SOME ASPECTS OF THE ECOLOGY AND BIOLOGY OF TWO CANCER SPECIES

I. CANCER MAGISTER: A REVIEW OF ITS ECOLOGY AND EXPLOITATION

II. CANCER PRODUCTUS: SALINITY EFFECTS UPON DISTRIBUTION AND ABUNDANCE IN COOS BAY, OREGON

by

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A Critical Essay Presented to the
FACULTY OF THE BIOLOGY DEPARTMENT
UNIVERSITY OF OREGON
In Partial Fulfillment of the
Requirements for the Degree
MASTER OF SCIENCE
(Biology)

December 1980

I. CANCER MAGISTER: A REVIEW OF ITS ECOLOGY AND EXPLOITATION

INTRODUCTION

As a commercially exploited species the Dungeness Crab, Cancer magister, has generated a fairly large, unconsolidated body of literature. Initial research undertaken in British Columbia, Washington, Oregon and California dealt with general biology and the fishery, with the goal of determining the adequacy of fishery regulations. At that time no danger of overfishing was thought to exist, although fishery effort was intensifying (Cleaver 1949). A number of authors also noted a coastwide cycling in abundance of crab landings. However, after the 1960-1961 season the central California fishery did not recover from low levels of abundance associated with a cyclic minimum. Concern for this fishery prompted a new wave of investigations of population dynamics, making use of recent ecological theory, computer analysis and modeling techniques. The possibility that the fishery could alter natural population cycles, resulting in drastically lowered population levels throughout the species' range, was suggested. The purpose of this paper is critically to review the ecology and exploitation of C. magister using the information gathered throughout the last 60 years.

Cancer productus, a congener often found in close proximity to C. magister, is considered in the final section of this paper, as the potential for competition with C. magister exists and very little published information concerning C. productus is available.

The results of a study of annual intertidal/subtidal distribution and abundance of C. productus in Coos Bay, Oregon are presented.

DISTRIBUTION

Cancer magister (Dana 1852) is a decapod crustacean of the suborder Reptantia, section Brachyura and family Cancridae. Common names include the edible crab, market crab and Dungeness crab. The most common and distinct name, Dungeness crab, is derived from a village on the Juan de Fuca Strait, Washington. The twenty species of the genus Cancer are limited in distribution by the 23.9°C and 4.4°C surface water isotherms (MacKay 1943). C. magister ranges along the Pacific coast of North America from Unalaska, Alaska to Magdalena Bay, Baja California (Schmitt 1921), occurring in greatest abundances between southeastern Alaska and San Francisco, California (Cleaver 1949).

Adult Dungeness crabs typically inhabit areas of sand or sandy-mud bottom within bays and estuaries as well as in the open ocean and may be found from mean low water to at least 91m. Although C. magister is occasionally found on rock or gravel substrates in offshore areas, similar habitats in more protected areas (bays, estuaries and protected outer coast) are typically dominated by Cancer productus, the red rock crab (MacKay 1942, Cleaver 1949, Waldron 1958).

LIFE HISTORY

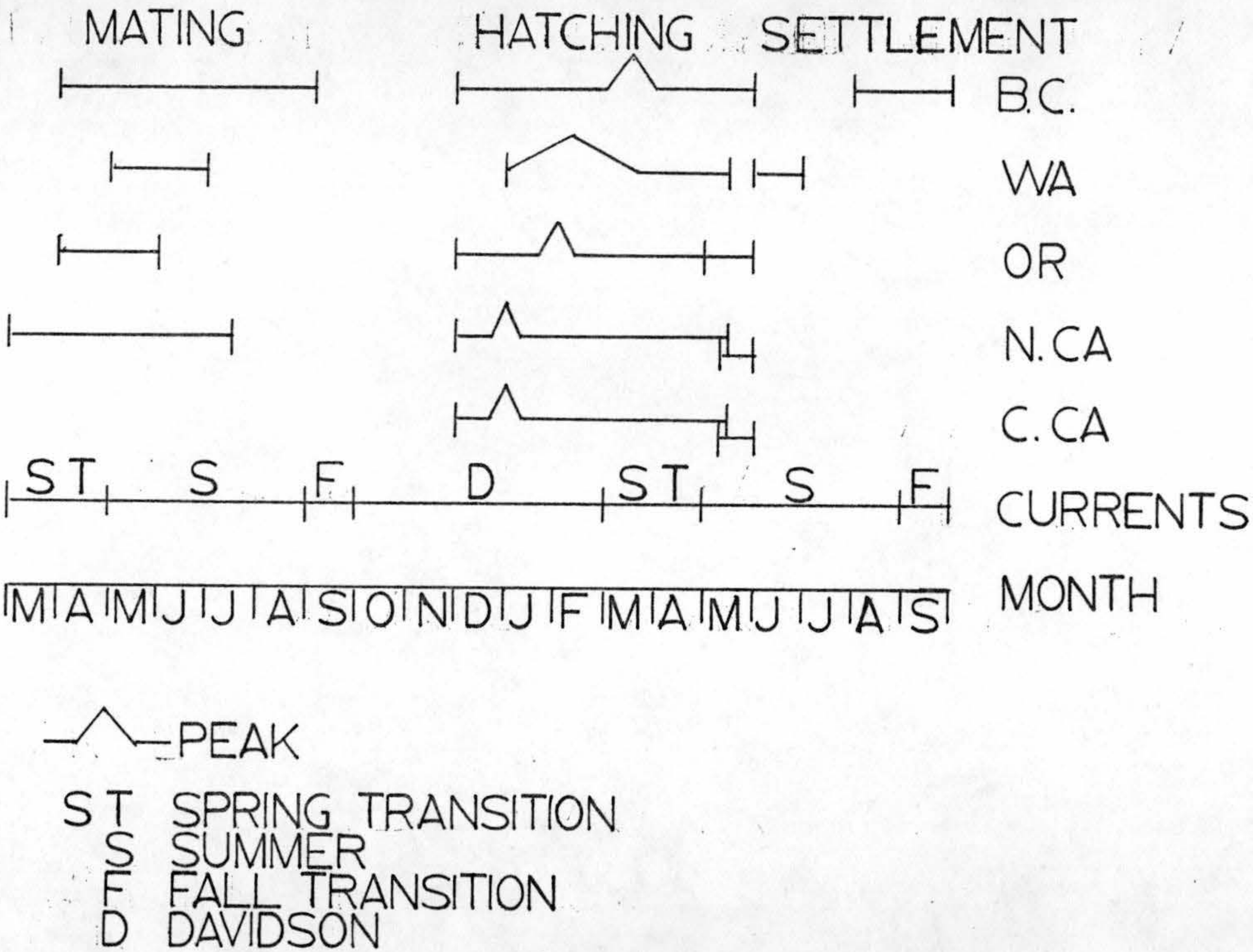
Mating and Ovigery

Mating of Cancer magister has been described by Spencer (1932), Butler (1960) and most thoroughly by Snow and Neilsen (1966). Introduction of a premolt female to a male usually elicits an immediate active response in the male: the male approaches, body held high, walking on the extreme tips of the walking legs. Hartnoll (1969) believes that the response is due to a sex-attractant pheromone released by the mature, premolt female. Ryan (1966) found evidence for such a pheromone in the urine of Portunus sanguinolentus (Brachyura, Portunidae); Hartnoll (1969) places the Cancridae and Portunidae into a similar courtship-and-mating group in a review of Brachyuran mating. Sex pheromones have been identified in Carcinus maenas, Micropipus holsatus, Pachygrapsus crassipes and Paratelphusa hypromus (Hartnoll and Smith 1979). Knudsen (1964) feels that a pheromone sex-attractant is present in Cancer productus but has no experimental data to support this contention. Hartnoll and Smith (1979), however, have found no evidence of such a male-stimulating hormone in the urine of courted premolt Cancer pagurus females. As molting and subsequent mating of C. magister occur on the edges of tideflats (Spencer 1932; MacKay 1937, 1942), the initial spatial contact may be behaviorally rather than pheromonally prescribed. Final recognition may depend upon tactile stimuli and passive or responsive behavior by the receptive female (Hartnoll 1969). Once a male has found a mature, receptive female the courtship and mating behavior follow. A premating embrace, in which the male "cages" the female with his walking legs and strokes her carapace with his chelipeds, lasts approximately seven days. The opening of the female's epimeral line, signalling the onset of exdysis, elicits a new, more aggressive behavioral pattern in the pair. The female then molts and the molted carapace is shoved away by the male. After a little more than an hour, presumably to allow the female's carapace to harden slightly, copulation occurs; the hardshell male inserts his gonopods into the spermathecae of the female, depositing spermatophores. Fasten (1918) believes spermatophores remain intact within the spermathecae. However, Butler (1960) found only free spermatozoa in the spermathecae. The sperm remain viable within the spermathecae until the ova mature (MacKay 1942, Butler 1960). Wild et al. (1978) observed four females which had participated in a spawning experiment to set sponges (egg masses) again after having done so once. None of these crabs had mated since setting first sponges. These findings demonstrate that at least two broods of eggs can result from a single mating episode. Further observations suggest that sperm present in the female at the time of ecdysis are retained and remain viable between molts as two of the aforementioned crabs molted after hatching larvae and oviposited new clutches of eggs. Transmolt retention of sperm followed by successful rearing of another brood has been demonstrated in Menippe and Portunus; retained sperm remains viable for more than a year in Callinectes and is utilized for repeated spawnings (Allen 1972).

The premating embrace of the male offers the female protection from predation as she undergoes and recovers from ecdysis and ensures both male and female an opportunity to mate (Hartnoll 1969). Spatial relationships of the crabs on the tideflats may necessitate such a ritual; a male remaining in the premating embrace with one female for up to ten days in a situation where more than one mature premolt female is available would have a lower Darwinian fitness than a male which fertilized as many females as possible; i.e., there would be many fewer progeny carrying the monogamist's genes. Because polygamy is believed to occur and has been observed in laboratory aquaria (Cleaver 1949, Butler 1960, Poole and Gotshall 1965), the mating scenario of C. magister suggests that the crabs are distributed sparsely on the tideflats. Once a pair forms it is to the male's advantage to maintain the premating embrace, to allow the female to molt and fertilize her before moving on in search of others. It also follows that spatial distributions of this type may implicate a pheromonal mechanism for the location and initiation of protection of a premolt female.

As mentioned above, mating occurs on the edges of tideflats where the paired crabs become partly or completely buried in mud and/or covered by algae or eelgrass (Zostera sp.) (Spencer 1932; MacKay 1937, 1942). Breeding pairs have been found in northern California from March through mid-July (Poole and Gotshall 1965), April in Coos Bay, Oregon (personal observation), primarily May and June in Washington coastal waters (Cleaver 1949) and from

FIGURE 1. TEMPORAL SEQUENCES OF NEAR-SHORE CURRENTS AND CANCER MAGISTER LIFE HISTORY PHENOMENA.


MATING
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CURRENTS
MONTH
M A M J J A S O N D J F M A M J J A S
PEAK
ST SPRING TRANSITION
S SUMMER
F FALL TRANSITION
D DAVIDSON

April through mid-September in various locations in British Columbia (Queen Charlotte Islands, Boundary Bay, Clayquot Sound) (Figure 1) (Spencer 1932; MacKay 1937, 1942; Butler 1956).

After mating and fertilization, the ova are extruded and attach to the pleopods on the abdominal flap. Brood size of mature females is estimated by the equation # eggs ($x\ 10^6$) = 0.29 carapace width (mm) + 2.45 (Mayer 1973). Oviposition must occur on a sand substratum in order to allow the formation of a burrow to hold the eggs until they have cemented to the abdominal setae. Substantial reductions in clutch size (estimated up to 50%) occur if oviposition occurs on a solid substrate (Wickham 1979b). The extruded eggs are bright orange and become progressively darker, as the yolk is consumed. At hatching they are dark brown or nearly black (Cleaver 1949, Waldron 1958).

The ovigerous period, i.e., the period when females are carrying developing eggs, has been reported as quite variable. In California, crabs set sponges from mid-September to late October in the laboratory. Spawning appears to coincide with or follow a gradual rise in seawater temperature (Orcutt et al. 1976, Wild and Haugen 1977, Wild et al. 1978). Waldron (1958) reports ovigerous females in the offshore waters of Oregon through March. Cleaver (1949) found females with eggs from November through February in Washington. In British Columbia, MacKay (1937, 1942) reports October through June in Boundary Bay, Spencer (1932) reports July through January or February in Clayquot Sound and Butler (1956) reports late September/early October until late

April in the Queen Charlotte Islands region.

Larvae

The time of larval hatching, like the ovigerous period, is reported to be quite variable. The difficulties in being absolute in such matters no doubt lie in environmental variables, e.g., temperature and salinity, which can drastically affect spawning and development (Reed 1969, Orcutt et al. 1976, Wild and Haugen 1977, Wild et al. 1978). Complicating this problem further is the detection of the planktonic larvae which may be patchy in horizontal, vertical and temporal distribution; e.g., a several week difference in the peak hatching period between two successive years in California was found (Tasto et al. 1977). Temperature effects upon development time have been experimentally demonstrated: 65 days after spawning at 17°C, 83 days after spawning at 11-15°C and 120-128 days after spawning at 10°C (Wild and Haugen 1977, Wild et al. 1978). In general, hatching occurs from December through mid-May with the peak in late December and early January in California (Tasto et al. 1977, Tasto and Reilly 1978, Tasto et al. 1979). Reed (1969) reports hatching in Oregon from December through April and Lough (1976) notes that the larvae appear in the plankton off the central Oregon coast in late January/early February. In Washington Cleaver (1949) reports the bulk of larval hatching as occurring from January through March and Mayer (1973) cites mid-February through mid-May. In British Columbia MacKay (1937, 1942) cites December through early June with the maximum in March, Spencer (1932) reports December through February and Butler (1956) quotes late April (Figure 1).

The larvae hatch as short-duration (11-60 minutes) proto- or prezoeae (MacKay 1937, 1942; Buchanan and Milleman 1969). This stage is followed by five zoeal instars. Mir (1961) describes the external morphology of the first three zoeal instars and Poole (1966) describes all five. The final larval instar is the megalops (MacKay 1942, Poole 1966, Reed 1969). Poole (1966) raised all instars in the laboratory in 111 days at 10.6°C and calculated the estimated developmental time under natural oceanic conditions in California to be 128-158 days.

Recent studies of larval distribution and abundance in Oregon and California (Orcutt et al. 1975, Lough 1975, Orcutt et al. 1976, Lough 1976, Tasto et al. 1977, Tasto and Reilly 1978, Tasto et al. 1979) suggest a possible spatial and temporal developmental scheme. Peak larval hatching occurs during late December and January within 5-16km of the California and Oregon coasts; development proceeds while the planktonic zoeae drift offshore. Offshore movement probably continues into late March or early April at which time either the stage V zoeae or megalopae, or both, reverse direction and move towards shore. It is most probable that movement onshore is accomplished by the megalopae as they have improved locomotory capabilities in comparison to those possessed by zoeae (MacKay 1942). The extent of movement offshore may be both considerable and variable. Lough (1976) found scattered occurrences of zoeal stages III-V and megalopae to 95km offshore. Tasto et al. (1979) found stages III-V to 185km in late March with peak occurrences to 100km. However, greater numbers of stage V zoeae close to metamorphosis were found from 101-185km, suggesting potential maximum drift to that extent. Analysis of 1950 CalCOFI plankton tows from transects off San Francisco (Tasto et al. 1977, Tasto and Reilly 1978) revealed stage III and IV zoeae at 177km in February and stage V zoeae to 247km in March. However, there is no evidence indicating that larvae drifting this far offshore are able to make the return to inshore settling areas. Nonetheless, it can be concluded that substantial offshore zoeal drift occurs during development. It can be conjectured that the offshore movement transports the larvae into an environment that is more stable than that of near shore and that an offshore dispersion limit is imposed upon the larvae past which unfavorable current transport and/or physical inability to make the inshore return occurs. Response surface analysis of temperature and salinity interaction effects upon C. magister larvae indicates that salinity exerts an immediate effect on survival while temperature effects become increasingly important with time (Reed 1969; Lough 1975, 1976). Offshore drift may circumvent potential low salinity and variable temperature stresses brought about by freshwater runoff occurring near shore during the winter and spring months. During April megalopae are moving towards inshore settling habitats and by late April are found within 1km of shore. The movement of megalopae into the nearshore area is accomplished in part by active locomotion of the megalopae (MacKay 1942) along with congregation by prevailing currents within approximately 8km of the coast (Lough 1976). Aid from the hydroid *Velella velella* is also possible (Tasto et al. 1977, Wickham 1979a). Due to annual variability of southerly and westerly wind, *V. velella* does not occur in the nearshore waters with absolute annual regularity (Ricketts et al. 1968) and densities of *V. velella* required for large scale megalopal movements are not known. Therefore, the use of *V. velella* for inshore transport is probably not a reliable phenomenon for larvae, but could be considered an opportunist behavior. Nevertheless, active, healthy *C. magister* megalopae have been found among the tentacles of *V. velella* feeding upon the hydroids (Tasto et al. 1977, Tasto et al. 1979, Wickham 1979a). It is concluded that *V. velella* could be providing a food source and shelter from predatory planktivores as well as some inshore transport.

The observed offshore-directed movements of *C. magister* are most likely attributable to interaction of vertical position in the water column with nearshore oceanographic events. Chuck Jacoby (personal communication) has experimental evidence indicating that all larval instars behave in a similar manner in the water column, responses being photo- and barotactic. Stage I zoeae reside at approximately 25-40m and stages II-V at approximately 25m during the day; the different zoeal instars migrate to various levels above 25m at night. Zoeal stages I, II and III have been found at 15-25m during the day and near the surface at night in the nearshore waters of California and Oregon (Holton and Elliot 1973, Tasto et al. 1978, Tasto et al. 1979). Tasto et al. (1979) have field data indicating similar behavior of zoeal stages IV and V. Megalopae exhibit like behavior (Chuck Jacoby, personal communication), but appear to become strongly photopositive at some point before metamorphosis and settlement as indicated by observations of daylight swarms of megalopae near shore (MacKay 1942, Cleaver 1949, Lough 1976) and response to night-lighting (Tasto et al. 1979).

The winter Davidson current, spring transition currents and summer currents are encountered near shore by newly hatched and developing larvae (Figure 1). The Davidson develops in the fall and runs in a northward direction along the coast to at least 48-50°N latitude and possibly as far north as 60°N latitude. It is characterized by relatively high and uniform temperature (approximately 10.8-11.4°C) and homogeneity to 25-50m. Intensifying spring northwesterly winds cause, at least in part, the spring transition currents of March and April which are variable in directional flow. By May the summer currents flow steadily southward (Sverdrup et al. 1946, Wyatt et al. 1972).

Peak larval hatching (Figure 1) from central California to Washington occurs during the period of the late Davidson current. Stage I zoeae hatched 5-16km offshore probably avoid onshore transport due to shoreward surface drift within 8km of shore that is associated with the Davidson (Wyatt et al. 1972). By residing at a depth of 25-40m during the day, stage I larvae may minimize northward current transport, thereby facilitating offshore movement by active swimming. The spring transition currents period (March-April) coincides with the period of maximal offshore drift by stage III zoeae (Tasto et al. 1979). The variable currents may minimize alongshore transport in either direction and the larvae positioned at a depth of 25m during the day could encounter low current velocities and direct themselves offshore. The possibility of Ekman spiral effects at 25m creating offshore-directed current motion is conceivable but lacks evidence. Reversal of offshore movement and commencement of inshore travel during late April coincide with megalopal surface swarming and the period of *Velella velella* abundance. This would indicate importance of the intensifying northwesterlies; wind generated surface currents coupled with relatively strong megalopal swimming abilities and *Velella* transport may provide the rather rapid movement back to inshore settling areas.

Juveniles

Subsequent to moving inshore the megalopae undergo metamorphosis to the first postlarval instar and settle to the bottom along channel banks of bays and inlets, probably as a result of being directed there by prevailing bottom currents. They then move from channel areas and concentrate in shallow areas (approximately 10m) of mudflats and sandy bottoms associated with eelgrass (*Zostera* sp.) or masses of detached kelp and other algae (Butler 1956, Orcutt et al. 1975, Tasto et al. 1977). In central California Tasto et al. (1977) estimate that up to 80% of a year class will spend its juvenile growth period, about a year, in the San Francisco Bay complex. Therefore, the eelgrass areas of the bays and inlets settled by the postlarval crabs may be considered nursery grounds (Poole and Gotshall 1965, Tasto et al. 1977), much as surfgrass (Phyllospadix sp.) habitats are for juvenile spiny lobsters (Panulirus interruptus) (Engle 1979). After spending a year or more in the nursery ground the majority of the young C. magister move into the deeper adult habitats, as evidenced by the central California population's movement from the San Francisco Bay into the Gulf of the Farallones (Tasto et al. 1977) and northern Californian crab movement out of Humboldt Bay (Poole and Gotshall 1965). However, there are segments of crab populations which appear to remain bay residents (Mayer 1973).

The first juvenile instars appear in August and September in the Queen Charlotte Islands region (Butler 1956) and August around Boundary Bay (MacKay 1942), both in British Columbia. Juveniles settle in late May and June in Washington (Cleaver 1949), May in Oregon (Waldron 1958) and May in California (Orcutt et al. 1975, Tasto et al. 1977, Tasto and Reilly 1978, Tasto et al. 1979).

The Cancer magister early life history can be summarized as follows. Mating occurs during the spring and early summer months. It appears possible that pair formation is accomplished via a sex attractant pheromone produced by the female. Once paired the male and female remain together in a premating embrace for up to a week. Copulation occurs on tideflats between a newly molted, softshell female and a hardshell male. Oviposition is accomplished on a sand substrate where the eggs are cemented to the abdominal setae. The eggs develop on the female's abdomen until the larvae begin hatching around December. A developmental period of four to five months is spent in the plankton of nearshore waters; developmental stages include a protozoea, five zoeae and a megalops. Development to zoeal stage V occurs as the larvae drift offshore. Around the time of attaining the megalopal stage a relatively rapid return movement towards inshore settling habitats begins. Once in the nearshore area the megalopae undergo metamorphosis to the first postlarval instar, settle to the bottom and concentrate in shallow "nursery" areas associated with eelgrass and algae. After a year or more the majority of the young crabs move to deeper adult habitats.

MOLTING AND GROWTH

Decapod growth requires periodic shedding of the calcareous exoskeleton, i.e., molting or ecdysis, resulting in incremental rather than continuous growth. The molt cycle, however, is virtually continuous with as much as 90% or more of an intermolt period involved with postmolt and premolt processes (Barnes 1974).

The onset of proecdysis is favored by darkness, moderate temperatures and solitude (Allen 1972); at the time of ecdysis, the most critical phase of the cycle, the animal is most susceptible to unfavorable environmental factors (e.g., salinity, temperature and oxygen concentration changes) and predators (Engle 1979). During ecdysis the body swells from the uptake of water and the soft crab emerges from the old exoskeleton. Following ecdysis the new exoskeleton calcifies and hardens. Immediately upon emergence C. magister individuals 85-160mm have obtained approximately 55-70% of the final postmolt size; the remaining increase occurs within approximately three hours via further water uptake. The absorbed water is subsequently replaced with new tissue over a period of approximately two months (Cleaver 1949, Waldron 1958, Barnes 1974).

Molting frequency is regulated by tissue growth via a molt-inhibiting hormone which is secreted until a minimum of tissue growth occurs. A molt can be delayed under dangerous or unfavorable conditions or accelerated under demanding conditions (e.g., loss of many pereiopods). Molting frequency is also temperature dependent due to direct effects on the metabolic rate. It is therefore possible to have gross variability and lack of homogeneity in size between individuals of the same age, as has been demonstrated in *Carcinus* (Adelung 1971, Allen 1972).

Numerous growth studies have been carried out using carapace width frequencies, mark and recapture methods, lab cultures and field molts (MacKay and Weymouth 1935; MacKay 1942; Cleaver 1949; Waldron 1958; Butler 1960, 1961; Orcutt et al. 1975). Many of these studies rely primarily upon laboratory reared animals for data. It has been found that a laboratory environment usually results in unnatural growth patterns and consequently unrealistic conclusions as to the extent of growth and the growth rate (Butler 1961, Orcutt et al. 1975). Therefore, those growth studies with field derived data will be emphasized in this discussion.

Postlarval instar sizes have been estimated by plotting postmolt carapace width versus premolt carapace width [measurements exclude the 10th anterolateral spines; I have corrected any data including the 10th anterolateral spines using the conversion $y = 0.9333x + 0.0271$ where x = carapace width (mm) including spines and y = carapace width excluding spines (Weymouth and MacKay 1936). Standard carapace width measurements are made excluding the spines.] and fitting lines by linear regression. Estimated postlarval instar sizes derived from regression equations for California, Washington and British Columbia are given in Table 1.

Regressions for juvenile males and females, adult males and adult females differ in their respective slopes, indicating differences in growth pattern associated with age and sex (Figure 2, Table 2) (Cleaver 1949, Butler 1961, Orcutt et al. 1975). Growth increments of instars of both sexes have been found to be comparable (slope = 1.22-1.23) up to the onset of sexual maturity (Butler 1961). Growth slows following the molt in which sexual maturity is attained (slope = 1.04-1.07 for males, 0.864-0.892 for females) and is thought to be a consequence of changes in energy allocation associated with gonad production. Females probably experience a greater decline in growth as a result of greater physiological demands for egg production as compared to that required for sperm production. Decreased percentage growth increments following the attainment of maturity offer further related evidence of the growth pattern (Figure 3) (Cleaver 1949, Butler 1961). Intersects of juvenile and adult regressions estimate the size at which sexual maturity is attained; estimated values for males range from 94.4-107.6mm premolt size (116.5-132.6mm postmolt size) and 82.5-83.4mm premolt size (102.0-103.9mm) postmolt size) for females (Table 2) (Butler 1961, Orcutt et al. 1975). Examinations of gonadal development have shown no male smaller than 93-122mm postmolt size (75.4-97.4mm premolt size) and no female smaller than 100mm postmolt size (80.2mm premolt size) to be sexually mature (Weymouth and MacKay 1936, MacKay 1937, Butler 1960, Poole 1967), agreeing well with estimates from regression intersects.

Age estimates have been determined for postlarval crabs by

TABLE 1

	INSTAR	CALIFORNIA	WASHINGTON		BRITISH COLUMBIA	
		MALE ONLY	MALE	FEMALE	MALE	FEMALE
JUVENILE INSTARS	1	7.3	5-7		6.5	
	2	10.7	9.9		9.4	
	3	14.2	13.4		12.8	
	4	18.4	17.7		17.1	
	5	23.6	22.9		22.4	
	6	29.9	29.3		28.8	
	7	37.6	37.1		36.8	
	8	47.0	46.6		46.5	
	9	58.6	58.2		58.6	
	10	72.7	72.3		73.4	
	11	90.0	89.5		91.5	
ADULT INSTARS	12	111.2	111.4	108.0	113.9	111.1
	13	136.5	134.2	124.0	139.6	128.6
	14	163.0	157.9	137.9	167.1	144.3
	15	190.9	182.6	149.8	196.5	158.2
	16	220.3	208.2	160.2	227.9	170.6

TABLE 1. Calculated instar size estimates derived from growth equations. All sizes exclude 10th anterolateral spines. Growth of juvenile males and females is equal up to sexual maturity (instar 11). Sources: Orcutt et al. (1975), data of Cleaver (1949), recalculated data of Butler (1961).

FIGURE 2. LINEAR REGRESSIONS OF _CANCER MAGISTER_ GROWTH IN WASHINGTON AND BRITISH COLUMBIA.

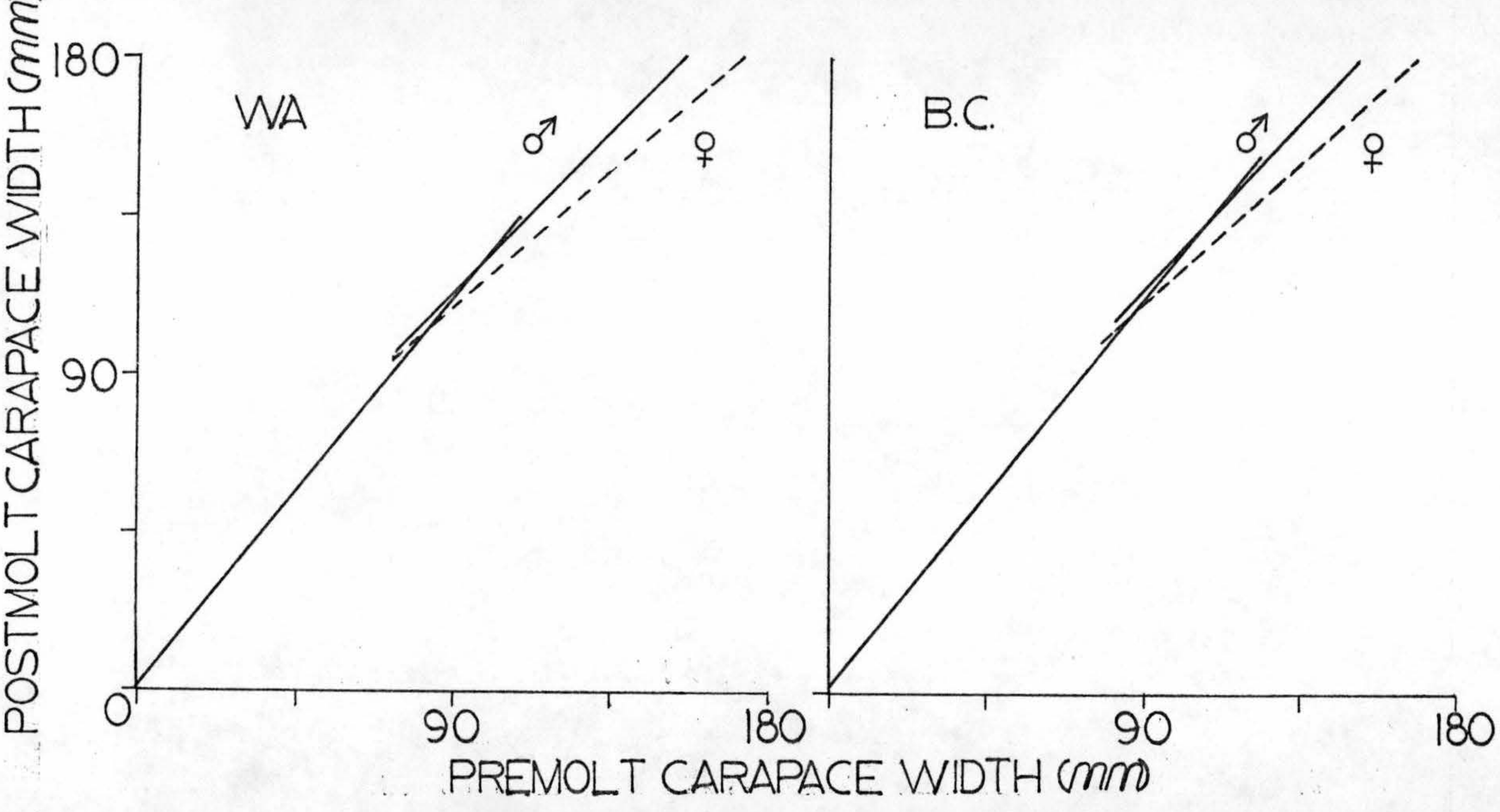
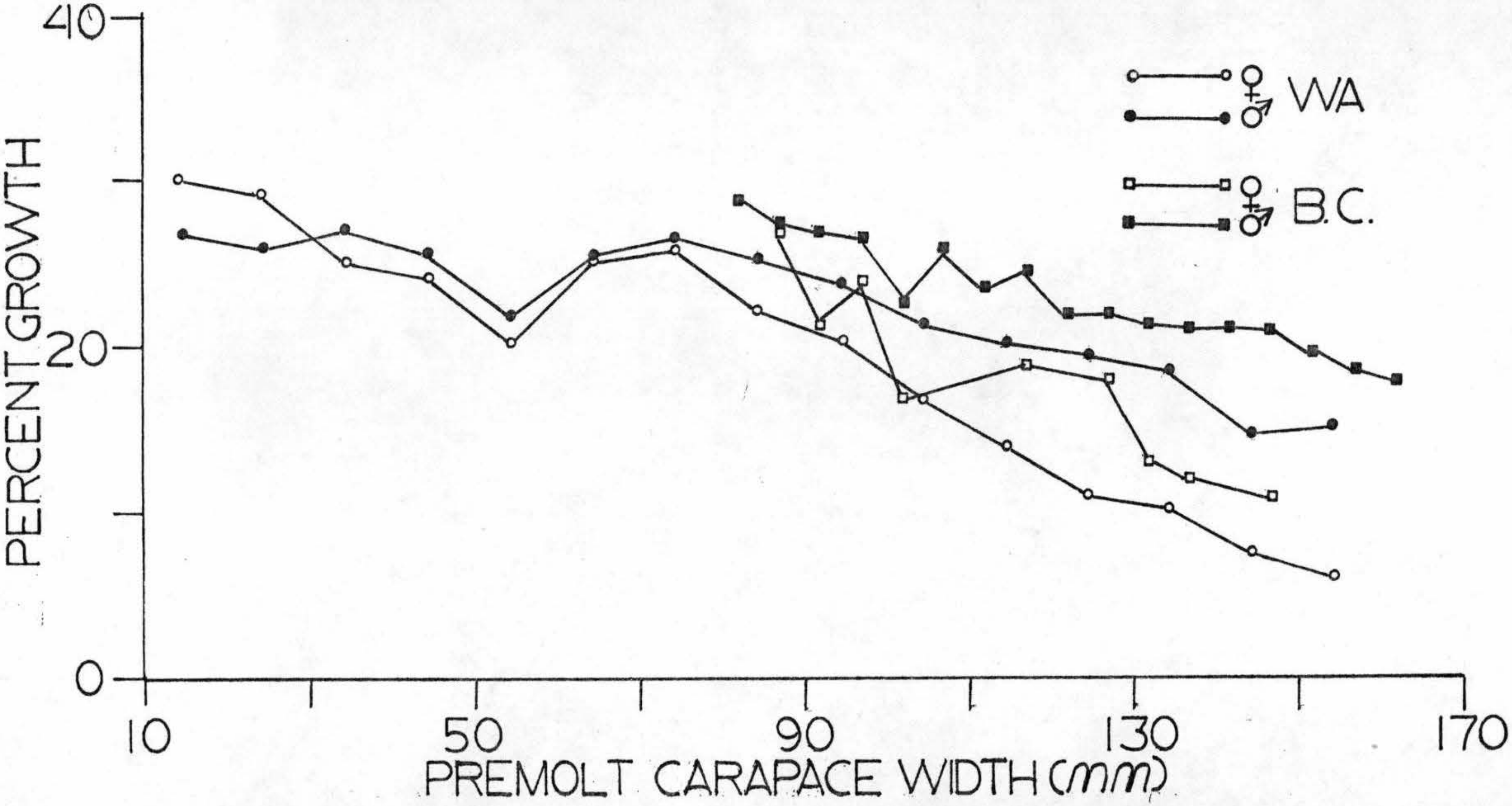

POSTMOLT CARAPACE WIDTH (mm)
180
90
0
WA
♂
♀
B.C.
♂
♀
90
180
90
180
PREMOLT CARAPACE WIDTH (mm)

TABLE 2

LOCATION	GROWTH PHASE	b	a	x COORDINATE (PREMOLT SIZE) of INTERSECTION of JUVENILE LINE WITH	SAMPLE SIZE	SOURCE
CALIFORNIA	JUVENILES	1.2233	1.0529			Orcutt et al. 1975
	ADULT MALE	1.0515	19.532	107.6		
ASHINGTON	JUVENILES	1.22	1.34		304	Data of Cleaver 1949
	ADULT MALE	1.04	18.33	94.4	87	
	ADULT FEMALE	0.864	30.71	82.5	152	
RITISH OLUMBIA	JUVENILES	1.23	1.32		6	Recalculated data of Butler 1961.
	ADULT MALE	1.07	17.7	102.4	284	
	ADULT FEMALE	0.892	29.51	83.4	44	

TABLE 2. Growth equation constants for linear regressions of the form $y = bx + a$, where y is postmolt carapace width and x is premolt carapace width.

FIGURE 3. CHANGES IN PERCENTAGE GROWTH WITH SIZE IN *CANCER MAGISTER*.


40
20
0
PERCENT GROWTH
10
50
90
130
170
PREMOLT CARAPACE WIDTH (mm)
○——○ ♀
●——● ♂ WA
□——□ ♀
■——■ ♂ B.C.

superimposing calculated instar size estimates on temporal series of carapace width frequency distributions (Table 3) (Cleaver 1949, Butler 1961, Orcutt et al. 1975). Age 0 is defined as the time of hatching and thus includes the 4-5 month larval period. Sexual maturity is estimated to occur at approximately 2 years for females and 2-3 years for males. The life span is 6-8 years (Cleaver 1949, Butler 1961).

Accelerated growth rate is reported for male crabs in the San Francisco Bay area population: at the age of one year juveniles in central California grow to instar 11 (approximately 85-105mm) as compared to growth to instars 4-7 (approximately 17-30mm) in Washington and British Columbia (Orcutt et al. 1975).

TABLE 3

Dungeness crab age-size estimates (males only)

Age (yr)	Central California	Washington	British Columbia
1	87-105mm (?)	30-35mm	22.4-28.8mm
2		95-106mm	91.5-113.9mm
3		150-154mm	139.6mm
4		175mm	167.1mm
5		≥200mm	≥196.5mm

Although no causative factors are hypothesized and age-size relationships for older crabs are not given, it can be conjectured that warmer southern water temperatures resulting in increased molting rates are responsible in part for this rapid growth. However, Orcutt et al. (1975) do not define age 0 for their age estimates;

if age 0 is taken by them to be metamorphosis from megalops to postlarval instar 1, then a crab aged one year would be 16-17 months old in the scheme in which hatching is defined as age 0. Butler (1961) estimates 17 month old (instars 9-10) British Columbia males to be approximately 80mm in size. If this were the case, comparable growth rates for central Californian and more northern crabs would be indicated.

BEHAVIOR

Predation and Prey

By probing in the sand with dactyls and partially opened chelae, foraging has been observed to take place at and near the surface of sandy substrates. Foraging is opportunistic and makes almost exclusive use of the benthic infauna (Butler 1954, Mayer 1973, Gotshall 1977, Pearson et al. 1979). Food items are located both tactilely and chemosensorily. Hairs on the chelae and walking legs are known to be mechanoreceptive (Butler 1954) and may also be chemosensitive (Barber 1960); distance chemoreception is facilitated by aesthetascs on the outer flagellum of the antennules (Barber 1960, Pearson et al. 1979). The feeding response involves an abrupt change in the orientation of the antennules, a sharp increase in antennular flicking rate, with the antennules usually becoming parallel and orienting upstream, and the rhythmic beating of the maxillipedal flagella (presumptive of gill bailing) (Pearson et al. 1979).

Feeding is greatly affected by the physiological state of the crab. Butler (1954) and Wild et al. (1978) note that feeding rates drop off significantly several days before molting, during ecdysis and a few days after molting. Passano (1960) estimates that approximately 15% of a Brachyuran intermolt period is spent feeding at a reduced rate (approximately 5%) or not at all (approximately 10%). For females, feeding rates are high before spawning, drop at the time of spawning, remain low during the ovigerous period and rise to normal after larval hatching (Wild et al. 1978). This may have evolved to minimize fecal material near the eggs in order to limit bacterial, algal and protozoan fouling of the brood. Rate of feeding has been found to increase with a rise in water temperature and vice versa (Wild et al. 1977).

C. magister feeds on crustaceans including gammarid amphipods, tanaids, decapods (including larval and juvenile C. magister), mysids, cirripeds, crangonid carideans, isopods and ostracods; molluscan bivalves; polychaetes; ophiuroids and small fish (Table 4) (MacKay 1931, 1942; Cleaver 1949; McMynn 1951; Butler 1954; Mayer 1973; Gotshall 1977; Pearson et al. 1979). Gammarid amphipods have been found to be the primary prey item in Washington and British Columbia (Butler 1954, Mayer 1973). C. magister tends preferentially to remove the "more commonly abundant" species from the infauna, therefore encountering the assemblage in a coarse-grained manner; infaunal diversity is increased and overall density decreased (Mayer 1973).

Information regarding larval feeding is unfortunately lacking. This is no doubt due to the larvae's planktonic existence, about which very little is known, small size and correspondingly small prey. Since the larvae are filter-feeders, an optimum size range of prey that can be captured by their filtering apparatus and consumed places constraints upon the larvae (Lough 1976). Reed (1969) fed C. magister zoeae Balanus glandula nauplii, Artemia salina nauplii and Mytilus edulis veligers and found that

TABLE 4

CRUSTACEA

  GAMMARID AMPHIPODS

    Photis lacia

    Heterophoxus occulatus

    Protomedia sp.

TANAIDS

    Leptognattea longiremus

OSTRACODS

    Euphilomedes productua

    E. carcharodonta

MOLLUSCA

  BIVALVES

    Transenella tantilla

ANNELIOA

  POLYCHAETES

    Praxiella gracilis

TABLE 4. Identified prey species of *Cancer magister* in Similik Bay, Washington. Source: Mayer 1973.

the M. edulis veligers (approximately 0.1- 0.3mm) were too small whereas the B. glandula and A. salina nauplii (approximately 0.37-0.42mm and 0.475mm respectively) were sufficient to sustain the zoeae. Unfed larvae survived 14 days. Megalopae have been observed to feed upon the hydroid Velella velella (Wickham 1979a).

Movements and Migrations

Cancer magister does not inhabit permanent burrows, but will bury into a sandy substrate when not moving about and/or foraging. When buried in the sand all but the eyes and antennae are concealed, allowing vision and chemoreception to continue (MacKay 1942). Individual crabs are active both day and night as evidenced by equally good crab catches occurring at both times (Spencer 1932).

Seasonal migrations undertaken by adult Dungeness crabs appear to be related to molting and breeding cycles and in general are restricted to inshore-offshore movements, but such movements are not universal within the species. There is no evidence suggesting extensive migrations (MacKay 1934; Butler 1957; Cleaver 1949, 1951; Allen 1966; Ricketts et al. 1968).

Crabs residing in sandy bottom subtidal habitats move inshore to intertidal mudflats during spring and summer to mate (Cleaver 1949, Butler 1957, Poole 1965). After mating, some portion of the population including the recently fertilized females begins to migrate offshore. Crab fishermen achieve best results by following these movements with their traplines (MacKay

1934). It is thought that by December, January and February in California and Oregon the crabs are approximately 5-16km offshore, where larval hatching occurs (Lough 1976). It is possible that females which did not mate during the spring and summer but still retain sperm from an earlier mating episode extrude a brood at some point offshore, with or without molting. By undergoing ecdysis in deep water instead of inshore by herself, i.e., in the absence of an embracing male, a female could reduce the chances of being preyed upon while in the soft, postmolt condition.

Information provided by returns from some tagging studies indicate only localized random or limited movements. A major flaw in most tagging programs has been placing the emphasis on tagging of males. This has been done to insure maximal returns as the majority of tags are returned by fishermen who carefully scrutinize only males. It is likely that further bias is introduced when legal males (159mm and larger) account for the preponderance of information. Small legal and sublegal males move as much or more than larger males (Cleaver 1949, Butler 1957), possibly accounting for the broadest migratory and least tagged segment of male crab populations. The winter offshore distribution of females has been inferred from the position of stage I zoeae as they appear in the plankton (Lough 1976).

In contrast to migratory crabs, large segments of *C. magister* populations in Oregon and Washington bays appear to be resident and remain within the home bay (Cleaver 1949, Waldron 1958, Mayer 1973). Through tagging it has been found that approximately 75% of bay recaptures are made within the bay of release in Oregon (Waldron 1958).

Predators

The eggs of C. magister are subject to predation by a species-specific nemertean worm, Carcinonemertes errans (Wickham and Fisher 1977, Wickham 1979c, Wickham 1980). Crabs begin carrying worms at a carapace width of 20mm and the worms continue to recruit throughout the crabs' life. C. errans infest females in virtually every protected crevice or joint while males have worms concentrated beneath the abdomen at the base of or on the gonopods. This suggests that worms on male crabs may move onto females around or at the time of copulation. One to two days after Cancer magister oviposition occurs the worms move off of the carapace and onto the eggs. The worms begin feeding within a day. Carcinonemertes errans is present on over 98% of all potential hosts in California and densities are increasing up the Pacific coast. Egg mortalities averaging over 50% are thought to be a major factor in the collapse of the central California crab fishery (see below).

Waldron (1958) distinguishes between two classes of C. magister predators: larval and adult. The first should be modified to include the predators of larvae as well as early postlarval juveniles.

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Waldron (1958) distinguishes between two classes of C. magister predators: larval and adult. The first should be modified to include the predators of larvae as well as early postlarval juveniles.

The only identified predators of zoeal C. magister are silver and chinook salmon. Undoubtedly there are other planktivores which prey upon the zoeal stages. Predators of megalopae and early postlarval juveniles (up to approximately 30-40mm) are dominated by fishes including silver salmon, chinook salmon, spring salmon, herring, pilchard, green sturgeon, white sturgeon, starry flounder, kelp greenling, rock sole and big skate (MacKay 1942, Waldron 1958, Tasto et al. 1977). Tasto et al. (1977) have found that as the strength of a crab year class increases the number of species of fish preying upon larval and juvenile crabs increases. Cannibalism of younger crabs and larvae has been reported and may exert a density-dependent controlling influence upon C. magister populations (see Population Dynamics section) (Cleaver 1949; Butler 1954; Botsford and Wickham 1975, 1978, 1979).

As the young crabs grow and approach maturity they attain a size refuge from the first class of predators. The size at which this refuge becomes effective is approximately 60mm and is reached in about six months in California (Tasto et al. 1977). Predators of adult crabs include wolf eels, halibut, ling cod, great marbled sculpin (cabezon), some rockfishes, octopus, other crabs and man (MacKay 1942, Waldron 1958, Spencer 1932, McMynn 1951, Gray 1964).

Wilkens et al. (1974) report that C. magister shows a "startle" response in which cardiac and scaphognathite pumping simultaneously cease when an abrupt stimulus occurs. They feel that this response may function as a predator avoidance tactic by concealing a motionless or buried crab from chemoreceptors and/or mechanoreceptors of a potential predator.

Competition

Competition may serve to structure observed Cancer magister habitat distribution. While interspecific competition per se is not addressed in the C. magister literature, conjecture about certain aspects of the subject can be made. Only speculation about competition in the oceanic habitat, i.e., the crabs' major habitat, is possible at this time. Competition for space is probably not a problem for C. magister as permanent burrows are not maintained and the crabs are quite mobile. Because C. magister is a predator of the infauna, it can be conjectured that competition occurs with those fishes and benthic predators, probably other crabs, that utilize the infauna. Within bays, where different habitat types are proximate and intergrade rapidly, niche overlap is possible and more intense competition for food resources can be envisioned. C. magister and C. productus both have been observed feeding on barnacles. C. productus may make slight use of the infauna, e.g., small clams (Pearson et al. 1979); C. magister makes almost exclusive use of the benthic infauna (Mayer 1973, Gotshall 1977, Pearson et al. 1979). However, the apparent modes of predation of the two crabs would appear to minimize competition for identical prey. C. magister sifts through the sandy bottom sediments with its slender chelae (Mayer 1973, Pearson et al. 1979) whereas C. productus with much heavier chelae forages in the more rocky high subtidal and intertidal for such prey items as barnacles, shore crabs and snails (Connell 1970; Pearson et al. 1979; Greg Daly, personal communication; personal observation).

Perhaps more significant than exploitative competition in limiting _C. magister_ to mostly sandy bottom habitats is interference competition. _C. productus_ is typically a more aggressive crab than _C. magister_ (personal observation). Antagonistic interactions involving _C. magister_ and _C. productus_ could serve to exclude _C. magister_ from rocky areas that can be foraged to some extent by them, e.g., for barnacles. _C. productus_, probably due to its large, less dextrous chelae, does not forage extensively on sandy bottoms. It is thus conceivable that the relatively limited areas of rocky substrate are contested for aggressively. The resulting outcome could be the observed distribution of _C. magister_ predominantly on sandy bottoms and _C. productus_ in rocky areas.

POPULATION DYNAMICS

Commercial crab landings, believed to represent an estimated 79-100% of total available legal males, are considered to be a good index of relative crab population size. It has often been noted that substantial yearly variations in C. magister landings, and therefore population sizes, occur (Cleaver 1949, 1951; Waldron 1958; PMFC 1959, 1961, 1962; Tegelberg 1963; Poole 1965) and recent catch statistics bear this out (Figure 4 and 5). Such variations in fisheries are considered normal and are assumed to be due to variability in year-class sizes (Cleaver 1949, Botsford and Wickham 1978). Fluctuations in recent Dungeness crab catches have been found to be cyclic with periods of 9 years in California and 12 years in Oregon and Washington (Botsford and Wickham 1975). However, the central California population declined to its cyclic minimum around 1960-1961 and has remained at very low levels (Figure 4). This situation has prompted a substantial amount of work attempting to determine factors causing the decline of this fishery, e.g., The Dungeness Crab Research Program conducted by the California Department of Fish and Game, and the population dynamics of C. magister in general.

Mayer (1973), Wild et al. (1978) and Wild and Haugen (1979) have experimentally determined that developing C. magister eggs are very sensitive to small temperature differences and temperatures above approximately 13°C cause acceleration of development accompanied with deterioration of egg masses on the abdomens of

FIGURE 4. COMMERCIAL DUNGENESS CRAB LANDINGS FOR NORTHERN AND CENTRAL CALIFORNIA, 1950-51 TO 1978-79.

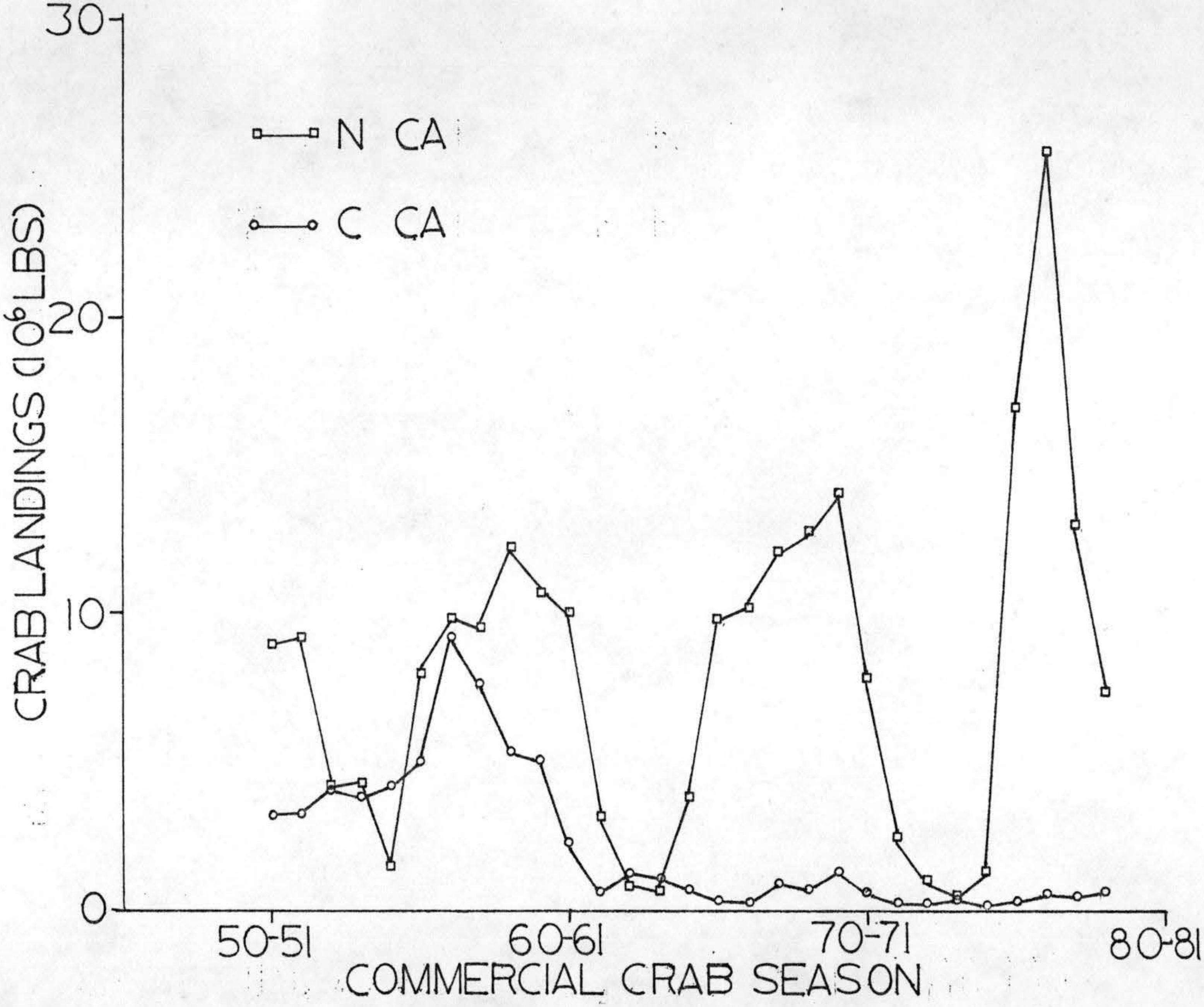
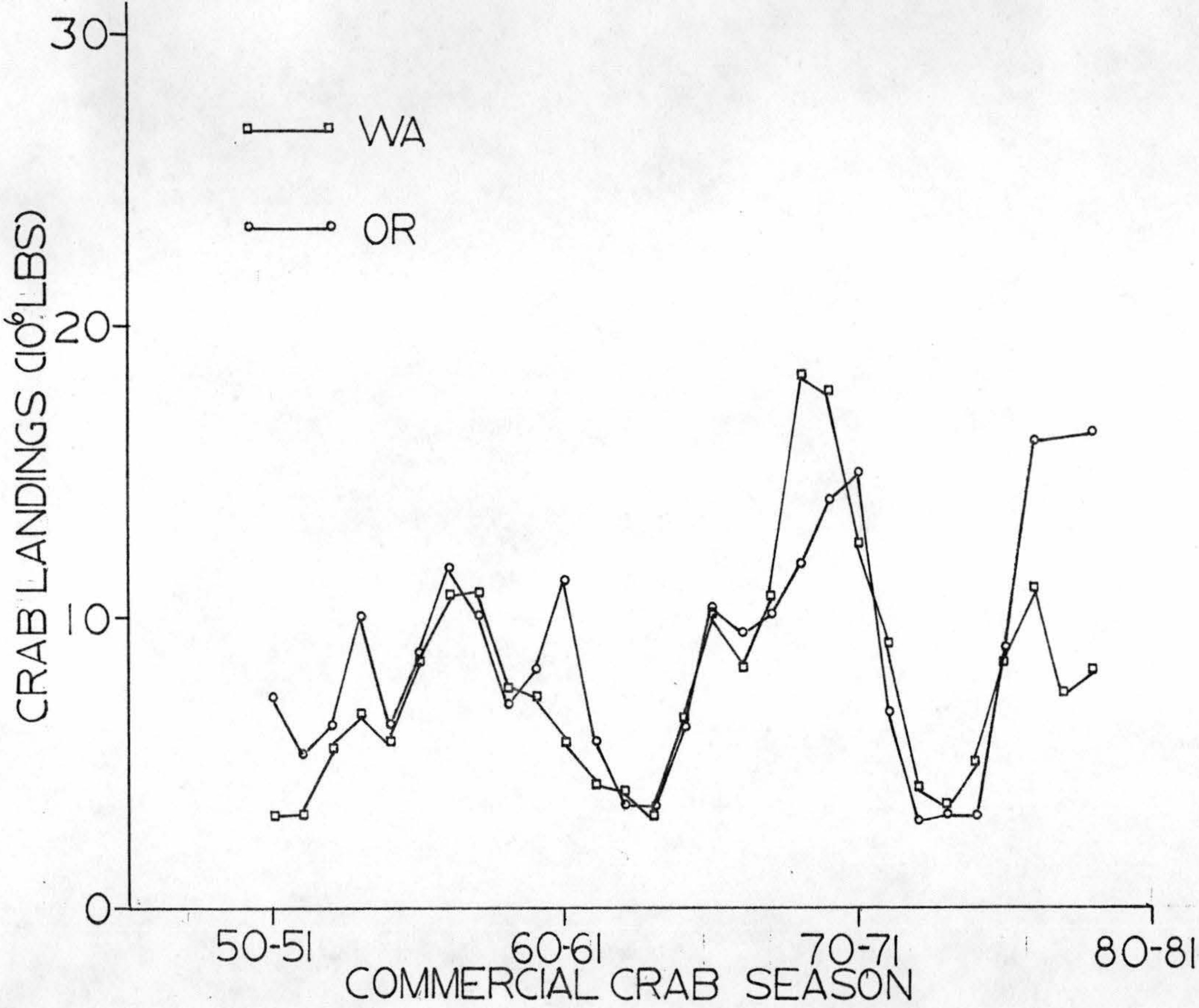

N CA
C CA
CRAB LANDINGS (10⁶ LBS)
30
20
10
0
50-51
60-61
70-71
80-81
COMMERCIAL CRAB SEASON

FIGURE 5. COMMERCIAL DUNGENESS CRAB LANDINGS FOR WASHINGTON AND OREGON, 1950-51 to 1978-79.



30
20
10
0
CRAB LANDINGS (10^6 LBS)
WA
OR
50-51
60-61
70-71
80-81
COMMERCIAL CRAB SEASON

female crabs. Decreased hatching success results. Historically, seawater temperatures of the central California C. magister environment have averaged 13.2°C (1922-1956) during the October to December spawning and egg brooding period. However, the 1957 October to December mean seawater temperature was 15.9°C and this trend has continued with an October to December mean seawater temperature of 14.2°C for the period 1957-1972. Since male crabs require approximately three years to enter the fishery at legal size, the decline and lack of recovery of the central California fishery/population has been hypothesized to be due, at least in part, to this change in the oceanic temperature regime.

Possible mechanisms driving the continuing population cycles in northern California, Oregon and Washington (Figure 4) have been pursued recently. Hypotheses examined include upwelling effects (Peterson 1973, Botsford and Wickham 1975), density-dependent interactions (Botsford and Wickham 1975, 1978, 1979) and egg predators (Wickham and Fisher 1977; Wickham 1979b, 1979c). Predation, both natural and by man, has also been suggested (Botsford and Wickham 1975, 1979; Lough 1976). However, the large number of predator species would most likely maintain a fairly constant level of predation unless a major predator (or predators) was cycling also. Human predation has been dismissed as the driving mechanism of the cycles since fishing concentrates upon large males that have mated and thereby responds to, rather than being the cause of, abundance. Fishing may alter the characteristics and stability of the natural cycles though. Larval and juvenile stages are considered the critical stages for maintenance of Dungeness crab populations and it is believed that their survival or lack thereof will drive the observed population cycles (Cleaver 1949, Orcutt et al. 1975).

Coastal upwelling intensity during spring and summer months is variable from year to year. Upwelling was found to be positively correlated with crab catches ½ year later in Washington and 1½ years later in California and Oregon. These lag times indicate that upwelling has no strong influence upon the abundance and survival of larval and juvenile crabs (Peterson 1973). Further analysis indicates that significant cycles in upwelling are not apparent while cycles in crab catch are (Botsford and Wickham 1975). However, it is thought that upwelling may circumvent declines in peak C. magister populations by increasing biological production in the pelagic environment which subsequently filters down to increase benthic production, hence the aforementioned lag times (Botsford and Wickham 1975).

Density-dependent interactions are at this time considered to be the most likely mechanism causing the cyclic fluctuations of C. magister populations. Mayer (1973) proposes density-dependent mortality of juveniles through cannibalism; cannibalism of young has been noted by many observers (e.g., Cleaver 1949, Butler 1954, Gotshall 1977). Botsford and Wickham (1975) also suggest cannibalism and have constructed a model of age-specific density-dependent mortality of juveniles (Botsford and Wickham 1978, 1979). In years of high crab abundance it is suggested that food resources are depleted, as evidenced by poor crab condition, resulting in adult cannibalism of juveniles which would have entered the fishery approximately three years later. Stability analysis of the model indicates that unregulated selective fishing of older age-classes, i.e., current fishery practices, can decrease stability of the population cycles. The result is an oscillating population with peaks of increasing amplitude and decreasing period. Such oscillations are currently evidenced by the northern California population (Figure 4) (Botsford and Wickham 1979). More field studies of the relationship between cannibalism and actual mortality are deemed necessary rigorously to implicate this mechanism. Botsford (in preparation) has preliminary results indicating that a stable equilibrium fishery may dampen current population cycles; the present Dungeness crab fishery is not of a stable equilibrium type (see below).

Intraspecific competition may also be acting in a density-dependent manner. Competition for food and/or space in which older crabs have the advantage over juveniles may result in reduced juvenile survival (Botsford and Wickham 1978).

Carcinonemertes errans, a nemertean egg predator host-specific to Cancer magister, is hypothesized to be a third possible density-dependent cause of population cycles (Wickham and Fisher 1977; Botsford and Wickham 1978, 1979). However, Carcinonemertes errans exhibits a density-dependent compensatory feeding inhibition which results in a consequent decrease in worm fecundity. Under normal circumstances, i.e., in unexploited crab populations, the worms remain at stabilized low densities on a portion of the available host population, thereby causing minimal egg mortalities (Wickham 1979c). This would seemingly discount C. errans as the generator of crab population cycles.

In the central California populations dense infestations of C. errans and correspondingly high levels of egg mortalities have been found. It is estimated that an annual loss of more than 50% of Cancer magister eggs is due to worm feeding. The possibility is good that the prolonged low population levels exhibited by the central California commercial crab catch (Figure 4) are related to this extreme mortality. Wickham (1979c) proposes a model in which C. magister populations exhibiting cycles of increasing amplitude and decreasing period (possibly due to fishing effort and/or the temperature change in the oceanic climate of central California, see above) act to drive the worm population to new high level equilibria as crab numbers drastically increase and subsequently decline. In the second, high level equilibrium the compensatory feeding inhibition response, resulting in decreased fecundity of individual worms, would not serve to limit overall worm-caused egg mortalities. The new compensatory response to high level worm density would be host availability. Egg mortality leading to long term low crab population levels could cause the worms and crabs to lapse into a direct predator-prey balance with high densities of worms on few crabs. Such a heterogeneous distribution of worms would probably not drive a C. magister population to extinction but would allow the population to persist at low levels, a situation seemingly quite similar to that occurring in central California at the present time. Wickham and Botsford (in preparation) will discuss this two equilibrium model in detail. Increasing densities of Carcinonemertes errans have recently been found in northern California, Oregon and Washington, suggesting that the bulk of the Dungeness crab fishery may be in danger of passing into the second, crab devastating equilibrium (Wickham 1979c; D. E. Wickham via Jerry Rudy, personal communication).

A second worm related source of C. magister egg mortality is epibiotic fouling of the eggs by a variety of bacteria, blue-green algae and stalked protozoans (Fisher 1977, Armstrong and Fisher 1977). Carcinonemertes errans has been shown to be a direct source of fouling via feeding activities and defecation. Detrital fouling and nutrient release from egg yolk promotes the growth of fouling organisms which may restrict gaseous exchange across the outer membranes of eggs (Fisher 1976, Fisher and Wickham 1976, Wickham and Fisher 1977, Wickham 1979b). Thus, the 50% egg mortality estimate due to C. errans is probably a conservative one, as such fouling in crustacean egg and larval cultures generally results in heavy mortalities (Armstrong and Fisher 1977; Wickham 1979b, 1979c).

In summary, Cancer magister populations experience coastwide cyclic fluctuations in abundance. A number of proposed cycle-producing mechanisms have been hypothesized and examined; modeling techniques implicate a density-dependent interaction as the most likely generalized mechanism. Adult cannibalism of juveniles is considered the most probable density-dependent interaction to impose such cycles upon crab populations. Stability analysis of the model indicates that unregulated fishing of older age-classes, i.e., current fishery practices, will result in an unstable mode in which oscillations of increasing amplitude and decreasing period can occur. The northern California fishery shows signs of such predicted oscillations and coastwide fishery effort is approximately twice that which would produce a maximum sustainable yield. Intraspecific competition may also act in a density-dependent fashion possibly resulting in abundance cycles. Such competition may in fact precede the initiation of cannibalism, juveniles first competing for limited food resources then becoming prey.

A species-specific nemertean egg predator, _Carcinonemertes errans_, has been implicated as the possible cause of continued low population levels in central California. _C. errans_, it is hypothesized, was able to increase to high densities during a period of unstable crab population oscillation in spite of the density-dependent compensatory worm feeding response which decreases worm fecundity. The speculated result is a system in which the crabs and worms lapse into a direct predator-prey cycle with the crabs maintaining depressed population levels. Worm related egg mortalities also occur as a result of worm feeding activities which cause bacterial, algal and protozoan fouling of eggs. In total, worm caused and worm related egg mortalities are estimated to be greater than 50% in a population afflicted by a heavy _C. errans_ infestation, e.g., central California.

Increasing _C. errans_ densities have been noted in northern California, Oregon and Washington. This would indicate a need to impose fishery effort management in order to avoid oscillations which could allow sufficient densities of _C. errans_ to accrue and potentially bring about permanently depressed coastwide population levels.

THE FISHERY

Cancer magister has presumably been fished since Pacific shores have been inhabited by man. Kroeber and Barrett (1962) note that Indians of northwestern California took crabs, predominantly Cancer antennarius and C. productus, from intertidal pools at low tides and C. magister may have been taken occasionally using shallow plateform [sic] baskets as traps.

The development and expansion of the present fishery began with the earliest coastal settlers (Cleaver 1949); the first reported landings in Oregon were in 1899 and production gradually increased up to 1931 (Waldron 1958). Early catches were limited by marketing difficulties as the perishable fresh cooked product was the earliest utilization of crab meat. The market was virtually restricted to coastal areas but processing advances, notably refrigeration, canning, freezing and improved transportation, occurred from about 1934 to 1943 and made a greatly expanded fishery possible (Cleaver 1949, 1951; Waldron 1958).

During the early years of the commercial fishery the bulk of the catches were taken in bays and other protected areas. In 1915 ocean catches had taken on importance in the Columbia river mouth fishery of Oregon and Washington. The offshore fishery increased until at present it accounts for approximately 95% of the commercial catch (Waldron 1958).

With the expansion of the fishery came an evolution of fishing gear. Small boats and crab rings or hoops (two iron hoops connected with netting) were common in the bay and ocean fisheries. Rings require frequent hauling and are limited to depths less than 18m as their open design allows the crabs a chance to escape. Therefore, the number a fisherman can handle is limited. Subsequently, crab pots or traps adapted from the east coast lobster pot were developed. Originally a wooden frame covered with wood slats with an entrance at each end, the crab pot is now constructed of iron rod and iron mesh. These pots came into common usage in the mid- and late 1930s and by the 1940s were almost the exclusive commercial crabbing gear. With the switchover to pots requiring less constant attention more gear per fisherman was possible; larger vessels carrying large numbers of pots became common and the ocean crab pot fishery is now conducted at depths from approximately 7-37m (MacKay 1931, Lahr 1939, Cleaver 1949, Waldron 1958). Although rings and pots are the principally used gear, rakes used intertidally supplied a small market in Coos Bay, Oregon in the past but now are legal only for sportfishing (Waldron 1958); there are not many crabs found intertidally with regularity any more (personal observation). In addition, modified sea bass gill nets were used in the 1920s in Monterey Bay, California because muddy bottom sediments precluded the use of rings. This method resulted in damaging many of the crabs as they were extracted from the nets, but did increase the catches in this area (Chute 1929);

nets are no longer legal. Incidental catches of crabs also occur in groundfish trawls and are legal to land, provided the crabs are of legal size, in California and British Columbia. Crab trawling of any kind is illegal in Washington and Oregon (Smith 1975, Miller 1976, Warner 1978).

The commercial Dungeness crab fishery extends from central California to Alaska with the bulk of the catches coming from northern California, Oregon and Washington (Figures 4 and 5). British Columbia contributes consistent but moderate landings. A Dungeness crab fishery arose around 1966 in western, southeastern, and central Alaska when the king crab (*Paralithodes camtschatica*) fishery declined. However, gear restrictions and a rapidly increasing tanner crab (*Chionectes tanneri*) fishery were probably responsible for a subsequent decline, around 1969, of the *C. magister* fishery there (Magoon 1969, Snow 1970).

Regulation of the Dungeness crab fishery is vested in individual state or provincial agencies: Alaska Department of Fish and Game, Canadian Fisheries and Marine Service, Washington Department of Fisheries, Oregon Fish and Wildlife Commission and California Department of Fish and Game. These agencies regulate legal size and sex, gear and open fishing seasons.

Size and sex limitations are imposed upon the fishery mainly for breeding purposes. Taking females is prohibited in California, Oregon, Washington and Alaska. Females are legally harvestable in British Columbia (Miller 1976). However, processors and fishermen in all localities are almost unanimously opposed to harvesting females (PMFC 1978). The minimum legal size for males in the commercial fishery is 159mm (6¼in) measured in a straight line directly in front of the 10th antero-lateral spines. At this size males are likely to have mated at least once before being removed from a population (Cleaver 1949, Miller 1976).

Commercial fishing gear is regulated to limit the fishery to crab rings and pots. Upon the recommendation of the Pacific Marine Fisheries Commission (PMFC 1978) two escape ports are now required by law (4 3/8in diameter in Washington and Oregon, 4½in diameter in California) on all crab pots to minimize handling mortality of females and sublegals; reduce injury inflicted on small crabs by larger, aggressive crabs; limit cannibalism; allow escape of sublegals and lessen the amount of sorting required of fishermen. Preliminary work has been done by the California Department of Fish and Game to develop a self-destruct mechanism for lost pots that continue to fish. However, a suitable design has not yet been developed (PMFC 1978).

Opening dates of the commercial crabbing season have undergone a good deal of discussion and revision of late. The closed season was originally enacted to protect molting and mating crabs, an economic as well as resource conserving move. Recently molted, or softshell crabs have not yet had time to allow their muscles, i.e., crab meat, to become firm and full after having taken up water during ecdysis. There is consequently a loss of up to 50%, by weight, of crab meat as compared to a crab in prime condition and the meat is watery and less marketable. In addition, sublegal softshell crabs that are discarded are subject to handling mortality of approximately 15-20% (PMFC 1960, 1978; Tegelberg 1963; Miller 1976). Recent experience has shown that November 15 and December 1 season opening dates have resulted in high incidences of softshell crabs being trapped in southern Oregon and California (PMFC 1960, Tegelberg 1963). Seasons in areas further north generally open either December 15 or January 1. Setting of season opening dates is complicated by the facts that crabs do not molt at exactly the same time each year and molting occurs later off northern Oregon and northward. The Pacific Marine Fisheries Commission (1972) recommended a coastwide January 1 opening date and later (PMFC 1978) reviewed the problem by considering uniform, staggered and flexible openings as well as a year round open season. Assessment criteria included meat yield, handling mortality, other fishing opportunities, opportunity costs for processors, costs of crab fishing, costs of crab processing and demand for crabs. In addition, a "skipper questionnaire" was used to provide input from within the industry. The January 1 opening was again thought to be the best uniform opening date as it produces the greatest net financial benefit for Oregon, Washington and California combined and is overwhelmingly endorsed by fishermen. Staggered opening dates in which the season in northern areas would usually open later, e.g., January 1, than in southern areas, e.g., December 1, to allow for maximum catches of prime crab could cause problems by allowing fishermen from southern areas to fish the earlier-opening areas and then to move northward to exploit unfished areas; Washington would suffer most in a situation such as this. Nonetheless, a coastwide net financial gain is predicted to result from such a scheme. A flexible season in which the season would be opened by "homogeneous areas" when crab condition criteria, essentially low softshell frequencies, were met would theoretically maximize meat yield and minimize handling mortality. However, coastwide monitoring of crab condition would be required, which would decrease net gains by creating the need for a monitor group or agency. Overall it appears that the January 1 coastwide opening endorsed by the PMFC (1972) would still be the most prudent from both fishery and conservational standpoints.

Further analysis of the fishery by the Pacific Marine Fisheries Commission (1978) indicates that effort levels, on the whole for Washington and Oregon and on the average for northern California, are exceeding the maximum sustainable yield (MSY). To attain the MSY a combined three state effort of approximately 60,000 pots is suggested; the present average effort is approximately 123,000 pots. The fishing effort is clearly intense. Waldron (1958) noted that average seasonal catch peaks in Oregon occurred in May. During the 1958-1959 season approximately 88% of the total central California catch was taken by the end of February (PMFC 1959). Poole (1965) found that owing to high opening prices and the fishermen's fear of not getting one's share of the potential catch, 90-95% of the available crabs are caught within seven weeks of the season opening, i.e., January or

February. It therefore seems necessary to effect some effort management program to avoid the possibility of a coastwide situation such as that now afflicting the central California fishery (see above). Three general approaches to effort management have been examined: license limitations, taxes on catch and gear and individual catch quotas (PMFC 1978).

The individual catch quota plan is thought to show the most promise (PMFC 1978). A predetermined allowable coastwide catch would be determined each year in advance of the season and then divided into shares among the fishermen, shares being transferable. The success of such a program would require accurate stock size prediction as well as support from fishermen in the form of accurate and reliable catch statistics.

Taxation of catch and gear would be the most direct and flexible plan but could hit fishermen harder than necessary. Underreporting catch and amount of gear would be financially beneficial to fishermen.

A license limitation program would license a given number of vessels representing the maximum allowable effort, a "substantial" annual license fee being involved. It is thought that a coastwide licensing agency would be preferable to individual state agencies to avoid the need for double licensing in border areas, e.g., the northern California-southern Oregon and Columbia River fisheries.

Implementing any such program obviously will bring about administrative costs as well as incur costs to fishermen, processors and marketers who are required to alter their traditional business methods. The PMFC (1978) is not able to conclude whether or not overall monetary benefits would be substantial enough to finance an effort management program. Therefore, no final recommendation has been made as of this writing. The evidence presented suggests that continuation of current unlimited fishery practices threatens the Dungeness crab resource. Coastwide fishery collapse, similar to that experienced by the central California fishery, is presently conceivable (see above). Management of fishing effort is clearly advisable.

RECOMMENDATIONS FOR FURTHER RESEARCH

The generalized life history of C. magister is fairly well understood at this time. However, the courtship and mating ritual of the crab still requires field documentation. Closely tied in with this is the question of presence or absence of a sex attractant pheromone released by the female. Other species, e.g., Hemigrapsus nudus and H. oregonensis, mate in aggregations and do not exhibit such ritualization (Knudsen 1964). Therefore, the need for a mating ritual such as that displayed by C. magister could implicate low densities of mature individuals on the tide-flats during mating season. It follows that a mechanism other than random search for location of a mate should exist to ensure mating success. Field studies of mate-finding and a search for presence or absence of a pheromone are necessary to substantiate this hypothesis.

Crab movements have been documented by tagging. However, tagging has emphasized legal males as they provide the "best" returns through the fishery. A program in which females and sub-legals also are tagged would provide better information on migratory behavior of the population as a whole. Location of larval hatching areas could also be discerned more accurately. Because female feeding rates are low during the ovigerous period, undoubtedly affecting their trapping rate, telemetry might be a useful technique to monitor their movements.

Examination of larval hatching peaks (Figure 1) indicates variations with latitude, peaks occurring earlier in southern areas, later in the north. The bulk of the information is from reports with no supporting data. Serial plankton tows conducted at stations from California to Washington are needed to quantify and implicate statistically this apparent trend. Oceanographic data, e.g., temperature and salinity, collected simultaneously may help to support any conclusions. Information obtained in such a program would provide baseline data to gain further insights into stock-recruitment relationships. Lough (1976) also outlines recommendations for future research on this subject.

The most urgent questions about _Cancer_ _magister_ are those concerning long term low population densities, a reality in central California, a possibility farther north. Imperative now is testing hypotheses that have been proposed; most important are those concerning the nature and modification of population cycles and _Carcinonemertes_ _errans_ effects.

Testing the proposed density-dependent mechanism, i.e., cannibalism, could be accomplished with a stomach content analysis program. By indexing numbers of cannibalized juveniles and comparing them with fishery levels at appropriately lagged intervals, approximately 3 years, a first estimate of cannibalism effects on recruitment could be had.

It is obvious that unexploited _C._ _magister_ populations are no longer available for study and for that reason the current situation must be taken as baseline. In order to discern ongoing fishery effects, especially the hypothesized decrease in cycle stability, fishery manipulation is probably necessary. Discrete populations of C. magister are believed to occur (e.g., see Gotshall 1978); for that reason it is recommended that a fishery moratorium be enacted in one population and a "stable equilibrium" fishery imposed upon another; populations with low egg predator burdens would be necessary to limit synergistic effects, i.e. it is hoped populations still exist which are not in immediate danger of lapsing into low abundance so just such a situation might be avoided. Comparison of the three treatments, unfished, "equilibrium" fished and intensely fished, over a period of 10-15 years would provide information on cycles, whether induced or natural, and provide fishery assessment and management criteria.

Unstable modes of population cycles have been hypothesized to result from unlimited fishing of older age-classes (Botsford and Wickham 1979). This may stem from direct effects on the mating success of the crabs. By removing the largest males each year, availability of large males the next year could be affected. Larger females may need to be overpowered by a male in order to accept him as a mate, i.e., the female must have the male's fitness "proven" to her by the male's size and ability to overpower. In addition, smaller males may be morphologically unable to copulate with a large female. Male mating activity is low during their first mating season (Poole and Gotshall 1965). In the past this could have been due to competition for females from older crabs and/or agonistic behavior of females. The result could be changes in population fecundity and/or gene pool changes. Such changes may be brought on by an increase in mating by small males of "unproven" fitness, i.e., they have not yet survived to large size. To begin pursuing this hypothesis relative numbers of large and small berried females should be compared; ideally the three fishing treatments suggested above would be sampled for this information. Should decreased mating success for large females be found, it would suggest alteration of fishery regulations. Should present unlimited fishery practices be continued it would be sensible to harvest large unfertilized females. However, the model (Botsford and Wickham 1979) suggests that a stable equilibrium fishery would dampen the unstable oscillations produced by the current fishery. Therefore, implementing such an equilibrium, i.e., cutback, fishery could possibly leave large males to mate with large females.

II. <u>CANCER</u> <u>PRODUCTUS</u>: SALINITY EFFECTS UPON DISTRIBUTION AND ABUNDANCE IN COOS BAY, OREGON

INTRODUCTION

The institution of a fishery for Cancer productus, the red rock crab, has been proposed by the National Marine Fisheries Service (Pat Rutten, personal communication) since the failure of the central California Dungeness crab, Cancer magister, fishery. However, very little is presently known about the ecology and biology of C. productus. Knudsen (1964) reviewed field observations on habitat, food and feeding habits, reproductive activity and copulation. Larval life consists of a prezoea (Roesijadi 1977), five zoeal instars and a megalops (Trask 1970). Adults typically inhabit rocky or gravelly bottoms (Weymouth 1914, Schmitt 1921, Cleaver 1949). It has been assumed since proposed by Weymouth (1914) that restriction to this type of habitat is due to the lack of a "straining apparatus" and for this reason C. productus do not inhabit sandy and muddy areas (Schmitt 1921, Ricketts et al. 1968). An alternative view explaining these findings, presented above (see Part I, behavior; competition), is that the mode of C. productus foraging limits success in sandy and muddy areas. It is suggested that the large chelae of C. productus are not dexterous enough for foraging efficiently in a sandy or muddy substrate, while the slender C. magister chelae are. Therefore, C. productus may not experience adequate predation success with much of the sandy bottom infauna utilized by C. magister. Schmitt (1921) also suggests that, aside from scarcity of favorable bottom, it is possible that the "great fluctuations in salinity" in upper San Francisco Bay may exclude *C. productus*. It has been reported that *C. productus* is an osmoconformer (Chuck Holliday and Robert Terwilliger, personal communications) although no published experimental verification has been available. This paper examines the hypothesis that *C. productus* is an osmoconformer and that local abundances are determined, at least in part, by changes in salinity.

MATERIALS AND METHODS

This study was conducted at a dredge-spoil island (PPSI) located north of Pigeon Point within Coos Bay, Oregon (43°22'N 124°18'W). Beginning 11 August 1978 the area was sampled once a month. Bimonthly sampling began 7 May 1979 and continued through 24 May 1980.

Subtidal and intertidal distribution and abundance were determined by trapping in the intertidal and subtidal habitats of PPSI. Trapping in the subtidal was done at and near slack low water at tidal heights of -3 to -5 feet; intertidal trapping was done at and near slack high water at tidal heights of approximately +2 to +3 feet. A trapline of three baited traps was set along a 100m transect parallel to the shore. A series of three sets of the trapline was made during each tide. Each set was fished for 30 minutes (defined as one unit of effort). Fresh red snapper and black cod carcasses were used as bait. Trapped crabs were sexed, marked by removing the dactyl of the first left walking leg and measured to the nearest mm. Measurements were made in a straight line across the back of the carapace just in front of and not including the 10th anterolateral spines.

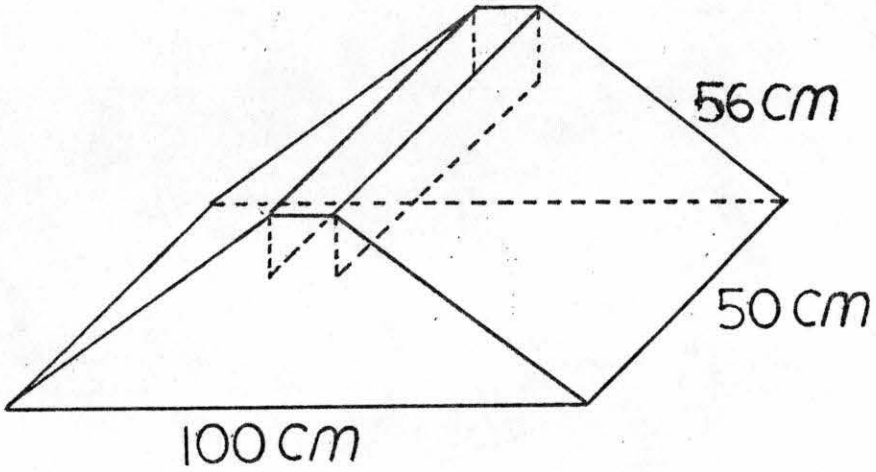
The traps used were of a top entry type (Figure 6) constructed of 1" x 1" galvanized hardware cloth. Polypropylene rope with painted plastic bottles as floats and markers were used for rigging.

Beginning 9 May 1979 water samples were collected at each tide for salinity measurements. Salinity determinations were made using density hydrometers provided by William Gilbert, Department of Oceanography, Oregon State University. Salinity was measured to the nearest tenth of a part per thousand (0.1 ^{o}/oo).

Salinity-tolerance experiments were performed 31 May and 1 June 1980. Six pools were filled with various dilutions of water from Coos Bay. The first trial consisted of dilutions to 28.5^{o}/oo, 25.5^{o}/oo, 21.4^{o}/oo, 18.8^{o}/oo, 16.1^{o}/oo and 13.1^{o}/oo and was terminated after 18.5 hours. The second trial was run with dilutions to 28.3^{o}/oo, 13.1^{o}/oo, 10.6^{o}/oo, 8.2^{o}/oo, 5.3^{o}/oo and 3.1^{o}/oo and ended after 6 hours.

Ten crabs were placed in each pool. Males and females of the size range 46-150mm were used. The pools were checked once an hour for moribund and dead crabs. A crab was considered moribund if no movement occurred when prodded and dead if the eyestalks were not retracted when touched and antennule flicking had ceased. Termperature was monitored each hour and salinity rechecked at the end of the experiment.

FIGURE 6. TOP ENTRY <u>CANCER</u> <u>PRODUCTUS</u> TRAP


56 cm
50 cm
100 cm

RESULTS

Cancer productus abundances at PPSI (Figures 7 and 8), quantified as monthly mean catch-per-unit-effort ($\overline{CPUE}$), went through a yearly cycle in both the intertidal and subtidal. Peaks and minima occurred in September-October and November-January, respectively. Monthly mean salinities ($\overline{SAL}$) (Figures 7 and 8) also varied through the year. Highest values were found from May-October; lower salinities occurred from November-April. Salinities recorded during sampling ranged from $19.1^{o}/oo$ to $33.2^{o}/oo$ in the subtidal and $21.0^{o}/oo$ to $33.2^{o}/oo$ in the intertidal. Linear regressions with $\overline{CPUE}$ as the dependent variable and $\overline{SAL}$ as the independent variable were significant (P 0.05) for the subtidal, but not significant for the intertidal (Table 5). Regressions with monthly change in $\overline{CPUE}$ ($\Delta\overline{CPUE}$) dependent and monthly change in $\overline{SAL}$ ($\Delta\overline{SAL}$) independent were significant ($P < 0.01$) for the subtidal, but not significant for the intertidal (Table 5). Intertidal $\overline{CPUE}$ was found to be positively correlated with subtidal $\overline{CPUE}$ ($P < 0.02$) (Table 5).

Salinity-tolerance data were analyzed for each salinity treatment by linear regression with time as the independent variable and survival as the dependent variable. All regressions were significant (Table 6). The results indicate greatly reduced survival at salinities below $13.1^{o}/oo$ (Figure 9, Table 6).

FIGURE 7. MONTHLY VARIATION IN SUBTIDAL $\overline{\text{CPUE}}$ AND $\overline{\text{SAL}}$ (± S.E.)

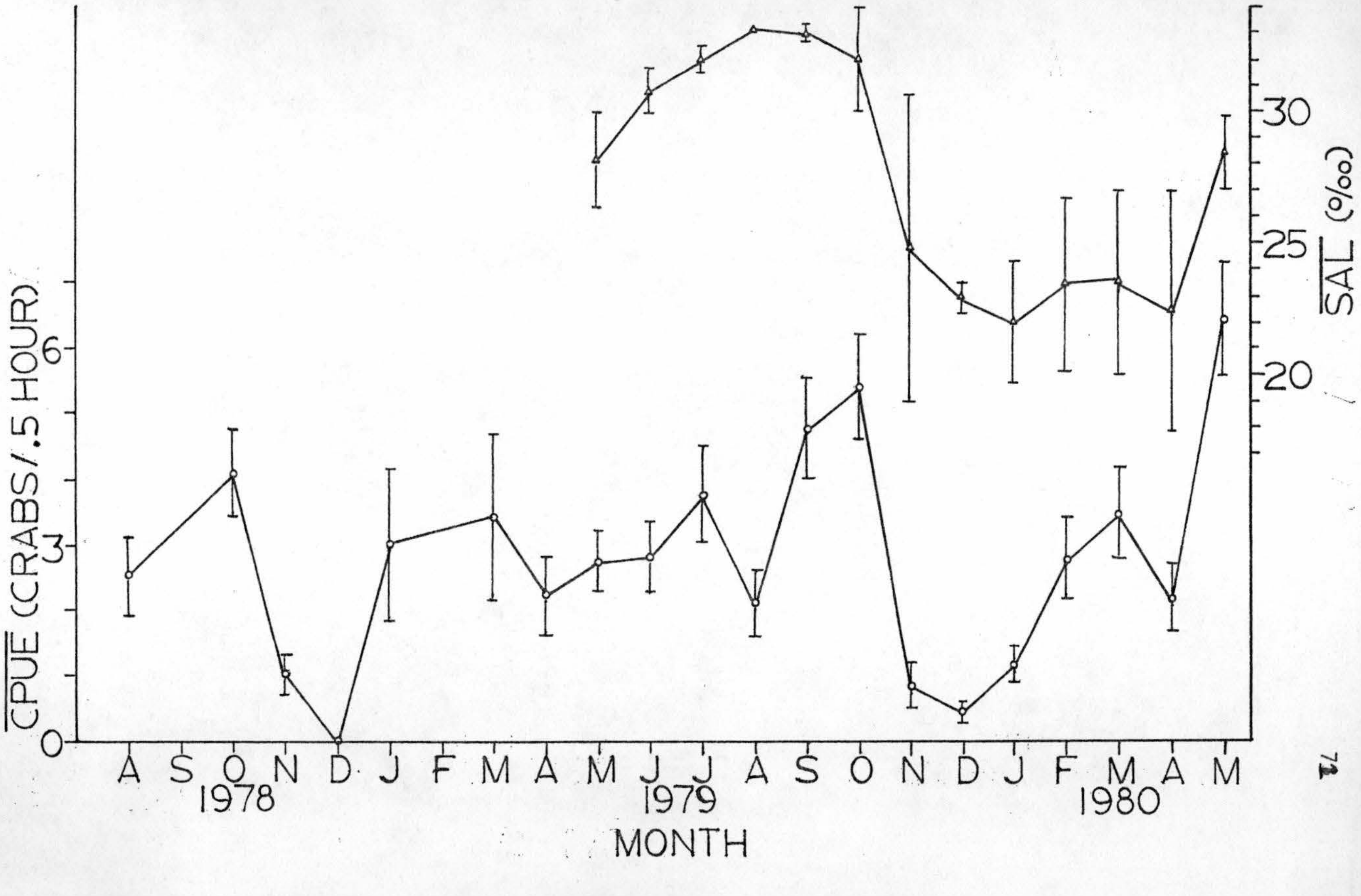

CPUE (CRABS/.5 HOUR)
0
3
6
SAL (‰)
20
25
30
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1978
1979
1980
MONTH

FIGURE 8. MONTHLY VARIATION IN INTERTIDAL $\overline{\text{CPUE}}$ AND $\overline{\text{SAL}}$ (± S.E.)

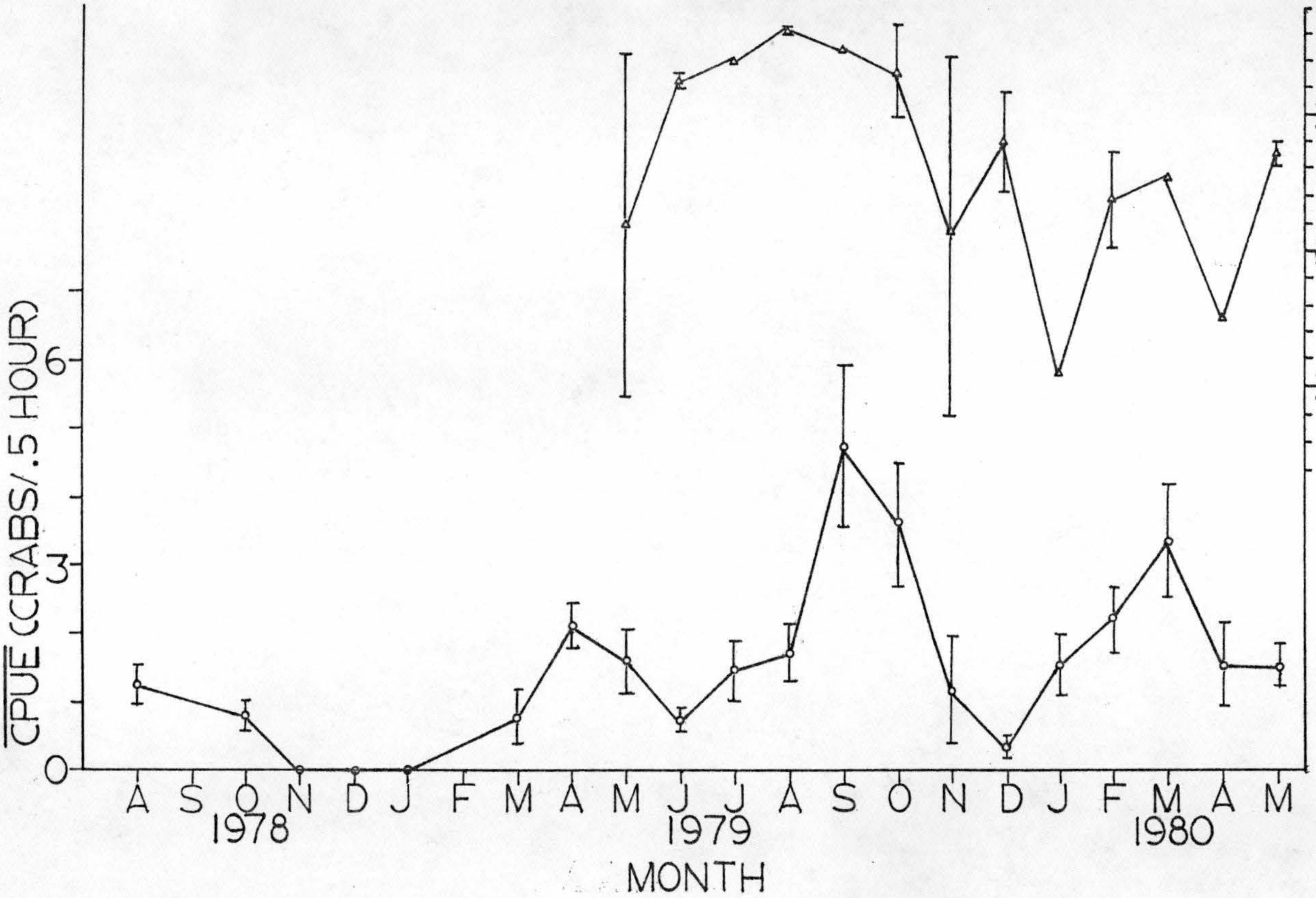

CPUE (CRABS/.5 HOUR)
0
3
6
SAL (‰)
20
25
30
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1978
1979
1980
MONTH

TABLE 5

RELATION	REGRESSION CONSTANTS AND STATISTICS						
	b	s_b	a	n	t	P	r^2
SUBTIDAL:							
$\overline{\text{CPUE}}$ DEPENDENT, $\overline{\text{SAL}}$ INDEPENDENT	0.2247	0.1009	-3.1658	13	212270	<0.05	0.3109
$\overline{\text{CPUE}}$ DEPENDENT, $\overline{\text{SAL}}$ INDEPENDENT	0.5649	0.1384	0.2900	12	4.0816	<0.01	0.6248
INTERTIDAL:							
$\overline{\text{CPUE}}$ DEPENDENT, $\overline{\text{SAL}}$ INDEPENDENT	0.0879	0.0923	-0.5154	13	0.9523	N.S.	0.0762
$\overline{\text{CPUE}}$ DEPENDENT, $\overline{\text{SAL}}$ INDEPENDENT	0.0427	0.0989	-0.0129	12	0.4317	N.S.	0.0183
INTERTIDAL $\overline{\text{CPUE}}$ DEPENDENT SUBTIDAL $\overline{\text{CPUE}}$ INDEPENDENT	0.4137	0.1481	0.3845	20	2.7934	<0.02	0.3023

TABLE 5. Linear regression constants and statistics for CPUE and SAL relations

TABLE 6

TRIAL	SALINITY ($^{o}/oo$)	b	s_b	a	n	t	P	r^2
1 (18.5 hrs.)	28.5	0.0		1.0000	11			
	25.5	-0.0100	0.0024	1.0487	11	-4.1667	<0.01	0.6506
	21.4	-0.0050	0.0012	0.9244	11	-4.1667	<0.01	0.6506
	18.8	-0.0150	0.0037	1.0731	11	-4.0541	<0.01	0.6506
	16.1	-0.0174	0.0020	1.0160	11	-8.7000	<0.001	0.8898
	13.1	-0.0251	0.0036	0.9862	11	-6.9722	<0.001	0.8462
2 (6 hrs.)	28.3	0.0		1.0000	6			
	13.1	0.0		1.0000	6			
	10.6	-0.1714	0.0165	1.1667	6	-10.3879	<0.001	0.9643
	8.2	-1400	0.0214	1.0400	6	-6.5421	<0.01	0.9147
	5.3	-0.1257	0.0345	0.9400	6	-3.6435	<0.05	0.7683
	3.1	-0.1486	0.0391	0.9533	6	-3.8005	<0.02	0.7830

TABLE 6. Linear regression constants and statistics for survival-time relations at various experimental salinities

FIGURE 9. LINEAR REGRESSIONS OF _CANCER_ _PRODUCTUS_ SURVIVAL THROUGH TIME AT VARIOUS EXPERIMENTAL SALINITIES

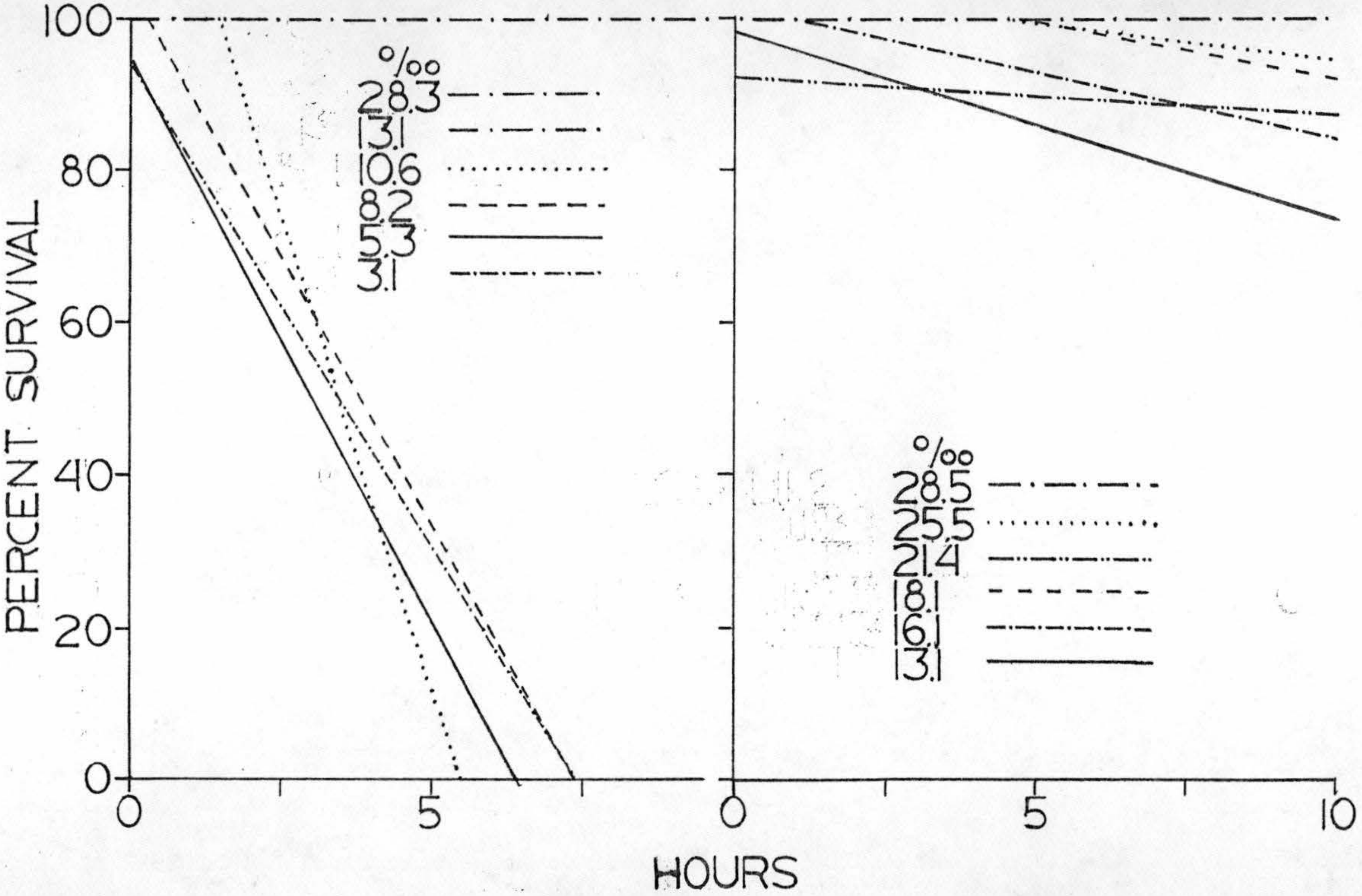
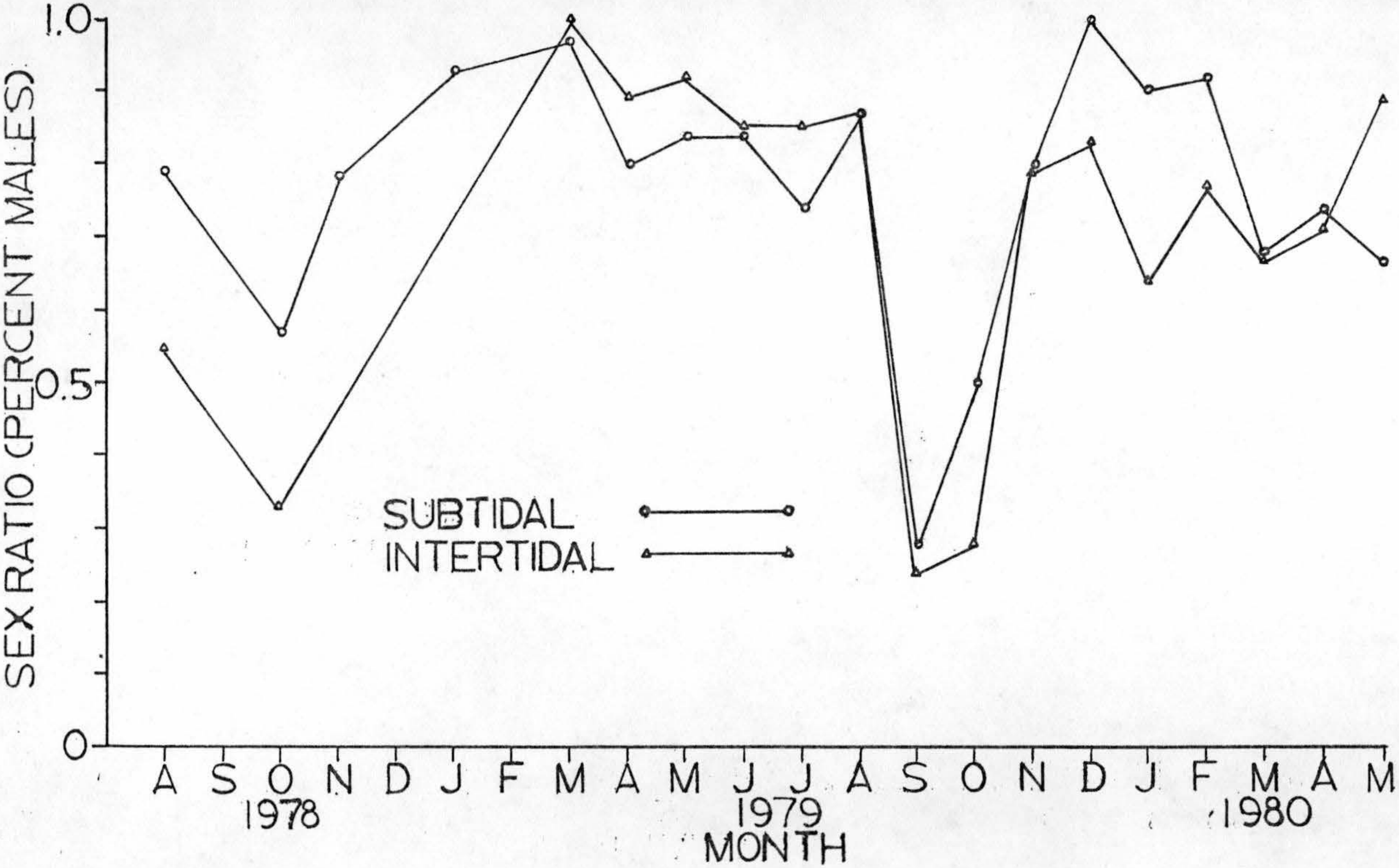

100
80
60
40
20
0
PERCENT SURVIVAL
‰
28.3
13.1
10.6
8.2
5.3
3.1
‰
28.5
25.5
21.4
18.1
16.1
13.1
0
5
0
5
10
HOURS

FIGURE 10. MONTHLY VARIATION IN *CANCER PRODUCTUS* SEX RATIO



SEX RATIO (PERCENT MALES)
1.0
0.5
0
SUBTIDAL
INTERTIDAL
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
1978
1979
1980
MONTH

DISCUSSION

Distribution and abundance of Cancer productus in Coos Bay, Oregon are responsive to salinity as indicated by the subtidal $\overline{CPUE}$-$\overline{SAL}$ and $\Delta\overline{CPUE}$-$\Delta\overline{SAL}$ regressions (Table 5); increases in mean salinity result in increases in mean crab numbers. The greater significance of the $\Delta\overline{CPUE}$- $\Delta\overline{SAL}$ relation, accounting for approximately 62% of the $\Delta\overline{CPUE}$ variation, suggests that month-to-month trends in crab abundance, rather than absolute numbers, are most predictable.

There are two apparently separate segments of the *C. productus* population. The nonsignificance of intertidal $\overline{CPUE}$-$\overline{SAL}$ and $\Delta\overline{CPUE}$-$\Delta\overline{SAL}$ relations is most likely due to crabs larger than 80mm carapace width, i.e., those crabs which are trappable, not residing in the intertidal. Daly (1981) sampled the PPSI intertidal from 1978 to 1980 and found that individuals less than 80mm are the only *C. productus* present there during low tide exposures. Knudsen (1964) observed that *C. productus* displays a negative rheotaxis in response to ebbing tides. Thus, individuals larger than 80mm found in the intertidal move up from the subtidal with the rising tide, forage in the intertidal during high tide and leave as the tide goes out. The positive correlation between subtidal and intertidal $\overline{CPUE}$'s (Table 5) is presumably due to this tidal migration, i.e., intertidally trapped crabs are a subset of the subtidal population. Crabs less than

80mm found in the exposed intertidal by Daly (1981) were essentially never caught intertidally or subtidally in traps. These crabs are probably juveniles and individuals which have recently attained sexual maturity, e.g., two females, 62 and 76mm, carrying eggs were found in the intertidal by Greg Daly (personal communication). After attainment of sexual maturity and/or a carapace width of approximately 80mm the crabs probably cease full-time intertidal residence and join the subtidal adult population. Juveniles and young adults may remain in the intertidal because it affords suitable shelter, minimizes agonistic/cannibalistic encounters with larger conspecifics and/or provides an adequate food resource.

The large November decreases in $\overline{\text{CPUE}}$ (Figures 7 and 8) and intertidal juvenile density (Daly 1981) (Figure 11) coincide with a marked drop in $\overline{\text{SAL}}$. The 24.8^{o}/oo subtidal and 25.6^{o}/oo intertidal November $\overline{\text{SAL}}$'s are considerably higher than the experimentally derived 13.1^{o}/oo critical, low-survival salinity. However, the standard errors of the November $\overline{\text{SAL}}$'s are the year's largest, indicating a change in the salinity regime. This suggests that *C. productus* responds to conditions signalling the potential for low salinity before critical, low-survival levels occur. The response may be due to salinity alone or a combination of external stimuli. This seems reasonable since salinities as low as 13.1^{o}/oo were not recorded during sampling. Periodic low salinities during the winter months of high Coos River runoff (December to February) (Bourke et al. 1971) occassionally result in low-survival salinities (Queen and Burt 1955). Initial salinity decreases, physical disturbances associated with the first large storms and/or photoperiod changes may trigger crab responses.

Knudsen (1964) believes that C. productus in Puget Sound, Washington may undergo a horizontal migration to deeper water during "periods of the year". It appears likely that C. productus in Coos Bay respond to decreasing salinity by migrating down-bay towards suitable habitats nearest the mouth of the bay. Physiological stress and mortality would be minimized in those habitats experiencing the least dilution of seawater. Queen (1930) found C. productus at two upper bay stations (near White Point and Kentuck Slough) only during the summer. Tom Polachek (personal communication) noted the absence of the crabs near Empire during January 1980. However, large numbers of C. productus can be found at Fossil Point throughout the year (Greg Daly, personal communication); the Fossil Point area and the Charleston small boat basin jetty and pilings, both near the Coos Bay mouth, are likely winter destinations of migrating crabs. A further consequence of the crabs being near the bay mouth may be facilitation of movement of the planktonic larvae, which hatch in late March/early April (Knudsen 1964), into the oceanic environment, assuming that is where development occurs.

Mating pairs were observed in eelgrass (Zostera sp.) at Fossil Point during June 1980. Fasten (1924) found full testes in late June/early July and most C. productus mating has been observed to occur from June to August (Spencer 1932, Knudsen 1964). It is probably significant that mating occurs during high-salinity months. Molting, which females undergo before copulation (Knudsen 1964), is a physiologically stressful period for crabs; as osmoconformers *C. productus* surely minimize such stress by mating at this time.

Peak $\overline{\text{CPUE}}$'s during September and October 1979 (Figures 7 and 8) were probably related to post-mating activities of the crabs. As indicated by the low sex ratio during these two months, the high $\overline{\text{CPUE}}$'s were a consequence of trapping a large number of females in addition to a normal contingent of males. Female *Cancer magister* exhibit high feeding rates after molting and mating and just before spawning; feeding rates drop off soon thereafter (Wild et al. 1978). It is reasonable to expect similar behavior from *C. productus*. In addition, younger crabs appear to have left the intertidal by October (Figure 11). Some crabs may also have begun down-bay migration at this time. Therefore, peak $\overline{\text{CPUE}}$'s in September and October are probably due to large numbers of post-mating, migrating adults and young-of-the-year moving past the PPSI area.

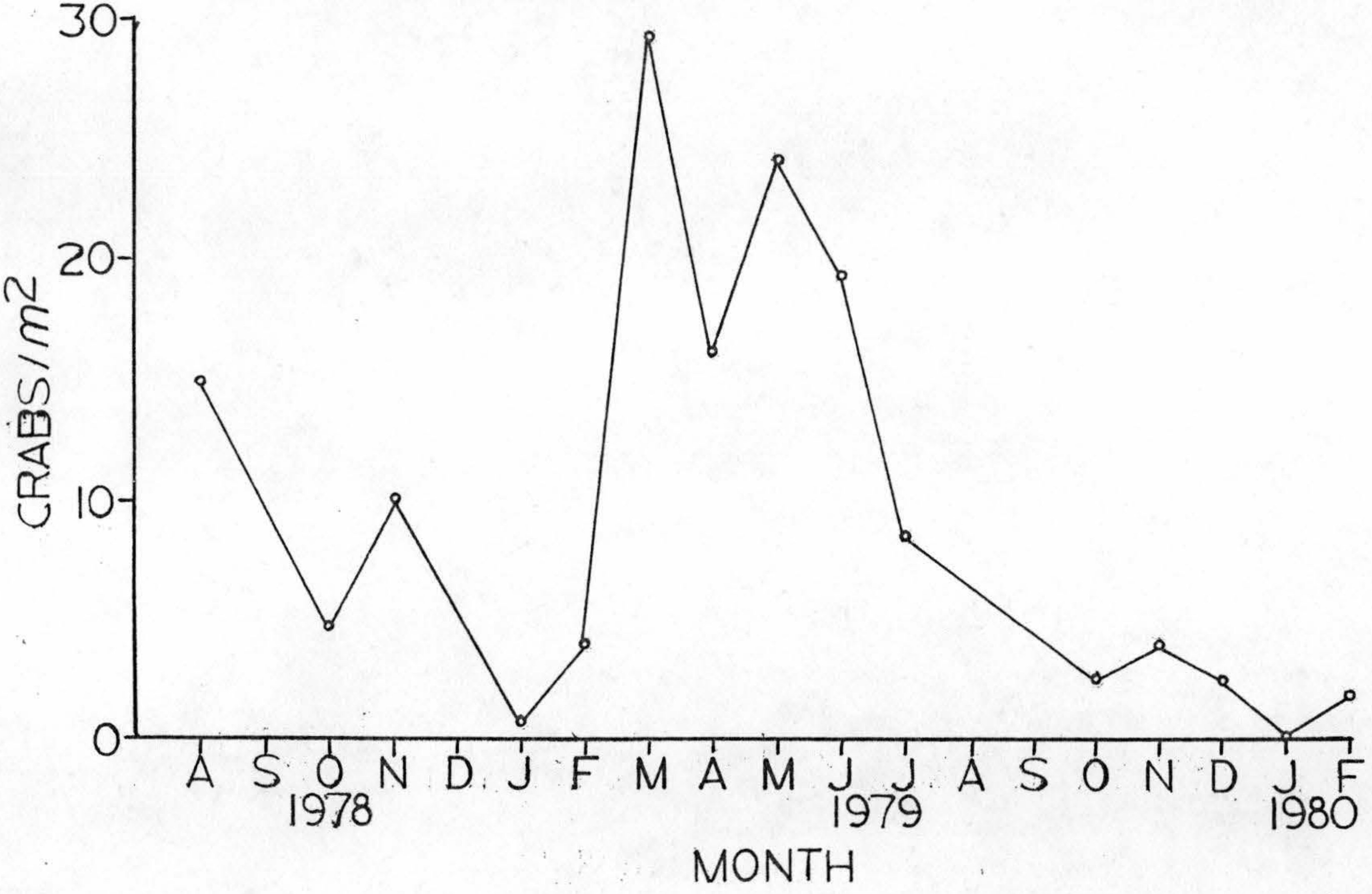
Subtidal $\overline{\text{CPUE}}$ returned to levels comparable to the preceding year in February 1980 (Figure 8). This suggests that a return migration could have begun or was occurring at that time. However, $\overline{\text{SAL}}$ was still low and quite variable from February through March (Figure 8). It may be that critically low salinities typically do not occur after January. Again it is possible that external stimuli, e.g., photoperiod, decreased storm intensities and/or rising salinities, could trigger the return migration to areas further up-bay.

Cancer productus appears to have recruited well in 1979. March, April and May 1979 densities of juveniles were high compared to April and May 1978 and March 1980 densities (Daly 1981) (Figure 11). This contention is further supported by the large May 1980 subtidal $\overline{\text{CPUE}}$ (Figure 8) which is significantly greater than the August and September 1979 yearly peak values. This May 1980 $\overline{\text{CPUE}}$ probably resulted from the one-year-olds which recruited during March through May 1979 (Daly 1981) leaving the intertidal and joining subtidal adults.

In summary, *Cancer productus* distribution and abundance in Coos Bay, Oregon are correlated with changes in salinity. It seems reasonable that the reaction is to salinity because the crabs are osmoconformers and experience low survival at salinities lower than 13.1^{o}/oo. They probably move down-bay during winter periods of low salinity caused by increased Coos River runoff. By removing themselves to habitats near the bay mouth, where seawater dilution is least, the crabs may minimize the possibility of mortality. A return migration which occurs around February is also suggested.

Adult *C. productus*, crabs larger than approximately 80mm, inhabit the subtidal and migrate into and out of the intertidal with the tides. Full-time intertidal residents are restricted to juveniles and crabs that have recently attained sexual

FIGURE 11. INTERTIDAL DENSITY OF JUVENILE CANCER PRODUCTUS THROUGH TIME. SOURCE: DATA OF DALY (1981)



30
20
10
0
CRABS/m^2
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
1978
1979
1980
MONTH

maturity, i.e., crabs smaller than approximately 80mm.

C. productus recruitment was good in 1979. Comparatively high densities of juveniles settled in the intertidal during March, April and May 1979. These juveniles probably appeared as adults in the large catch of May 1980.

Further research on C. productus is necessary to document the down-bay migration hypothesized above. Sampling throughout the year at stations up- and down-bay would aid in the proof or disproof of the hypothesis. It is essential to gain a working knowledge of C. productus ecology and biology as the crab may become a commercially exploited species in the wake of potentially failing Dungeness crab (Cancer magister) fisheries.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. Peter Frank, my committee chairman, for encouragement, constructive criticism and for always keeping me honest. Thanks are due to my other committee members, Drs. Paul P. Rudy and Daniel Udovic for suggestions, comments and review of the manuscript. I also thank Dr. Paul Rudy for the use of the Oregon Institute of Marine Biology, Charleston, Oregon, facilities.

I would especially like to thank Dr. Greg Daly for providing me with project suggestions, many hours of valuable discussion and guidance, review of the manuscript and the use of the Stinky Cove Marine Laboratory and Seafood Kitchen. Thanks also to Sheryl and Jacob.

I would like to acknowledge the financial assistance afforded me by the University of Oregon Graduate Research Committee, Fred Munz, chairman. This support permitted construction of crab traps and provided travel expenses.

Acknowledgement is due my friend Betsy Vander Schaaf for typing the paper and providing a calming effect.

I dedicate this paper to my wife Carolee. Without her love, understanding and support I could not and would not have done it.

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