mu$  Nitex, and

<sup>&</sup>lt;sup>8</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.



FIGURE 2.—Prevailing surface circulation off the British Columbia-Washington coast in winter and summer. Broken arrows indicate uncertain currents. Numbers give speeds (cm s<sup>-1</sup>) (modified from Thomson 1981).

was the same size as that on the bongo gear. The neuston sampler was towed at 4 kn approximately 10 m from the side of the vessel to reduce hull avoidance by the larvae. Tow duration was usually 15 minutes but was shortened when crab larvae occasionally became very abundant at dawn and dusk.

Bongo gear was a modified SCOR design (Mason et al. 1984), having a mouth opening of 25 cm (each side) with the outboard (left) net of 500  $\mu$  Nitex and the inboard (right) net of 230  $\mu$  Nitex. A General Oceanics flowmeter was mounted in the mouth of each net. Sampling procedure followed that described by Smith and Richardson (1977<sup>4</sup>). At stations <100 m water depth, the bongo was fished in an undulating fashion from the bottom to the surface in order to filter a standard volume of water (about 300 m<sup>3</sup>).

The epibenthic sled (Phillips and Mason 1986) used in inshore waters had a 60 cm mouth opening and 1 mm Nitex netting; it was towed for 10 minutes at 2–3 kn. Nine tows were made over bottoms of unknown characteristics. The modified beam trawl (Gunderson and Ellis 1986), also used in inshore waters, had a 3 m mouth opening, a 7 mm mesh net, and a 3 mm mesh cod end; it was towed for 10 minutes at about the same speed as the sled. For both gear types, distance towed was calculated by radar triangulation to reference points on land.

#### **Data Analysis**

All plankton samples were preserved initially in a 4% formaldehyde solution of saltwater. In the laboratory, settled volume was determined, and general composition of the plankton noted. Samples were then sieved, and Cancer larvae picked by hand and returned to a 2% formaldehyde solution before their identification. *Cancer magister* megalops are readily identifiable by their larger size (Trask 1970; Lough 1975), but the currently used key (Lough 1975) was not always effective in separating C. oregonensis and C. productus. Presence of lateral spines is a subjective criterion, and morphological dimensions and counts of setae were two variable to distinguish species. These smaller megalops were finally concluded to be C. oregonensis after rearing hundreds of larvae to the juvenile stage and finding no C. productus.

With beam trawl samples, the catch was sorted

on deck to remove juvenile crabs, and the megalopae were preserved as above. Species composition of the catch was noted.

For the bongo tows, the volume of water filtered was used to calculate a haul factor (Mason et al. 1984), which accounted for tow depth and allowed expression of the data as the integrated number of organisms beneath 10 m<sup>2</sup> of sea surface.

For neuston tows, relative abundance was expressed as area swept rather than as volume filtered and again expressed as number of animals under 10  $m^2$  of sea surface.

Calculations of larval abundance are necessarily conservative, and direct comparisons between different gear types are not presently possible, given our current understanding of gear efficiency and larval catchability, which varies with both depth and time of day. Numbers of larvae reported here are thus directly comparable only within each gear type used. For bottom gear, numbers of crabs were calculated with no consideration of gear efficiency.

### Molt Staging

State of development within the megalopal stage was determined for all *Cancer* megalopae collected at a station, or 25 randomly selected individuals of each species if the number collected exceeded 25. The sequence of epidermal changes occurring during this intermolt period has been described for Dungeness crab by Hatfield (1983), and her procedures and staging criteria were applied for both species. Whole megalopae were stained with 0.25% Fast Green dye in either water or polyvinyl lactophenol for 2-18 hours, and then the second maxillipeds were removed and mounted. Megalopae were identified to 1 of the 13 intermolt stages recognized by Hatfield (1983); these were then combined to form 3 groups: early (stages 1-4), middle (stages 5-8), and late (stages 9-13) megalopae. Temporal durations of these three groups in laboratory studies were 5.8, 15.4, and 6.3 days, respectively (Hatfield 1983). Corresponding durations for C. oregonensis are unknown. Stages were grouped into the three categories described for simplification of analysis; many of Hatfield's stages were of <48-h duration, and this was considered too fine a resolution for our purposes.

#### RESULTS

### Water Temperature

Water temperature at the surface ranged from

<sup>&</sup>lt;sup>4</sup>Smith, P. R., and S. L. Richardson. 1977. Manual of methods for fisheries resource survey and appraisal. Part 4. Standard techniques for pelagic fish egg and larval surveys. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Adm. Rep. No. 77-11.

 $8.4^{\circ}$  to  $14.4^{\circ}$ C, and from 7.6° to  $8.8^{\circ}$ C at 50 m, during the period 17 April to 7 July (Table 1). Warmest surface temperatures were in May and July, and at 50 m, were warmest in June.

### **Species Occurrence**

Three species of crab larvae predominated in the plankton collected. The porcellanid crab, *Petrolisthes cinctipes*, predominated in waters within 8 km of shore, while *C. oregonensis* and *C. magister* dominated in more offshore waters. Other crab species were present but at much lower abundance than these three species. Megalopae of *C. oregonensis* were of comparable abundance to *C. magister* at most stations sampled.

### Surface Abundance

Presence of crab megalopae at the surface was dependent on time of day, with slight differences in timing of maximal abundance occurring between the two *Cancer* species (Fig. 3). At 9.3 km offshore in June, *C. oregonensis* was several orders of magnitude more abundant and also seemed to peak in abundance a little earlier in the evening and later in the morning than did *C. magister*. Relative abundance of both species declined in the middle of the night.

Data in Figure 3 was smoothed by eye (Fig. 4) to allow megalopal abundance data from the transect to be weighted by time of capture at night. Multiplier values were determined, and these were used to adjust actual abundance data by sampling time for the May and June sampling periods (Tables 2, 3). Only these data were weighted, and since day length changes with time of year, ad-

justment of data collected more than two weeks on either side of 14 and 15 June was considered inappropriate.

In hindsight, some data (indicated by asterisks in Tables 2, 3) was found to have been collected at a time when megalopae were just beginning to reach, or had just left, the surface. The calibration slope (Fig. 4) is very steep at both these times and it was impossible to estimate accurately a meaningful scaling multiplier for these data. Our estimated megalopal abundance at these stations should be viewed with particular caution; a zero value may not indicate that megalopae were absent, but only that they were not at the surface.

Bongo tows during the day poorly sampled the abundance of C. magister megalopae (Table 4) shown to be present by nighttime neuston tows (Tables 2, 3). This was possibly due to sampling the total column below only a few square meters of sea surface, because of integration of the results, or to avoiding the net by the megalopae. It was unlikely because of failure to sample deeply enough, since on the continental shelf, tow depth approached bottom depth. Megalopae (maximum per tow was 4) were primarily collected by bongo gear at stations where they were abundant in neuston samples at night, but relative abundance estimates obtained from bongo nets are considered only useful in a general qualitative sense because of the low absolute numbers caught.

## Temporal Occurrence (Time of Year)

No Cancer megalopae were found in samples collected shortly after dusk on 27 February-4 March. Cancer megalopae were first observed on the next

Distance offshore (km)	Depth (m)											
	April			May			June			July		
	0	20	50	0	20	50	0	20	50	0	20	50
0	8.8	8.8		12.2	9.2		12.2	11.4		_		
9	8.8	8.7		13.4	9.5		12.2	9.0		13.5	11.0	
19	8.7	8.1	7.9	13.4	8.6	7.6	12.3	10.4	8.0	14.0	9.0	7.6
28	8.8	8.8	8.2	13.1	9.6	7.9	12.8	12.3	8.0	13.3	10.0	7.7
37	8.6	8.6	8.3	13.8	9.3	7.9	12.7	9.4	8.3	13.3	10.7	7.7
56	8.7	8.7	8.2	13.3	9.8	8.2	12.9	10.5	8.1	14.4	13.3	8.6
74	8.7	8.6	8.2	11.8	10.0	8.2	12.9	12.0	8.7	14.4	13.3	8.6
93	8.5	8.5	8.2	11.9	10.3	8.2	12.8	12.2	8.5			
111	8.5	8.4	8.0	11.5	10.5	8.1	12.7	12.2	8.5	_		
130	_	_		—			12,7	12.4	8.6	_		
148	8.5	8.5	8.0	11.0	10.0	8.7		—	—		~	
185	8.4	8.6	8.4	11.4	10.0	8.4	_	_	_	_		

TABLE 1.—Water temperatures (°C) by depth (m) at the stations sampled off Tofino, B.C. on 17 April, 31 May, 14 June, and 6 and 7 July 1985.

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FIGURE 3.—Neustonic abundance of *Cancer magister* and *C. oregonensis* megalopae observed during sampling through one night at a station 9 km off the coast off Tofino, B.C.



FIGURE 4.—Smoothed abundance of Cancer magister and C. oregonensis megalopae observed during sampling through one night at a station 9 km off the coast off Tofino, B.C.

TABLE 2.—Scaling values used to standardize the actual number of megalopae caught (unscaled) to the estimated number which would have been caught at the times of peak nocturnal abundance, 22:40 and 23:40 hours, for *Cancer oregonensis* and *C. magister*, respectively, on 30 and 31 May 1985. \* = Value uncertain because of time of sampling. Values rounded to one decimal place.

Time	Dictores		C. magister (N 10 m <sup>-2</sup> )		C. oregonensis $(N \ 10 \ m^{-2})$			
	(km)	Multiplier	Unscaled	Scaled	Multiplier	Unscaled	Scaled	
18:12	0	00	2.3	?*	80	0	0*	
19:02	9	36.7	0.2	7.2*	00	4	?*	
19:43	19	26.8	0.0	1.1*	80	Ó	0*	
20:26	28	20.0	0	0	00	0	0*	
21:09	37	11.0	0.4	4.7	80	Ó	0*	
21:52	46	3.9	14.4	56.4	5.2	2.2	11.5	
22:35	56	1.6	29.9	47.0	1.0	0.1	0.1	
23:37	74	1.0	17.0	17.0	_	0	0	
00:47	93	3.3	36.0	119.9	24.8	1.0	25.7	
01:55	111	5.0	2.6	13.3	40.0	1.8	72.1	
03:56	148	110.0	1.1	118.4*	2.5	0.1	0.2	
05:57	185	00	0	0*	80	0	0*	

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sampling date, 16 and 17 April, but maximum abundance (unweighted as to diel time of sampling) occurred in late May and the second week of June (Fig. 5). *Cancer magister* megalopae were collected as late as 24 August, the last sampling date, but relative abundance along the transect was low after the beginning of July.

Cancer oregonensis megalopae were caught in April but occurred in abundance only in the late May and mid-June surveys, with peak abundance in June.



FIGURE 5.—Neustonic abundance of megalopae observed along the transect line during April to August 1985 surveys.

TABLE 3.—Scaling values used to standardize the actual number of megalopae caught (unscaled) to the estimated number which would have been caught at the times of peak nocturnal abundance, 22:40 and 23:40 hours, for *Cancer oregonensis* and *C. magister*, respectively, on 14 and 15 June 1985. \* = Value uncertain because of time of sampling. Values rounded to one decimal place.

Time	Distance		<i>C. magister</i> (N 10 m <sup>-2</sup> )		<i>C. oregonensis</i> (N 10 m <sup>-2</sup> )			
	(km)	Multiplier	Unscaled	Scaled	Multiplier	Unscaled	Scaled	
01:42	0	_	0	0	37.1	8.8	327	
00:58	9	3.6	0.1	0.4	27.4	170.5	4,671	
00:09	19	1.2	0.1	0.1	16.3	0.1	2.3	
23:19	28	1.0	0.2	0.2	2.7	7.6	20.5	
05:36	37	8	0.1	?*	00	0	0*	
03:52	56	55.0	52.2	2,871*	2.6	15.7	40.9	
02:02	74	5.2	3.7	19.2	40.0	4.8	192	
00:25	93	2.4	8.9	21.6	20.8	1.5	30.4	
22:45	111	1.2	8.4	10.3	1.0	12.5	12.5	
21:10	130	_	0	0	-	0	0	

TABLE 4.—Tow characteristics and number of *Cancer magister* megalopae (10 m<sup>-2</sup> of sea surface) caught by 0.25 m<sup>2</sup> bongo tows off Tofino, B.C., on 31 May and 14 June 1985.

Distance offshore (km)			м	ay		June					
	Time (h)	Water volume (m <sup>3</sup> )	Max. depth (m)	No. megalops	Megalopae (N 10 m <sup>-2</sup> )	Time (h)	Water volume (m <sup>3</sup> )	Max. depth (m)	No. megalops	Megalopae (N 10 m <sup>-2</sup> )	
0	19:27	210	33	1	1.6	08:00	240	36	3	4.5	
9	18:52	182	55	1	3.0	08:55	220	55	0	0	
19	18:16	114	72	0	0	09:51	222	75	0	0	
28	17:37	166	120	0	0	10:50	209	115	0	0	
37	16:55	199	151	0	0	11:47	284	146	1	5.1	
56	15:30	352	250	4	28.4	13:32	381	192	0	0	
74	14:07	327	250	1	7.6	15:21	338	200	1	5.9	
93	12:42	326	250	3	23.0	17:04	296	200	2	13.5	
111	11:17	360	250	1	6.9	18:56	269	200	0	0	
130	_					21:12	327	200	2	12.2	
148	08:55	400	250	0	0	_					
185	06:18	319	250	0	0	_					

### **Cross-Shelf Spatial Distribution**

With both species, no clear pattern in cross-shelf distribution was evident from the April data, perhaps because of relatively low overall megalopal abundance. In late May (Table 2), scaled abundance (weighted as to time of night) of *C. magister* was highest at 93 km offshore, but megalopae were generally abundant (>10 10 m<sup>-2</sup> sea surface) from 46 to 148 km offshore. In mid-June, the basic pattern observed in late May was still evident, although megalopal abundance near shore had declined (Table 3). Highest estimated *C. magister* abundance was at 56 km offshore.

With C. oregonensis, scaled abundance in late May peaked (>20 10 m<sup>-2</sup>) 93-111 km offshore (Table 2). An exceptionally large number of megalopae (4,671 10 m<sup>-2</sup>) was found 9 km offshore in June (Table 3), while from 56 to 111 km offshore, abundance remained high (>20 10 m<sup>-2</sup>).

Sampling of inlet waters around Tofino with neuston gear showed that a few *Cancer* megalopae were present but that no substantial (average was <1 10 m<sup>-2</sup>) numbers occurred. Maximum *C. magister* megalopal abundance was 2.9 megalopae 10 m<sup>-2</sup> on 5 June, with megalopae observed only between 29 May and 19 June. Maximum *C. oregonensis* abundance was 2.3 megalopae 10 m<sup>-2</sup> on June 19, with megalopae observed only between 4 and 19 June.

#### **Intermolt Stage**

All C. magister megalopae collected in April were of early developmental stage (Fig. 6), whereas all those collected in August were mid-stage megalopae. In May, June, and July, the general pattern of offshore distribution by molt stage was for late stage larvae to be nearest inshore and early stage larvae to be furthest offshore.

Cancer oregonensis megalopae had a similar developmental distribution pattern to those of C. magister (Fig. 7); late molt megalopae were most abundant closest to shore. However, in late May, most megalopae were early stage, in contrast to C. magister, whereas by mid-June, all three intermolt groups were present.

When the scaled megalopal abundance at distance offshore (Tables 2, 3) is multiplied by the percentage at each molt stage at a specific location (Figures 6, 7, for each species, respectively), the actual abundance by molt group with distance offshore is determined (Figures 8, 9, respectively). In late May, late stage C. magister megalopae were relatively abundant 9 km offshore, indicating that some Dungeness crab settlement may have occurred. However, larval sampling in the inlets and bays showed few megalopae present. In contrast to previous years, no recently settled juvenile crabs (0 age-class crabs) were found by local fishermen in intertidal areas or on floating objects, confirming that the magnitude of megalopal settlement in 1985 was relatively small. In mid-June, there were few C. magister megalopae of any intermolt stage present within 40 km of the coast and little evidence of late stage megalopae offshore. Early and mid-stage megalopae were most abundant from 56 to 111 km offshore.

For C. oregonensis, the opposite was observed (Fig. 9). Few late stage megalopae were present in late May, and unlike C. magister, megalopae were not concentrated in nearshore waters. However, megalopae in all three intermolt stages were abundant inshore in mid-June, with late stage megalopae dominating at the coast. The timing of occurrence



FIGURE 6.—Percentage of the three *Cancer* magister megalopal intermolt groups observed at each station during the April to August 1985 surveys.

of late stage megalopae at the coast thus differed between the two species.

### **Inshore Benthic Sampling**

Survey of commercial crab habitat with beam trawls and an epibenthic sled yielded few newly settled megalopae or juvenile C. magister (Table 5). A maximum of 83 crab/10,000 m<sup>2</sup> was collected, well below densities which might be expected if settlement had been substantial. No C. oregonensis were caught, perhaps because of the habitat being sampled, and no larval settlement of either species was observed when intertidal mud flat areas were searched by foot. In a concurrent study, no signifi-

cant abundance of 0 age-class C. magister was observed during monthly sampling throughout the remainder of the year.

### DISCUSSION

#### Megalopal Source

Temporal duration of *C. magister* larval stages has been estimated both by laboratory rearing (Poole 1966; Reed 1969; Brugman 1972; Gaumer 1973; Ebert et al. 1983) and the first appearances of larval stages in field studies (Poole 1966; Lough 1976; Reilly 1983). The length of the total larval period has been estimated as 105–125 days by Reilly (1983),



FIGURE 7.—Percentage of the three Cancer oregonensis megalopal intermolt groups observed at each station during the May to July 1985 surveys.

	Depth (m)	Gear type	Area swept (m <sup>2</sup> )	Catch	of crabs	<u>No. 10<sup>4</sup> m<sup>-2</sup></u>		
Area				Juveniles	Megalops	Juveniles	Megalops	
Templar Channel	7	trawi sled	2,650 375	5 0	0 0	26 0	0	
Chesterman Beach	5	trawi sled	300	- 0	0	0		
Cox Bay	8 7	trawi sled	2,500 400	1 3	0 0	4 75	0 0	
	13 15	trawi sled	2,600 420	7 2	0 0	27 48	0 0	
	30 23	trawi sled	2,260 360	0	0 3	0	0 83	
Lennard island	25	trawi sled	350	0	0	0	0	
Long Beach	. 7	trawi sled	2,700 400	5 2	0	18 50	0 0	
	13	trawi sled	2,650 400	6 2	1 1	23 50	4 25	
	23	trawi sled	220	0	1	0	 45	

TABLE 5.—Beam trawl and epibenthic sled catches from nearshore waters around Tofino, 16--18 June 1985.



FIGURE 8.—Scaled abundance of *Cancer magister* megalopae by intermolt group observed at each station during the May and June 1985 surveys. \* = Value uncertain because of time of sampling.



FIGURE 9.—Scaled abundance of *C. oregonensis* megalopae by intermolt group observed at each station during the May and June 1985 surveys. \* = Value uncertain because of time of sampling.

130 days (range: 89-143) by Lough (1976), 45 and 108 days at 17.8° and 10.0°C, respectively, by Reed (1969), and 128-158 days under natural conditions by Poole (1966). In laboratory studies, Poole (1966) found the total time required was 111 days at 10.5°C. Since water temperatures typically range from about 8° to 13°C off the British Columbia-California coast during January-February (Thomson 1981), the total larval period in the study area is assumed to be about 110 days.

Off Vancouver Island, megalopae can be collected in abundance in open coast waters from mid-April to August. Ovigerous Dungeness crab, collected at Tofino and held in ambient temperature seawater at Nanaimo, hatched their eggs from January to March, with most hatching occurring in February (G. Jamieson, unpub. data). This suggests that megalopae collected between April and June could be from local populations whereas most megalopae collected in July and August may have largely originated elsewhere.

Lough (1975) stated that the hatching period of *C. oregonensis* off Oregon extends from January to July, with two broods indicated, one primarily hatching in February and the other in May-June. He estimated larval duration of a brood at 155 days (range: 123-203 days) from field sampling, but there was possible intermixing of the larvae from different broods, as well as population variability in the timing of hatching. We have no data on the hatching period of this species in British Columbia.

Given the currents off the west coast of Vancouver Island, then, *Cancer* larvae present there in the spring could theoretically have originated anywhere between northern California to perhaps southern Alaska. It seems very unlikely that the larvae are entirely the progeny of adult crabs on the west coast of Vancouver Island.

### **Onshore Movement**

Geographical location of larval settlement is very dependent on currents. Adult *Cancer* of both species are largely found in nearshore, shallow-water habitats (Hart 1982), and such environments are apparently both the origin and preferred destination of larval crabs (Butler 1956). Along the open coast, Dungeness crab larvae are known to settle in both estuarine and nearshore areas (Wild and Tasto 1983; Stevens and Armstrong 1984; Armstrong and Gunderson 1985). In waters largely surrounded by land, such as Puget Sound, Georgia and Queen Charlotte Straits, and, to a lesser extent, Hecate Strait, Dixon Entrance, and southeastern Alaska, larval crabs may perhaps remain nearshore throughout their entire developmental period. However, studies suggest that while larvae may be hatched nearshore along the outer coast, they subsequently move offshore and then inshore (Lough 1976; Reilly 1983). The extent to which this may occur can profoundly affect the degree of dispersal of a local region's progeny.

Evidence for an offshore-onshore movement of C. *magister* during the larval development period is ambiguous. In the field, three studies of the offshore spatial pattern of larval distribution have been undertaken: off central and northern California (Reilly 1983), off Newport, Oregon (Lough 1976), and off Tofino, British Columbia (this study). The California study extended to about 185 km from shore from San Francisco north to Cape Mendocino, with some earlier CALCOFI data (1949-75) extending to about 275 km offshore included. Sampling consisted of discrete-depth and oblique plankton tows and was mostly during the day. The sampling gear (0.5 m diameter opening) most often used was preceded by the towing cable and bridle (P. Reilly<sup>5</sup>), and gear avoidence by same megalopae may have occurred. Because of the gear and protocol used, it is difficult to interpret Reilly's (1983) results in a quantitative sense. However, offshore movement of larvae during zoeal stages II-V was indicated, as was the later presence of megalopae in nearshore waters following a period when stage V zoeae were generally absent from within 40 km of shore, but a mechanism to explain the onshore transport of megalopae was not established. As part of the overall study (Wild and Tasto 1983), Hatfield (1983) determined the intermolt stage of many larvae collected by Reilly (1983). Earlier stage megalopae were in general collected further offshore, earlier in the year, and at a lower latitude.

The Oregon study (Lough 1976) was on one trackline extending 110 km offshore off Newport, with mostly daytime, oblique bongo samples collected at specified stations. Although early stage zoeae of both species were abundant nearshore, late stage zoeae were not, and were largely collected at the offshore stations. Lough (1975) noted that *C. oregonensis* megalopae were found further offshore and later during the summer upwelling season than were *C. magister* megalopae. In 1970, large numbers of *C. magister* megalopae, which were not intermolt staged, were found inshore. In 1971, virtually no *C. magister* larvae older than stage III were collected

<sup>&</sup>lt;sup>5</sup>P. Reilly, California Department of Fish and Game, Menlo Park, CA 94025, pers. commun. February 1988.

at any of the stations, and Lough suggested that a mass mortality of C. magister larvae might have occurred. In contrast, C. oregonensis larvae were in greater abundance during 1971 than 1970.

Results from the current study and Booth et al. (1985) suggest that the sampling gear and procedures used by Reilly (1983) and Lough (1976) gave poor abundance estimates of megalopae. The number of megalopae caught during daylight is relatively low, and the presence or absence of only a few megalopae can greatly influence the estimated megalopal density per unit of sea surface. This sensitivity to bias can only be compensated for by many replicate samplings, and it is logistically easier to estimate absolute megalopal abundance by sampling at night when megalopae are concentrated in a relatively easily sampled, narrow depth range, namely the neuston (Booth et al. 1985). Reilly (1983) sampled once both day and night at 12 stations, and noted no significant differences in megalopal density between day and night at the surface and in oblique tows. However, his surface tows were not neuston tows, and consisted of a 0.5 m diameter net towed about 0.25-0.5 m below the water surface. or below the wave troughs if the surface was rough (P. Reilly fn. 5). This qualifies his observations, and may explain the suggested low abundance of megalopae in his study area (maximum density was 43  $100 \text{ m}^{-3}$  at the surface).

On occasion, megalopae have been observed to be in association with *Velella velella* at the surface during daylight (Wickham 1979; Reilly 1983; G. Jamieson unpub. data), but we have generally observed relatively few megalopae in surface waters during the day in comparison to the number observed present at night. Accepting that relative megalopal abundance is best determined at night from neuston tows, megalopae off British Columbia were shown to be abundant in specific areas offshore and at these locations, early and mid-stage megalopae predominated.

All three studies indicate that 1) later stage C. magister larvae are found offshore and, since they are hatched at inshore locations, some mechanism must be transporting them away from shore, 2) megalopae are found inshore, with Hatfield (1983) and this study showing that earlier stage megalopae predominate furthest offshore, and 3) while longshore drift of larvae may occur, it is difficult to establish its significance in the absence of simultaneous current and larval distribution data, both geographically and vertically in the water column. None of these studies demonstrates conclusively that larvae which ultimately settle inshore were ever

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very far offshore, and while it is shown that larvae can be carried offshore in abundance, this may well represent larval wastage, in that relatively few of them, if any, may ultimately return inshore to survive at settlement. The same is assumed to apply for *C. oregonensis*.

The California data on larval distribution, which is the most extensive spatially, are somewhat ambigious in that they may be interpreted either as onshore-offshore-onshore movement, or as a general offshore dispersal coupled with northwards-southwards drift of those larvae remaining inshore. To account for an absence of middle stage larvae in the nearshore waters of Reilly's (1983) study area, the latter scenario assumes that larval crab production south of the Gulf of the Farallones is relatively low. and that the water mass entering the sample area from the south as part of the Davidson Current contains few larvae. Little data appear to exist to refute this possibility; the commercial fishery for Dungeness crab only exists at a few locations south of San Francisco, and then only sporadically (Warner 1985). Our data and Lough's (1976) data are inadequate to investigate longshore drift because biological samples in each study were only collected along one offshore transect and no data on currents was simultaneously obtained.

Off the west coast of Vancouver Island, we found that megalopae may be concentrated in areas between surface currents flowing in opposite directions, specifically in the shear between the Vancouver Island Coastal Current and the outer Shelf-Break Current. Megalopae were abundant 40-70 km from shore, with C. magister megalopae particularly concentrated about 50 km from shore. In 1985, there was no major crab settlement observed on the outer coast near Tofino, suggesting that the Coastal Current may sometimes be an effective barrier to onshore movement and successful settlement. Understanding the horizontal and vertical distributions of crab larvae in the water column now seems essential if transport mechanisms of larvae and their movement from hatching to settlement are to be understood.

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