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CONTAMINANT PROBLEMS AND MANAGEMENT OF LIVING CHESAPEAKE BAY RESOURCES

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Chapter Ten

FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF THE BLUE CRAB IN CHESAPEAKE BAY

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ABSTRACT

That environmental conditions in the Chesapeake Bay are optimal for the blue crab population is suggested by the fact that hard crab landings by Virginia and Maryland watermen accounted for almost 48% of the total of East and Gulf coast landings in 1985. Estimates of total mortality from the egg to the adult stage range from 0.999973 to 0.999996. Commercial fishing removes an additional 0.0000031 to 0.0000251, leaving 0.0000024 to 0.000001 as the rates of removal by other sources. Physical and chemical pollutants, predators, and plants and animals symbiotic with the blue crab are part of the environment that must be acknowledged as actual or potential factors affecting the rates of reproduction, growth and survival, and the behavior and distribution of the blue crab population. The impact of parasites and disease, predation, salinity, temperature, dissolved oxygen, heavy metals, polynuclear aromatic hydrocarbons, and halogenated substances on the blue crab are described.

THE FISHERY

Since the beginning of the commercial fishery for blue crabs in the Chesapeake Bay over 100 years ago, large interannual and longer oscillations in landings have occurred (Fig. 1). The perspective provided by the longer record does not indicate any long-term change. The decline in landings from an all-time high in 1966 to the recent low in 1976 has been overemphasized by some correspondents; similar events occurred from 1930-1941 and from 1950-1959.

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Comparison of 1981-1985 hard crab landings with those from any earlier period is feasible only on a state-by-state basis, since the data acquisition method in Maryland was changed in 1981. Maryland's 5-year mean landings were 45.5 million (M) pounds, double the mean of 21.2 M for 1976-1980 and of 23.2 M for the 21 years of 1960-1980. These numbers do not include estimates of the recreational crabbers catch. No perceptable change in the accounting method occurred in Virginia: the 1981-1985 mean of landings in Virginia was 44.4 M, a marked increase from the previous 5-year mean of 35.3 M but only slightly different from the 21 year mean of 43.3 M.

Principal explanations for fluctuations in landings may lie in variations of any one or a combination of the following factors: 1) fishing effort; 2) the parent-progeny relationship; and 3) the atmospheric and oceanographic environment. Progress in uncovering relationships for any of these three has been hindered by the unavailability or incompleteness of biological, environmental and landings data, and particularly the uncertainty of their reliability.

Daily landings of crabs are determined by 1) their availability, that is, the portion of the total population susceptible to capture, and 2) the intensity of fishing. While availability is a function of the effects of varying environmental conditions on crab distribution, significant deviations from the normal environment are not likely to occur in the short term, and changes in catch are likely to be of short duration. Similarly, while cessation of fishing may be caused by an oversupply of crabs or crab meat, strikes by watermen demanding higher prices for their catch, unusual weather conditions that have destroyed fishing gear and/or vessels or have prevented normal fishing effort, these conditions

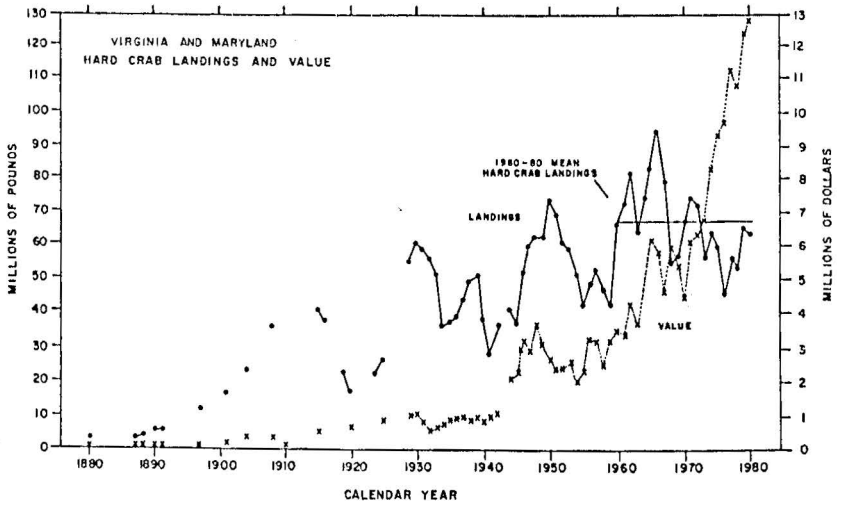

FIGURE 1. Virginia and Maryland hard crab landings and value.

have almost always been of such short duration that the losses in catch are negligible.

Landings over the long term depend primarily on the "fishable" portion in the crab population, which is derived (recruited) by growth from the younger portion. Since "stock density", which is a measure of the proportion of different age or size groups in the population, varies seasonally and interannually, estimates of abundance of each portion of the population are important in understanding the effects of environmental variables and of fishing on the population and on recruitment.

Since the blue crab fisheries are confined to state territorial waters, responsibility for fisheries management rests with the states. Regulatory authority concerning seasonal, geographic, size, sex and catch limits, gear restrictions, and other licensing controls over harvesting is generally retained by the state general assemblies, but may be delegated to commissions that have various degrees of authority to invoke management action at the local level as the need arises.

Despite the stated intention that regulations are for conservation of the blue crab population, most, if not all, regulations of the blue crab fisheries in the United States have been based on local or regional economic, political or sociological demands. Little or no regard has been given for scientific investigations of the status of the population and the fishery before regulations are put into effect nor has regard been given for observing and analyzing conditions in the fishery at later intervals. Such regulations are trial and error efforts to manipulate the fishery to effect whatever objective the management agency is seeking. Untested regulations usually result in the underutilization of the resource.

The historical and popular conception of the life history of the blue crab in the Chesapeake Bay is that the population is self contained within the Bay, that zoeae and megalopae are produced and retained in the highly saline portions of the southern end of the Bay and that their further development to juveniles within the Bay precedes migration to the nursery grounds in the lower salinity regions of the tributaries and the upper Bay. Regulations reflecting this viewpoint have been enacted by Virginia and Maryland over the last 70 years.

"Stock density" implies that there is a relationship between the number of crabs of different age groups in the population. Usually only the relationship between the parents (spawners) and their progeny is considered important enough for study. Seldom mentioned is the competition between crabs, which may be age specific, for food and space.

Most often, the parent-progeny relationship is thought of in the classical sense, that is, the effects that the density (numbers) of adult females may have on the density of very early life-history stages (zoeae and megalopae). Obtaining even relative estimates of the numbers of these early stages is a newly developing area of study and difficult at best. Numbers of these early stages will be less

closely correlated than 2 to 12-month old juveniles with the resultant adult stock, probably because of relatively large and fluctuating rates of mortality (affected by food, space and water quality requirements, predation by plankton feeders, and dispersion through water transport). In contrast to the parent-progeny relationship, the relationship between the early stages or the juveniles and the resultant stock is more properly termed a "recruitment" or "spawner-recruit"curve. At present, too little is known of the mode and time of transport of the transition phase between zoeae and megalopae from the open waters of the lower Bay and the adjacent continental shelf waters to the juvenile stage on the nursery grounds to justify speculation on the factors that could affect their survival.

There are three approaches to modeling populations: 1) an empirical method in which trends in the fishery are associated with trends in environmental variables, 2) the surplus-yield "conceptual" model which requires an input of catch and effort data, and 3) the dynamic pool "conceptual" model for which we need details of the biological characteristics of the stock, such as growth, mortality and recruitment rates.

An examination of the life history pattern of the Chesapeake Bay blue crab and its population parameters suggests that a spawner-recruit model would not be useful in setting a management policy, as it is not density-dependent. The species is characterized by the annual production of a large number of young, large interannual fluctuations in production, rapid growth, early attainment of maturity, high mortality rates and a short life span. Those are the characteristics of a density-independent species, exposed to a variable environment in which the population's resources are spent mostly on reproductive (*r)* functions! In short, the blue crab appears to be an *r* selected strategist. Because of these characteristics, the blue crab can be fished at high levels of fishing effort, and, because of the short life span and rapid succession of year classes, would have a quick recovery if overfishing occurred. Species with such characteristics are strongly affected by physical, chemical and biological environmental factors! It is axiomatic that for populations fluctuating widely as a response to environment variation that the maximum sustained yield cannot be realistically estimated.

Although the exact mechanisms through which environmental factors affect yearclass strength are only partially known, it is believed that they occur at critical times early in the life cycle of the blue crab.

BIOLOGY, LIFE HISTORY AND DISTRIBUTION

Spatial, seasonal and size distributions of the pre-recruit stages are evidence that chemical, physical and biological factors effect survival and growth.

Female blue crabs mate only once, in the soft shell state at the terminal molt, sometime between early May and the end of October, and shortly thereafter

migrate from the brackish waters of the tributaries and the upper Bay to the saltier waters of the southern end of the Bay. Most females of the same age group (year class) reach the terminal molt stage and mate in late summer, July through September, the second summer of life, and do not extrude eggs until the following spring: they may produce two or more egg masses at least two months apart. A varying number of females of the same year class do not reach the terminal molt stage and mate until May or June in the third year and may not extrude eggs until August in the third summer. During the third winter of life, aged females carrying egg remnants on the swimmerets from previous extrusions comprise about 5% of the stock of adult females in the southern end of the Bay[2] and, conceivably, some of them may extrude eggs the fourth summer, although that has not been verified. Adult females are commonly called "sooks", and those with extruded eggs are usually called "sponge crabs" but occasionally called "busted sooks".

Zoeae hatch within 10-14 days and progress through seven, occasionally eight, stages in one month, then metamorphose to the megalopal stage. In the Bay, Stage 1 zoeae are found predominantly in the surface waters along with some later stages, but most later stages, including the megalopa, are in subsurface layers or bottom waters.

In summary, zoeae appear in the Bay plankton June through September, are most numerous in July and August and rarely occur in May, October or November. They are most numerous at the baymouth and occur in rapidly decreasing numbers upestuary. In some years they may be found in large numbers at least 75 km inside the baymouth. Stages I-VII and the megalopa are present in the water column, but most zoeae, predominantly Stage I, are found in the upper 10-15 cm of the surface waters. Evidence of vertical migration was not found by Goy[3] from day and night samples in Hampton Roads, although the results are inconclusive because of the small numbers found. Grant and Olney[4] suggested diurnal migration of the larvae, based upon the large proportion of megalopae and zoeae in subsurface samples in the daytime, in contrast to their relative scarcity in the neuston. They concluded that "this difference in depth distribution of developmental stages may reflect a behavioral adaptation of the species that aids in recruitment of populations to the estuary" (p. 48). Provenzano et al.[5] found peaks of abundance of zoeae at 3 m depth after late night or morning high slack tide at stations occupied just inside the baymouth in 1979. They suggested that the peaks were associated with a night time ebbing and could be due to the input of new zoeae into the water column due to an apparent synchronized hatch. Support for vertical migration was not observed. McConaugha et al.[6,7] reported large numbers of zoeae of all stages and megalopae collected in 1980 from stations located inside and outside the baymouth.

Collection of large numbers of blue crab zoeae and megalopae in continental shelf waters in the last 15 years has revived interest in dispersal and retention

mechanisms. Specifics of the distribution and abundance of zoeae and megalopae outside the baymouth and on the continental shelf, and of the site-specific hydrographic conditions where samples are collected, are clues to the abilities of these stages to survive and exist under those conditions, and to the extent of the transport of those stages. These collections do not tell us where the stages originated, nor of the transport mechanisms involved.

Comparison of temperature-salinity conditions in the Bay and on the shelf with tolerances of zoeae and megalopae determined in the laboratory may lead to unwarranted conclusions that in some seasons the natural environmental conditions are too rigorous to sustain life or permit molting. Possibly, tolerances may have been too narrowly defined when temperature-salinity ranges were selected to determine optimal responses, e.g., 15-30°C, 5-19 ppt.[8] Responses to combinations of temperature and salinity of 10-20°C/10-20 ppt and 10-20°C/30-35 ppt are needed to predict survival and growth in the Bay and on the shelf.

Following metamorphosis of the megalopa to the first true crab stage, young-of-the-year crabs move into the tributaries of the southern end of the Bay and into Maryland waters, occasionally as far north as Eastern Bay, Maryland. Information on the distribution and abundance of megalopae and the earliest true crab stages, 1st to 3rd instars, 2-5 mm wide, is scanty. The time of their first appearance as 6-25 mm wide crabs in the lower Bay's tributaries is usually early September, but varies considerably from year to year, rarely mid-August or as late as mid-November. These pre-recruits are seldom as numerous in late summer and fall trawl net catches, taken in monitoring surveys, as in the following spring and summer. Maximum numbers are recorded in June, July and August, the second summer. In June, the usual width range is 25-60 mm.

Growth is rapid. Crabs hatched in late May or early June become five inches in width or larger by mid-August or early September the following year, but those hatched in late August will not reach five inches in width until May or June the third year. Sexual maturity of males is attained a year after hatching and before the crab is fully grown, and during its last three growth stages may mate with one or more females. Females hatched in June become sexually mature in 14 months and mate in the soft shell stage in the terminal molt.

The influence of environmental variables on yield has been demonstrated for a number of crustacean fisheries. In each instance long time series of data were used and regression analyses, consisting of current landings as the dependent variable, were run against combinations of previous years' landings, fishing effort and lagged environmental variables as the independent variables.

Temperature, salinity, substrate and food have been found to be the primary factors affecting growth, survival and distribution of many crustaceans. That these factors are optimal in the Chesapeake Bay is suggested by the fact that hardshell blue crab landings by Virginia and Maryland watermen accounted for almost 48% of the total of East and Gulf coast landings in 1985.[9] In a multiple

correlation analysis, 86% ($r^2 = 0.86$) of the variation in commercial hard crab landings from 1964 through 1975 (in the Biological Year, September through August) was explained by fluctuations in Norfolk, VA cooling degree days in May, Delaware Bay meridional wind stress in January and the log transformation of the York River juvenile crab catch per tow in the year of the hatch and through August the following year![0]

Physical and chemical pollutants, predators, and plants and animals symbiotic with the blue crab are part of the environment that must be acknowledged as actual or potential factors affecting the rates of reproduction, growth and survival, and the behavior and distribution of the blue crab population. Research to identify and describe those factors that could have an impact on the blue crab population has attained marked progress since the mid-1960's.

ESTIMATES OF MORTALITY

Known sources of total mortality of the blue crab, that occur at any stage of its life history, do not account for the low survival rate obtained from estimates of the reproductive and fishing mortality rates. Estimates of the mortality rate from the egg to the adult stage can be made by applying a number of initial assumptions: 1) commercial fishing removes 75 to 90% of the adult stock; 2) the commercial fishery removed 46 to 90 million (M) pounds of crabs a year over the 21-year period from 1960-1980; 3) fecundity rate of adult female blue crabs, which are one-half the survivors, varies from 0.725×10^6 to 2.0×10^6; and 4) there are three crabs in each pound of the commercial catch.

Estimates of the mortality rate range from approximately 0.9999725 to 0.9999959. Commercial fishing removes an additional 0.0000031 to 0.0000251, leaving 0.0000024 to 0.000001 as the rates of removal by other sources. If it is assumed that the commercial catch is grossly underestimated, that the landings could be as much as 150 M pounds, the estimates of the total mortality rate are unchanged: 0.9999725 to 0.9999959.

A second estimate of total mortality can be based on a tenet held by ecologists, that for a population to maintain its position in a community, i.e., to continue to occupy the same niche, on the average over several generations no more than two individuals from each brood may survive to adulthood. If more than two individuals survive, the population will soon outgrow its niche; if less than two individuals survive, the population will be threatened by extinction or must adopt a smaller role in the composition of the community. If reproductive potential averages 1×10^6 eggs per female, the survival rate is estimated as 2×10^{-6} and the mortality rate up to the adult stage is estimated as 0.999998.

SYMBIONTS

At least 84 kinds of viruses, algae, diatoms, bacteria and invertebrates, some identified only to genus, are symbionts of the blue crab on the Atlantic or Gulf coasts (Table 1). Twenty-two (26.5%) of them occur as commensals that may be found on or attached to the external shell or in the gill chamber of the crab as part of the normal flora and fauna, such as algae, bacteria, sponges and corals, coelenterates, mollusks, annelids, barnacles and amphipods, bryozoans, and tunicates. None of these fouling organisms is usually considered a threat to the crab's existence.

The other 62 species occur as parasites or diseases, ten of which have been implicated with mortality of crabs: four viruses, a bacterium, four photozoans, and a fungus. In addition, a nemertean, *Carcinonemertes carcinophila* and a ciliated protozoan, *Lagenophrys callinectes* may occur on the gills in such large numbers as to interfere with gas diffusion across the gill membranes and diminish the capacity of the crab to respire. Mortality caused by parasites and disease is believed to be small, except in crabs infected with the protozoan *Paramoeba perniciosa,* and crab eggs that are infested with the fungus *Lagenidium callinectes. Paramoeba* infections are usually limited to high salinity environments and mortality may reach 14-18%.[11] A large winter mortality of blue crabs in Chincoteague Bay in the late 1960's may have resulted from a combination of cold temperature and *Paramoeba* infection.[11] Fungi may infest from 25-50% of the extruded eggs on as many as 87% of sponge crabs in the Chesapeake Bay in a wide range of salinities, and some or all of the larvae grown in culture.[12]

Effects of the remaining 50 parasites and diseases are not now known to threaten the existence of the blue crab population: 18 bacteria, five viruses, one fungus, eight protozoans, one bryozoan, two nematodes, seven trematodes, one cestode, three annelids, three barnacles, and one isopod.

Bacteria have been found inside the body and in the hemolymph of wild crabs.[13,14,15,16,17,18,19,20,21,22,23,24,25] Stress on crabs, such as injuries, exposure to temperature extremes and dehydration, which may occur during commercial fishing, probably results in decreased effectiveness of resistance mechanisms, and is related to increases in hemolymph bacterial numbers.[24] Infections by viruses of natural, "wild" populations of crabs are relatively unknown. Accumulations of viruses by crabs could occur by feeding on infected tissues, by direct transmission from the water or through wounds, but concentration of viruses by the host has been considered unlikely because of the crab's feeding habits. Mortality of peeler and soft crabs in shedding tanks may result from preexisting viral (or bacterial or amoebic) infections, occurring in crabs before they were caught, or those acquired by contact in the tanks with infected crabs, aggravated by the stress of capture and confinement. Human illness from eating crabs that have accumulated viruses has not been reported.

Several bacteria associated with crabs that have been in contact with fecal pollution, are potential human pathogens, causing gastroenteritis when crabs that are improperly cooked are eaten.[13,14,15,16,17,20,21,26,27,28,29,30,31,32,33] Wound infections on humans can occur when live crabs are carelessly handled.[16,17]

TABLE 1

Symbionts of the Blue Crab

FOULING ORGANISMS

Algae.

1. (34)

Bacteria

2. coliforms. (21,35)

Porifera

3. zoanthid. *Epizoanthus americanus.* (36)
4. soft coral. *Leptogordia vingulata.* (36)
5. stony coral. *Astrangia danae.* (36)
6. sponge. (36, Van Engel unpubl. data)

Coelenterates

7. *Obelia bidentata.* (34,37)
8. *Bougainvillia* sp. (34,37)

Mollusks

9. *Crassostrea virginica.* (34,37, Van Engel unpubl. data)
10. *Mytilus edulis.* (34,38, Van Engel unpubl. data)

Annelids

11. polychaetes. (34, Van Engel unpubl. data)

Barnacles

12. *Balanus eburneus.* (Van Engel unpubl. data)
13. *Balanus improvisus.* (Van Engel unpubl. data)
14. *Balanus venustus niveus.* (32,34,35)

Amphipods

15. (34,36)

Bryozoans

16. *Acanthodesia tenuis.* (39, Van Engel unpubl. data)
17. *Alcyonidium mytili* (= *polyoum).* (36,39, Van Engel unpubl. data)
18. *Alcyonidium verrilli.* (39, Van Engel unpubl. data)
19. *Membranipora crustulenta.* (39, Van Engel unpubl. data)
20. *Membranipora tenuis.* (34)
21. *Conopeum tenuissium.* (34)

Tunicates

22. *Molgula manhattensis.* (36, Van Engel unpubl. data)

PARASITES (Species that are lethal to the host are marked *)

Viruses. Viruses marked with brackets [ ] were seeded to water for accumulation studies, and were not found naturally occurring in blue crabs.

Baculovirus. (32,40,41,42). No overt disease.

23. *Baculovirus* A. (19,41,43)
24. *Baculovirus* B. (19,43)
    [Coxsachievirus. (44-seeded)]
    [echovirus. (44-seeded)]
25. enterovirus. (35)
26. enveloped helical virus. (19,45)
27. *herpes-like virus. (19,32,42,43,46,47,48). Lethal.
28. *picorna-like virus. (19,32,42,43 [49 is incorrect]. Lethal.
    [poliovirus. (40, 44-seeded)]

TABLE 1 (continued)

Symbionts of the Blue Crab

29. *reo-like virus. (19,32,42,43,47,48,49,50). Lethal combination with rhabdo-like virus.
rhabdo-like virus (2 or 3 kinds).
30. *rhabdo-like virus A. (42,43,45,51,52,53). Lethal combination with reo-like virus
31. rhabdo-like virus B. (45)
[simian rotavirus. (40, 44-seeded)]

Bacteria. (18,23,54)
chitonoclastic. (19,54,55,56,57,58)
32. *Acinetobacter* sp. (15,19,21)
33. *Aeromonas* sp. *(hydrophila?)* (17,21)
34. *Bacillus* sp. (15,21)
35. *Benekea* type 1. (32,58,59)
36. *Clostridium perfringens* (?). (17)
37. *Clostridium botulinum.* (25,60)
38. *Enterobacter aerogenes* (?) (35)
39. *Escherichia coli.* (21)
40. *Flavobacterium* sp. (15,19,21)
41. gram-negative, unidentified. (19,61)
42. *Leucothrix mucor.* (filamentous). (19,65). (Probably only a fouling organism).
43. *Pseudomonas* sp. *(bathycetes ?).* (21,59)
44. *Staphylococcus aureus.* (17)
45. *Vibrio* spp. (14-in water, 15,16,17,21,22,24,35,59,62).
46. *Vibrio alginolyticus.* (17).
47. *Vibrio cholerae.* (14-in water, 16,17,22,30)
48. *Vibrio fischeri.* (21)
49. **Vibrio parahaemolyticus.* (13, 14-in water, 15,16,19,20,21,22,23,26,27,28,29,31,32,33)
50. *Vibrio vulnificus.* (16,17)

Fungi
51. **Lagenedium callinectes.* (19,32,63,64,65,66,67,68,69,70)
52. *Thraustochytrium* sp. (65)

Protozoans
Dinoflagellate
Hematodinium sp. (71)
53. **Hematodinium perezi.* (11,32,72). May be lethal.
Amoebae
54. **Paramoeba perniciosa.* (11,12,32,72,73,74,75,76,77,78,79,80,81). Lethal.
Microsporidians
Ameson sp.
55. **Ameson (Nosema) michaelis.* (11,32,72,78,82,83,84,85,86). Lethal.
56. *Ameson sapedi.* (11,78,84,87,88,89)
57. *Ameson* sp. (new) (84)
58. *Pleistophora cargoi.* (11,72,78,84,90)
59. *Thelohania* sp. (91,92)
Haplosporidians
60. **Haplosporidium* sp. (*Minchinia*-like). (11,32,72,93). Lethal
61. *Urosporidium crescens.* (11,32,72,78,84,87,88,89,94)
Suctorian
62. *Acineta* sp. (32,84)
Peritrichs
63. **Lagenophrys callinectes.* (11,32,72,95,96,97). May be lethal in shedding floats.
64. *Epistylis* sp. (32)
Holotrich ?
65. (32)

TABLE 1 (continued)

Symbionts of the Blue Crab

Bryozoans
66. *Triticella elongata.* (34,39, Van Engel unpubl. data)
Nematodes
67. other. (34,89)
68. *Hysterothylacium* sp. (34)
Trematodes
69-70. digeneans. (2 others) (34)
71. *Levenseniella capitanea.* (32,34,37,98,99)
72. *Microphallus basodactylophallus.* (32,34,37,98.100)
73. *Microphallus nicolli.* (34,101)
74. *Microphallus pygmaeus.* (34,102)
75. *Megalophallus diodontis.* (34)
Cestode
76. (32)
Nemertean
77. **Carcinonemertes carcinophila.* (32,34,36,37,103,104,105,106)
Annelid
78. *Myzobdella lugubris.* (32,34,37,107,108,109)
79. *Calliobdella vivida.* (34)
80. *Cambrincola vitreus (= mesochoreus?)* (32,34,37)
Barnacle
81. *Chelonibia patula.* (32,34,36,37,103,110,111,112, Van Engel unpubl. data)
82. *Octolasmis mulleri.* (32,34,36,37,103,110,113,114,115,116,117, Van Engel unpubl. data)
83. *Loxothylacus texanus.* (32,34,37,118,119,120)
Isopods
84. In gill chamber of blue crabs, carapace width approx. 8-25 mm, York River (Gloucester Banks area) and Chisman creek, VA, 1948-1949. W.A. Van Engel collection.

PREDATION

Predation intensity on blue crabs varies with the species of predator, its size, life history stage, physical characteristics and feeding habits, whether it is a resident or migratory species, and the chemical and physical conditions of the environment, but overall appears to be slight or insignificant, judging from gut content analyses. Generally, fish predators <250 mm standard length (SL) preferentially feed on micro- and macroplankton, small fishes and epibenthos; however, changes in diet may occur with increase in predator size. The frequency of occurrence of blue crabs in the diet is small in lie-in-wait predators and in those fishes whose mouths are not morphologically equipped to capture small blue crabs. Some migratory predators consume blue crabs only in fresh to brackish water, but seek other prey in saltier waters. Throughout a migrant's range, its food may include any abundant organism. Resident fishes are less frequent consumers of blue crabs than migratory megapredators.

Whether predation varies with the life history stage and size of the blue crab cannot be determined from published reports, since the prey stage or size is almost never reported. Predation on blue crab zoeae and megalopae is largely unknown: remains of early-stage brachyurans in fish stomachs are seldom if ever identified other than as "crab zoeae", brachyura zoea" or "megalopae" (see e.g., 121,122,123,124,125,126). However, blue crab megalopae were found in the gut contents of a few juvenile weakfish (*Cynoscion regalis*) on the York River nursery grounds.[127] The role of predators that could be consumers of blue crab megalopae in brackish and salt marshes, in particular the ubiquitous mummichog, *Fundulus heteroclitus,* has been partially investigated. In tidal brackish marshes from Massachusetts to Georgia, larval, juvenile and adult mummichogs forage at high tide in daylight on the marsh surface, primarily on detritus, polychaetes and small crustaceans such as amphipods.[121] Consumption of "crab zoea" by small, 9.5-23.4 mm SL mummichogs collected in the wild has been observed, but consumption of blue crab megalopae has not been confirmed; some sites of study were beyond the natural range of the megalopae, and because the rate of digestion of food by mummichogs is so rapid, fish guts are often empty or the contents unidentifiable.[121] Other ubiquitous small-size fishes and palaemonid crustaceans, which also occur in tidal marshes, have not been investigated as potential predators of megalopae.

Post-megalopal-stage blue crabs seldom appear in the gut contents of fishes that are residents or are coastal species utilizing the inshore, mid- to low-salinity (5-20 ppt) crab and fish nursery grounds along the eastern Atlantic coast and on the Gulf coast. For numerous species, less than 15% of the individuals (= frequency of occurrence) occasionally consume blue crabs (Table 2).

TABLE 2

Species and common name.	Size, mm	Reference
Carcharhinus leucas bull shark	780-805	(128)
Raja eglanteria clearnose skate		(129)
Ictalurus catus white catfish		(127)
Ictalurus furcatus blue catfish	60-229	(128)
Ictalurus punctatus channel catfish		(128*)
Arius felis sea catfish	170-229	(128)
	240-360	(128*)
Bagre marinus gafftopsail catfish		(128*)
Opsanus tau oyster toadfish	58-337	(130)
	32-252	(131)
		(132)
Morone americana white perch	204	(133)
Micropterus salmoides northern largemouth bass	175-209	(128)
Pomatomus saltatrix bluefish	122-870	(133)
	450 mean SL	(134)

Archosargus probatocephalus sheepshead	218-410	(128)
	190-365	(128*)
	145-449 SL	(135)
Lagodon rhomboides pinfish	65-74	(128)
Aplodinotus grunniens freshwater drum	211-347	(128)
Bairdiella chrysura silver perch	70-143	(128)
	20-150	(133)
		(136)
Cynoscion arenarius sand seatrout	59-320 SL	(135)
Cynoscion nebulosus spotted seatrout	275-555	(128*)
	400-495	(138)
	73-532 SL	(135)
Cynoscion regalis weakfish	320-580	(133)
	121-180	(136)
		(137)
	403 mean SL	(134)
		(127)
Leiostomus xanthurus spot	20-150	(133)
Micropogonias undulatus Atlantic croaker	100-199	(128)
	<39- >180 SL	(124)
	95-350 SL	(138)
	135-142	(136)
		(137)
Pogonias cromis black drum	205-460	(128*)
		(135)
		(127)
		(136)
Sciaenops ocellata red drum		(128*)
Ancylopsetta quadrocellata ocellated flounder	25-199 SL	(139)
Citharichthys spilopterus bay whiff	50-149 SL	(139)
Paralichthys lethostigma southern flounder	113-380	(128)
	168-410 SL	(135)

Footnote. Body lengths are shown as designated by the author; lengths that are missing were not provided by the author. Citations designated with an * include reviews of other authors.

There are a few heavy consumers of blue crabs in estuaries (Table 3); the percentage of fishes sampled that had eaten blue crabs (frequency of occurrence) is shown in parenthesis.

Sandbar sharks in the Chesapeake Bay preferred soft blue crabs but occasionally consumed hard crabs, 35-115 mm wide;[133] however, at the mouth of the Chesapeake Bay and on the adjacent continental shelf, between May and October, large sandbar sharks (545-2070 mm TL) fed mostly on epibenthic fishes and some pagurid and brachyuran crustaceans, but no blue crabs.[142] Feeding preferences of the red drum appear similar in Mississippi Sound (usually 6-15 ppt salinity), Lake Pontchartrain (1.2-18.6 ppt);[128] the bay side of the eastern shore of Chesapeake Bay (14-21 ppt);[133] and in waters of Texas, Louisiana and Florida.[141] In Lake Pontchartrain, feeding by red drum on blue crabs varied seasonally, more in spring and summer than fall and winter, with a preference

TABLE 3

Species and common name	Size, mm	Frequency of occurrence, %	Reference
Carcharhinus plumbeus			
sandbar shark	435-852 SL	(57)	(133)
	600-1125	(41.3)	(140)
Lepisosteus oculatus			
spotted gar	405-555	(70)	(128)
			(128*)
Lepisosteus spatula			
alligator gar	903-1472	(65)	(128)
		(87)	(128*)
Ictalurus furcatus			
blue catfish	230-411	(24)	(128)
Opsanus tau			
oyster toadfish	58-337	(36)	(130)
Strongylura marina			
needlefish	380-403 SL	(90)	(133)
Tylosurus acus			
agujon	970-1140	(71.4)	(133)
Roccus mississippiensis			
yellow bass	130-195	(18.5)	(128)
Centropristes striatus			
black sea bass	72-158 SL	(25)	(133)
Cynoscion regalis			
weakfish	403 mean SL	(38)	(134)
Micropogonias undulatus			
Atlantic croaker	200-325	(21.7)	(128)
Sciaenops ocellata			
red drum	384-765 SL	(100)	(133)
	184-625	(62)	(128)
			(128*)
	190-780 SL	(17.3)	(141)

Footnote. Body lengths are shown as designated by the author. Citations designated with an * include reviews of other authors.

for crabs in the lower salinity waters near Lake Pontchartrain and for shrimp in waters in or near Gulf of Mexico waters.[141] In Mississippi Sound, red drum (190-780 mm SL) were frequent feeders on the blue crab but more drum were consuming the "lesser blue crab", *Callinectes similis.*[141]

Frequently the gut contents are described by the common name "crabs", either because the remains cannot be further identified or because the investigators are unfamiliar with decapod crustacean species types. Probably, but not certainly, the "crabs" are xanthid or grapsoid crabs, since such reports relate more often to in-faunal or epibenthic feeders. Fishes consuming "crabs", "zoeae and megalopae" are listed in Table 4.

TABLE 4

Species and common name	Size, mm	Reference
Carcharhinus leucas bull shark		(128*)
Squalus acanthias spiny dogfish		(129)
Gymnura micrura butterfly ray		(129*)
Lepisosteus osseus northern longnose gar	706-1180	(128)
Elops saurus ladyfish		(128*)
Synodus foetens lizard fish		(129*)
Arius felis sea catfish	240-360	(128*)
Bagre marinus gafftopsail catfish		(129*)
Urophycis regia spotted hake		(129)
Roccus mississippiensis yellow bass		(128*)
Micropterus salmoides northern largemouth bass	203-432	(128*)
Caranx hippos crevalle jackfish		(128*)
Lagodon rhomboides pinfish	51-100	(128*)
Bairdiella chrysura silver perch		(128*)
		(143)
Cynoscion arenarius sand seatrout	100-406	(128)
		(128*)
Leiostomus xanthurus spot		(128*)
Menticirrhus saxatilis northern kingfish	19-72	(126)
Menticirrhus americanus southern kingfish	80-250	(126)
Micropogonias undulatus Atlantic croaker		(128*)
		(144)
		(145)
Pogonias cromis black drum	80-200	(128*)
Stellifer lanceolatus star drum	21-80	(126)
Prionotus carolinus northern searobin		(129)
Paralichthys dentatus summer flounder		(129)

Footnote. Body lengths are shown as designated by the author; lengths that are missing were not provided by the author. Citations designated with an * include reviews of other authors.

Some fish species in confinement may prey on blue crabs, whereas in an open environment such predation by the species is rare or has been unreported: the northern puffer (*Sphaeroides maculatus*) in confinement preys on blue crabs and Tangier, Virginia, watermen have used blue crabs in crab pots as bait for puffers (Van Engel unpubl. data). Cannibalism by blue crabs has been reported from stomach content analyses of crabs >30 mm width,[128,146] although in approximately 3200 stomachs crab remains represented only nine % of the dry weight, almost all consumed by crabs >60 mm wide![146] Blue crabs have been observed to feed on crab scraps or injured or dead crabs discarded at piers or from boats or found in peeler crab shedding tanks, since they are opportunistic feeders and scavengers (147,148, Van Engel unpubl. data), and all sizes of paper-shell crabs, which are those that recently molted, regularly consume their own molted exoskeletons.

Sub-adult loggerhead (*Caretta caretta*) and Atlantic ridley (*Lepidochelys*

kempii) turtles forage in the lower Chesapeake Bay from May through October. The stocks of these turtles in the Chesapeake Bay regions is not large. Loggerheads consume mostly horseshoe crabs and rock crabs, some blue crabs, spider crabs and clams. Destruction by loggerheads of wire pots set to catch blue crabs in the south end of Chesapeake Bay has been frequently reported by local watermen. Atlantic ridleys feed exclusively on blue crabs.[149,150,151]

River otters (*Lutra canadensis*) in small intertidal ponds and streams in salt marshes and freshwater swamps consume mammals, birds, fishes and invertebrates. In eastern North Carolina, in a 4-year fall and winter collection, 39% of the otters consumed crayfish, blue crabs and shrimp, in that order of preference.[152,153] In southern Louisiana, almost 20% of the otters in salt marshes in a 3-year winter collection consumed blue crabs, second in abundance to cyprinodont fishes, but in swamps 4% of the otters ate blue crabs and 34% ate crayfishes.[154] Little seasonal difference in predation is believed to occur.[154] Mink *(Mustela vison)* in eastern North Carolina marshes preferred fishes, and fewer mink consumed mammals, arthropods, birds, amphibians, and reptiles, in that order; no blue crabs were observed in stomach contents.[153]

CHEMICAL AND PHYSICAL FACTORS

Numerous chemical and physical pollutants occur in the Chesapeake Bay and its tributaries. Sediments, fertilizers, pesticides, herbicides, heavy metals, sewage and petroleum products arrive in the marine environment from both point and non-point sources. Their effects on estuarine biota are not well known. Chronic and acute effects of most of these parameters of water quality on the various life history stages of the blue crab, and their secondary effects on a crab's behavior, caused by the destruction or alteration of the habitat or the depletion of the food supply, are even less well known. Field evidence is difficult to obtain since only large departures from normal water quality parameters may influence changes in the seasonal and spacial distributions of organisms, which otherwise are primarily influenced by temperature, salinity and food availability. Laboratory studies provide data on the effects that specific pollutants may have in enclosed, controlled environments, but field evidence is required to substantiate any lethal or behavioral responses. For example, storm-water runoff from deforested land may contain tannic, folvic and lignic acid components that lower the pH and raise water color. Laboratory studies of blue crabs of all sizes in low salinity water, 0-2 ppt, adjusted artificially with dilute hydrochloric acid between pH 4.6 to 8.2, have shown significant, maximal avoidance to pH <6.0.[155,156] However, field collections of blue crabs from creeks in East Bay, part of the Apalachicola Bay system, Florida, which exhibit a range of pH from 4.0 to 8.8, have shown greater numbers of juvenile crabs, $<$ 60 mm width, and lesser numbers of larger crabs in regions where pH was <6.0. The extremely

low pH values were usually preceded by moderate to heavy rainfall. Furthermore, seasonal migrations of small blue crabs, January-February and July-August, have been shown to occur in Apalachicola Bay, Florida, when large pH fluctuations occur in East Bay.[155,156] Supportive evidence comes from other laboratory studies which have demonstrated that during upstream migration, as blue crabs acclimate to increasingly lower salinities and a more acidic medium, when salinity falls below 27 ppt they change from osmoconformity to osmoregulation.[157]

The differences between "pollution" and "inorganic or organic enrichment" are in the degree of departure from normal values and the possibility for potential harm. While temperature and salinity of the environment are not usually considered pollutants, large departures from normal can have deleterious effects on the biota. For example, a few adult female blue crabs with extruded eggs (sponge crabs) may first appear in the southern end of the Chesapeake Bay in late April, but intensive activity does not begin until mid-June, and usually ceases by early September. Hatching of crab eggs has been observed to occur in 8-11 days at 25-26°C (77-79°F);[158] at water temperatures that normally occur in the southern end of Chesapeake Bay from mid-June through mid-September, but may not be attained until mid-July and may drop below 25°C in late August, sometimes in the same year.[159] However, at 16°C (60°F) hatching occurs in approximately 45 days;[158] a mean water temperature of 16°C is normally attained in the southern end of the Chesapeake Bay in early May, but may occur anytime from late April to mid-May, and may drop below 16°C in mid-October.[159] Eggs extruded on May 1 may not hatch until June 15, while those extruded on June 15 may hatch on June 25. If mortality due to predation and disease on the eggs and embryos during the early 45-day hatching period is larger than that occurring in the later 10-day period, and if the rates of development of the vectors in the two periods are not substantially different, timing egg extrusion to the warmer temperature would have extreme survival value to the blue crab population. The rate of warming in the spring, after late April, and the time of cooling in the fall may have a marked effect on the success or failure of a year class of crabs. Cooling degree days in May in the year of the hatch, observed at Norfolk, VA, was one of three variables used in a multiple correlation analysis, in which 86% ($r^2 = 0.86$) of the variation in commercial hard crab landings one and a half years later, from 1964 through 1975 was explained.[160]

In the lore of Chesapeake Bay watermen, sub-freezing winter temperatures are associated with the deaths of adult female crabs in the southern end of the Bay. Dead females are often seen in the winter dredge catch, varying geographically and with decreasing salinity from the southern end of the Bay to the Virginia-Maryland border.[161]

Whenever below-average rainfall in late summer and fall and concomitant increases in salinity in the Bay's tributaries occur, juvenile blue crabs have been found more numerous in higher reaches of the tributaries (Van Engel unpubl.

data). In those areas, since space and food are less than occur in the normal nursery areas, competition between individuals promotes stress and thus potentially limits the success of the year class.

Although sediment is the most significant contribution from agriculture to the marine environment, particularly during storm-water runoff, the only known direct effects, reported by local watermen, are losses of soft crabs in shedding houses and a decrease in peeler crab catch following heavy rainfall; the latter is probably the result of a change in crab behavior in the wild in water containing suspended sediment. Secondary effects of sediment transport and deposition are the physical alteration of habitat and the increase in turbidity, resulting in decreased light penetration. Decreased photosynthesis is considered a factor in the decline in abundance of eelgrass (*Zostera*), although excessive nutrients, nitrogen and phosphorus, which promote fouling of the fronds, are probably the major cause.[162]

Less well known are winter mortalities occurring when frequent low pressure centers pass over the southern end of the Bay and on the adjacent ocean coast and create wind tides. Subsurface currents, enhanced in a storm in the relatively shallow Bay and coastal area, sweep crabs along the bottom, where their exoskeletons are severely abraded, resulting in uncounted deaths of crabs along the ocean shore and up to 20% of the dredge catch in the Bay.[161]

Perhaps the most insideous parameter of water quality that can affect blue crabs is a deficiency of dissolved oxygen (DO). The duration and extent of anoxic water in the Bay have accelerated since 1950, primarily in the portion of the Bay from the Patapsco River, MD, south to the vicinity of Reedville, VA, and at depths between the bottom and the halocline (8-14 m in depth). Volume of water with DO concentrations equal to or less than 0.7 mg L^{-1} (defined as "low" value) is estimated to be 15 times more in 1980 than in 1950,[162] and the duration now extends from early May into September. Reduction in DO is primarily due to decomposition of organic material, but there are seasonal differences related to temperature and salinity effects on oxygen solubility. Oxygen deficiencies or barriers may be encountered by juvenile blue crabs migrating to nursery grounds in the estuary. Migration routes, and the depth of water in which migration occurs, are not well understood. If normal migration primarily occurs on flood tide at depth, the presence of anoxic water could be a barrier or a trap, either preventing further migration or forcing crabs to move to shallower waters.[163]

Municipal wastewater discharge, atmospheric fallout and surface runoff contribute trace metals to the marine environment, but the amounts contributed vary with potential sources in each geographic site. Some of the trace metals are essential, in moderation, in nutrition and growth (e.g., copper, zinc, manganese and cobalt) and others potentially toxic (e.g., cadmium, silver, mercury, lead and chromium).[164] A substance in the hepatopancreas and in the gills of the blue crab, a metallothionein-like protein, is involved with trace metal metabolism and with metal-detoxification.[165,166] Bioconcentration of cadmium

from seawater by the blue crab has been found to occur primarily at the gills, and lesser amounts occur in the hepatopancreas and hemolymph. Although cadmium has been found associated with hemocyanin in the hemolymph, the low levels of cadmium found are estimated not to affect hemocyanin-mediated oxygen transport.[167] Copper, zinc and nickel have been found in gills and hepatopancreas from environmentally-exposed blue crabs.[168]

Unsubstituted polynuclear aromatic hydrocarbons (PAHs) enter the marine environment from atmospheric fallout of vehicle exhaust, industrial smoke and wood fires. Localized concentrations of hydrocarbons are contributed by effluents from domestic and industrial treatment facilities, oil spillages and urban run-off. PAHs are toxic, and some are believed to be carcinogenic or mutagenic or both when activated through metabolism.[169] Blue crabs have been shown to take up PAHs directly from the water and from food, pass some of it directly through the intestinal tract and rapidly metabolize most of the remainder, converting lipid-soluble to water-soluble compounds.[170] Metabolism of the lipophylic compounds is believed to be carried out by mixed-function oxygenases (MFO), which are enzymes. The main site of metabolism is either in the hepatopancreas[171] or in the green gland, which is essentially an excretory gland.[172] Concentrations of these oxygenases vary with the molt stage of the blue crab, being highest during the intermolt and least during the molt.[172] The y-gland molt-promoting hormone crustecdysone, a steroid hormone, exhibits a cycle opposite that of the oxygenases. Oxygenases are also required in the synthesis and breakdown of crustecdysone. It has been proposed that in instances of exposure to high levels of PAHs, oxygenase activity could be concentrated on detoxifying the PAHs instead of the production of the ecdysone, resulting in a breakdown in the molting sequence and prolonging the intermolt state.[172,173,174] PAH in lipid reserves may be relatively inert. Benzene, an aromatic hydrocarbon, has been shown to delay limb-bud growth and limb regeneration and to cause an increase in the intermolt stage in the blue crab.[175]

Chlorination of wastewater to improve its hygienic quality, may be either insufficient to minimize water-borne disease or produce substances that have an adverse environmental impact. Several compounds have been identified with highly chlorinated wastewater, such as chloramines in freshwater and bromamines in seawater, and their oxidation products. Few studies have been conducted of the effects of any of these substances on marine crustaceans of commercial value. In laboratory studies of acute-toxicity, adult blue crabs have been found more tolerant of chlorine-produced oxidants than most other marine species tested.[176] Respiration rate, ventilation rate and most blood serum constituents were unaffected by the levels of oxidants tested.[176]

Halogenated substances in the marine environment, such as pesticides, solvents and other industrial compounds, are contributed from industrial and domestic wastewaters, including runoff, but some may have been derived from the chlorination of wastewater. Among the toxicants are Kepone, chlorinated

phenols, polychlorinated biphenyls, dieldrin, mirex, heptachlor, methoxychlor and DDT and its derivatives. A blue crab primarily accumulates most of its body burden of pesticides through its dietary habit as an opportunistic scavenger. Laboratory studies of blue crabs, involving the bioconcentration of DDT from water treated with low levels of 0.25 and 0.50 ppb to higher levels of 0.01 to 1.0 ppm, exposed from nine months to 12 hours, respectively, have shown no differences in mortality rates between control and treated crabs.[177,178] In one study, uptake appeared to occur primarily at the gills, but DDT and its metabolites were found sequestered in the gills, gonads, claw and backfin muscles, the heart and the hepatopancreas, principally in the latter organ.[177] The number of molts of control crabs and those exposed to low levels of DDT was not found to be significantly different, but crabs exposed to 0.50 ppb DDT experienced fewer molts.[178] In field studies, moribund crabs contaminated with DDT exhibit lack of equilibrium and tremors, and large scale mortality, up to 90% of the population, eventually ensues (179,180,181, Van Engel unpubl. data).

Relatively small amounts of Kepone and low levels of toxicity have been found to occur in juvenile blue crabs that have bioconcentrated Kepone from water.[182] However, crabs that accumulated Kepone through feeding underwent fewer molts and suffered over 80% mortality, and depuration of Kepone was found to be relatively slow.[183] In another study, no statistical differences were found in mortality and molting rates between crabs provided food either uncontaminated or contaminated with Kepone.[184] Concentrations of Kepone have been found to differ in male and female blue crabs, in amount and site of concentration: male crabs concentrated more Kepone in the backfin muscle, and adult females had more Kepone in the ovary and secondarily in the hepatopancreas.[185] Depuration of Kepone in the female blue crab, through the extrusion of Kepone-laden eggs, has been suggested.[186] No effects of contamination in the eggs on hatching or survival have been found.[187] The potential impact of Kepone contamination on the wild blue crab stock has been estimated to be minimal, based on the estimate that the natural diet of crabs contains lower levels of Kepone than used in laboratory studies.[188]

The sorption of some pesticides by the chitin of crustacean exoskeletons has been documented, but no statements have been made of the potential impact on the host animal. Dicamba, 2, 4-D and DDT have been found sorbed by chitin, but not atrazine, propanil or paraquat.[189]

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