NOAA Technical Report NMFS Circular 426

Synopsis of Biological Data on the Rock Crab, *Cancer irroratus* Say

May 1979

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Synopsis No. 123

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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

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U.S. DEPARTMENT OF COMMERCE
Juanita M. Kreps, Secretary

National Oceanic and Atmospheric Administration
Richard A. Frank, Administrator

National Marine Fisheries Service
Terry L. Leitzell, Assistant Administrator for Fisheries

PREFACE

This synopsis of the literature is intended to summarize all biological and biochemical studies involving *Cancer irroratus* published before early 1977. Included are some unpublished observations, drawn primarily from work completed at the U.S. Environmental Protection Agency laboratory in Narragansett, R.I.

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*As no information was available, these sections were omitted.

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Synopsis of Biological Data on the Rock Crab, *Cancer irroratus* Say

Thomas E. Bigford[1]

ABSTRACT

The rock crab, *Cancer irroratus* Say, is a common member of the benthic community along the east coast of North America. The species inhabits sandy bottom areas but may occur on gravel or rocky substrates. Bottom trawls and trapping via pots frequently yields high numbers of rock crabs. A growing market may create an increased demand for this underexploited species.

Cancer irroratus typically occurs from Labrador south to Florida. Within this range the crab is distributed in specific patterns with respect to temperature, salinity, depth, substrate, and time of year. Many of these factors, plus light, pressure, and gravity, affect larval distributions.

The literature includes several papers in general life history. Patterns of molting and growth have been studied in the laboratory and field for all of the life stages. Larval development and responses to environmental variables are also well described.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name (from Rathbun 1930)

Cancer irroratus Say, 1817, J. Nat. Sci. Phila., vol. 1, p. 59, pl. 4, fig. 2; Smith, 1871-1872 (1873), Rep. U.S. Commer. Fish., vol. 1, p. 312 (18), 530(236), 546(252); Rathbun, 1884, Fish. Fish. Ind. U.S., sec. 1, p. 766, pl. 260, figs. 1-3; Sumner, 1911, Bull. Bur. Fish., vol. 31, pt. 2, p. 671; Hay and Shore, 1915-1916 (1918), Bull. Bur. Fish. 35: 369-475, pl. 35, fig. 1.

1.12 Synonomy (from Rathbun 1930)

Platycarcinus irroratus Milne Edwards, Hist. Nat. Crust., vol. 1, 1834, p. 414; DeKay, Nat. Hist. New York, pt. 6, Crust., 1844, pl. 2, fig. 2.

Cancer sayi Gould, Rep. Invertebr. Mass., ed. 1, 1841, p. 323 (type-localities, Cape Ann, Nahant, etc.; types not located).

Platycarcinus sayi DeKay, Nat. Hist. New York, pt. 6, Crust., 1844, p. 7.

Cancer borealis Packard, Mem. Boston Soc. Nat. Hist., vol. 1, 1867, pl. 303; not *C. borealis* Stimpson.

Cancer amoenus Connolly, Contrib. Can. Biol., n. s., vol. 1, 1923, p. 337, text-figs. 1 and 2, pls. 1-4. Not *C. amoenus* Herbst, 1799.

1.2 Taxonomy

1.21 Affinities

Suprageneric

Phylum Arthropoda
  Class Crustacea
    Subclass Malacostraca
      Series Eumalacostraca
        Superorder Eucarida
          Order Decapoda
            Suborder Reptantia
              Section Brachyura
                Subsection Brachygnatha
                  Superfamily Brachyrhyncha
                    Family Cancridae

Generic *Cancer* (from Nations 1975)

"*Cancer* Linnaeus 1758:625. Type species *C. pagurus* Linnaeus 1758.

"*Alpheus* Weber 1795:91. Type species *A. pagurus* (*Linnaeus* 1795). Not *Alpheus* Fabricius 1798:380.

"*Pagurus* Berthold 1827:255. Type species *P. pagurus* (Linnaeus 1827). Not *Pagurus* Fabricius 1775:410.

"*Trichocera* DeHaan 1833:4,16. Type species *T. gibbosula* (DeHann 1833). Not *Trichocera* Meigen 1803:2.

"*Platycarcinus* Milne Edwards 1834:412. Type species *P. pagurus* (Linnaeus 1834).

"*Romaleon* Gistle 1848:11. Substituted for *Trichocera*.

"*Metacarcinus* Milne Edwards 1862:33. Type species *M. magister* (Dana 1862).

"*Trichocarcinus* Miers 1879:34. Type species *T. gibbosula* (DeHaan 1833). Substituted for *Trichocera*."

Generic (from Glaessner 1969)

"Carapace very wide, finely granulate, anterolateral margins very long, curved, with about 10 denticulate

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[1] U.S. Environmental Protection Agency, Environmental Research Laboratory, Narragansett, RI 02882; present address: Center for Natural Areas, 1525 New Hampshire Avenue, N.W., Washington, DC 20036.

lobes; gastrocardiac regions marked; orbits small, deep, with 2 fissures; front narrow, with 3 teeth, epistome narrow, chelae subequal, with 5 longitudinal blunt ridges on their outer surfaces."

Subgeneric *Cancer*, sensu stricto (partially from Nations 1975)

Front produced; frontal teeth rounded, medial one not acute but forming a rounded lobe nearly as wide or wider than those of the adjacent pair. Anterolateral teeth broad, truncate to slightly produced, separated by closed fissures; first tooth wider than second. Outer margin of anterolateral teeth forming an obtuse angle. Carapace and chelipeds smooth. Usually colored with purple or crimson spots dorsally on a light brownish-red background; Gulf of St. Lawrence crabs may lack purple, with a yellow-brown color predominating and a ventral color of pale yellow to cream (Stasko[2]).

Specific *irroratus*

Nine anterolateral and two posterolateral teeth (usually obscure). Carapace ovular and convex, bordered anteriorly by the anterolateral teeth and posteriorly by a raised carina with two teeth. Anterolateral teeth generally shallow, with notches between adjacent teeth extending into the carapace as short fissures (Fig. 1). Haefner[3] described specific morphological differences between *C. irroratus* and similar crabs.

Chelipeds shorter than first pair of pereiopods and granulate (not denticulate); upper margin of merus ending in a short, subdistal tooth; carpus with a sharp, inner tooth overlapping propodus. Legs long and compressed, with merus (arm), carpus (wrist), and propodus (hand) with the dactylus visible from above on all five pairs of legs. Side margins of fifth and sixth abdominal segment in male converging distally. Pleopods, except for first and second (modified for copulation), are reduced.

Diagnosis: Nine anterolateral and two posterolateral teeth on the carapace; edges of teeth entire. Chelipeds granulate, not denticulate (Fig. 1).

1.24 Standard common names, vernacular names

Rock crab, stone crab, mud crab, and cancer crab.

1.3 Morphology and description

1.31 External morphology

As described above in Section 1.21.

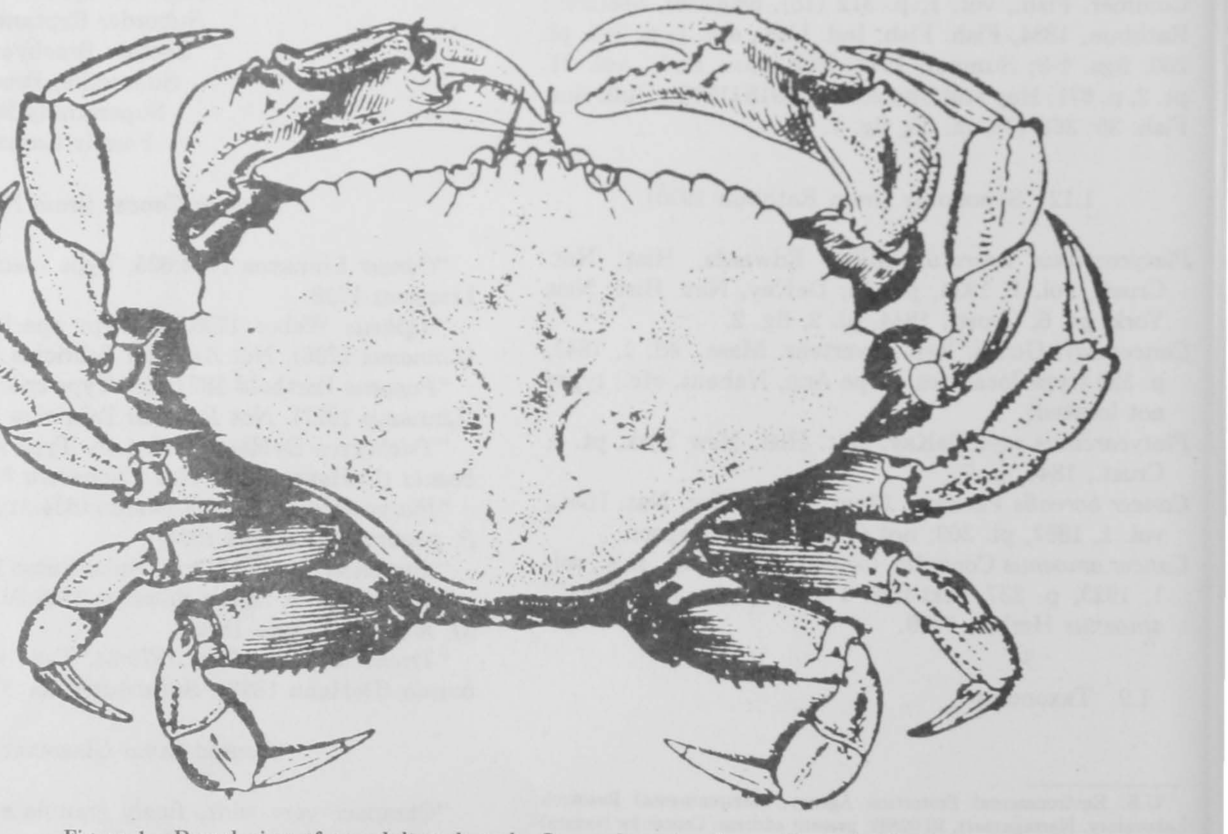

Figure 1.—Dorsal view of an adult rock crab, ***Cancer irroratus*** Say. (From Rathbun 1930.)

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[2] A. B. Stasko, Fisheries and Marine Service, Biological Station, St. Andrews, New Brunswick, Canada, EOG 2X0, pers. commun., Oct. 1977.

[3] P. A. Haefner, Jr. 1976. *Cancer* crabs: aids to identification. Virginia Institute of Marine Science, Advisory Service #10, Gloucester Point, Va.

1.33 Anatomical and biochemical characteristics

Skobe and Nunnemacher (1970) studied the fine structure of the circumesophageal nerve. One rock crab (carapace width 65 mm) had a connective nerve of 0.29 mm in diameter. Within the connective were numerous fibers, ranging from <1 μ (fine) up to 25 μ (large). Fine fibers (<1 μ) and small (1-3 μ) fibers comprised the majority of all fibers with 41 and 47%, respectively. Medium-sized fibers (3-9 μ) accounted for 11%, and only 1% of the fibers were rated as large (9-25 μ).

Various organs and fluids of C. irroratus have been analyzed for biochemical content. Cooke and Goldstone (1970), upon examining the pericardial organs for monoamines, found a green-fluorescing and a yellow-fluorescing system of axons and terminals.

Functional organization of the propus-dactylus organ consisted of paired neurons in one scolopidium that were sensitive to the same directional stimulus (Hartman 1966; Hartman and Boettiger 1967). Certain movement cells showed position sensitivity.

Blood sugar analysis by Telford (1968) revealed a mean glucose level of 8.1 mg/100 ml in animals collected off Maine during May and June. Reducing substances were 11.9/100 ml. No difference was found between sexes. Jeffries (1966) found a mean concentration of 2.11 mg glucose/100 ml serum and 2.41 mg phosphate/100 ml serum in the rock crab.

A study to determine the characteristics of hemolymph upon infection by the bacterial pathogen *Gaffkya homari*, recently renamed *Pediococcus homari* (Section 3.3.5), determined several hemolymph protein values: mean hemolymph serum protein 23.0 mg/ml ± 10.5; mean hemocyte values/mm^3 × 10^4 were 2.24 ± 1.14, correlation coefficient (cells/serum protein) of 0.723; ratio of hemocytes (Lga:Sga:Ly or large granule amoebocytes: small granule amoebocytes: lymphocytes) of 16:10:1; and a hemolymph pH of 7.38 ± 0.1 at 20°C (Stewart and Dingle 1968).

Biochemical analyses of digestive gland enzymes in the rock crab (Hiltz and Lightle 1970) determined the mean activities of β-glucuronidase and arylsulphatase as 53 and 115 μg phenol liberated/g powder per h, respectively.

Carbohydrase analyses of *C. irroratus* tissue homogenates revealed a strong activity on the substrates glycogen and maltose, a moderate activity on amylose and amylopectin, and a very slight activity on trehalose, raffinose, α-lactose, β-lactose, cellobiose, and laminarin. No activity was recorded on sucrose, mannan, turanose, melezitose, melibiose, cellulose, fucoidin, lichenin, galactin, xylan, methyl glucoside, or innulin (Telford 1970).

Blood samples taken directly from the heart of male rock crabs were analyzed by Dean and Vernberg (1965) for the chromatographic presence or absence of blood carbohydrates. Of the carbohydrates tested, maltotetraose, maltotriose, maltose, glucose, galactose, and a galactan derivative were present and mannose and fucose were absent.

2 DISTRIBUTION

2.1 Total area

Cancer irroratus inhabits the continental shelf and slope waters from Labrador to South Carolina (Rathbun 1930; Squires 1966; Williams 1965; Nations 1975); Jeffries (1966) listed the southernmost limit as Florida while Carpenter[4] has positively identified *C. irroratus* in the Straits of Florida. The crab typically occurs in shallow waters in its more northern habitats (Williams 1965; Templeman 1966), in deeper, sandy-bottom regions further south (MacKay 1943), and in bays and inlets in intermediate areas (Jeffries 1966). Most of these distributional patterns vary seasonally, especially south of Massachusetts and Rhode Island.

2.2 Differential distribution

2.21 Spawn, larvae, and juveniles

Sastry and McCarthy (1973) found ovigerous females with eggs nearing hatch from late April (water column 5°C) to early June (15°C at bottom, 19°C at surface) in Narragansett Bay. Other collections have found ovigerous females from late December through late August in Rhode Island waters (Bigford[5]).

Larvae hatch from late spring throughout the summer months. In Canadian waters, Connolly (1923) and Scarratt and Lowe (1972) collected *C. irroratus* larvae between June and September. Fish (1925) collected larvae at Woods Hole from May to August. Hillman (1964) first found *Cancer* larvae in Narragansett Bay in late May while Frolander (1955) found larvae from April to late October in the same waters. Coastal New Jersey plankton surveys by Sage and Herman (1972) revealed *C. irroratus* larvae in late spring samples. In Delaware Bay, larvae were collected in April, May, and June (Deevey 1960). Sandifer (1973) found *C. irroratus* zoeae (stages I-IV) in lower Chesapeake Bay from May to October, exluding August.

Hillman (1964) first found larvae in Narragansett Bay plankton samples when the bottom-water temperature was 9.2°C and found them last when the surface waters reached 18.4°C. Note that these data were collected prior to verification of the larval description (Section 3.22). These temperature limits are significantly lower than those reported for other decapod larvae within the bay (Hillman 1964). Water reached 9.2°C in late May or early June in Narragansett Bay.

Larval distributions in plankton collections indicated that zoeae hatch offshore. This pattern of occurrence more seaward was observed by Sandifer (1972) in the Chesapeake Bay area and predicted by laboratory experiments by Bigford (1976, 1977). As development proceeds, larvae may be found nearer to shore.

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[4] R. Carpenter, formerly with the Virginia Institute of Marine Science, Gloucester Point, VA 23062, pers. commun., Jan. and June 1978.

[5] T. E. Bigford, formerly with the U.S. Environmental Protection Agency, Narragansett, RI 02882. Unpubl. data.

Juveniles appeared to migrate, or are carried by currents, to shallow waters and the intertidal zone. Krouse (1977) reported an abundance of small juveniles (5-40 mm carapace width) buried in the pebble, rock, and shell debris of the shoreline in Maine.

2.22 Adults

Adult rock crabs are distributed in specific patterns with respect to depth, time of year, substrate, and water temperature. A complete, but dated, listing of the place of capture, substrate, and depth for a series of collections is given by Rathbun (1930). Most collection efforts have been concentrated in the summer months, thereby biasing annual collection data.

Depths of occurrence vary with time of year and sex. Migrations of each sex yield changing patterns of distribution, particularly in coastal waters. In the northern part of its range the rock crab is found along the coast year-round; in the south, frequent shelfward migrations apparently occur that spread the population into deeper (>170 m) waters in the summer months. Tagging studies would verify these migrations.

In southern New England waters the rock crab has been collected at depths up to 170 m (Jones 1973; Reilly 1975); surveys in more southern waters have revealed a tendency toward even deeper waters. Musick and McEachran (1972) found *C. irroratus* at 274 m off the Chesapeake Bight; Haefner (1976) collected rock crabs in the Mid-Atlantic Bight region at depths to 751 m. Rathbun (1930) reported collecting several individuals at 592 m near North Carolina.

Movements of rock crab populations were noted by several researchers. The southern trend, as observed by Jones (1973) in Rhode Island and Cerame-Vivas and Gray (1966) and Shotton (1973) in Virginian waters, is apparently for the crabs to migrate offshore into cooler water temperatures in the summer. Northern populations remain predominantly inshore throughout the year (Krouse 1972; Stasko see footnote 2).

With respect to substrate, the rock crab is found primarily on sand-mud substrates south of Cape Cod (Jeffries 1966; Weiss 1970; Stewart 1972; Shotton 1973; Steimle and Stone 1973). Gulf of St. Lawrence's populations appear to be less selective of substrates in the summer, with crabs common on rock, gravel, sand, and mud (Stasko[6]). Fall collections (Scarratt and Lowe 1972) indicate that these same Canadian crab populations may prefer rock outcroppings in cooler water temperatures. Interspecific competition affects distribution patterns, as discussed in Section 3.33.

Distribution patterns, including migrations, are closely related to time of year and hence water temperatures. During the winter months, southern rock crabs tend to move inshore. In the Chesapeake Bay the shoreward migrations are initiated when water temperatures fall below 15.5°C (usually late October or early November) (Shotton 1973). In Rhode Island waters the inshore movements also begin in mid-autumn (Jones 1973; Bigford see footnote 5).

2.3 Determinants of distribution changes

Cancer irroratus is distributed in specific patterns with respect to temperature, salinity, light, gravity, pressure, substrate, depth, and carapace size. The relative effect of each factor varies with age and time of year.

Zoeae and megalopae were found (Sastry 1970; Sastry and McCarthy 1973) to survive differentially in various temperature-salinity regimes depending upon the stage of development. Tables 1 and 2 show the trend in development and mortality toward an apparent optimum at 15°C and several salinites or 20°C and 25‰. Sandifer (1973) collected zoeae in temperature-salinity ranges of 13.0°-27.9°C and 23.31-32.03‰, respectively. Few larvae were collected above 25°C or below 25‰, reflecting the optima shown in Tables 1 and 2.

Rock crab larvae show differential survival in various temperature regimes. Research by Sastry (1976) showed that both the mean temperature and the range affect survival during larval development. Percent survival of each larval stage was higher under cyclic temperatures; a range of 10°C (10°-20°C or 15°-25°C) resulted in higher survival than cycles with 5°C ranges (Figs. 2, 3; Table 3).

Thermal tolerance limits (LD_{50}) for all five zoeal stages, shown by Sastry and Vargo (1977) were approximately 28°C. Stages II and IV larvae exhibited a slightly higher LD_{50} than the other three zoeal stages; megalopae show a lethal temperature for 50% of the test population at about 27°C, slightly below the zoeal limits.

Adult rock crabs are abundant in Narragansett Bay, R.I., where water temperatures range from 1°C to about 23°C annually (Bigford see footnote 5). Mid-Atlantic Bight populations have been reported in waters of 5.1°-

Table 1.—Stage of development reached by larvae of *Cancer irroratus* in different combinations of temperature and salinity. I-V, zoeal stages; M = megalops stage; C = crab stage. (From Sastry and McCarthy 1973.)

Temp.	Salinity				
(°C)	15	20	25	30	35
10	I	II	M	M	M
15	II	C	C	C	C
20	I	M	C	M	M
25	I	I	I	I	I

Table 2.—Percentage mortality of each stage of *Cancer irroratus* larvae reared in 30‰ salinity at different temperatures. (From Sastry and McCarthy 1973.)

	Temperature			
Stage	10°C	15°C	20°C	25°C
I	16.6	5.5	27.7	100.0
II	13.8	3.7	5.5	
III	25.0	5.5	13.8	
IV	2.7	0	13.8	
V	0	3.7	11.1	
Megalops	41.6	20.3	27.9	

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[6] A. B. Stasko. 1976. Northumberland Strait Program: lobster and rock crab abundance in relation to environmental factors. Int. Counc. Explor. Sea, Doc. CM 1976/k:25, 13 p.

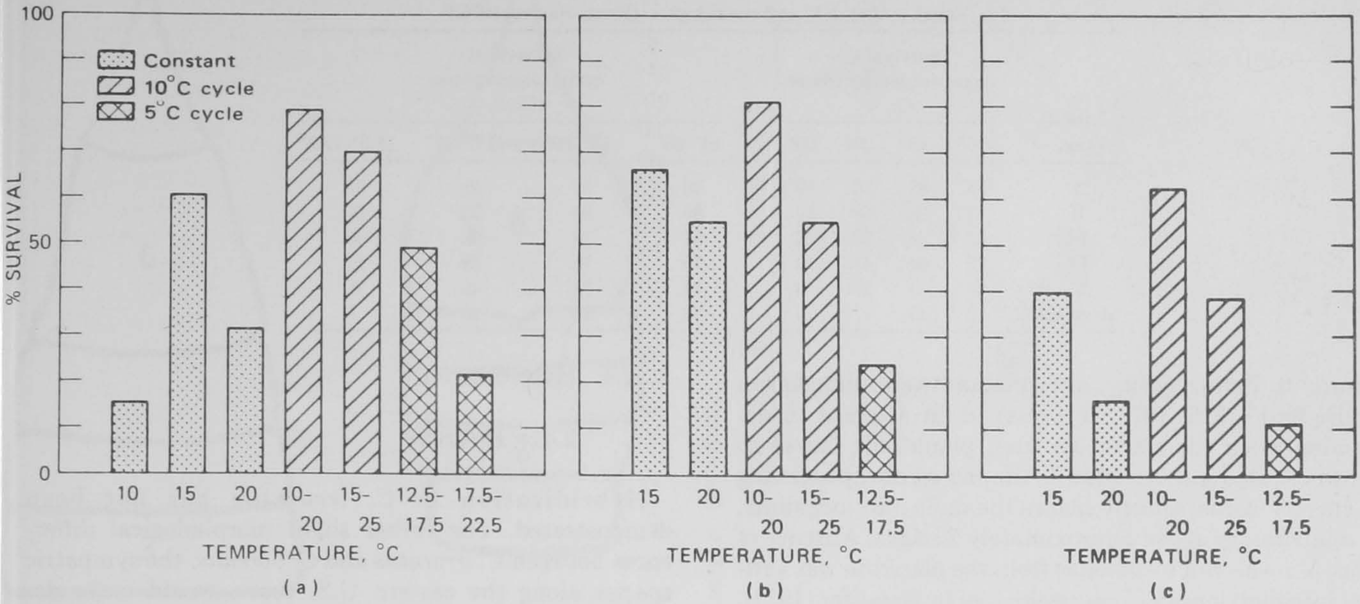

Figure 2.—Percentage survival of *Cancer irroratus* larvae at constant and cyclic temperatures. (a) Hatch to megalops, (b) megalops to crab, (c) hatch to crab. (From Sastry 1976.)

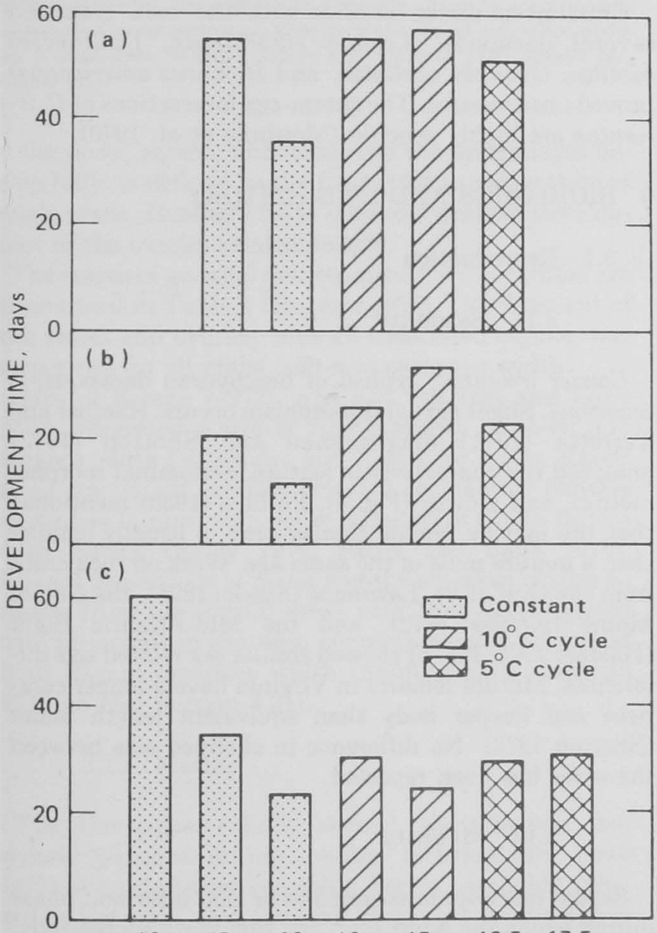

Figure 3.—Duration of larval development in *Cancer irroratus* at constant and cyclic temperatures. (a) Hatch to crab, (b) megalops, (c) hatch to megalops. (From Sastry 1976.)

14.4°C during June sampling (Haefner 1976). Near North Carolina, *C. irroratus* have been collected at temperatures up to 30°C in February and 32°C in May (F. J. Vernberg and W. B. Vernberg 1970). Maximum abundance, as reported by Haefner (1976) for the mid-Atlantic region in June, occurred at 8°-9.9°C, with density slightly lower between 10° and 13.9°C.

MacKay (1943) hypothesized that the key factor affecting the distribution of *Cancer* crabs is temperature. Temperature governs distribution along the entire geographical range of the rock crab, imposing latitudinal and shore-to-shelf gradients. The crabs are rarely found north of the 4.4°C mean surface water temperature isotherm or south of the 23.6°C isotherm.

The influence of salinity is perhaps less severe than temperature. Zoeae, megalopae, and juveniles can survive in salinities ranging from 20 to 35‰ (Table 1). Synergistic effects of temperatures are important in determining the effects of salinity (Sastry and McCarthy 1973). Adult and juvenile crabs are typically oceanic in Narragansett Bay and New England waters; salinity preference appears to be approximately 25-30‰, much like the larvae. (See section 3.35.)

Sastry and Vargo (1977) studied possible seasonal variation in temperature-salinity responses. Results thus far indicated that larvae from winter hatches completed development in 30‰ at 10°C and in 25-35‰ at both 15° and 20°C. Larvae hatching in the spring metamorphosed in 25-35‰ at 10° and 20°C and in 20-35‰ at 15°C. Fall-hatched zoeae completed development in salinities of 20-35‰ at 15°C and 25-35‰ at 20°C. Survival to the first crab stage was highest in spring hatches and lowest in winter hatches. Sastry and Vargo (1977) proposed that previous thermal history, plus the stage of egg development at collection, could influence these changing temperature-salinity limits.

Laboratory studies on the responses of larval *C. ir-*

Table 3.—Survival of *Cancer irroratus* larvae at constant and cyclic temperatures. Zoeal stages I-V and megalops. (From Sastry 1976.)

Larval stage	Survival at constant temperatures (C), %				Survival at cyclic temperatures (C), %			
	10°	15°	20°	25°	10°-20°	15°-25°	12.5°-17°	17.5°-22.5°
I	54	85	76	39	88	87	82	76
II	37	78	68	17	86	83	72	60
III	32	72	58	6	84	78	66	40
IV	20	66	47	0	79	75	58	27
V	15	60	31	0	78	71	49	20
Megalops	0	40	17	0	63	39	12	0

roratus to light, gravity, and pressure were undertaken by Bigford (1976, 1977, in press) in an attempt to determine when the transition from planktonic larvae to benthic crab occurred. Results showed an abrupt settling in stage V zoeae, shortly before the molt into megalopa, at a laboratory age of approximately 20 days. Absence of stage V zoeae and megalopae from the plankton was verified by collections in Chesapeake Bay by Sandifer (1973).

Rock crabs are abundant from nearshore to the continental slope. In the Mid-Atlantic Bight, Haefner (1976) found highest densities of adults between 40 and 60 m on the continental shelf. Densities in Haefner's collection (June) were consistently higher in the shelf zone than either the slope or adjacent canyons. Within these areas there are rather extensive migrations related to water temperature. In Narragansett Bay the population moves into shallow (about 6 m) waters during early autumn and returns to deeper waters (>20 m) during the spring (Jones 1973); Shotton (1973) observed a more widespread migration to depths of 274 m in the warmer months off Virginia. Sexes may migrate independently, as suggested by Jones (1973).

Size has been correlated with population distributions in *C. irroratus* by Haefner (1976). Crabs ≤50-mm carapace width ranged in depth from 10 to 150 m, with both males and females within this stratum. Intermediate-sized crabs (51-100 mm) were most abundant in the shelf-slope areas at 150-400 m. Large crabs (≥101 mm) were mostly in nearshore waters at 20-60 m.

The distribution studies of Haefner (1976) also included analysis of the relationship between crab size and water temperature. As stated by Haefner (1976): "Male crabs ≤50 mm were not found in temperatures ≤6°C, nor females ≤50 mm at ≤8°C. Otherwise this size group was equally abundant from 8 to 13.9°C. Crabs 51-100 mm in size had the broadest temperature range (4-13.9°C for males; 6-13.9°C for females), and were most abundant within the 8-9.9°C temperature stratum. The large male crabs (≥101 mm) were taken within the 8-13.9°C temperature range." Note that these conclusions were based on collections in June only; data for September, November, and January are in preparation by Haefner[7].

2.4 Hybridization

2.41 Hybrids

Hybridization in *C. irroratus* has not been demonstrated. The rather slight morphological differences between *C. irroratus* and *C. borealis*, the sympatric species along the eastern U.S. coast, would make determination of hybridization on the basis of physical characters difficult (Jeffries 1966). However, biochemical analysis of serum phosphate could reveal hybrids (Jeffries 1964, 1966).

Cross-insemination studies with the rock crab and several decapods (*Libinia emarginata, Callinectes sapidus, Ovalipes ocellatus,* and *Homarus americanus*) proved unsuccessful. The sperm-egg interactions of *C. irroratus* are highly specific (Mowbray et al. 1970).

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Cancer irroratus, typical of brachyuran decapods, is dioecious. Slight sexual dimorphism occurs. Haefner and Terretta (1971) diagrammed and Shotton (1973) analyzed the characteristic feature, abdominal morphometrics, and growth (Fig. 4). Phillips (1939) mentioned that the mature female *Cancer* crab is usually smaller than a mature male of the same age. Work on rock crabs from the Gulf of St. Lawrence (Stasko 1975), the Gulf of Maine (Krouse 1972), and the Mid-Atlantic Bight (Haefner 1976; Fig. 5) showed similar sex related size differences. Mature females in Virginia have a longer carapace and deeper body than equivalent length males (Shotton 1973). No difference in cheliped size between the sexes has been reported.

3.12 Maturity

Sexual maturity is assumed to be that intermolt phase during which the adult crab can first mate successfully, as defined by Hartnoll (1969). In males, maturity is accompanied by the presence of fertile spermatozoa within the spermatophores of the vasa deferentia. In females, gonad maturation apparently does not occur until after copulation. Hence, the molt of puberty, where-

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[7] P. A. Haefner, Jr., Biology Department, Rochester Institute of Technology, Rochester, NY 14623, pers. commun., Jan. 1978.

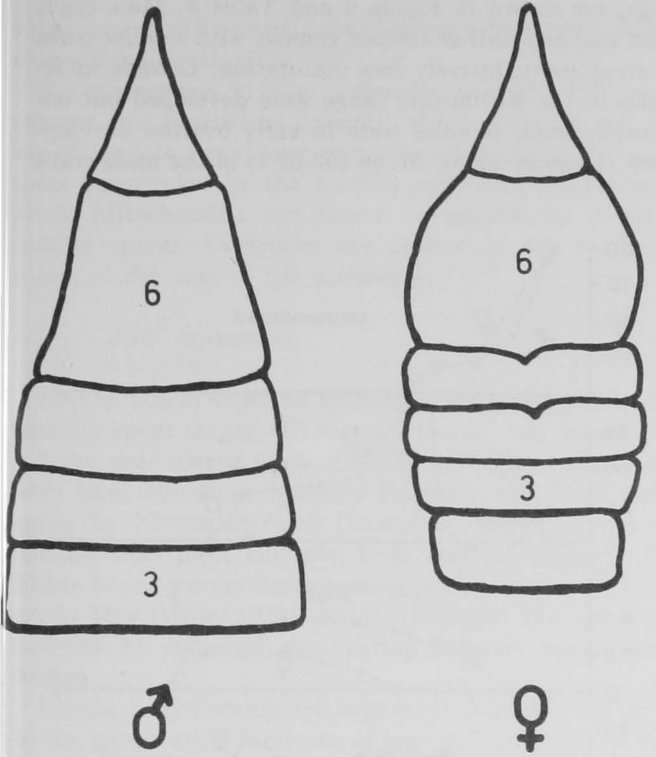

Figure 4.—Sexual dimorphism in abdomen shape in mature male and female *Cancer irroratus*. View is of the dorsal side when abdomen is extended. (From Haefner and Terretta 1971; Stasko text footnote 2.)

by the body, organs, abdomen, and the appendages develop fully, is defined as the final stage in maturation of female crabs. Haefner (1976) showed a gradual development of the ovaries related to size.

The stages of gonadal development for *C. irroratus* are summarized in Table 4 (Haefner 1976). Development of both testes and ovaries, plus all associated organs, was categorized for all crabs >50-mm carapace width.

Data of Krouse (1972), and also Scarratt and Lowe (1972), suggested a size at first maturity of 55-60 mm carapace width for females and 70 mm for males. Rhode Island population samples revealed egg-bearing females as small as 14 mm, with many collected in the 14-25 mm width ranges (Reilly 1975; Reilly and Saila 1978). Gonadal inspections of males and the presence of eggs on females from the coastal areas near Virginia suggested that individuals in southern populations may mature at about 30-mm carapace width (Shotton 1973; Terretta 1973; see also Section 4.31).

3.13 Mating

The Cancridae exhibit several characteristic behavioral patterns during mating. Scarratt and Lowe (1972) suggested that courtship begins, probably initiated by the male, with the male clasping a female across her carapace. (The cradle carriage position is described by Terretta (1973).) This has also been observed in *C. pagurus* and *C. magister* (Hartnoll 1969). At this point the female molts, with mating following shortly thereafter. Typically, the clasping is followed by a postcopu-

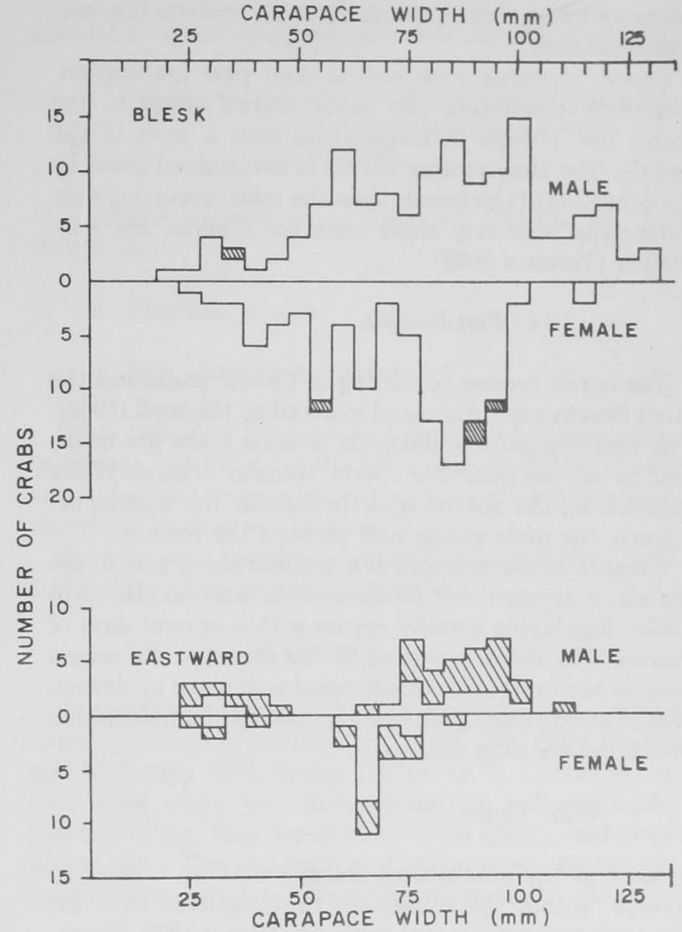

Figure 5.—Width frequency distributions of *Cancer irroratus* collected on two cruises: *Blesk*—30 September-12 October 1971, at 48 stations from Cape Cod (lat. 41°09′N) to Cape Hatteras (lat. 35°37′N) and *Eastward*—24-30 April 1973, off coast of North Carolina. Intermolt (C_1-C_4) stage is represented by the blank area; soft and papershell (A_1-B_2) by the hatched area. Males frequencies are above the line, females below. (From Haefner 1976.)

Table 4.—Stages in gonadal development of *Cancer irroratus*. (From Haefner 1976.)

Stage of development	Male	Female
Undeveloped	Gonads not observed under 40× magnification	
Very slight	Vasa deferentia threadlike, detectable with scope. Colorless.	Ovary threadlike, detectable with scope. Colorless.
Slight	Thickened strands of vasa deferentia evident without scope. Colorless.	Thickened ovary with naked eye. Colorless to white.
Moderate	Testes and vasa deferentia equal approximately one-fourth volume of hepatopancreas. White.	Ovary about one-half volume of hepatopancreas. White, tan to light orange.
Well-developed	Volume of male organs subequal to that of hepatopancreas. White.	Volume of ovary subequal to hepatopancreas. Light orange to orange.
Very well	Testes and vasa deferentia, the dominant internal organs. White.	Ovary larger than hepatopancreas; eggs are obvious. Orange.

latory embrace, during which the male protects the softshelled female.

Cancer irroratus continues to molt past maturation. Therefore, copulation can occur several times in the crab's life, always in conjunction with a molt of the female. The time mating occurs is determined more by the condition of the female than the male, occurring only during the relatively short time the females are softshelled (Terretta 1973).

3.14 Fertilization

The entire process of mating in *Cancer* crabs and the other Brachyura is discussed in detail by Hartnoll (1969). The first two pairs of pleopods in male crabs are modified to act as penislike sperm transfer organs. While transferring the sperm, and throughout the mating sequence, the male grasps and protects the female.

Because of the presence of a seminal receptacle in the female, it appears that fertilization is internal (Hartnoll 1969). Egg-laying usually occurs within several days of mating. The delay is caused by the presence of a semen plug or seal on the receptacle opening (caused by deposition of semen during copulation) and by the maturation of the ovaries after mating.

3.15 Gonads

Most of the brachyuran crabs, including *Cancer irroratus,* within the subsection Brachygnatha have the same generalized internal anatomy (Barnes 1973; Terretta 1973). Both sexes have paired gonads. For the most part, the gonads lie within the thorax (Haefner see footnote 7), occasionally extending to the first few segments of the abdomen. Each branch of the testes and ovaries bears many diverticulae.

The terminal portions of the gonads are adapted for mating and fertilization. In males, the end of the sperm duct is musculated for use an an ejaculatory organ. Usually the duct opens to the outside near the base of the coxa or at a joint of the coxa and sterna. In females, the terminal portions of the ovaries are modified into seminal receptacles which receive sperm from the male pleopods.

The relationship between gonad development and carapace width, and gonad development and intermolt stage, are shown in Figure 6 and Table 5. Male crabs ≥101 mm had well-developed gonads, with smaller crabs showing comparatively less maturation. Gonads in females in the 80-100 mm range were developed but not ripened; small females were in early ovarian development (Haefner 1976). Many (52-82%) of the male crabs

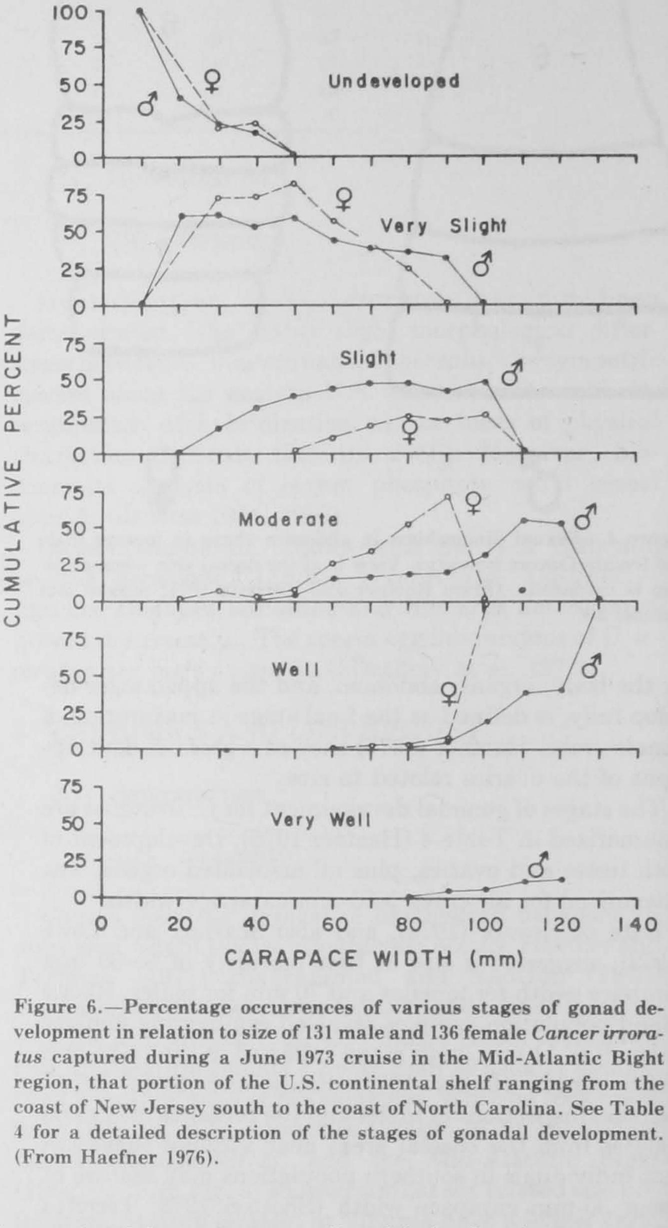

Figure 6.—Percentage occurrences of various stages of gonad development in relation to size of 131 male and 136 female *Cancer irroratus* captured during a June 1973 cruise in the Mid-Atlantic Bight region, that portion of the U.S. continental shelf ranging from the coast of New Jersey south to the coast of North Carolina. See Table 4 for a detailed description of the stages of gonadal development. (From Haefner 1976).

Table 5.—Relationship of intermolt stage and gonad development in 267 *Cancer irroratus* collected during June in the Mid-Atlantic Bight. N = numbers of crabs; % ΣN = percent of the total for each sex; C_1, C_4, etc. = molt stages (see Table 11 and Drach (1939) for explanation). (From Haefner 1976.)

	Male					Female				
Gonad development	ΣN	% ΣN	C_1-C_4	D_2-D_4 (% N)	A_1-B_2	ΣN	% ΣN	C_1-C_4	D_2-D_4 (% N)	A_1-B_2
Undeveloped	6	4.6	16.7	16.7	66.6	7	5.3	14.1	0	85.9
Very slight	27	20.6	14.8	3.7	81.5	26	19.1	7.6	11.5	80.9
Slight	40	30.5	22.5	15.0	62.5	26	19.1	42.4	11.4	46.2
Moderate	29	22.1	38.0	10.2	51.8	71	52.1	80.2	11.2	8.6
Well	23	17.6	60.9	0	39.1	6	4.4	66.7	0	33.3
Very well	6	4.6	83.3	0	16.7	0	—	—	—	—
N	131					136				

with only slight gonadal development had hard-shell characteristics (Haefner 1976).

Spermiogenesis in the Cancridae, including *C. irroratus*, was studied by Langreth (1969). Mature sperm are aflagellate, consisting primarily of a spherical acrosome surrounded by the nucleus with short, radiating arms. Mitochondria are absent or degenerate in the mature sperm. Centrioles are present in the nucleoplasm at the base of the acrosome.

3.16 Spawning

Krouse (1972) reported collecting newly berried and recently spent (egged-off) females periodically throughout the year in the Gulf of Maine. Ovigerous females were most abundant between February and May and again in November and December. Recently spent females were most common from June to August. In Rhode Island waters the spawning peaks are also February to May (Reilly 1975). Jones (1973) and Bigford (see footnote 5) collected egg-bearing females until late August.

Unripe, bright orange-red eggs occur from late fall until the temperature increases of late spring (Reilly 1975; Krouse 1972). The eggs darken to a brick red as summer approaches and development proceeds. A pale grey-brown color typifies an ensuing hatch.

3.17 Fecundity

Reilly (1975) counted the number of eggs from 33 ovigerous females (carapace widths 21-88 mm) and derived a regression equation[8] to estimate the egg count:

$$\log_{10} \text{no. of eggs} = -0.33459 + 3.01016 \log_{10} \text{carapace width (mm)}$$

$$r = 0.986.$$

Egg counts ranged from 4,430 to 330,400 for the specimens.

3.2 Preadult phases

3.21 Embryonic phase

Embryonic development of *C. irroratus* proceeds within the egg. At hatching the larvae are usually fully developed stage I zoeae, although a prezoeal stage has been observed (Bigford see footnote 5).

Eyespots and heartbeats are visible several days prior to hatching (Bigford see footnote 5).

3.22 Larval phases

Cancer irroratus typically has five zoeal stages and one megalopa stage (Connolly 1923; Sandifer 1973; Sastry and McCarthy 1973; Sastry 1977) (Fig. 7). Larvae in the first zoeal stage are characterized by well-developed thoracic limbs, long dorsal and rostral spines, and large lateral eyes. The abdomen and telson show the typical segmentation. As zoeal development proceeds, the seta-

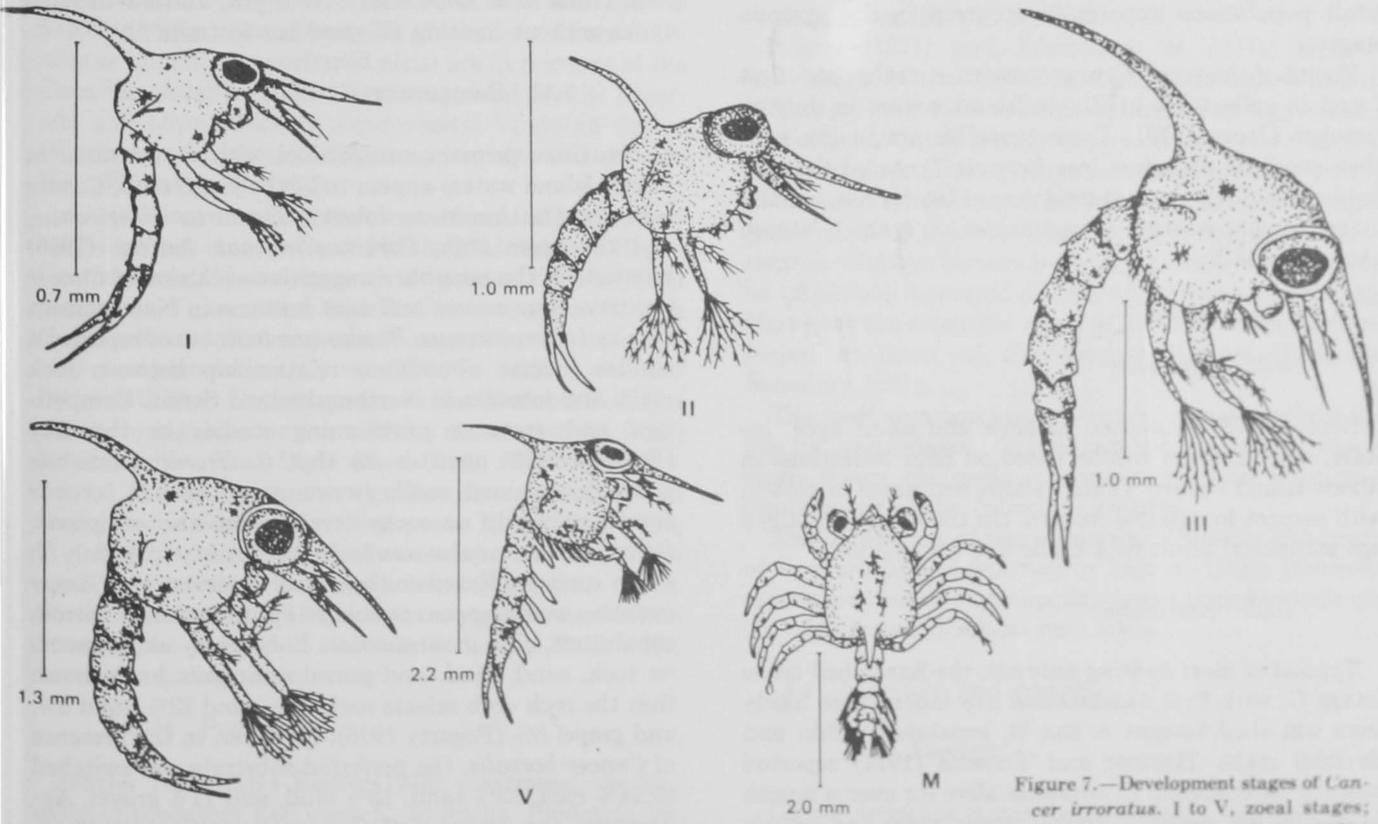

Figure 7.—Development stages of *Cancer irroratus*. I to V, zoeal stages; M, megalops. (From Sastry 1976.)

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[8] Extraction of back-transformed data may involve bias, see Beauchamp and Olsen (1973).

tion patterns on the appendages change and the pleopod buds grow (see summary in Table 6).

Cancer spp. larvae have several morphological features that distinguish them from other southern New England decapods (Hillman 1964). Each abdominal segment bears one pair of small lateral spines; the telson is bifurcate, with 3 inner and 1 lateral spine per fork. Hillman further described the general characteristics of the five zoeal stages. *Cancer* spp. have a long backward curved dorsal spine and a straight rostrum of about equal length. The abdomen bears a pair of hooked spines on the second segment and a pair of smaller spines on segments 3, 4, and 5. The cornua of the telson have a pair of dorsal and a pair of lateral spines. Three pairs of spines are on the lateral margin of the telson. A concave depression lies between the spines.

3.23 Adolescent phases

Little research has been done on juvenile rock crabs, i.e., those crabs that have developed beyond megalopa but are not yet sexually mature. Reilly (1975) calculated mortality rates for subadults on the basis of stomach content analysis of cod, *Gadus callarias,* and little skate, *Raja erinacea.* Results showed that juveniles inhabit both bay waters and saltwater ponds in the Narragansett Bay watershed. Krouse (1977) found juveniles concentrated in the rocky intertidal zones of Maine.

Zooplankton surveys (e.g., Sandifer 1973, 1975) and laboratory experiments (Bigford 1976, 1977, in press) inferred that rock crab larvae settle out of the plankton outside the bay waters they inhabit as adults. Mass migrations or other passive movements to inshore adult populations apparently occurred in the juvenile stages.

Young-of-the-year *Cancer irroratus* crabs are first found in collections in Rhode Island waters in July to October (Jones 1973). These juveniles are in the soft-shell condition. Haefner (see footnote 7) stated that the hardening of the exoskeleton takes at least 1 mo, usually longer in cold weather temperatures, in crabs >50-mm carapace width.

3.3 Adult phase

3.31 Longevity

Reilly (1975) estimated juvenile and adult ages, instars, and carapace widths based on field collections in Rhode Island waters. Table 7 shows estimates in growth with respect to age and instars. On the basis of Reilly's age estimator, adult rock crabs live up to 8 yr.

3.32 Hardiness

Typical of most molting animals, the hard-shell crabs (stage C, with firm exoskeleton) are much more hardy than soft-shell (stages A and B, exoskeleton thin and flexible) crabs. Haefner and Terretta (1971) reported keeping hard-shelled *C. irroratus* alive for over a month in circulating seawater tanks. Adult male and female rock crabs have been held over a year in flow-through tanks without molting (Bigford see footnote 5).

Table 6.—Diagnostic features of stages during larval development of *Cancer irroratus*. (Part from Sastry 1977 and Bigford see text footnote 5.)

Prezoeae	Dorsal and rostral spines lacking; maxilliped natatory hairs reduced; bifurcate telson not pointed and rather blunt, with stage I spines.
SI	Dorsal and rostral spines present; eyes not stalked; maxillipeds 1 and 2 with 4 natatory hairs; each furca of telson with 3 setae on inner side; mandible with one point.
SII	Eyes stalked; maxillipeds 1 and 2 with 6 natatory hairs; each furca of telson with 3 setae on inner side; mandible blunt, without point.
SIII	Maxillipeds 1 and 2 with 8 natatory hairs; each furca of telson with 4 setae on inner side; posterior edge of carapace with 4-6 hairs.
SIV	Maxillipeds 1 and 2 with 10 natatory hairs; each furca of telson with 5 setae on inner side; sixth abdominal segment present; pleopod buds present.
SV	Maxillipeds 1 and 2 with 12 natatory hairs; sixth abdominal segment bilobed; pleopods developed; single palp on mandible.

Table 7.—Estimated age (years) and corresponding instars and carapace widths (mm) for male and female *Cancer irroratus*. (From Reilly 1975.)

	Males		Females	
Age	Instar	Carapace width	Instar	Carapace width
1	IV	13.7	IV	13.7
2	VIII	39.9	VIII	39.9
3	X	65.9	IX	50.8
4	XI	80.4	X	61.1
5	XII	97.3	XI	70.9
6	XIII	116.9	XII	80.1
7	XIV	139.6	XIII	88.9
8			XIV	97.2

3.33 Competitors

The three primary competitors with *C. irroratus* in Rhode Island waters appear to be the jonah crab, *Cancer borealis,* the American lobster, *Homarus americanus,* and the green crab, *Carcinus maenas.* Jeffries (1966) pointed out the possible competitive exclusion of *Cancer irroratus* from coarse sediment bottoms in Narragansett Bay by *H. americanus.* Stasko (see footnote 6) reported a similar inverse abundance relationship between rock crabs and lobsters in Northumberland Strait. Competition and resource partitioning studies in the Bay (Fogarty 1976) have shown that *C. irroratus* inhabits solely fine-grained, sandy environments, and *C. borealis* occurs primarily on rocky terrain, but also on gravel; *Carcinus maenas* also was found by Fogarty to be only on sandy surfaces. Based on these field observations, *Cancer irroratus* would appear to compete with its sandy bottom cohabitant, *Carcinus maenas.* Laboratory experiments on rock, sand, mud, and gravel sediments have shown that the rock crab selects rock 62%, sand 23%, mud 8%, and gravel 6% (Fogarty 1976). However, in the presence of *Cancer borealis,* the preferred substrate was switched to 24% rock, 52% sand, 13% mud, and 11% gravel. Apparently, the presence of *C. borealis* competitively excludes the rock crab from its preferred substrate. *Carcinus maenas* and *Cancer irroratus* pairings were not studied.

The competitive resource could be shelter. Fogarty (1976) has shown that *C. irroratus* will utilize a laboratory shelter 100% of the time when no jonah crabs are present. With rock and jonah crabs both in the tank, *C. irroratus* achieved control of the protective shelter in only 28% of the cases, with 64% having *C. borealis* and the remainder shared by both species. This again confirms displacement of *C. irroratus* by *C. borealis.*

As a result of the competitive pressures of *C. borealis,* the rock crab is found primarily on sandy substrates. This limitation appears to be by behavioral competition and not its physical attributes (Fogarty 1976). Interspecific agonistic encounters between the *Cancer* congeners show that *C. borealis* induces direct avoidance reactions in *C. irroratus;* the rock crab causes no such behavior in the jonah crab (Fogarty 1976).

Rock crab survival on sandy substrates, including avoidance of competitors (*Carcinus maenas*) and predators, is enhanced by burial in the upper layers of sediment. As shown by Jeffries (1966), *Cancer irroratus* is better suited to extended locomotory efforts than *C. borealis.* Fogarty (1976) has shown a similar advantage for the rock crab in burial time; *C. irroratus* can completely bury itself in an average of 16.3 s, while *C. borealis* requires about 48.9 s. Slightly larger pereiopods may assist the rock crab in its burial activity. The complete sequence of burial is described by Fogarty for *C. irroratus.*

These competitive pressures do not exist throughout the range of the rock crab. In the absence of either *C. borealis* and/or *Homarus americanus,* the rock crab is found in rocky areas. Examples of locations where *C. irroratus* inhabits its preferred niche are in portions of the Canadian Atlantic coast (Northumerland Strait) (Scarratt and Lowe 1973), in some coastal Virginian waters (Haefner and Terretta 1971), and in parts of Delaware Bay (Winget et al. 1974).

A coefficient of association was calculated by Haefner (1976) for rock crabs collected in the Mid-Atlantic Bight. Contingency tables were used to compute Cole's (1949) coefficient of association (C_7) for *C. irroratus* paired with *C. borealis* and *Homarus americanus.* Results showed a very close association ($C_7 = 1.000, P = 0.025, t = 4.427$) between the two *Cancer* species in the Chesapeake Bight region during June and a negative association for October in the New York Bight ($C_7 = 0.483, P = -0.025, t = 2.322$). The rock crab was significantly associated with the lobster in June in the Chesapeake Bight ($C_7 = 0.766, P = 0.025, t = 2.353$), which was expected due to the positive association between lobster and jonah crabs. Stasko (see footnote 6) has shown a negative association between the rock crab and lobster in the Gulf of St. Lawrence during the summer.

3.34 Predators

Jeffries (1966) and Reilly (1975) mentioned the activity of predatory fish upon *C. irroratus.* Predation by cod, *Gadus callarias,* and little skates, *Raja erinacea,* on the Rhode Island rock crab population has been used as an indicator of predation (Reilly 1975). Reilly showed that there was a tendency for skates to prey upon juveniles <20 mm wide more extensively than cod do. Other fish known to feed on rock crab juveniles and adults include smooth dogfish, *Mustelus canis;* red hake, *Urophycis chuss;* ocean pout, *Macrozoarces americanus;* longhorn sculpin, *Myoxocephalus octodecimspinosus;* toadfish, *Opsanus tau;* cunner, *Tautogolabrus adspersus;* tautog, *Tautoga onitis;* striped bass, *Morone saxatilis;* and goosefish, *Lophius americanus* (Field 1907; Bigelow and Schroeder 1953; Reilly 1975; Reilly and Saila 1978).

Ennis (1973) reported that in Bonavista Bay, Newfoundland, *C. irroratus* and several other decapods make up a total of almost 50% of the stomach contents of *Homarus americanus.* The intensity of predation varied seasonally, reaching a minimum in midsummer. Rock crabs also comprised about 28% of the stomach contents of lobster in Nova Scotia seaweed communities (Miller et al. 1971).

Mention was made by Sastry (1971) that *C. irroratus* larvae are cannibalistic under laboratory conditions. For this reason individualized culture systems are frequently used.

3.35 Parasites, diseases, injuries, and abnormalities

Many of the common fouling organisms observed on adult rock crabs were identified by Haefner and Van Engel (1975) and Haefner (1976). As noted in Table 8, the fleshy ectoproct *Alcyonidium* is abundant on *C. irroratus* in waters <75 m deep.

Sastry (1971) and Johnson et al. (1971) reported infestations of the bacterium *Leucothrix mucor* in both laboratory and field studies, primarily on egg masses. Use of penicillin G greatly depressed bacterial counts in the recirculating seawater systems used by Sastry (1971).

Cornick and Stewart (1968) found a moderate pathogenic effect of the bacterium *Gaffkya homari* on *C. irroratus. Gaffkya homari* is the transmittor of gaffkemia, an often fatal bacterial disease of *Homarus americanus.* Note that the scientific name of *Gaffkya homari* was rejected in favor of *Pediococcus homari* (Editorial Secretary 1971).

The most common injury observed in rock crabs is the loss of appendages. Trawl samples frequently reveal crabs minus chelipeds or pereiopods. This may be a direct result of the collection process.

The occurrence of two immature albinistic specimens of *C. irroratus* was reported by Dexter (1968). However, albinism is rare in anthropods; these two individuals are the only recorded albino rock crabs.

3.4 Nutrition and growth

3.41 Feeding

Cancer irroratus is mostly carnivorous, and cannibalistic to an extent. The degree of cannibalism appears to

Table 8.—Incidence and type of fouling organisms observed on *Cancer irroratus* captured in June in the Mid-Atlantic Bight. See Table 11 for a description of the molt stages. (From Haefner 1976.)

	Hard and peeler crabs			Papershell crabs		
Depth (m)	Total no.	Fouled (%)	Fouling organisms	Total no.	Fouled (%)	Fouling organism
10-20	5	40.0	*Alcyonidium* sp.	2	0.0	—
		20.0	Gastropod eggcase			
20-40	60	20.0	*Alcyonidium* sp.	51	3.9	*Alcyonidium*
		3.2	*Octolasmis loweii*			
		1.6	*Hydractinea* sp.			
40-60	40	15.0	*Alcyonidium* sp.	29	0.0	—
		2.5	*Octolasmis loweii*			
		5.0	*Hydractinea* sp.			
75-150	15	0.0	—	28	0.0	—
150-400	15	0.0	—	11	0.0	—
Total	133	20.0		121	1.6	

be density dependent. It may be that cannibalism is solely a laboratory phenomenon; Scarratt and Lowe (1972) reported that parts of rock crab shell were found in the stomach of only one rock crab collected in the field.

Feeding is accomplished with the aid of both the chelipeds and pereiopods, which hold the food up to the mouthparts. Food is torn up by opposing movements of the mouthparts.

3.42 Food

Rock crabs held in the laboratory were fed combinations of chopped quahaug, *Mercenaria mercenaria;* blue mussel, *Mytilus edulis;* assorted fish; and thawed adult brine shrimp, *Artemia salina* (Bigford see footnote 5). Haefner and Van Engel (1975) offered squid, although only papershell (molt stages A_2 and B_1) crabs accepted it. No studies were conducted relating the nutritive value of these foods to the needs of the crabs. Gut content analyses (Table 9) revealed that pelecypods such as the mussel, plus other animal and plant tissues, are consumed by field populations of *C. irroratus.*

3.43 Growth and morphometry

In the laboratory, the duration of completion of the five zoeal and one megalopa stages varies depending on temperture cycles, salinity, culture conditions, and food. With a constant temperature regime, development proceeded fastest (37 to 58 days) to first crab stage at 15°C and 30‰ (Sastry 1970, 1971). The duration of zoeal development was usually shorter and megalopal development longer when larvae were reared in cyclic (5° or 10°C range; 10°-25° minimum, maximum) temperatures at 30‰ (Sastry 1976).

Growth of *C. irroratus* adults has been studied by Shotton (1973), Reilly (1975), and Haefner and Van Engel (1975). Results from Shotton's morphometry studies (Table 10) implied that length-width relationships in the rock crab are linear. One exception was the curvilinear ratio of propodus length on carapace width in males ≥30 mm (Table 10). Generally, the various body proportions showed an abrupt change at approximately 30-mm carapace width. This was particularly true of abdomen width, an indicator of sex and maturity (see Sections 3.11 and 3.12).

Krouse (1977) suggested that at carapace widths below 60 mm both sexes have the same growth rate. One linear regression (see footnote 8), $Y = 0.556 + 1.247X$ (where Y = postmolt carapace width and X = premolt carapace width), described the growth rates for crabs ranging in size from 9 to 48 mm. Beyond that size, changes due to sexual maturity complicated the growth relationship.

Studies by several investigators have shown that male rock crabs are larger than females in carapace dimensions. Maximum carapace widths were 141 mm for males and 106 mm for females in Virginian waters (Shotton

Table 9.—Analysis of stomach contents (number with each food, percent total, weight of food) of *Cancer irroratus* in the Gulf of St. Lawrence, Canada. (From Scarratt and Lowe 1972.)

	6-30 June 1967			21 Sept.-5 Oct. 1967		
Item	No.	%	g/kg	No.	%	g/kg
Total examined	202	—	—	28	—	—
Empty	50	29.2	—	—	—	—
Amorphous matter	71	35.1	1.6	23	82.1	2.2
Liquid	36	17.8	1.0	10	35.7	0.9
Polychaeta	39	19.3	1.0	5	17.8	0.3
Shell fragments	31	15.3	0.4	5	17.8	0.1
Sand	21	10.4	0.2	—	—	—
Eelgrass (*Zostera*)	9	4.4	0.1	—	—	—
Sea urchin (*Strongylocentrotus*)	8	4.0	<0.1	3	10.7	<0.1
Mussel (*Modiolus*)	6	3.0	0.2	9	32.2	0.1
Amphipoda	5	2.5	<0.1	1	3.6	<0.1
Pelecypoda	4	2.0	0.1	1	3.6	<0.1
Gastropoda	3	1.5	<0.1	1	3.6	<0.1
Porifera	3	1.5	0.1	—	—	—
Rhodophyceae	3	1.5	<0.1	—	—	—
Tunicata	3	1.5	<0.1	1	3.6	<0.1
Cumacea	2	1.0	<0.1	—	—	—
Asteroidea (*Asterias*)	2	1.0	<0.1	4	14.3	0.2
Chiton	1	0.5	<0.1	2	7.1	<0.1
Foraminifera	1	0.5	<0.1	—	—	—
Isopoda	1	0.5	<0.1	—	—	—
Turbellaria	—	—	—	1	3.6	<0.1
Cancer irroratus	—	—	—	1	3.6	<0.1

1973). Boothbay Harbor, Maine, populations were also sexually dimorphic (Krouse 1972). Industrial trawl samples from Rhode Island revealed a maximum carapace width of 126 mm for males and 100 mm for females (Reilly 1975). Differences in carapace length between the sexes are reflected in the regression equations shown in Table 10.

The adult width-weight relationship has been calculated for crabs from Casco Bay and Boothbay Harbor by Krouse (1972)n from Narragansett Bay by Fogarty (1976), and from Chesapeake Bay by Haefner and Van Engel (1975). Krouse's calculations, based on wet weights taken to the nearest 10 g, yielded an exponential curve. The regression equations (see footnote 7) showed a slight difference between the two Maine sites:

Boothbay Harbor—

$$\log_{10} \text{weight} = -3.39 + 2.82 \log_{10} \text{carapace width}$$

Casco Bay—

$$\log_{10} \text{weight} = -3.60 + 2.94 \log_{10} \text{carapace width.}$$

Sexes were grouped during Krouse's analysis since there were no significant differences in regressions (see footnote 8) between males and females. Haefner and Van Engel also determined the width to weight relationship:

$$\log_{10} \text{premolt weight} = -4.06 + 3.14 \log \text{premolt width}$$

$$\log_{10} \text{postmolt weight} = -4.14 + 3.14 \log \text{postmolt width.}$$

Differences in regression equations reported by these researchers arose from both methodology and the conditions of the crabs. While Krouse (1972) recorded weights to the nearest 10 g, Haefner and Van Engel (1975) used 0.1-g calibrations. Krouse also used a different method of determining carapace width than did Haefner and Van Engel. Scarratt and Lowe (1972) have also calculated width-weight regressions, but they used preserved crabs. All other studies reported here utilized fresh crabs. Haefner and Van Engel presented a detailed discussion of crab width to weight relationships.

Table 10.—Regressions of body measurements from juvenile and adult *Cancer irroratus* in Virginia waters. (From Shotton 1973.)

Measurement	Sex	Size (mm)	Regression equation
Carapace length (CL) on carapace width (CW)	M	<30	CL = 1.48+0.63 CW
	F	<30	CL = 0.94+0.69 CW
	M	≥30	CL = 2.17+0.62 CW
	F	≥30	CL = 2.91+0.62 CW
Left cheliped propodus length (PL) on carapace width (CW)	M	<30	PL = 0.89+0.40 CW
	F	<30	PL = 0.47+0.42 CW
	M	≥30	PL = 3.76+0.31 CW +0.00131 CW^2
	F	≥30	PL = 1.25+0.47 CW
Body thickness (BT) on carapace width (CW)	M	<30	CT = 0.42+0.33 CW
	F	<30	CT = 0.04+0.38 CW
	M	≥30	CT = 0.50+0.34 CW
	F	≥30	CT = 1.35+0.34 CW
Thickness (CT) on width (CW)	M	all	CT = 0.32+0.34 CW
	F	all	CT = 0.87+0.35 CW
Width (CW) on thickness (CT)	M	all	CW = −0.28+2.91 CT
	F	all	CW = 1.66=2.84 CT
Abdomen width (AW) to carapace width (CW)	M	<30	AW = 0.09+0.13 CW
	F	<30	AW = 0.71+0.22 CW
	M	≥30	AW = 0.90+0.15 CW
	F	≥30	AW = 3.75+0.30 CW

3.44 Metabolism

Oxygen consumption rates in the zoeal and megalopa stages (Figure 8) were studied by Sastry and McCarthy (1973) and Sastry and Vargo (1977). Stage I zoeae, which are the most insensitive to temperature, showed a relatively constant Q_{10} of <2 in temperatures ranging from 5° to 20°C. Second stage zoeae showed a marked increase in Q_{10} between 5° and 15°C, with a maximum Q_{10} of 6.26. As with stage I and II zoeae, the third stage larvae

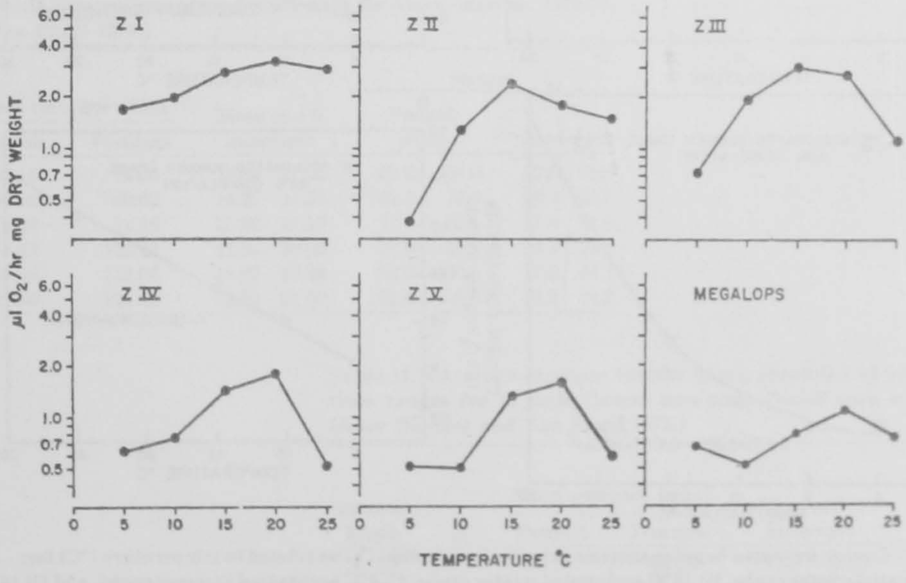

Figure 8.—Metabolic-temperature response curves for the five zoeal and one megalopal stages of *Cancer irroratus*. (From Sastry and McCarthy 1973.)

exhibited depressed oxygen consumption above 20°C. The last two zoeal stages showed an increase in Q_{10} between 10° and 15°C. Generally, these zoeal Q_{10} values inferred a more stenothermal tendency in later stage larvae. At the optimal temperature range of 10°-15°C or 15°-20°C, Sastry and McCarthy (1973) found a typical Q_{10} of about 1-2; one exception was the fifth zoeal stage, which had a Q_{10} of 7 at 10°-15°C.

The metabolic adaptation of adult rock crabs to temperature acclimation was studied by Jones (1973). Oxygen consumption of winter-collected crabs from Rhode Island increased for the first 3 wk of laboratory holding. During this period the consumption rate changed from 0.84 μl O_2/mg dry wt per h for field animals to 1.50 μl after 1 wk at 18°C and 0.90 μl after 3 wk. This latter value appeared to be the acclimated oxygen consumption value for 18°C.

Specific patterns of organ respiration varied according to the collection and holding temperatures (Figure 9). Acclimation to temperatures near the seasonal temperatures resulted in a linear regression line; acclimation to out-of-season temperatures caused a curvilinear response of hepatopancreas oxygen consumption to temperature.

Metabolic rates, measured by oxygen consumption, of rock crabs collected in South Carolina waters revealed seasonal shifts and a tendency to decrease above 20°C (W. B. Vernberg and F. J. Vernberg 1970). Highest oxygen consumption, found at 10° and 15°C, was 53.73 and 92.55 μl O_2/h per g, respectively.

3.45 Molting

The molt stages of *C. irroratus* have been categorized according to exoskeleton firmness (Table 11). Molt times varied with geographical location, age, and sex. Investigations by Krouse (1972) in the Gulf of Maine showed that months of peak shedding varied for each sex. The percent male shedders was highest in February and March; female shedders were most common in September and October. In Virginia coastal waters, the sexes also showed different molting cycles; recently molted males outnumbered females in winter and spring trawl catches (Shotton 1973).

Cancer irroratus populations near the Maine coast molt in late winter or early fall, depending on the sex (Krouse 1972). Boston Harbor populations molt between December and April (Turner 1954). In Narragansett Bay, percentages of postmolt rock crabs increase progressively between December and April, falling off in May (Jones 1973). Jeffries (1966) claimed that most sheddings occur between May and June in Narragansett Bay. In Chesapeake Bay molting occurs in January in both sexes (Haefner and Terretta 1971); by mid-Febru-

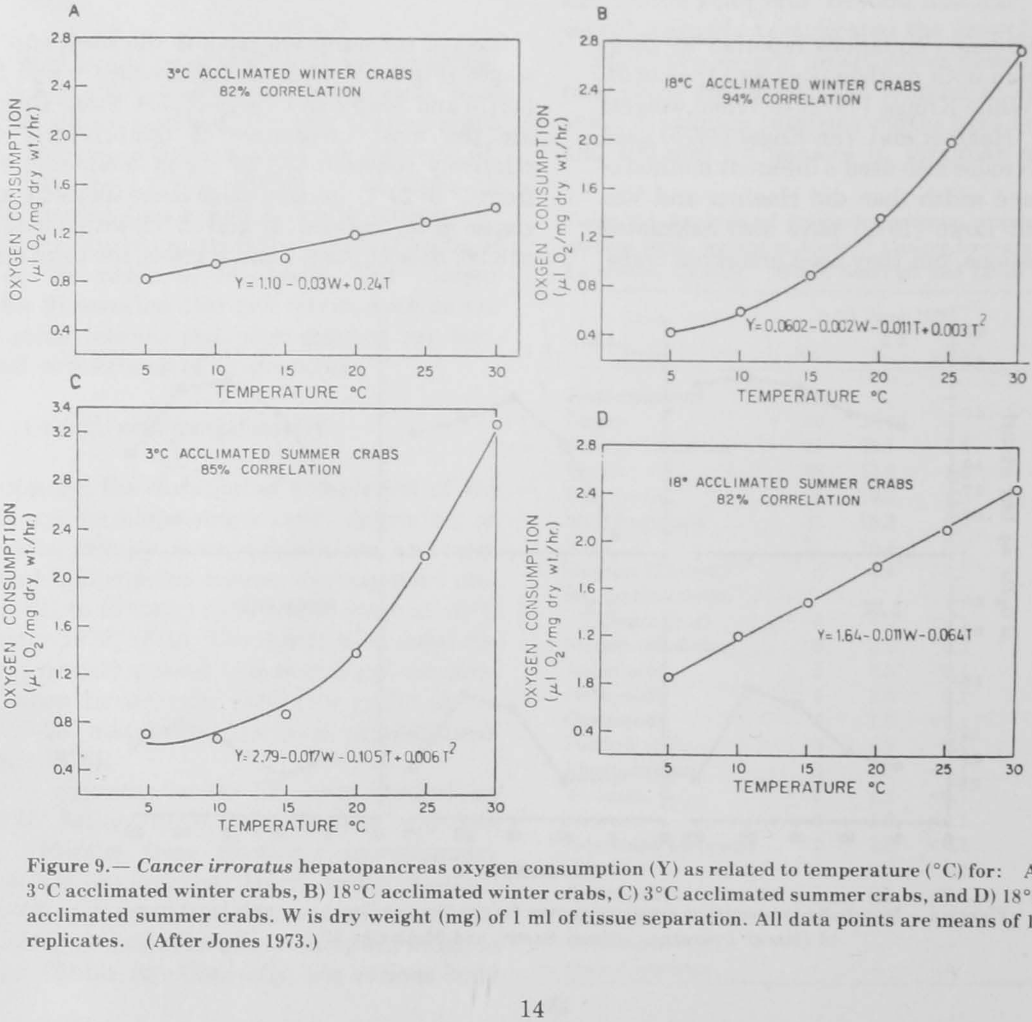

Figure 9.— *Cancer irroratus* hepatopancreas oxygen consumption (Y) as related to temperature (°C) for: A) 3°C acclimated winter crabs, B) 18°C acclimated winter crabs, C) 3°C acclimated summer crabs, and D) 18°C acclimated summer crabs. W is dry weight (mg) of 1 ml of tissue separation. All data points are means of 10 replicates. (After Jones 1973.)

Table 11.—Molt cycle stages of *Cancer irroratus*. Modified from Drach (1939). (From Haefner and Van Engel 1975.)

Condition	Stage	Description
Hard	C_1-C_4	Shell very firm, strong; finger pressure on subbranchial area of carapace does not cause indentation or flexing of shell. No limb buds present at site of lost appendages.
Early peeler	D_0-D_1	Shell firm, but finger pressure along subbranchial ecdysial suture line reveals slight flexibility. Limb buds may be present.
Advanced peeler	D_2-D_3	Shell firm, but finger pressure along ecdysial suture line reveals marked flexibility without cracking the line. Limb buds may be present and may be well developed.
Early buster	D_4	Ecdysial suture cracks with light finger pressure. Limb buds when present usually well developed.
Buster	D_4	Ecdysial suture visibly separated; separation measureable at posterior edge of carapace at its junction with the abdominal segments 1 and 2. Limb buds, when present, usually well developed.
Soft	A_1	Newly molted. Skeleton very soft. Still in process of water uptake.
Early papershell	A_2	Exoskeleton leathery, pliable to the touch.
Mid-papershell	B_1	Exoskeleton thin, brittle; dents under finger pressure but returns to normal shell configuration when pressure is released; merus and propodus of legs bend without breaking.
Late papershell	B_2	Exoskeleton brittle but thick; finger pressure may fracture shell; merus and propodus crack when bent; anterolateral spines hard.

ary more than 90% of the crabs were papershells (Terretta 1973). Early summer collections in the mid-Atlantic reveal that 67% of the crabs were in molt stages A_1-B_2, indicating a recent molt. Of the remaining crabs, 12% were preparing to molt (D_2-D_4) and only 12% were hard shell (C_1-C_4) or in the intermolt period (Haefner 1976).

Detection of premolt signs was discussed by Haefner and Van Engel (1975). The best single characteristic to describe the different molt stages was shell rigidity, on which Table 11 is based. However, numerous secondary observations were recorded. Detachment of the epidermis and the formation of new setae on maxillae and maxillipeds marked the development of a new exoskeleton. These traits were visible at 15-20× magnification. No changes in color were observed to accompany the succession of intermolt stages preceded by the molt.

A technique has been described by Haefner and Van Engel (1975), to determine proximity to molting by dislocating and removing the dactyl of a cheliped. If the break is clean and the new exoskeleton emerges undamaged, the crab is nearing a molt; rough breaks resulting in torn tissue are indicative of a hard-shell crab.

Each molt is accompanied by several changes in body proportions, especially carapace width, carapace length, and weight. The changes are typically linear increases (Haefner and Van Engel 1975) of approximately 20-25% (Scarratt and Lowe 1972; Haefner and Van Engel 1975; Reilly 1975), decreasing slightly as size increases (Tables 12, 13, 14). Size regressions (see footnote 8) between premolt and postmolt size have been described by Haefner and Van Engel (1975) and Reilly (1975):

Postmolt width (mm) = 3.93 + 1.16 premolt width (mm) for 125 males

Postmolt length (mm) = 1.61 + 1.16 premolt length (mm) for 60 crabs sexes combined)

Postmolt weight (g) = −5.33 + 163 premolt weight (g) for 57 males (28.7-141.6 g; $r^2 = 0.9506$).

Further changes in weight occurred during the many molt stages. A 0.5-3% loss from initial weight was

Table 12.—Average carapace widths (mm), absolute and precentage increments, and their ranges for 125 male *Cancer irroratus*. Pooled data for three seasons, 1970-73. (After Haefner and Van Engel 1975.)

Premolt width	*N*	Mean carapace width		Mean and % increment		Ranges			
		Premolt	Postmolt			Premolt width		Increment	
51-60	4	58.15	74.03	15.88	27.25	57.6	59.0	10.5	19.0
61-70	22	66.42	80.62	14.20	21.38	61.5	70.0	10.4	23.0
71-80	40	75.23	91.16	15.93	21.18	71.0	80.6	11.6	21.6
81-90	37	85.63	103.47	17.84	20.83	81.0	90.7	10.4	23.0
91-100	18	95.29	113.96	18.67	19.59	92.0	100.3	17.0	27.1
101-110	4	102.96	125.60	22.63	21.98	101.8	105.0	18.2	24.0

Table 13.—Average carapace lengths (mm), absolute and precentage increments, and their ranges for 43 male *Cancer irroratus*. Pooled data for three seasons, 1970-73. (After Haefner and Van Engel 1975.)

Premolt length	*N*	Mean carapace length		Mean and % increment		Ranges			
		Premolt	Postmolt			Premolt length		Increment	
31-40	2	38.70	44.15	7.45	19.10	37.5	39.9	5.3	9.6
41-50	15	45.93	55.89	10.73	23.13	41.1	50.8	6.8	14.2
51-60	17	55.45	65.85	10.41	18.82	51.1	60.6	5.7	16.1
61-70	10	64.51	76.60	12.09	18.68	62.6	66.6	8.5	15.7

Table 14.—Average weights (g), absolute and percentage increments, and their ranges for 57 male *Cancer irroratus*. Arranged according to carapace width (mm). Pooled data for three seasons, 1970-73. (After Haefner and Van Engel 1975.)

Premolt width	*N*	Mean weight		Mean and % increment		Ranges			
		Premolt	Postmolt			Premolt weight		Increment	
51-60	3	30.1	54.6	24.5	81.8	28.7	32.4	22.3	26.8
61-70	16	47.0	71.1	24.1	52.0	35.7	58.8	14.5	38.1
71-80	22	69.4	106.3	36.9	52.6	49.0	86.7	16.4	63.1
81-90	14	99.6	159.1	59.5	59.3	89.2	120.5	31.7	74.1
91-100	2	138.7	220.2	81.5	58.7	135.7	141.6	74.8	88.2

observed during the first 2-3 days premolt. When the ecdysial sutures opened, the body weight may increase up to 90% due primarily to water uptake (Haefner and Van Engel 1975). Typically, the water content remained constant at approximately 65-70% during molt stages C_4, D_0, D_2-D_3, and D_4 (identified in Table 12). During D_4, water is absorbed until the percent content reaches 80-90% in stage A_1. Stages A_2, B_1, and B_2 also exhibit this higher water content level.

Comparisons of crab weights from various collections may necessitate some form of standardization for varying calcification rates. Richards and Richards (1965) described a decalcification technique for *C. irroratus.*

Cancer irroratus, like all brachyurans, possess a series of neurosecretory complexes within their eyestalks that control the molting process. Removal of a portion of the eyestalk (Simione and Hoffman 1975) affects one of these endocrine organs (Y-organ) specifically. Resultant changes in the Y-organ include an increased rate of RNA synthesis and an increased cell volume. Both of these Y-organ changes occur immediately following partial eyestalk ablation and persist for 4 or 5 days thereafter.

Larval diet studies have been undertaken by Bigford (see footnote 5). Measurements of zoeae reared on a diet of newly hatched brine shrimp, *Artemia salina,* are presented in Table 15. At these stages sexes could not be differentiated.

Measurements of juvenile crabs collected intertidally are listed in Table 16. Predicted sizes based on regression equations and values from crabs reared in the laboratory are also presented. Note that the molt instars used by Krouse (1977) (Table 16) do not coincide with those used by Reilly (1975) (Table 7). The field carapace widths (of both Krouse and Reilly) are slightly larger than those of laboratory-reared animals.

Table 15.—*Cancer irroratus* larval carapace measurements (mean ± standard deviation, mm), based on a diet of newly hatched brine shrimp nauplii. Stages I-V = zoeae; M = megalopae. (From Bigford see text footnote 5.)

Larval stage	*N*	Dorsal Spine height	Carapace width	Carapace length
I	15	0.688±0.033	0.936±0.034	0.664±0.028
II	15	0.702±0.036	0.951±0.048	0.691±0.032
III	15	0.722±0.027	0.984±0.066	0.771±0.027
IV	15	0.913±0.082	1.186±0.039	0.990±0.037
V	15	1.140±0.098	1.450±0.050	1.360±0.049
M	15	—	1.892±0.069	2.396±0.120

3.5 Behavior

3.51 Migrations and local movements

Mass movements of *C. irroratus* adult populations have been recorded near Narragansett Bay and Chesapeake Bay. In Rhode Island, movements occurred primarily within the Narragansett Bay region (Jones 1973). Jones (1973) found a definite change in population center from inside the bay in the winter and early spring to outside the bay in late spring and summer. Similar movements were observed in coastal waters near Virginia and Chesapeake Bay (Shotton 1973). Mature crabs moved offshore late in the spring and returned to shallow waters the following winter. However, in Boston Harbor waters a tagging study found the adult crab population to be essentially nonmigratory (Turner 1953, 1954); Dean[9] and

Table 16.—Comparison of mean juvenile and adult *Cancer irroratus* carapace widths (mm) based on: field collections and derived regressions (Column A; Krouse 1977), regression values only (Column B; Krouse 1977), Krouse's regression values and Haefner's (text footnote 8) projections beyond stage X (Column C), and Laboratory reared (Column D; Bigford text footnote 5). Krouse's regression equation (text footnote 8): Postmolt carapace width = 0.566 + 1.247 premolt carapace width.

	A	B	C		D	
Instar	I-V: Actual measurements VI-XIII: regression values	Regression values (based on Stage I actual measurements)	Projections of column B and lab reared		Lab reared	
			N	$\bar{x}$	*N*	$\bar{x}$
I	2.6	2.6	—	—	5	2.4
II	3.7	3.8	—	—	5	3.5
III	4.6	5.3	—	—	4	4.4
IV	5.9	7.2	—	—	3	5.6
V	7.4	9.5	—	—	2	7.2
VI	9.6	12.4	—	—	2	9.6
VII	12.5	16.1	—	—		
VIII	16.2	20.6	—	—		
IX	20.8	26.3	—	—		
X	26.4	33.3	—	—		
XI	33.5	42.1	N/A	42.6		
XII	42.4	53.0		53.3		
XIII	53.4	66.7		65.8		
XIV				80.2		
XV				97.0		
XVI				116.4		
XVII				139.0		

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[9] D. Dean (editor). 1972. The University of Maine's coherent project Sea Grant program. Unpubl. manuscr., 25 p. University of Maine, Orono.

Stasko (see footnote 2) reported that rock crab populations in Maine and Canadian waters remained inshore throughout the year.

Cancer irroratus adult migrations show marked differences between sexes. Mostly, ovigerous females exhibit the seaward migration to the mouth of Narragansett Bay in June to October (Jones 1973). Males tend to remain in the shallow (20 m or less) regions of the inner bay.

3.53 Responses to stimuli

Effects of temperature shock on locomotion in adult rock crabs were investigated by Jeffries (1966). Increased activity, especially walking, was observed upon exposure to a +8°C shock from 6° to 14°C. If reversed, the −8°C shock decreased activity. In terms of locomotory activity the optimal temperatures were determined to be 14°-18°C.

Studies of the response of adult *C. irroratus* to hyposaline conditions suggest that rock crabs can withstand a wide range of salinities for a short time (McCluskey[10]). Adults (sexes not differentiated) were found to be euryhaline, surviving in salinities ranging from 10 to 20‰ (Table 17) for 3 days at 5°-8°C. Crabs normally occur in waters with salinities up to 35‰.

Hall (1973) studied behavioral responses of *C. irroratus* to changes in external salinities. Behavior was monitored in terms of dactyl chemoreception.

4 POPULATION

4.1 Structure

4.11 Sex ratio

Sex ratios appear to vary both by season and location. In Northumberland Strait, males outnumbered females by a ratio of 5.9:1 in summer collections (Stasko see footnote 6). Studies by Krouse (1972) revealed changes in sex ratios at various locations off the coast of Maine. Between 1968 and 1971 in Boothbay Harbor more females were collected than males; there were more males than females in 1969 landings from Casco Bay. The overall percentages were 62% female in Boothbay Harbor and 32% female in Casco Bay. These differences may be the result of population movements, which may be restricted to one sex (Jones 1973), and therefore cause landings to be mostly unisexual. Dean (see footnote 9) reported a predominantly male sex ratio in other Maine waters.

Table 17.—Percent mortalities of *Cancer irroratus* adults held at different salinities in the laboratory for 3 days. (From McCluskey text footnote 10.)

Salinity (‰)	*N*	Mortalities	% mortalities
20	69	1	1.44
15	18	2	11.10
10	24	7	29.10
0	18	18	100.00

Rock crab populations in the Gulf of St. Lawrence showed some seasonal variations in sex ratio (Scarratt and Lowe 1972). Females outnumbered males all year, but the ratio varied from 1.31:1 in the spring to 1.47:1 in the fall.

Changes in the sex ratio of *C. irroratus* were also reported in Narragansett Bay (Jones 1973). The percentage of females in the populations at sampling sites near the mouth of the bay was generally lowest in February, March, and April. During this time the females were ovigerous and had moved into shallower waters on their way to their summer habitats in deeper water (Jones 1973).

Haefner (1976), studying rock crabs in the Mid-Atlantic Bight, found the male:female sex ratio for adults to range from 1.0:1.4 to 1.9:1 (Table 18). In all water depth strata, except 20-40 m, this male dominance was significantly different from 1:1. The size class 51-100 mm had ratios of 1.7:1 on the continental slope at 150-700 m to 4.6 and 4.9:1 at 75-150 m in canyons and on slopes. Sex ratios in these data seemed dependent on carapace size, collection depth and location. In Maine, the sex ratio of juveniles below 40-mm carapace width is 1:1 (Krouse 1977), and in the Delaware Bay, the male:female sex ratio was approximately 12:1 (Winget et al. 1974).

Shotton (1973) reported a preponderance of males in the coastal waters of Virginia. In crab pot catches the

Table 18.—Sex ratios, by area and depth (m), for *Cancer irroratus* captured in June 1973 in the Mid-Atlantic Bight. Larger than expected deviations from the 1:1 ratio are labelled significant (sig) in the chi-square column. The ns denotes not significant. *P* level not given by author. (From Haefner 1976.)

		≤50 mm width				51-100 mm width				All crabs			
Area	Depth	Male	Female	Ratio	Chi^2	Male	Female	Ratio	Chi^2	Male	Female	Ratio	Chi^2
Shelf	10-20	62	54	1.3:1	ns	3	3	1:1	ns	65	57	1.2:1	ns
	20-40	95	101	1:1.1	ns	28	86	1:3.1	sig	132	187	1:1.4	sig
	40-60	96	60	1.6:1	sig	60	54	1.1:1	ns	159	114	1.4:1	sig
Slope	75-150	77	57	1.4:1	ns	50	11	4.6:1	sig	127	68	1.9:1	sig
	150-400	0	2	0:2	ns	45	27	1.7:1	sig	49	29	1.7:1	sig
Canyon	75-150	53	57	1:1.1	ns	44	9	4.9:1	sig	97	66	1.5:1	sig
	150-400	1	1	1:1	ns	30	19	1.6:1	ns	33	20	1.7:1	ns

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[10] W. J. McCluskey. 1975. The affects of hyposaline shocks on two species of *Cancer*. Unpubl. manuscr., 15 p. Narragansett Marine Laboratory, University of Rhode Island, Narragansett, RI 02882.

male:female ratio ranged from 4.6:1 to 111.7:1. Trawl catch data ranged from 0.6:1 to 12.5:1, with only the 0.6:1 station reporting more females than males.

4.12 Age composition

The mean age composition of any particular field collection is especially dependent upon sample location and time of year (Jones 1973). These factors relate to population migrations and changing sex ratios.

Fishing efforts tend to concentrate on larger males (Scarratt and Lowe 1972). This pressure could alter the age composition by removing the larger and older males, resulting in a younger age structure.

4.13 Size composition

Krouse's (1972) studies in the Gulf of Maine showed that male rock crabs dominate the carapace width classes over 90 mm. At Boothbay Harbor the mean female and male carapace widths were 81.7 and 92.4 mm, while at Casco Bay the values were 77.1 and 107.0.

Industrial trawl samples in Rhode Island coastal water revealed mean carapace widths of 57.3-102.9 mm for males and 59.7-79.5 mm for females (Reilly 1975). Larger sample means coincided mostly with the spring months and more seaward sample stations.

Size-frequency distributions of juvenile and adult crabs in Delaware Bay (Winget et al. 1974) indicate a bimodal or polymodal distribution (Fig. 10). This relationship presumably changes in response to factors such as year class strength and mortality.

It should be noted that collecting gear, i.e., trawls and pots, may be size selective. Carapace measurements could be skewed in favor of some size classes by various trawl nets or pot entrance and escape hole sizes.

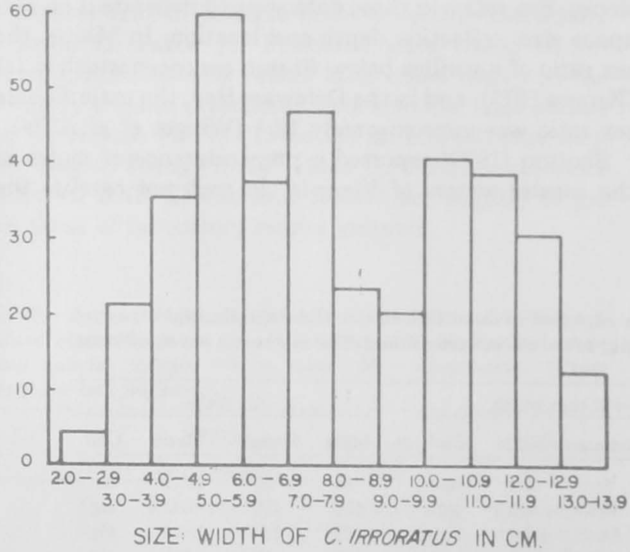

Figure 10.—Carapace width size frequencies of *Cancer irroratus* collected with crab pots in Delaware Bay from November-April 1969-70. (From Winget et al. 1974.)

4.2 Abundance and density

4.22 Changes in abundance

Larval stages of *C. irroratus* were most abundant in the Gulf of St. Lawrence from August to September (Scarratt and Lowe 1972). The numbers of larvae varied tremendously each year, with the highest abundance usually occurring in late summer. In Rhode Island waters, larvae occurred from late May to early September, with a peak in midsummer (Hillman 1964). Frolander (1955), in plankton collections at two stations in Narragansett Bay, found larvae present from April to late October, with peak abundance in June and early July.

Highest abundance of *Cancer irroratus* adults in the coastal waters of Virginia occurred in February, March, and April, when inshore waters were coldest (Shotton 1973). Sampling trawls in Narragansett Bay netted most crabs between November and March, which also corresponded to time of lowest temperatures. In warmer months the Narragansett Bay rock crab population presumably moved seaward to areas of lower temperatures (Bigford see footnote 5).

4.23 Average density

Plankton studies in Narragansett Bay between May and December 1961 revealed a mean density of 2.9 *Cancer* spp. (*C. irroratus* and *C. borealis*) larvae/m^3, with a range of 0-10 larvae/m^3, depending on location within the bay (Hillman 1964).

Scarratt and Lowe (1972) calculated the average standing stock of adult rock crabs in Kouchibouguac Bay, Canada, to be 3.7 g/m^2 on rocky substrates and 1.3-2.2 g/m^2 on sand and bedrock. Adult densities were surveyed from a submersible by Caddy (1970) in the Northumberland Strait in Canada. On the basis of three dives the density was 0.01 adults/m^2. Fogarty (1976) found a mean density of 2.1 crabs/5 m^2 (0.4/m^2) in his diving quadrats in Narragansett Bay waters.

4.3 Natality and recruitment

4.31 Reproduction rates.

Rock crabs typically mate at the onset of the female postmolt (A_1, A_2, B_1, or B_2) period while the female is still soft (Terretta 1973). The minimum carapace width at which mating can occur, and the reproduction rates thereafter, have not been fully elucidated. Reilly (1975), Reilly and Saila (1978), and Bigford[11] reported the occurrence of ovigerous females as small as 14-mm carapace width. Females may produce more than one egg mass from one copulation by storing the spermatophores.

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[11] T. E. Bigford. 1975. Occurrence of an unusually small ovigerous rock crab, *Cancer irroratus*, in Narragansett Bay. Unpubl. manuscr., 4 p. U.S. Environmental Protection Agency, Narragansett, RI 02882.

4.32 Factors affecting reproduction

The close relationship between molting and mating infers that variables affecting one could influence the other. Most molts occur in the fall, with reproduction occurring in the fall, winter, and spring months. Egg masses are carried until the larvae hatch; temperature controls the length of embryonic development. For example, an unusually warm week in April 1976 resulted in an abrupt bottom water temperature increase in Narragansett Bay from 6.5° to 10.0°C in 1 wk. Shortly thereafter, all females collected in the bay lacked eggs but showed evidence of recent hatches (Bigford see footnote 5). This unusually early hatch seemed correlated with the temperatures in previous weeks.

4.33 Recruitment

Ovigerous rock crabs tend to migrate offshore prior to hatching (Jones 1973; Sandifer 1975). The larvae are therefore most abundant offshore near the hatching grounds. Recruitment back into the bay waters (e.g., Narragansett and Chesapeake) is apparently either by chance in the zoeal stages or by migration in the megalopa and juvenile crab stages (Sandifer 1975), with the latter method most probable on the basis of laboratory experiments (Bigford 1976; Bigford in press).

4.4 Mortality

4.41 Mortality rates

Estimates of adult mortality were made by Reilly (1975) using the rate of total instantaneous mortality, Z. This relationship is based on the commercial catch curve and year classes, with the restriction that the latter do not vary significantly from year to year. In the male population of Narragansett Bay, the year classes did vary and an estimate of mortality was not possible. Calculations of Z for females revealed a change in mortality as the carapace size increased. Total annual mortalities for a sample collected in April 1974 were 54% for females <82.5 mm and 93% for crabs >82.5 mm. A May 1975 sample gave 60% for crabs <86.5 mm and 94% for larger crabs.

Field collections of juvenile (<40 mm) *C. irroratus* and an analysis for annual natural mortality gave juvenile mortalities of 94% and 64% for two samples (Reilly 1975). The method involved stomach content analysis of *Raja erinacea* and *Gadus callarias*. Analysis of cod stomachs revealed mortalities of 59-84% for juvenile crabs.

When categorized by estimated age, mortalities calculated by Reilly (1975) were 75-85% for the second year and 65-80% for the third year. With increased size, predation by fish became less important compared to fishing mortalities.

4.42 Factors causing or affecting mortality

Many of the predators, competitors, parasites, diseases, and injuries responsible for field and laboratory mortalities are discussed in Sections 3.33, 3.34, and 3.35.

Laboratory studies by Sastry (1970, 1976) indicated high mortalities in rock crab larvae reared under less than optimal conditions of temperature and salinity. Effects of temperature were especially lethal. Salinity may alter oxygen consumption (Hanlon 1958) and survival.

Attempts to culture larvae on a variety of laboratory diets indicated that the ciliate *Euplotes vannus* could be responsible for rapid mortalities (Bigford see footnote 5). This ciliate was added to the culture as a food organism but does occur naturally in seawater systems.

Cornick and Stewart (1968) reported high mortalities of adults in high density holding systems. Cannibalism is a frequent problem in holding systems for larvae and adults.

4.5 Dynamics of population

See Sections 2.21, 2.22, and 3.51 for discussions of population dynamics.

4.6 The population in the ecosystem

Jeffries (1966) described *C. irroratus* as being an open sand dweller in Narragansett Bay; the congeneric *C. borealis* inhabits the rockier areas. Absence of the rock crab from coarse sediment types (Steimle and Stone 1973) is peculiar considering its common name. Jeffries (1966) and Fogarty (1976), as discussed in Section 3.33, suggested that *C. borealis, Carcinus maenas,* and *Homarus americanus* may be competing for sediment space and type with the rock crab. Juvenile rock crabs outnumber lobsters in both rocky and boulder-strewn areas off Canada (Scarratt and Lowe 1972). Tendencies for the rock crab to bury in sand and lobsters to excavate burrows may permit limited coexistence without competition.

Fogarty (1976) studied *Cancer irroratus* in its own niche and in the ecosystem, based on both extensive diving surveys in Narragansett Bay and laboratory experiments. Niche breadth calculations, based on Levins' (1968) formulation, revealed that *C. irroratus* has a highly specialized pattern of resource use; the niche breadth value was 1.00, indictive of the fact that all rock crabs collected in Narragansett Bay were found on a sandy substrate. The role of the rock crab in the community matrix was calculated from the probability of occurrence of the rock crab and its decapod cohabitants (*Cancer borealis, Homarus americanus,* and *Carcinus maenas*) on rock, mud gravel, or mud substrates. Matrix values showed an extensive overlap of *C. irroratus* with *C. maenas,* but not with *H. americanus* or *C. borealis.*

Adult rock crabs have been observed to inhabit the upper regions of mantis shrimp, *Squilla empusa,* tunnels and abandoned lobster burrows in Narragansett Bay (McCluskey[12]).

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[12] W. J. McCluskey, Narragansett Marine Laboratory, University of Rhode Island, Narragansett, RI 02882, pers. commun., June 1977.

5 EXPLOITATION

5.1 Fishing equipment

5.11 Gear for capture

Crabs of all species are commonly collected by various nets and traps. Bottom trawls, with either otter or German nets, and dredges are towed from fishing vessels; traps resemble lobster pots, with specific designs highly variable (Bigford see footnote 5; Turner 1953, 1954). Typically, the pots are semicylindrical and 0.6-1.3 m long. Entrances may be constructed so as to eliminate certain size ranges. In Canada, various types of cylindrical, rectangular, or conical and metal or plastic traps have been tried (Caddy et al. 1974). Shotton (1973) mentioned that rock crabs are often attracted to Virginia sea bass pots where trapped fish serve as bait.

Stasko (1975) researched relative efficiencies of various trap materials, entrance shapes, and entrance sizes. A long rectangular opening of 44.5 mm wide permitted crabs to enter while preventing passage to most legal-sized lobsters. Modified lobster pots with the entrance on top fished exclusively for crabs. A study by Stasko and Graham[13] on seven trap types revealed that wooden traps with a 5-cm metal entrance on top caught the most crabs. The 5 cm by 27.5-62.5 cm metal entrance eliminated lobsters, while a wooden trap caught more crabs than any metal trap. In Massachusetts, rock crabs are caught primarily by means of pots (Turner 1954). Most pots used commercially in Massachusetts waters are rectangular, about 0.3 m high, 0.6 m wide, and 1 m long. Oak is usually used for framework and heavy netting for the funnellike entrances. This crab trap differs from the lobster pot in that the twine funnels are shaped to meet the contours of the crab and, secondly, small holes are drilled in the framework to permit escape of juvenile crabs (Turner 1954). A detailed description of the fishing gear and its manufacture is given by Marchant and Holmsen (1975). Hipkins (1972) described crab pots used in the Dungeness crab, *Cancer magister,* fishery on the west coast of North America.

Many baits are used depending upon cost and availability. In general, fresh bait is cheaper than the frozen or salted varieties. Common baits are fish processing wastes, unwanted fish caught by trawls (skates, ocean pout, sea robins), and industrial fish (menhaden, herring, flatfish, and mackerel) (Marchant and Holmsen 1975).

Bait fish is usually placed in bags and hung in the pot. Approximately 1-2 kg of fish is placed in each "purse" for inshore fishing; 2-3 kg are used for offshore grounds.

5.12 Boats

Chesapeake Bay and Narragansett Bay area fishermen catch most crabs incidentally while trawling, dredging, or pot trapping for another species. In Canadian waters, a majority of the crabs are caught in lobster pots (Stasko see footnote 2). Lobster and trawler boats used in such operations are typically wooden, open, and 4-14 m long, with offshore vessels larger than inshore vessels.

Offshore fishing vessels are usually equipped with onboard refrigeration systems. Holding tanks are maintained at or near bottom temperatures and are well aerated.

5.2 Fishing areas

5.21 General geographic distribution

Rock crab populations are large enough to support a commercial fishery from the Chesapeake Bay region north to the Canadian provinces. Continental shelf populations both nearshore and in deeper waters have been harvested.

5.22 Geographic ranges

The first commercial fishery for rock crabs began in Massachusetts about 1900 (Turner 1953; Wilder 1966z. Shortly thereafter the fishery moved into the other New England states, Canada, and the Chesapeake region. Small canning operations began in Prince Edward Island and New Brunswick (Caddy et al. 1974); fresh crab markets developed in Massachusetts (Turner 1953), Maine (Wilder 1966), and the middle Atlantic (Haefner et al. 1973).

Several areas appear to have the potential for commercial exploitation. In Canadian waters, Northumberland Strait and other nearshore waters are promising (Scarratt and Lowe 1972). Up to 97% of the total catch in some Canadian waters at some times of the year exceeded the arbitrary minimum market size of 89-mm carapace width (Scarratt and Lowe 1972). Southern New England and mid-Atlantic waters, where crabs migrate seasonally, may have commercially productive populations in offshore and onshore waters, depending on the season.

5.23 Depth ranges

As stated above, populations in shallow (<50 m) waters may prove most valuable in the northern range of the rock crab. In more southern areas, crabs may be fished seasonally in coastal bays (Narragansett and Chesapeake) or on the continental shelf.

5.24 Conditions of the grounds

Since the crab industry is still growing, all grounds show large standing stocks of crabs. Due to the lack of populations studies there are no reliable bases for estimating stocks or potential yields (Caddy et al. 1974). Small surveys and recent catches in the crab fishery in Canada reveal that the sustained yield of the southern Gulf of St. Lawrence region could be 1.3-2.3 million kg annually. Smaller commercial stocks exist in the north-

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[13] A. B. Stasko and D. E. Graham. 1976. Preliminary report on rock crab trap comparison. Unpubl. manuscr., 2 p. Fisheries and Marine Service, Biological Station, St. Andrews, New Brunswick, Canada, EOG 2X0.

ern Gulf area, off Newfoundland and off Nova Scotia (Caddy et al. 1974).

5.3 Fishing seasons

5.31 General pattern of season(s)

Cancer irroratus typically molts between December and May in southern populations and from December to as late as October in northern ranges. Due to the reduced meat yield of newly molted crabs, fishermen attempt to avoid fishing during peak periods of molting. This constraint limits the primary fishing seasons to the late spring, summer, and fall months (Turner 1953; Caddy et al. 1974).

5.32 Dates of beginning, peak, and end of season(s)

Collections by Krouse (1972) at Boothbay Harbor, Maine, indicated peak abundance of *C. irroratus* in July, Augustn and September. These crabs would be marketable size with high meat to wet weight ratios. Throughout the remainder of the year, *C. irroratus* was less abundant in Boothbay Harbor than during these months. This apparent decrease in abundance could be attributed to the fact that crabs are much less active during the winter months than at other times (Stasko see footnote 6). Peak abundance in Northumberland Strait, Canada, occurs when waters exceed 10°C.

In Rhode Island waters, a similar peak in abundance occurred (Jones 1973). Trawl catches peaked in late summer offshore and in cooler months nearshore (see Section 4.22). Weather permitting, harvesting may last 12 mo in Rhode Island and about 7-8 mo in Maine. Molting of crabs could restrict these fishing seasons. See Section 6.12.

5.4 Fishing operations and results

5.41 Effort and intensity

Because lobsters are the primary target of pot fisheries, it can be assumed that rock crabs are caught with little extra physical effort. However, additional capital is needed to store the crabs onboard and to replace bait typically used in landing lobsters.

Marchant and Holmsen (1975) calculated the feasibility of harvesting rock crabs. They concluded that the additional effort would generally result in a significant increase in income. At the 1974 prices, a full-time offshore lobsterman with an average business could earn $3,000-$16,000/yr from crabs alone.

Rees (1963) suggested that the rock crab meat ranks high in flavor and should be utilized commercially. According to Haefner et al. (1973), newly molted "peeler" crabs appeared to have potential as a commercial resource. Catches of these soft-shell crabs are particularly high in December and early January in the Chesapeake Bay area, where the resource may be exploited soon. Northern Atlantic populations could also be exploited.

The economic returns to the fishermen depend upon the efficiency of his operation (Van Engel and Haefner 1975). Crabs should be eaten the same day they are dressed. Meat discoloration that affects marketability may occur during dressing (Van Engel and Haefner 1975). Production of minced rock crab meat involves separation of shell fragments from the meat. Sims and Anderson (1976) devised a chemical method for calculating the amount of shell particles in the meat. In good crab meat, the concentration of shell particles remaining on a 20-mesh sieve should be $<0.3\%$; particles remaining on a 50-mesh sieve should not exceed 1.05%; and total shell contents should not exceed 1.25%, based on a dry weight (Sims and Anderson 1976). Haefner et al. (1973) discussed a processing plant operation for commercial purposes.

Ex-vessel landing prices are highly variable. In 1965, cans of prepared crab meat retailed for $1.50-$1.79/kg (Wilder 1966). By 1967, prices for live crabs were 11-24.4¢/kg in Rhode Island (Gates et al. 1974); Canadian landing prices for inshore and offshore crabs from Rhode Island were 32¢ and 55¢/kg by 1974 (Marchant and Holmsen 1975).

Meat yields from whole boiled crabs were calculated to be 21% of the live weight (Wilder 1966). However, considering that some useful parts of the crab are not utilized, the present commercial yield may be closer to 10% (Wilder 1966). Table 19 summarizes the changes in meat yield over the course of the fishing season. Carbonneau (1965a, b), in addition to Wilder, discussed the potential of the species as a source of crabmeat.

Table 19.—Catch data and meat yields (kg) from the Boston Harbor *Cancer irroratus* population. Traps used are described in Section 5.11. (From Turner 1954.)

Month	Daily catch per trap	Crabs per kg meat	Average meat yield of daily catch per trap
Apr.[1]	125-150	77-84	2
May	50-75	42-46	About 1
June	35-50	42-46	About 1
July	35-50	[2]57	Under 1
Aug.	20-40	[2]66	About 0.5
Sept.	20-40	[2]66	About 0.5
Oct.	20-40	[2]73	Under 0.5
Nov.	30-50	88	About 0.5

[1] Experimental fishing.

[2] Increase in small crabs in catch.

5.42 Selectivity

Crab pots have been developed that will select specifically for rock crabs, as discussed in Section 5.11 (Stasko see footnote 6; Stasko and Graham see footnote 13). Various baits, gear types or pot entrances may be used to select size; spider crabs, *Libinia emarginata*, and lobsters, *Homarus americanus*, are frequently caught in crab pots.

5.43 Catches

The rock crab fishery began between 1890 (Haefner et al. 1973) and 1900 (Turner 1953; Wilder 1966) and developed slowly. Up to 1962, the total U.S. catch was only 1 million kg, with a value of $91,000 (Wilder 1966). Since 1962, the industry has developed more quickly. Annual catches increased but never exceeded 230,000 kg in Canada (Caddy et al. 1974). Commercial landings in New Jersey began in 1959; since then catches have increased steadily up to 157,000 kg in 1974 (McHugh and Williams 1975). Figure 11 and Table 20 summarize *Cancer* species landings in Rhode Island including rock and jonah crabs. Per vessel catches in Canada are described by Wilder (1966). In 1963, the daily crab catch per boat varied from 68 to 1,818 kg. One boat in the Pugwash, Nova Scotia, region reportedly averaged 863 kg/day from 5 September to 10 October.

Catches per crab pot are discussed in Shotton (1973) and Stasko (see footnote 6).

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

6.11 Limitation or reduction of total catch

At present, there are no limits on total catch of *C. irroratus* on an annual basis. However, some states have general laws concerning "edible crabs." For example, Chapter 130, Section 37 (Lobsters and crabs; license, regulations; violations) of the Massachusetts General Laws specifies that noncommercial, daily catches shall not exceed 50 crabs in 1 day. Permits are required for all fishermen taking edible crabs commercially or noncommercially in Massachusetts (Chapter 130, Sections 38 and 83). Commerical fishermen must pay $15 for a general shellfish license and $50-$100 for a boat license, depending on the total length of the vessel. Noncommercial licenses for crabs for use with up to 10 pots or diving are $15.

6.12 Protection of portions of population

Miller (1976) detailed the regulations of all North American commercial crab fisheries. *Cancer irroratus* was not included in the study since the extent of its exploitation did not warrant protection. Instead, some states and Canada have legislated protective measures that are applicable to all fisheries or the edible crabs.

Competition among fishermen for the New England rock crab populations led to legislative action at the state level as early as 1937. At that time Massachusetts passed a law prohibiting the taking of rock crabs between 1 December and 31 March (Massachusetts General Laws, Chapter 130, Section 40).

Collection of female crabs is regulated in several states. Massachusetts (Gates et al. 1974) and Rhode Island require special permits from the respective Department of Natural Resources before collecting females. Section 43 of the Massachusetts General Laws (Chapter 130) lists the conditions under which ovigerous females may be taken.

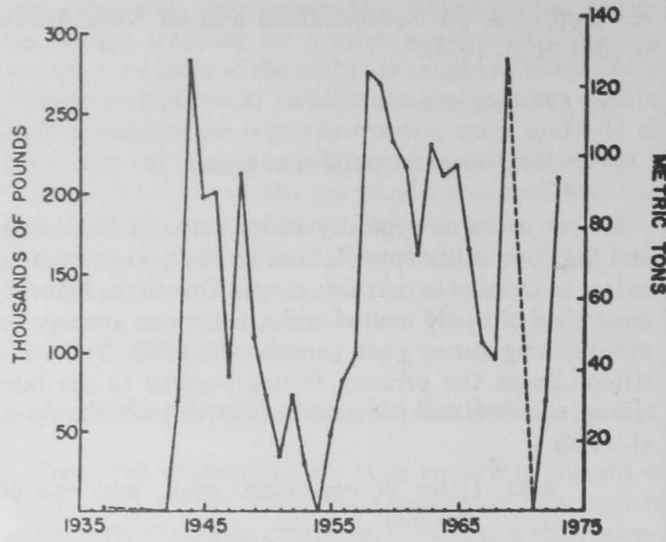

Figure 11.—Rhode Island commercial landings for the *Cancer irroratus* and *C. borealis* combined. (From Olsen and Stevenson 1975.)

Table 20.—Commercial crab (*Cancer irroratus* and *C. borealis* combined) landings and values in Rhode Island waters between 1971 and 1973. (From Olsen and Stevenson 1975.)

Year	kg × 1,000	% total kg	$ × 1,000	% total $
1971	0	—	0	—
1972	31.9	0.1	19	0.1
1973	93.6	0.2	46	0.3

No minimum carapace width has been established in law; practicality and percent meat yields have effectively placed a lower limit on commercial crab sizes of 89-mm carapace width (Scarratt and Lowe 1972). Even under the most favorable ratios of meat to wet weight, up to 45 crabs are required to yield 1 kg (approximately 20 crabs for 1 lb) of meat (Turner 1953). (See Table 19.)

To gather statistics and maintain proper management efforts, the Commonwealth of Massachusetts requires the Director of Marine Fisheries to collect catch data (number of crabs, type of gear used, cost of gear, and number of employees) from each gear or boat owner (Chapter 130, Section 33 of Massachusetts General Laws).

6.3 Control or alteration of chemical features of the environment

6.31 Water pollution control

Many metals are important in the maintenance of enzymatic and respiratory systems in *Cancer irroratus*. These metals often form the active centers for key organic molecules. Martin (1973, 1974) analyzed several adult rock crabs in attempts to study the metal content as related to the crabs' needs. To minimize variability, all crabs were in intermolt stage C_4 (Passano 1960). Table 21 summarizes the whole body concentrations of metals in rock crabs collected from "nonpolluted" waters.

In his more recent studies, Martin (1975, 1976) has analyzed rock crab eggs and ovaries for concentrations of

Fe, Cu, Zn, Mg, Mn, and Co. Some of the metals (Fe, Mn, and Mg) induced increased metabolism rates during embryogensis that were independent of the water content of the embryos. Decreases in concentrations of Cu and Zn were correlated to increased water content in embryos.

Possible effects of hydrocarbons have also been studied. The water accomodated fraction (WAF) of No. 2 fuel oil has been shown by Bigford (1976, 1977) to significantly alter larval responses to light, pressure, and gravity. In general, exposure to 0.1 and 1.0 ppm WAF depressed movements of larvae in the early stages and enhanced many of the same movements in late stage larvae. When compared to the control larvae (approximately 0.0 ppm), the oil-exposed larvae were significantly lower in vertical column tests during zoeal stages I-III and higher in stages V and megalopae; stage IV was similar in all three oil treatments. These differences in larval behavior could lead to exposure to various physical factors (water currents, temperature, salinity) that could alter mortality and recruitment. Losses via volitilization during the above study (Bigford 1976, 1977) reduced the oil concentrations sufficiently to permit larval development at the 1.0 ppm WAF concentration. However, continuous exposure experiments indicated that 1.0 ppm WAF is lethal to rock crab larvae within several days (Pechenik et al. in press).

Adult rock crabs surveyed in Chedabucto Bay, Nova Scotia, throughout the year exhibited bunker C oil accumulation ranging from 2.5 to 17 times that of controls (Scarratt and Zitko 1972).

6.4 Control or alteration of the biological features of the environment

6.43 Control of parasites and disease

Antibiotics have been used to control bacterial infestations in laboratory cultures of rock crab larvae. Sastry (1970) added penicillin to his cultures. Bigford (see footnote 5) used streptomycin and penicillin in small, individualized cultures. In the latter case, a comparison between the treated and untreated cultures revealed that survival and development times were significantly better in the treated water. Suvival to megalops and the first crab stages were 83.3% and 61.1% with antibiotics and 16.6% and 2.7% without.

Table 21.—Average concentrations of metals (ppm) in whole *Cancer irroratus* adults expressed as ratio of wet weight, dry weight, and ash, ±1 standard deviation. A, average body size in mm; B, average % H_2Oas ratio of wet weight; C, average % ash as ratio of dry weight. (From Martin 1974.)

Metal	Wet weight	Dry weight	Ash
Zn	30.5± 10.2	103.0± 29.5	284.8± 87.8
Cu	19.9± 11.8	66.8± 37.2	184.2± 105.2
Fe	60.0± 28.0	205.6± 105.3	570.7± 294.3
Mn	10.6± 4.2	35.8± 13.8	98.9± 41.1
Mg	3100.9± 340.0	10,556.5± 854.8	28,994.3± 1,965.4
Ca	51,169.0±5,471.4	174,408.6±13,713.0	478,539.0±15,941.5
Sr	673.3± 70.4	2,293.5± 150.0	6,297.9± 234.2
Na	8,854.9±1,799.5	30,343.8± 6,526.4	83,428.0±18,010.2
K	2,949.3±1,023.5	10,080.4± 3,450.0	27,820.9± 9,813.3
	A	B	C
	78.97± 15.56	70.65± 3.22	36.43± 2.40

Ultraviolet sterilizing units have been attached to some laboratory culture systems (Sastry 1970) to minimize bacterial infestations.

7 CULTURE

No information is available concerning concentrated rock crab culture efforts. However, Bigford[14] has summarized the culture methodology used in hatching and maintaining larvae in the laboratory.

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[14] T. E. Bigford. 1977. Culture manual for the rock crab, *Cancer irroratus*, Say. Unpubl. manuscr., 42 p. U.S. Environmental Protection Agency, Narragansett, RI 02882.

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